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Potential distribution and invasiveness of recently naturalised alien plants under climate change

Christine Sabine Sheppard

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Biological Sciences, The University of Auckland, 2013.
Abstract

Climate change and plant invasions have been studied extensively as individual factors, but few studies have considered their combined and potentially synergistic impacts. This thesis aims to test if climate change may provide opportunities for alien plants to expand into regions where they previously could not survive and reproduce. Using three recently naturalised plants in New Zealand from warmer native ranges as model species (Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla), I assessed their potential invasiveness under climate change. Following an investigation into the importance of variable selection for species distribution models, I modelled potential distributions of these three species under a range of climate change scenarios. I conducted experiments in controlled environments to study growth responses to elevated temperature, CO$_2$ and drought. Furthermore, I investigated effects of competition on closely related native species. To validate the models, I conducted field trials to test whether these alien plants perform as expected in sites of differing climate suitability (as identified by the models). The species distribution models indicated that the alien plants are likely to expand their range (by 2090) on average by 101% (A. cunninghamiana), 70% (P. guajava) and 112% (S. actinophylla). The controlled environment experiments showed that biomass of S. actinophylla under doubled CO$_2$ was increased by 45%, while P. guajava seeds germinated faster under elevated temperature. The three species showed high drought tolerance, with a seven week drought reducing biomass of P. guajava only. Effects of competition from the alien species under high densities were strong compared to intraspecific competition among the native species, particularly for A. cunninghamiana. The field trials showed high performance of the alien plants in the sites identified as suitable, and growth and survival were high even during a severe drought. Shoot biomass and survival generally correlated well with predicted suitability of the models. The combined results from the models, field trials and controlled environment experiments provide strong evidence of the potential invasiveness of these plants. By having higher confidence in the potential risk of new weeds, cost-effective management actions can be taken to control alien plants at an earlier stage of their naturalisation.
To Mami – to my late mother Irène Joggi –

who had such a huge role in shaping who I am

and what I have achieved.

How I wish you were here now.
Acknowledgements

My PhD journey of the last 3.5 years has been exciting, challenging, instructive and frustrating - I discovered my first white hair (was it when my field site got bulldozed, the many delays in building the shadehouse, or the third time rabbits ate all my plants? Maybe it was the devastating spider mite attack? Was it when I had to remove 57 dog poos from a field site while being barked at, or when the neighbour’s cattle escaped with its taste for palms?); anyhow, there is a number of people whom I would like to thank for helping along the way.

First of all, a huge thank you to my main PhD supervisor Margaret Stanley – I really valued your support, your humorous attitude, your efficiency in getting back constructive comments on my drafts, and dealing with all my administrative issues! Many thanks also to my co-supervisor Bruce Burns for your guidance along the way. Thank you both for your inputs into this study, helping to develop this project into a fantastic piece of research.

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Thanks to everyone who helped me get this far on the journey of my scientific career. I am excited about the next step that lies ahead!
Publications

Chapters 2-7 of this thesis were prepared as a series of stand-alone papers as allowed under the 2011 PhD Statute and Guidelines (for relevant co-authorship forms see next pages). These Chapters are based on the following publications:

Chapter 2:

Chapter 3:

Chapter 4:

Chapter 5:

Chapter 6:
Sheppard CS & Burns BR. Effects of interspecific alien versus intraspecific native competition on growth of native woody plants. Under review at Plant Ecology.

Chapter 7:
Sheppard CS, Burns BR & Stanley MC (in press) Predicting plant invasions under climate change: are species distribution models validated by field trials? Global Change Biology. DOI: 10.1111/gcb.12531
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Chapter 4. Published as: Sheppard CS & Stanley MC (in press) Does elevated temperature and doubled CO2 increase growth of three potentially invasive plants? Invasive Plant Science and Management. DOI: 10.1614/IPSM-D-13-00038.1

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CHAPTER 1

Introduction
Chapter 1: Introduction

1.1 Biological invasions

1.1.1 Introduction and definitions

Biological invasions are an important driver of global change, posing a major threat to biodiversity (Lambertini et al. 2011). Invasive species have multiple impacts on native species, communities and ecosystems via different mechanisms, such as: competition; predation or herbivory; parasitism that results in disease; and alteration of fire or nutrient regimes (Mack et al. 2000). Biological invasions also result in economic damage, such as losses in crops, fisheries, forestry or grazing capacity (Mack et al. 2000). A decade ago Pimentel et al. (2001) calculated that the 120,000 species of plants, animals and microbes that have been introduced to six major countries (USA, UK, Australia, India, South Africa, Brazil) have resulted in economic damage that totals more than US$336 billion per year – not including costs of losses in biodiversity and ecosystem services.

Although it is usually invasive animals that are implicated as leading causes of species extinctions (Blackburn et al. 2004; Clavero & García-Berthou 2005), invasive plants have been shown to severely affect native plant communities. A recent meta-analysis calculated that invasive plants reduced fitness of native plant communities on average by 41.7%; growth by 22.1%; species abundance (measured by plant numbers, density or cover) by 43.5%; and diversity (measured by alpha diversity, richness or evenness) by 50.7% (Vilà et al. 2011).

For this thesis I will use the following terms, adapted from definitions by Richardson et al. (2000) and Richardson & Pyšek (2006): alien plants are defined as plants, which occur in an area as a result of human-mediated transport. Casual plants are alien plants that occasionally occur outside cultivation, but do not persist. Naturalised plants are alien plants that form self-sustaining populations. Invasive plants are a subset of naturalised plants that have high reproductive capacity and spread over wide areas. Invasive plants are also often called weeds, and an environmental weed is defined as an alien plant invading natural ecosystems and threatening the conservation of native plants and animals.

1.1.2 Plant invasions: predicting successful invaders

The ‘paradox of invasion’ (Sax & Brown 2000) attempts to understand why alien species that had no opportunity to adapt to local conditions are able to not only establish in their new range, but sometimes even outcompete native species, which have long since adapted to the local environment. Much research in the last few decades has focused on determining what attributes make a successful invader, and what attributes make a community invasible (Richardson & Pyšek 2006).
Reviews and meta-analyses summarising these studies show that invasive species often share traits, such as high relative growth rates, high specific leaf area, smaller seed mass and phenotypic plasticity (Ordonez et al. 2010; van Kleunen et al. 2010; Davidson et al. 2011; Lamarque et al. 2011). Such traits are thought to infer higher competitive ability and predict invasion success. However, as traits vary considerably amongst both invasive and non-invasive species, prediction power based on traits of species is limited (Schlaepfer et al. 2010). While there is ongoing effort to find the ultimate explanation for all invasions, many have come to the conclusion that species and ecological communities are idiosyncratic, and particular invasions have to be studied in detail to explain local patterns (Simberloff 2010).

To understand the success or failure of invaders, I will look at the pathway a new alien plant (or animal) takes before eventually becoming invasive. The invasion process can be categorised into four stages: transport, introduction, establishment and spread (Figure 1.1). Invasive species must overcome various barriers at every stage of the invasion process, and at each barrier they are likely to fail (Blackburn et al. 2011).

![Figure 1.1: A unified framework for biological invasions, reproduced from Blackburn et al. (2011)\(^1\). The invasion process is divided into four stages, and for each stage there are barriers that need to be overcome. Relevant terminology and appropriate management interventions are shown along the pathway. The codes inside the arrows designate different categories of alien plants; for detailed descriptions see Table 1 in Blackburn et al. (2011).](image)

1.1.2.1 Transport stage

To invade a new range, a species must first cross a geographical barrier by being transported to the recipient region. Generally, species with larger ranges are more likely to be transported to a new location, and thereafter also more likely to establish successfully due to their wide environmental tolerance (Goodwin et al. 1999). Alien species have been globally dispersed by humans via three mechanisms: importation of a commodity; arrival of a transport vector; and natural spread from an already invaded neighbouring region (Hulme et al. 2008). Globalisation and economic growth are primary drivers of biological invasions (Hulme 2009). Human population density and wealth have been shown to be important factors explaining the numbers of alien species in a region (Pyšek et al. 2010), but alien species richness is also associated with indicators of socioeconomic activity around a century ago (Essl et al. 2011).

1.1.2.2 Introduction stage

Once a species has been transported to a new location, there are still many barriers to colonisation. While deliberately introduced species such as ornamentals first have to escape cultivation, other species may skip that barrier and be directly released into the environment (Blackburn et al. 2011). For alien plants the main pathway of introduction is escape: that is, plants that were originally imported as a commodity subsequently escape unintentionally (Hulme et al. 2008). Even successful invasive species often have undergone multiple failed introductions before they eventually become established and highly successful (Sax & Brown 2000). Most local introductions simply fail because propagules are dispersed to unsuitable locations, which do not meet the basic physiological requirements of a species (Sax & Brown 2000). Propagule pressure, which refers to both the numbers of individuals released in a release event (propagule size), and the number of discrete release events (propagule number), is a key factor affecting invasion success (Lockwood et al. 2005; Simberloff 2009). Although difficult to measure directly, various studies have shown how proxies for propagule pressure affected invasion success: for example, availability and price in the horticultural market affected invasion success of ornamental alien plants in Britain (Dehnen-Schmutz et al. 2007), and forestry use was most important in determining pine introductions and naturalisations (McGregor et al. 2012). If propagule pressure is high, the effects of reduced genetic diversity and harmful population bottlenecks can be averted (Allendorf & Lundquist 2003; Lockwood et al. 2005). Indeed, genetic diversity in alien populations can be very high because multiple introductions lead to new combinations of alleles (Allendorf & Lundquist 2003; Suarez & Tsutsui 2008).
1.1.2.3 Establishment stage

If propagule pressure is sufficiently high and an alien plant is able to overcome the various abiotic and biotic barriers (Figure 1.1; Blackburn et al. 2011), it may succeed in surviving and reproducing, leading to establishment of a self-sustaining population. Successful establishment at a particular location will depend on both the specific traits of the alien plant and the attributes of the invaded community (Richardson & Pyšek 2006).

A recipient community must provide opportunities to invade; that is, niche opportunities or the abiotic and biotic conditions that promote invasions (Shea & Chesson 2002). First of all, climatic conditions must allow the survival and reproduction of a plant. Climate is the dominant factor influencing the distribution of all plants (Woodward 1987). Climatic niche shifts have been shown to be rare among terrestrial plant invasions (Petitpierre et al. 2012); that is, upon introduction to a new range, a species will establish in recipient regions of similar climatic conditions as in the native range.

At smaller spatial scales, other abiotic factors become important. Invasive species often show greater performance in high nutrient conditions or in disturbed conditions, both of which have often resulted from human activities (Daehler 2003). Davis et al. (2000) proposed a theory stating that a community becomes more susceptible to invasion whenever the amount of unused resources increases. This might occur either because the native community’s resource consumption declines, which could be due to damage from a disturbance event or because the resource supply increases at faster rates than the community uses it, for example as a result of eutrophication. Increasing nitrogen deposition associated with global change may thus promote establishment of alien species (Dukes & Mooney 1999).

Biotic factors, such as competition from resident plant species and the presence of natural enemies, will also determine establishment success (Levine et al. 2004). For a long time it has been thought that communities of higher diversity would be more resistant to invasion, due to competitive effects of resident species (Elton 1958). However, conflicting results for both a negative and a positive relationship between native species diversity and level of invasion have been reported (Fridley et al. 2007). While evidence for the positive relationship has come from models and experimental studies at small scales, large scale observational studies often showed the opposite: more diverse regions also had more invaders (Levine & D’Antonio 1999; Shea & Chesson 2002; Davies et al. 2005; Fridley et al. 2007). What drives the change to a positive relationship at larger spatial scales is debated, although with increasing spatial scale the drivers of the relationship generally change from biotic to environmental (Fridley et al. 2007). Thus, the conditions that favour native species diversity also favour alien species diversity at large spatial scales (Levine & D’Antonio 2004).
A popular explanation for invasion success is the enemy release hypothesis, which predicts that when a species gets introduced to a new area its specialist enemies will be absent (Keane & Crawley 2002). Extending on the enemy release hypothesis, the evolution of increased competitive ability hypothesis states that due to enemy release, selection will favour plants that allocate fewer resources to herbivory defence and more to improved competitive abilities, such as increased growth and reproduction (Blossey & Nötzold 1995). Yet another explanation, termed the novel weapons hypothesis, states that some invaders may use new competitive mechanisms to negatively affect their native neighbours, such as production of chemicals to which natives are not adapted (i.e. chemical allelopathy) (Callaway & Aschehoug 2000).

The importance of these factors will vary for each invasion event, but in general, propagule pressure and abiotic factors act early in the invasion process, with climate being particularly important at a regional scale. Biotic factors may then affect establishment at a more local scale (Richardson & Pyšek 2006; Fridley et al. 2007). However, the specific combination of these various factors, including traits of the invaders and anthropogenic influences, will determine if a particular species establishes at any given location.

1.1.2.4 Spread stage

To spread across the landscape, an alien species must have high dispersal ability and overcome the environmental barrier, which refers to the increasingly wide range of environmental conditions a species encounters as it spreads further (Blackburn et al. 2011). Minimum residence time (time since first record of occurrence outside cultivation) has been shown to be strongly associated with landscape spread (Ahern et al. 2010). In New Zealand, a study of 100 alien plant species showed average spread rates of 2-42 km/year (Aikio et al. 2010a). Many alien species undergo a lag phase, which means that their populations remain small and inconspicuous for decades before becoming abundant and widespread (Mack et al. 2000). Such species have been defined as sleeper weeds: species that have naturalised in a region, but not yet increased their population size exponentially (Groves 1999). It has been suggested that woody perennials on average take centuries to naturalise (Caley et al. 2008). In Europe it has been estimated that an alien plant takes on average about 150 years to reach its maximum range (Gassó et al. 2010). For plant invasions in New Zealand, lag phases of several decades are common, averaging 20-30 years from first naturalisation to spread (calculated from a data set including a high proportion of herbaceous weeds; Aikio et al. 2010b). The time lag has been explained by demographics (alle effect, leading to reduced population growth because of low population density); ‘invasional meltdowns’ (where two invasive species facilitate each other’s spread); or a change in the invaded habitat (Simberloff 2009), as occurred when a combination of
factors including rabbit control and increased fertilisation induced the spread of hawthorn (*Crataegus monogyna*) in New Zealand (Williams et al. 2010). A lag phase might also be occurring because a species is undergoing evolutionary adaptations to the new environment (Suarez & Tsutsui 2008).

### 1.1.2.5 Probability of successful invasion

What is the probability that an alien species manages to cross all the barriers at the various stages of the invasion pathway? The tens rule predicts that 10% of species brought into a new region become casual and of these 10% become naturalised, and again 10% of naturalised species become invasive (range 5-20%; Williamson & Fitter 1996). However, while plants roughly seem to follow this rule (see Lockwood et al. 2001), more recent research showed that the tens rule does not hold for vertebrates, where approximately 50% have been found to establish (i.e. naturalise) and of these 50% have been found to spread (i.e. become invasive) (Jeschke & Strayer 2005). In New Zealand, of about 25,049 alien plant species having been introduced, 2146 have naturalised (9%), representing 53% of the total flora (Diez et al. 2009). Of those, the Department of Conservation lists 328 species (15%) as environmental weeds (Howell 2008). Although it has frequently been suggested that islands are inherently more invasible than the mainland (Sax & Brown 2000; Pyšek & Richardson 2006), Diez et al. (2009) found no support for this in New Zealand. Numbers of alien species may not provide a useful measure of invasibility, because the higher proportions could simply result from more introduction attempts (Allen et al. 2006). Furthermore, contradictory to Darwin’s naturalisation hypothesis (stating that alien species with higher phylogenetic relatedness to native species will be less successful), it has been found that plants that have congeneric relatives in New Zealand were more likely to naturalise, possibly because they share traits pre-adapting them to the new environment (Duncan & Williams 2002; Diez et al. 2009).

### 1.2 Climate change

Climate change, as another driver of global change, has the potential to have a wide variety of impacts on the global economy, human health and ecosystems. During the past century, a warming of 0.74°C has already been observed globally (IPCC 2007). Eleven of the 12 years between 1995 and 2006 were among the 12 warmest years since the beginning of global surface temperature records in 1850. More intense and longer droughts, increased frequency of heavy precipitation events and extreme temperature events have also been observed (IPCC 2007).
By the end of the century, temperature is projected to increase by 1.1-6.4°C across a range of emission scenarios (Figure 1.2) (IPCC 2007). Increased precipitation is very likely at higher latitudes, while decreased precipitation is likely in the subtropics (IPCC 2007). For New Zealand, predicted warming is somewhat below the global average, with projections ranging from 0.2-2°C by 2040 and 0.7-5.1°C by 2090, with best estimates of 1 and 2°C respectively (Ministry for the Environment 2008). Precipitation changes will vary seasonally: in winter and spring westerly winds are projected to increase, bringing more rainfall in the west of both islands and drier conditions in the east and north. In summer and autumn however, predictions indicate that decreasing westerly winds bring drier conditions in the west of the North Island and increased precipitation in the east (Ministry for the Environment 2008). Frost risk and snow cover are predicted to decrease, while the frequency of high temperature events and extreme daily rainfalls are predicted to increase, as well as possible strong winds (Ministry for the Environment 2008).

Figure 1.2: Past and projected temperature increase until the end of the century, reproduced from IPCC (2007), Figure SPM.5: “Solid lines are multi-model global averages of surface warming (relative to 1980–1999) for the scenarios A2, A1B and B1, shown as continuations of the 20th century simulations. Shading denotes the ± 1 standard deviation range of individual model annual averages. The orange line is for the experiment where concentrations were held constant at year 2000 values. The grey bars at right indicate the best estimate (solid line within each bar) and the likely range assessed for the six SRES marker scenarios. The assessment of the best estimate and likely ranges in the grey bars includes the AOGCMs [Atmosphere-Ocean General Circulation Models] in the left part of the figure, as well as results from a hierarchy of independent models and observational constraints.”
Climate change will affect species, communities and ecosystems in many different ways. For many species, climate will very likely change too rapidly for evolutionary adaptations to take place (IPCC 2007). Increased carbon dioxide levels will affect plants directly, and although responses will be species specific, in general, an increase in photosynthesis rates and reduction in stomatal conductance and respiration is expected (IPCC 2007). Climate change has a major effect on phenology: spring phenology events correlate with spring temperatures in the preceding months, and accordingly spring activities have been occurring progressively earlier since the 1960s (Walther 2004). Specifically, a mean earlier onset of 2.3 days per decade in spring phenology has been observed across a range of taxa, including plants, birds, butterflies and amphibians (Parmesan & Yohe 2003).

Most importantly, however, climate change will affect geographic ranges of species (Thuiller et al. 2007). While local evolutionary responses to climate change have frequently been observed, no change in absolute climate tolerance has been observed in any study. That is, no major evolutionary responses have been observed at the species level, such as novel phenotypes, that would allow conservation of current geographic distribution in the face of climate change (Parmesan 2006). For 99 species of birds, butterflies and alpine herbs, ranges have already shifted on average 6.1 km per decade poleward or 6.1 m upward in altitude (Parmesan & Yohe 2003). Many species are at risk from range losses due to climate change. For example, for alpine plants in the European Alps average range size reductions of 44-50% by the end of the century have been predicted (Dullinger et al. 2012). Moreover, across a wide range of taxa and regions, species extinctions are predicted to range between 22-52% by 2050 assuming there is no dispersal, or 9-32% assuming universal dispersal (Thomas et al. 2004). Similarly, a study of 1350 plant species in Europe calculated an average expected species loss of 27-42% with migration, or 45-63% when assuming no migration, by 2080 (Thuiller et al. 2005). Migration will be limited by the fragmentation of natural habitats brought on by anthropogenic land use. In New Zealand, the high degree of endemism with the associated restricted geographical and climatic ranges implies that many species are at great risk from rapid climate change (IPCC 2007). It has been estimated that a 3°C rise could lead to extinction of 33-50% of native alpine vascular plants in New Zealand (Halloy & Alan 2003).

While some species react directly to climate change by shifting their range, in many cases there may be indirect effects of climate change, such as altered species interactions, or altered physical structure of habitats (Thomas 2010). Rates of adaptation to climate change will vary between species; some species will do better than others. Therefore, competitive balances will shift,
and species dominance will change as well as community composition and even ecosystem functioning (Walther 2004).

1.3 The effects of climate change on plant invasions

While climate change and plant invasions each have been studied extensively, few studies have considered their combined and potentially synergistic impacts (Thuiller et al. 2007). However, climate change provides opportunities for invasive plant species to expand into regions where previously they could not survive and reproduce (Walther et al. 2009). Constraints, such as a reduced growing season, will be lifted for alien species originating from warmer areas introduced into temperate areas (Walther et al. 2009). Ornamental plants already present in gardens may naturalise and subsequently become invasive as conditions become more favourable (Dukes & Mooney 1999; Vilà et al. 2007; Pyke et al. 2008).

It has often been suggested that invasive plants will be favoured under climate change. By definition invasive species are suited to succeed in novel environments (Bradley et al. 2010a). Invasive species may be favoured because they may possess traits that facilitate adaptation to the new climate: invasive species often show rapid dispersal abilities (Dukes & Mooney 1999), they usually tolerate a wide range of climate conditions, and often do not depend on coevolved pollinators or seed dispersers (Vilà et al. 2007). The greater phenotypic plasticity of many invasive species (Daehler 2003; Davidson et al. 2011) will also assist in responding to a changing climate. An increase in the frequency and severity of extreme weather events may also facilitate invasions by creating disturbances and altering resource availability (Jiménez et al. 2011). Additionally, resistance of communities to invasion could decrease as climate change affects native species and disturbs the equilibrium maintaining the community (Thuiller et al. 2007). Furthermore, climate change may also change human activities, which in turn may affect plant invasions (Walther et al. 2009). New plant species will be transported in response to altered demand due to changing conditions, for example the proposed use of invasive species as biofuels in order to reduce greenhouse gas emissions (Pyke et al. 2008). More imports and greater planting effort will result in more plant invasions (Bradley et al. 2010a).

Actual empirical evidence of the impacts of climate change on plant invasions is limited. Among the few studies investigating effects of elevated temperature, open-top chamber studies have shown enhanced growth of two invasive thistles under elevated temperature (Zhang et al. 2012), while in a similar study, native herbaceous species were shown to be less productive while alien congeners showed no response (Verlinden & Nijs 2010). Experimental studies, mostly of
herbaceous species and some vines, also generally show greater response to elevated CO$_2$ in alien species compared to native congener (Dukes & Mooney 1999; Vilà et al. 2007). Moreover, the already observed increase in CO$_2$ in the 20$^{th}$ century resulted in a far greater increase in biomass of some invasive herbaceous species than any other examined species (Ziska 2003). The combined effects of temperature and CO$_2$ on invasive plants has rarely been investigated (but see Hely & Roxburgh 2005; Lee 2011). Studies on the impacts of extreme events on plant invasions are also rare (Bradley et al. 2010a). Most evidence on the effects of climate change on invasive plants has in fact come from modelling studies. Species distribution models are a useful tool to predict an invasive species potential range by relating occurrence data of a species to the environmental conditions at these locations (Elith & Leathwick 2009). These models have been extended to investigate how distributions may change with future climate, with results from such studies frequently predicting range expansions of invasive plants (e.g. Kriticos et al. 2003; Bradley et al. 2010b; Kleinbauer et al. 2010), but sometimes also range contractions (e.g. Bradley et al. 2009; Gallagher et al. 2013).

Indeed, climate change does not favour invasive plants in every case; instead it could reduce the risk of some plant invasions (Bradley et al. 2010a). A recent meta-analysis showed only weak evidence that terrestrial native and alien species responded differently to changes in temperature, precipitation or CO$_2$ levels (Sorte et al. 2013). However, overall it is likely that climate change, together with other major drivers of global change, including increased nitrogen deposition and land use change, will predominantly favour invasive species, thus increasing negative impacts of invasions on ecosystems (Dukes & Mooney 1999).

1.3.1 Plant invasions and climate change in New Zealand

The large pool of alien species present in New Zealand provides multiple sources for ongoing naturalisation (Allen et al. 2006). Most naturalised plant species are still at an early stage of the invasion curve, populations are small and geographic spread limited, with very few weeds appearing to occupy their full environmental range (Williams & West 2000). With climate change, it can be expected that, in particular, species originating from warmer regions will be able to increase their populations and expand to wider areas under climate change (Walther et al. 2009). The predicted warming in New Zealand of 2°C by 2090, combined with fewer frosts (Ministry for the Environment 2008), may enable subtropical or tropical alien species to establish or expand their range southwards (towards higher latitudes). Climate change will thus provide a great challenge for the management of invasive plants. However, to date there have been no comprehensive studies addressing the effects of climate change on invasive plants in New Zealand.
Studying recently naturalised species from warmer native ranges is therefore critical in order to understand whether such species may become invasive and to allocate control efforts accordingly. Indeed, it is at this stage of early naturalisation that control efforts should be focused, as the cost/benefit ratio will be very high. It was found that late control (i.e. action is delayed until infestation is widespread or dense) was on average 40 times more expensive than early control (i.e. small infestation up to 400 m$^2$) (Harris & Timmins 2009). However, as there are too many naturalised species in their early stages of spread to contain them all, it is of utmost importance to be able to predict which naturalised species will become problematic weeds, in order to prioritise and allocate management resources effectively (Kelly & Sullivan 2010). A recent Department of Conservation report on climate change effects on New Zealand biodiversity stated that “the arrival of new weeds and increased invasiveness of existing weeds is one of the most troubling likely consequences of climate change” (McGlone & Walker 2011). Yet, because of the lack of research or evidence available, weed management does not account for climate change. Although ecological theory may suggest which species are more likely to benefit from climate change, the idiosyncratic nature of plant invasions along with the complex interactions with climate change necessitate more experimental research.

1.4 Study species

This thesis focuses on recently naturalised plant species in New Zealand, with limited spread to date, but having the potential to become environmental weeds with climate change. The study species were selected to fulfil various criteria: they should be newly naturalised or naturalising in the Auckland region (i.e. early stages of the invasion), originating from native ranges in warmer subtropical or tropical regions. If the selected species’ native range is Australia, there had to be clear records of its introduction to confirm it was indeed human-introduced. Current distribution of the species had to be limited to the northern North Island – assuming they may be climate-limited and thus may spread further south with a warming climate. The species should be known to be invasive in other countries. The focus is on woody species, as they are rapidly increasing in importance as major plant invaders globally (Richardson & Rejmánek 2011). Almost half of the environmental weeds controlled by the Department of Conservation in New Zealand are trees or shrubs, even though this group only amounts to about 25% of all naturalised species (Howell 2008). Potential spread should not be dispersal-limited; the selected species should be sold in nurseries and be bird-dispersed. Birds are an important dispersal mechanism in habitats favoured by them, such as native forests, and bird-dispersed species are thereby able to spread over wide areas (Williams 2006; Williams et al. 2010; Jordaan et al. 2011). Adhering to these criteria narrowed the selection to three
species listed on the Auckland Council’s Regional Pest Management Strategy in the ‘Research Plants’ category (Auckland Regional Council 2007). This list includes species that are considered to be potential weeds, but require further assessment in order to be listed as banned pest plants. The three species chosen are *Archontophoenix cunninghamiana* (bangalow palm), *Psidium guajava* (common guava) and *Schefflera actinophylla* (Queensland umbrella tree) (Figure 1.3).

![Image](image-url)

**Figure 1.3:** The three study species: a) *Archontophoenix cunninghamiana*; b) *Psidium guajava* (photo by Forest & Kim Starr); and c) *Schefflera actinophylla*.

### 1.4.1 *Archontophoenix cunninghamiana*

*Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. et Drude (bangalow palm) is a native of eastern Australia in the family Arecaceae. This species has been introduced to New Zealand as an ornamental from as early as 1898, and as a popular garden plant it naturalised in 1992 (Cameron 2000a). *Archontophoenix cunninghamiana* is a long lived rainforest palm, growing up to 14 m tall in New Zealand, with pinnately divided leaves up to 6 m length with up to 77 pairs of leaflets (Cameron 2000a). It has a grey trunk of uniform diameter, a green crown shaft and lilac flowers (Jones 1996). This species is self-fertile and produces a large amount of seeds, which in New Zealand are dispersed by blackbirds (*Turdus merula*) and kereru (New Zealand wood pigeons, *Hemiphaga novaeseelandiae*) (Cameron 2000a).

*Archontophoenix cunninghamiana* grows in gullies, stream banks and swampy areas, in shaded areas and under the canopy (Jones 1996). It usually grows in monospecific stands, which can be dense enough to exclude most other species (Jones 1996). This species is cold-sensitive and does not like heavy winds, but is shade tolerant, although it grows faster with more light (Cameron 2000a).
Archontophoenix cunninghamiana has been introduced to Hawaii, New Caledonia, Egypt, Singapore, The United States and South Africa, but it is not reported as invasive (USDA 2010; Invasive Species Specialist Group 2013; US Forest Service 2013). However, A. cunninghamiana has been reported to be invasive in Brazil, with studies documenting its invasion in a small Atlantic rainforest fragment near São Paulo, to the extent of being the species with the highest density (Dislich et al. 2002; Dislich & Pivello 2002; Christianini 2006; Mengardo et al. 2012). In New Zealand, A. cunninghamiana has shown a lag phase of more than 90 years, with the first wild seedlings found in Whangarei in 1992, in native forest 2-300 m away from the nearest adult (Cameron 2000a). One of the largest populations in New Zealand is found in St John’s College bush in Meadowbank, Auckland, where A. cunninghamiana has been widely naturalising (Cameron 2000b). Although this population was eradicated in 2006 (Ewen Cameron, personal communication), new seedlings have since established (personal observation).

1.4.2 Psidium guajava

Psidium guajava L. (common guava) belongs to the family Myrtaceae. A native of Central America (Mexico to northern South America), it first naturalised in New Zealand on the Kermadec Islands in 1965 (Sykes 1982). It is a perennial small tree that grows up to 3 m with a smooth bark and leaves that are densely hairy when young. The fruit is yellow with pink flesh, with a diameter of up to 4 cm (West 1996). The fruits are dispersed by birds, but rats also eat the fruit although they destroy many of the seeds in the process (West 1996). Psidium guajava has the ability to re-sprout vigorously from cut stumps (West 2002).

As P. guajava needs light, it is found in light gaps or at the forest edge (West 1996). This plant can form dense thickets and therefore displace native species. It tolerates a wide range of frost-free climatic conditions and is a drought tolerant species, growing in both humid and dry environments (Yadava 1996). Psidium guajava has been introduced to most subtropical and tropical regions due to its edible fruit (Invasive Species Specialist Group 2013). It has been reported as invasive in many Pacific Islands, islands of the Indian Ocean, Australia, China and South Africa (US Forest Service 2013). In the United States it is present in the states of Florida, Louisiana, Hawaii, and the territories of Puerto Rico and the Virgin Islands (USDA 2010). It is listed on Florida’s list of invasive plant species in category 1 (i.e. “invasive exotics that are altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridising with natives”) (Florida Exotic Pest Plant Council 2011). In New Zealand it is commonly found near old orchards and roadsides (Auckland Regional Council 2007). Attempts to eradicate P. guajava present
on Raoul in the Kermadec Islands commenced in 1972 (West 1996), but the species has persisted at low levels (West 2002).

1.4.3 *Schefflera actinophylla*

*Schefflera actinophylla* (Endl.) Harms (Queensland umbrella tree) is a native species of Australia and New Guinea in the family Araliaceae. It has been introduced to New Zealand for horticulture and its escape from cultivation was first discovered when it was growing as an epiphyte on an old olive tree in Cornwall Park, Auckland, in 2005 (Wilcox 2005). This tree species can grow up to 10 m tall, often with multiple trunks. It has glossy green leaves consisting of five to ten leaflets around 30 cm long that radiate out from a central stalk, and a terminal inflorescence up to 1 m long with small red flowers and scarlet fruit (Walters 1998). It is a prolific seed producer and its seeds are dispersed by birds (Thayer 1998; Walters 1998). The trees also have a vigorous root system, and tolerate heavy pruning, quickly regenerating after being cut (Walters 1998).

*Schefflera actinophylla* can be found in a range of habitats from dry sand dunes to dense shaded canopies (Thayer 1998). It can form large monospecific stands. While growing best in tropical and subtropical areas, the species is robust enough to grow in temperate regions (although smaller at 3-5 m maximum), especially coastal areas, as long as it is protected from frost (Walters 1998). *Schefflera actinophylla* is a shade tolerant plant, which is thereby capable of invading remnant bushland and undisturbed forests (Martin *et al.* 2009). *Schefflera actinophylla* has been reported as invasive in many Pacific Islands, some islands of the Indian Ocean and Singapore (US Forest Service 2013). In the United States it is present in the states of Florida, Hawaii, and the territories of Puerto Rico and the Virgin Islands (USDA 2010), being listed on Florida’s list of invasive plant species in category 1 (description see above) (Florida Exotic Pest Plant Council 2011).

1.5 **Aims and layout of thesis**

In this thesis I will use the three species described above as a model to determine how climate change may affect potential new weeds from subtropical and tropical regions. I aim to investigate whether these three recently naturalised alien species may become more invasive in the Auckland region with climate change, and whether they may spread further in New Zealand. The three selected species have been chosen because they are typical of the weeds that naturalise in New Zealand and become a problem: they are woody, bird-dispersed species of horticultural origin. The thesis combines modelling, controlled environment and field experiments in a holistic approach, aiming to comprehensively assess potential invasiveness of the alien species under climate change
Although the application of species distribution models to predict climate change effects on invasive species has greatly increased in recent years, the results of these studies are rarely validated with field studies and experiments, which is one of the major objectives of this thesis. Another objective is to test growth rates of the alien plants under actual climate change conditions. Furthermore, as competitive displacement is an important impact mechanism of alien species, performance of the alien species will be compared to performance of closely related native species across different climates, and the effects of competition will be assessed. Only when improved knowledge is gained as to how climate change and plant invasions interact, can appropriate management actions be taken to minimise adverse effects of these two principal drivers of global change.

Figure 1.4: Conceptual diagram of the thesis.
The thesis is made up of the following self-contained chapters (Figure 1.4): Chapter 2 will investigate a methodological aspect of species distribution models; how do different sets of climate variables influence model predictions? Chapter 3 will explore the potential distribution of the study species under a range of climate change scenarios using species distribution models. Is the potential range of the study species likely to expand under climate change, and if so, which areas of New Zealand are most at risk? In Chapter 4, seedlings of the study species are grown in the controlled conditions of an environmental chamber under current temperatures and CO₂ levels, compared to the temperatures and CO₂ levels predicted by 2090. It addresses the question, as to whether the alien species may grow more vigorously under future climate conditions. Chapter 5 experimentally tests growth responses of the alien species to drought, an extreme event which is expected to become more frequent with climate change. How is growth and survival of the alien species affected by two different durations of drought? Chapter 6 is a shadehouse experiment examining the impacts of alien species competition on native relatives. How does competition with alien species at differing seedling densities affect growth of native seedlings, and how does it compare to intraspecific competition among the native species? In Chapter 7, seedlings of the study species and native relatives are grown in six sites across the country, differing in suitability (according to the species distribution models). Their performance in relation to the differing climates is measured. Do the alien species perform as expected in suitable, potentially suitable and unsuitable habitats, as previously determined by the species distribution models? How does growth of native relatives in these sites compare to growth of the alien species? Furthermore, Chapter 7 also addresses the question, as to whether the study species may benefit from enemy release. The general discussion (Chapter 8) is a synthesis of all the above chapters, discussing the potential invasiveness of the three study species under climate change, as well as general implications for plant invasions under climate change.
Chapter 1: Introduction

1.6 References


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Chapter 1: Introduction


Chapter 1: Introduction


CHAPTER 2

The effects of climate variable selection on predictions of alien plants’ distributions

Abstract

Species distribution models are an important tool to predict the potential spread of invasive plants. While recent progress has improved model performance, there is still concern about the validity of such models, especially when applied to novel geographic regions or climates. This study investigated how different sets of variables influence predicted distributions, considering several measures of model performance and how extrapolation to novel geographic regions may affect results. Potential distributions of three recently naturalised alien plants in New Zealand (Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla) were modelled, by training a model based on global data from native and introduced ranges and projecting it to New Zealand, using Maxent. For each species four models were calibrated: first with a full set of 19 bioclimatic variables, then with a customised set with selection based on analysis of response curves, and finally with two reduced sets of uncorrelated variables. Although AUC across all models was very high (AUC ≥ 0.9), correlations amongst models ranged between 0.27-0.98. Inclusion of all variables predicted larger areas to be suitable in the projected region, with highly unlikely predictions in some areas; especially where bioclimatic variables showed values outside the range of the training data (new environments). Conversely, minimal extrapolation and more realistic predictions of species distributions were obtained from models including a customised set of variables, and even more so from models including only a reduced set of variables. This study shows that careful selection of variables and investigation into extrapolation are vital in aiming towards more realistic predictions of invasive species’ distributions.

2.1 Introduction

Species distribution models (SDMs) are an important tool used to make predictions of a species’ potential distribution by relating occurrence data to environmental conditions (Elith & Leathwick 2009), and particularly, climatic conditions. Climate has for a long time been recognised as the dominant factor influencing the distribution of plants (Woodward 1987). One of the more recent applications of such models is predicting the spread of invasive plants (e.g. Robertson et al. 2001; Dunlop et al. 2006; Follak & Strauss 2010; Kriticos et al. 2011). This is of vital importance, as alien plant invasions drive native population declines (Baider & Florens 2011). Being able to predict the potential range of an invasive plant provides a valuable insight to its threat to biodiversity and assists weed management programs (Follak & Strauss 2010; Kriticos et al. 2011).

A major assumption in species distribution modelling is often violated when models are applied to invasive species, namely that a species is at equilibrium with its environment (i.e. it occurs in all potentially suitable habitats) (Jones et al. 2010). Furthermore, there is uncertainty whether a species’ niche is conserved when introduced into a new range (Broennimann & Guisan 2008). However, a recent study showed that niche shifts are rare for terrestrial plant invaders (Petitpierre et al. 2012). Moreover, by using data from both the native and introduced range, the fitted model will include eventual differences in niche (Broennimann & Guisan 2008). Models for invasive plants trained at a global scale may thus be used to predict suitable habitat in a recently invaded region (Jones et al. 2010). Predictions to new environments (i.e. data outside the range of the training data; Elith et al. 2010) are often necessary for applying SDMs to invasive species. This may pose a number of problems, one being that the fitted response may extrapolate unrealistically at the extreme of the sampled climate variables (Elith et al. 2010). However, such models are often the only way to forecast invasions, therefore they remain useful, as long as methods and results are critically evaluated (Elith & Leathwick 2009). Although clearly important, extrapolation to new environments is a factor of uncertainty that has received little attention (Fitzpatrick & Hargrove 2009).

One methodological issue with SDMs is the selection of appropriate predictors. Users generally rely on automatic parameterisation and variable selection procedures to train SDMs, assuming that the algorithm will select the ones most influential for the actual distribution (Jiménez-Valverde et al. 2011). However, selecting appropriate variables is particularly important when models are to be used in different regions or climates (Peterson & Nakazawa 2008; Elith et al. 2011). A balance between overfitting the model by using too many variables and underfitting by excluding an important variable should be aimed for. Ideally the choice would be based on good knowledge of the abiotic requirements of these species (Beaumont et al. 2005). As this is often not available, other
methods that have been used are preliminary PCA (Robertson et al. 2001) or multicollinearity analyses (Giovanelli et al. 2010) and investigations of response curves of individual variables (Beaumont et al. 2005). Recent studies have suggested that inappropriate selection of predictors may lead to a failure of predicting distributions in the invaded range and with it a premature conclusion of a niche shift (Peterson & Nakazawa 2008; Rödder et al. 2009). In particular, there may be some bioclimatic variables that are more conserved compared to others that may be subject to niche shift, and thus the selection of predictors may affect transferability of a model (Rödder & Lötters 2010).

Another issue concerns the evaluation of the models. Prediction accuracy, commonly tested with measures such as area under the curve (AUC) of receiver-operating characteristic (ROC) plots (Fielding & Bell 1997) is frequently used to compare model performance. Other methods of comparing and evaluating models have however not received enough attention (Syphard & Franklin 2009). Model exploration tools should be incorporated into model development and evaluation (Elith et al. 2010). Measuring the amount of map overlap among predictions may provide important information, as the accuracy of different modelling approaches may not always be apparent from global measures such as AUC (Syphard & Franklin 2009).

By applying predictive models to alien plants at an early stage of the invasion, they have the potential to inform land managers and decision-makers at a time when their actions to control these plants may still be effective (Jones et al. 2010). However, to reduce the cost of monitoring and control, high-accuracy predictions are essential. This is of vital importance in New Zealand, as there is a large pool of alien plant species, but relatively few of them occupy their full environmental potential (Williams & West 2000). In this study three newly naturalised (sub-) tropical alien plants in New Zealand are modelled. Models calibrated with a full set of 19 bioclimatic variables are compared to models calibrated with subsets: a customised set with selection based on analysis of response curves, and two reduced sets comprising uncorrelated variables. To evaluate models critically, a range of model exploration tools are used instead of solely relying on AUC. The objective of the study is to investigate how inclusion of different sets of climate variables affects predicted distributions in a new geographic region.
2.2 Methods

2.2.1 Study species

This study models the distribution of *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. et Drude (bangalow palm), *Psidium guajava* L. (common guava) and *Schefflera actinophylla* (Endl.) Harms (Queensland umbrella tree), three species from subtropical or tropical native ranges. They are all newly naturalised plants in New Zealand, with limited spread to date in the northern part of the North Island, but are a concern as potential weeds. They are woody, bird-dispersed species and recorded as invasive in other parts of the world.

*Archontophoenix cunninghamiana* is a native of eastern Australia in the family Arecaceae. In Brazil, *A. cunninghamiana* has invaded a small forest fragment near São Paulo to the extent of having become the species with the highest density (Christianini 2006). *Psidium guajava* belongs to the Myrtaceae. A native of Central America (Mexico to northern South America), it has been introduced to most subtropical and tropical regions due to its edible fruit, and has become invasive in many countries (Randall 2007). *Schefflera actinophylla* belongs to the Araliaceae and is native to Australia and New Guinea. *Schefflera actinophylla* can form large monospecific stands and is considered very invasive in the Pacific Islands (Randall 2007).

2.2.2 Occurrence and climate data

Occurrence data across the globe from both the native and introduced ranges was used, but excluding data from the region of interest (i.e. New Zealand, where they only recently naturalised). The majority of occurrence data originates from the Global Biodiversity Information Facility (GBIF; [http://data.gbif.org/](http://data.gbif.org/)) and Australia’s Virtual Herbarium (AVH; [http://avh.chah.org.au/](http://avh.chah.org.au/)), retrieved in November 2010, and some additional records from Tropicos ([http://www.tropicos.org/](http://www.tropicos.org/)) and, for *A. cunninghamiana*, from the literature (Christianini 2006).

Occurrence data was cleaned before use: occurrence records were compared to an administrative shapefile of the world, to check if the recorded country name in the occurrence records matched the actual geographical country based on the coordinates (Hijmans *et al*. 1999). Most of such unmatched records were deleted, but in some cases new coordinates were assigned if a locality description was available, as generally the coordinates are more likely to be erroneous than the locality descriptions (Hijmans *et al*. 1999). Duplicates were removed. After cleaning the data, 81 global records remained for *A. cunninghamiana*, of which 88% are from its native range;
152 for *S. actinophylla* with 70% from its native range; and 1741 records for *P. guajava* with 52% from its native range (Figure 2.1).

![Figure 2.1](image)

**Figure 2.1:** Global occurrence data used for species distribution modelling. Records of *A. cunninghamiana* are represented as red squares, *P. guajava* as green triangles, and *S. actinophylla* as blue circles.

Models were trained using global climate data and then applied to New Zealand data. To train the model, data from Worldclim was used in 2.5 arc minutes resolution across the globe ([http://worldclim.org/](http://worldclim.org/); Hijmans et al. 2005). The model was then projected onto New Zealand-specific climate layers, which were provided by the National Institute of Water and Atmospheric Research (NIWA; layers accessed November 2010). These layers were created using the maximum number of weather stations available in New Zealand, resulting in higher accuracy data than global climate layers such as Worldclim. Layers from NIWA are in 0.05° resolution (i.e. 3 arc minutes; approximately 5 x 5 km).

### 2.2.3 Modelling approach

Distribution models were built using maximum entropy; a general-purpose machine learning method, implemented in Maxent Version 3.3.3e ([www.cs.princeton.edu/~schapire/maxent/](http://www.cs.princeton.edu/~schapire/maxent/); Phillips et al. 2006). Maxent estimates a target probability distribution by finding the probability distribution of maximum entropy, i.e. the most spread out or closest to uniform, while respecting a set of constraints representing the incomplete information about the target distribution (Phillips et al. 2006). Maxent consistently has been ranked amongst the highest performing SDMs (Elith et al. 2006;
Roura-Pascual et al. 2008; Giovanelli et al. 2010; Dupin et al. 2011). Maxent has been shown to perform well even when dealing with spatial uncertainty of occurrence data and when only few occurrence records are available (Hernandez et al. 2006; Wilson et al. 2009). Default settings were used in Maxent. The logistic output was used as a suitability index (Elith et al. 2011).

Four models were calibrated for each species, including different sets of climate variables. For each model, a ten-fold cross-validation was applied by using 90% of occurrence data for training the model, leaving out a different 10% of data for testing of each of the model runs. The average output was used to assess the distributions of the species.

To begin, models were calibrated using all 19 bioclimatic variables (hereafter termed ‘full set’) (Table 2.1). While this uses the maximum information available, this approach has been criticised as it includes predictors that may not be ecologically relevant (Elith & Leathwick 2009), and it may promote overfitting (Jiménez-Valverde et al. 2011).

Secondly models were calibrated excluding certain variables (hereafter termed ‘customised set’). The chosen set of variables differed among species. If both monthly and quarterly variables describing the same patterns existed, only the monthly variables were retained. Thereafter other variables were excluded based on analysis of response curves in a model calibrated with only the corresponding variable. These curves are part of the Maxent output and give an indication of whether a specific variable may be informative. If the curves showed a clear pattern (normal distribution or skewed distribution) they were included in the model (adapting the ideas of Beaumont et al. 2005 who instead examined the histograms of the bioclimatic variables), however if the curves showed a high standard deviation for the ten cross-validated runs or random patterns, they were excluded. Adhering to these criteria, ten variables were retained for A. cunninghamiana and 12 each for P. guajava and S. actinophylla (Table 2.1).
Table 2.1: The 19 bioclimatic variables used in the full set of variables, with crosses indicating the variables used in the customised sets for A. cunninghamiana (AC), P. guajava (PG) and S. actinophylla (SA); and the variables used in the reduced set and the reduced NIWA set.

<table>
<thead>
<tr>
<th>Bioclimatic variable</th>
<th>Customised set</th>
<th>Reduced set</th>
<th>Reduced NIWA set</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIO1 Annual mean temperature</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO2 Mean diurnal range (mean of monthly (max temp–min temp))</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO3 Isothermality (BIO2/BIO7) (*100)</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>BIO4 Temperature seasonality (standard deviation*100)</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>BIO5 Max temperature of warmest month</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO6 Min temperature of coldest month</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO7 Temperature annual range (BIO5-BIO6)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO8 Mean temperature of wettest quarter</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO9 Mean temperature of driest quarter</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>BIO10 Mean temperature of warmest quarter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO11 Mean temperature of coldest quarter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO12 Annual precipitation</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>BIO13 Precipitation of wettest month</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO14 Precipitation of driest month</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>BIO15 Precipitation seasonality (coefficient of variation)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO16 Precipitation of wettest quarter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO17 Precipitation of driest quarter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO18 Precipitation of warmest quarter</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>BIO19 Precipitation of coldest quarter</td>
<td></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

In a third approach a small set of variables (hereafter termed ‘reduced set’) was chosen using ecologically relevant variables that avoid problems of multicollinearity. The selected variables do not contain highly correlated pairs (i.e. correlation > 0.8; Giovanelli et al. 2010), as assessed by calculating Pearson correlations between the Worldclim climate variables in a pairwise fashion (Table 2.2). As temperature variables are frequently highly correlated, only three variables could be retained (BIO2, 5, 6); and to avoid overemphasizing the precipitation variables, only three of the non-correlated precipitation variables were included (BIO13, 15, 18) (Table 2.1). For comparison, another reduced set was built (termed ‘reduced NIWA set’), when Pearson correlations were calculated among the NIWA climate layers (projected region) instead. For these climate layers, the precipitation variables are all highly correlated with exception of BIO15 (Table 2.3). Thus, the variables that were retained using this approach were BIO5, 6, 7, 8, 15 and 18.
Table 2.2: Pearson correlations between bioclimatic variables in the training region (using 9,025,130 data values for each Worldclim climate layer). Values > 0.8 are highlighted in bold.

| BI01 | BI02 | BI03 | BI04 | BI05 | BI06 | BI07 | BI08 | BI09 | BI10 | BI11 | BI12 | BI13 | BI14 | BI15 | BI16 | BI17 | BI18 | BI19 |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 0.521 | 0.387 | -0.892 | -0.210 | -0.833 | 0.764 | 0.355 | 0.888 | 0.059 | 0.861 | 0.886 | 0.831 | 0.988 | 0.825 | 0.866 | 0.931 | 0.987 | 0.866 | 0.825 | 0.967 | 0.866 | 0.825 |

Table 2.3: Pearson correlations between bioclimatic variables in the projected region (using 11,624 data values for each NIWA climate layer). Values > 0.8 are highlighted in bold.

| BI01 | BI02 | BI03 | BI04 | BI05 | BI06 | BI07 | BI08 | BI09 | BI10 | BI11 | BI12 | BI13 | BI14 | BI15 | BI16 | BI17 | BI18 | BI19 |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| -0.043 | 0.462 | 0.619 | 0.784 | 0.091 | 0.340 | 0.553 | 0.519 | 0.915 | 0.549 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 | 0.994 |

2.2.4 Model evaluation

The models were evaluated with several measures of model performance. The threshold-independent receiver operating characteristic (ROC), which characterises the performance of a model at all possible thresholds by a single value, the area under the curve (AUC) has been extensively used to evaluate SDMs. The AUC can be interpreted as the probability, that if comparing
a random presence and a random absence site, the presence site will have a higher predicted value than the absence site (Elith et al. 2006). In case of presence-only data, instead of distinguishing presence from absence, it distinguishes presence from random (Phillips et al. 2006). Models that are no better than random have an AUC value of 0.5, whereas models with perfect predictive ability have an AUC approximating 1. The use of AUC in SDMs has recently been criticised (Lobo et al. 2008; Jiménez-Valverde 2012); consequently while AUC is reported in this study, other measures of model performance were given greater importance.

Further model evaluations required a threshold, converting the map of continuous suitability into a binary map of suitable/unsuitable. The threshold was chosen as the value that maximises the sum of test sensitivity and specificity under the receiver operating curve. A comparative study of 12 commonly used thresholds showed that this approach achieved both high sensitivity and specificity (Liu et al. 2005). To test if the accuracy of the predictions is greater than expected by chance, a one-tailed binomial test was used to test the omission rate. To compare test AUC, the selected threshold value, the area predicted suitable globally and in New Zealand, and the testing omission error among the ten cross-validated models calibrated with the different variable sets, a Wilcoxon Rank Sum (Mann-Whitney U) test was employed using R (R Development Core Team 2010, version 2.11.0 for Windows).

All the above reported values, however, only indicate how good the model is before projection to a new region. To investigate similarity of the predicted distributions from the four variable sets in the projected region, Pearson’s correlation coefficient was used on a cell by cell basis, pairwise between models (Syphard & Franklin 2009). After applying the threshold, the overlap between the areas predicted suitable in New Zealand of the four models calibrated with different variable sets was calculated.

As transferability of models may be limited if correlation structures among predictors are not consistent across regions, the correlation matrixes of the Worldclim and NIWA variables (Tables 2.2 and 2.3) were compared using a Mantel test. The test was carried out in R with 1000 permutations (Jiménez-Valverde et al. 2009) for correlation structures among all 19 bioclimatic variables as well as all subsets used. Furthermore, the contributions of bioclimatic variables to the models were investigated, as determined by Maxent.

As introduced range models often need to extrapolate for values outside the training data, care needs to be taken. Maxent uses an exponential model for probabilities, which can give very large predicted values for environmental conditions outside the training range (Phillips et al. 2006).
The multivariate environmental similarity surface (MESS) was therefore investigated, which is part of the Maxent outputs. These maps show the similarity of a point (in predicted area) to a reference set of points (training data) in regard to the predictor variables. Negative values indicate that at least one variable has a value that is outside the range of the training data (Elith et al. 2010). The locations of these sites were investigated and the percentage of all cells in New Zealand with negative values calculated. This calculation was repeated for the area predicted suitable after applying the threshold, to see whether the negative MESS values may indicate questionable predicted suitability. To furthermore investigate if differences in predicted suitability across the four models were mostly due to negative MESS values, the overlap between the areas predicted suitable between models was calculated again, but this time omitting in the calculation all cells with negative MESS values.

2.3 Results

2.3.1 Comparison of models calibrated with different variable sets

Models calibrated with the full, customised, reduced or reduced NIWA sets of variables produced different predictions, with the most notable difference being the area of the Southern Alps, which is predicted to be highly suitable if using the full set of variables, whereas it is not when using the customised or the two reduced sets of variables (Figure 2.2).

Test AUC was high across all models (AUC ≥ 0.9; Table 2.4). There were no significant differences in test AUC for either A. cunninghamiana or S. actinophylla between the full, customised and the two reduced sets of variables. However for P. guajava, AUC of the two reduced sets of variables was significantly lower than the customised and full set (reduced set: \( P = 0.023 \) and \( P < 0.001 \); reduced NIWA set: \( P = 0.003 \) and \( P < 0.001 \)).

For all models, omission error was ≤ 5% (Table 2.4). One-tailed exact binomial tests of omission error showed \( P < 0.001 \) for each of the individual cross-validation models across all species and variable sets. When a threshold was applied, there were no significant differences among the selected threshold or the testing omission error for the different sets of variables for any of the species (Table 2.4).
Figure 2.2: Model predictions using the logistic output for a-d) *A. cunninghamiana*; e-h) *P. guajava*; and i-l) *S. actinophylla*. The first map in each row (a,e,i) shows results from the models calibrated with the full set of variables, the second map (b,f,j) with the customised set, the third map (c,g,k) with the reduced set, and the fourth map (d,h,l) with the reduced NIWA set of variables.

The global area predicted suitable was significantly larger for *P. guajava* using the reduced set of variables compared to the full set ($P = 0.005$), and for *S. actinophylla* it was significantly larger for the model with either of the reduced sets of variables compared to both customised and full set models (reduced set: $P = 0.005$ and $P = 0.009$; reduced NIWA set: $P = 0.029$ and $P = 0.035$).
proportion of area predicted suitable in New Zealand (Figure 2.3), however, was significantly larger for all species with the full set models than the customised, reduced or reduced NIWA sets (A. cunninghamiana: \( P = 0.002, P < 0.001, P = 0.002; P. guajava \) and S. actinophylla: all \( P < 0.001 \) (Table 2.4). For A. cunninghamiana, the reduced set area predicted suitable in New Zealand was also smaller than the other two sets (both \( P < 0.001 \)). For P. guajava the area predicted suitable in New Zealand for the model with the customised set was significantly larger than the reduced NIWA set (\( P = 0.023 \)). For S. actinophylla, the reduced set area predicted suitable in New Zealand was smaller than the reduced NIWA set (\( P = 0.002 \)).

**Table 2.4:** Mean test AUC ± standard deviation, the selected threshold, mean test omission error and area predicted suitable (proportion of whole world and proportion of New Zealand) ± standard error for ten cross-validation models. Significant differences are indicated by differing lower case letters; for \( P \)-values see text.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>AUC ± sd</th>
<th>Threshold</th>
<th>Omission error ± se</th>
<th>Area ± se</th>
<th>Area NZ ± se</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. cunninghamiana</em></td>
<td>Full set</td>
<td>0.986 ± 0.0218</td>
<td>0.258</td>
<td>0.013 ± 0.0125</td>
<td>0.028 ± 0.0079</td>
<td>0.210 ± 0.0112</td>
</tr>
<tr>
<td></td>
<td>Customised set</td>
<td>0.983 ± 0.0203</td>
<td>0.325</td>
<td>0.038 ± 0.0267</td>
<td>0.065 ± 0.0087</td>
<td>0.163 ± 0.0039</td>
</tr>
<tr>
<td></td>
<td>Reduced set</td>
<td>0.981 ± 0.0228</td>
<td>0.345</td>
<td>0.038 ± 0.0267</td>
<td>0.025 ± 0.0075</td>
<td>0.124 ± 0.0034</td>
</tr>
<tr>
<td></td>
<td>Red. NIWA set</td>
<td>0.983 ± 0.0187</td>
<td>0.279</td>
<td>0.038 ± 0.0267</td>
<td>0.031 ± 0.0097</td>
<td>0.162 ± 0.0055</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td>Full set</td>
<td>0.919 ± 0.0086</td>
<td>0.219</td>
<td>0.047 ± 0.0096</td>
<td>0.212 ± 0.0098</td>
<td>0.426 ± 0.0180</td>
</tr>
<tr>
<td></td>
<td>Customised set</td>
<td>0.913 ± 0.0093</td>
<td>0.239</td>
<td>0.049 ± 0.0094</td>
<td>0.218 ± 0.0131</td>
<td>0.303 ± 0.0117</td>
</tr>
<tr>
<td></td>
<td>Reduced set</td>
<td>0.901 ± 0.0091</td>
<td>0.217</td>
<td>0.036 ± 0.0052</td>
<td>0.255 ± 0.0069</td>
<td>0.271 ± 0.0115</td>
</tr>
<tr>
<td></td>
<td>Red. NIWA set</td>
<td>0.898 ± 0.0091</td>
<td>0.250</td>
<td>0.048 ± 0.0065</td>
<td>0.241 ± 0.0062</td>
<td>0.261 ± 0.0142</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td>Full set</td>
<td>0.977 ± 0.0146</td>
<td>0.145</td>
<td>0.036 ± 0.0160</td>
<td>0.057 ± 0.0072</td>
<td>0.133 ± 0.0060</td>
</tr>
<tr>
<td></td>
<td>Customised set</td>
<td>0.974 ± 0.0122</td>
<td>0.178</td>
<td>0.050 ± 0.0186</td>
<td>0.056 ± 0.0077</td>
<td>0.035 ± 0.0021</td>
</tr>
<tr>
<td></td>
<td>Reduced set</td>
<td>0.966 ± 0.0156</td>
<td>0.182</td>
<td>0.029 ± 0.0117</td>
<td>0.094 ± 0.0142</td>
<td>0.030 ± 0.0014</td>
</tr>
<tr>
<td></td>
<td>Red. NIWA set</td>
<td>0.960 ± 0.0093</td>
<td>0.164</td>
<td>0.035 ± 0.0192</td>
<td>0.120 ± 0.0171</td>
<td>0.035 ± 0.0026</td>
</tr>
</tbody>
</table>

Correlations of predicted suitability in New Zealand between the reduced and customised set models were generally high, whereas correlations of these sets of models compared to the full set were always lower than 0.6 (Table 2.5). Overlaps of the areas predicted suitable in New Zealand between the four models ranged between 62-95%, except for S. actinophylla comparing the full set to the other three sets, where overlaps ranged between 33-41%.
Figure 2.3: Areas predicted suitable (shaded) for a-d) A. cunninghamiana; e-h) P. guajava; and i-l) S. actinophylla. The first map in each row (a,e,i) shows results from the models calibrated with the full set of variables, the second map (b,f,j) with the customised set, the third map (c,g,k) with the reduced set, and the fourth map (d,h,l) with the reduced NIWA set of variables.
Table 2.5: Pearson correlation between models and percent overlap between areas predicted suitable in New Zealand when a threshold was applied (i.e. 2 x number of cells, where both models predict suitability, divided by sum of total number of cells with predicted suitability of model 1 and 2), and in brackets percent overlap when cells with negative MESS values were excluded from the calculation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Full - customised</th>
<th>Full - reduced NIWA</th>
<th>Full - red. NIWA</th>
<th>Customised - reduced</th>
<th>Customised - red. NIWA</th>
<th>Reduced - red. NIWA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Correlations</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. cunninghamiana</em></td>
<td>0.534</td>
<td>0.578</td>
<td>0.561</td>
<td>0.978</td>
<td>0.949</td>
<td>0.953</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td>0.451</td>
<td>0.521</td>
<td>0.500</td>
<td>0.889</td>
<td>0.930</td>
<td>0.944</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td>0.362</td>
<td>0.322</td>
<td>0.276</td>
<td>0.866</td>
<td>0.841</td>
<td>0.921</td>
</tr>
<tr>
<td><strong>Overlap</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. cunninghamiana</em></td>
<td>64.22 (72.12)</td>
<td>62.98 (71.12)</td>
<td>62.94 (70.66)</td>
<td>84.69 (84.62)</td>
<td>88.23 (88.47)</td>
<td>84.53 (84.46)</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td>72.86 (74.50)</td>
<td>69.21 (70.99)</td>
<td>76.01 (78.09)</td>
<td>75.08 (74.97)</td>
<td>83.26 (83.45)</td>
<td>82.38 (82.38)</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td>40.97 (55.30)</td>
<td>32.56 (44.15)</td>
<td>35.39 (47.63)</td>
<td>74.14 (74.14)</td>
<td>76.66 (76.66)</td>
<td>94.76 (94.76)</td>
</tr>
</tbody>
</table>

Mantel tests showed significant correlation structures between the training and testing region variables (Worldclim and NIWA) for all sets, with correlations lowest for the customised set of *S. actinophylla* (0.473; \(P = 0.005\)) followed by the reduced NIWA set (0.530; \(P = 0.069\)) and highest for the reduced set (0.637; \(P = 0.009\)) (Table 2.6). Variable contributions differed among models (Table 2.7); with the most important variable in the reduced set models for all species being BIO6 (minimum temperature of the coldest month). The six variables of the reduced set, for instance, explained only 16.0% of the *A. cunninghamiana* model calibrated with the full set, 8.6% of the *P. guajava* model, but 33.3% of the *S. actinophylla* model.

Table 2.6: Mantel tests comparing similarity of correlation structure between Worldclim (global) and NIWA (New Zealand) bioclimatic variables.

<table>
<thead>
<tr>
<th>Bioclimatic variables</th>
<th>Correlation</th>
<th>(P)-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>All 19 variables (full set)</td>
<td>0.594</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Customised set <em>A. cunninghamiana</em></td>
<td>0.533</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Customised set <em>P. guajava</em></td>
<td>0.635</td>
<td>0.002</td>
</tr>
<tr>
<td>Customised set <em>S. actinophylla</em></td>
<td>0.473</td>
<td>0.005</td>
</tr>
<tr>
<td>Reduced set</td>
<td>0.637</td>
<td>0.009</td>
</tr>
<tr>
<td>Reduced NIWA set</td>
<td>0.530</td>
<td>0.069</td>
</tr>
</tbody>
</table>
Chapter 2: The effects of climate variable selection on predictions of alien plants’ distributions

Table 2.7: Variable contributions [%] for the four models with different sets of variables, for A. cunninghamiana (AC), P. guajava (PG) and S. actinophylla (SA).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Full set</th>
<th>Customised set</th>
<th>Reduced set</th>
<th>Reduced NIWA set</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AC</td>
<td>PG</td>
<td>SA</td>
<td>AC</td>
</tr>
<tr>
<td>BI01 Annual mean temperature</td>
<td>0.8</td>
<td>2.1</td>
<td>0.7</td>
<td>17.9</td>
</tr>
<tr>
<td>BI02 Mean diurnal range (mean of monthly (max temp – min temp))</td>
<td>1.0</td>
<td>1.2</td>
<td>7.1</td>
<td>7.1</td>
</tr>
<tr>
<td>BI03 Isothermality (BI02/BI07) (*100)</td>
<td>34.4</td>
<td>1.0</td>
<td>11.7</td>
<td>11.7</td>
</tr>
<tr>
<td>BI04 Temperature seasonality (standard deviation*100)</td>
<td>7.6</td>
<td>35.1</td>
<td>13.2</td>
<td>-</td>
</tr>
<tr>
<td>BI05 Max temperature of warmest month</td>
<td>5.6</td>
<td>0.2</td>
<td>0.5</td>
<td>6.3</td>
</tr>
<tr>
<td>BI06 Min temperature of coldest month</td>
<td>0.2</td>
<td>0.2</td>
<td>9.3</td>
<td>25.6</td>
</tr>
<tr>
<td>BI07 Temperature annual range (BI05-BI06)</td>
<td>0</td>
<td>22.6</td>
<td>26.8</td>
<td>7.1</td>
</tr>
<tr>
<td>BI08 Mean temperature of wettest quarter</td>
<td>0</td>
<td>0.2</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>BI09 Mean temperature of driest quarter</td>
<td>0</td>
<td>0</td>
<td>2.2</td>
<td>0.6</td>
</tr>
<tr>
<td>BI10 Mean temperature of warmest quarter</td>
<td>1.2</td>
<td>0.9</td>
<td>0.8</td>
<td>-</td>
</tr>
<tr>
<td>BI11 Mean temperature of coldest quarter</td>
<td>8.8</td>
<td>12.4</td>
<td>0.2</td>
<td>-</td>
</tr>
<tr>
<td>BI12 Annual precipitation</td>
<td>0.6</td>
<td>2.6</td>
<td>1.6</td>
<td>-</td>
</tr>
<tr>
<td>BI13 Precipitation of wettest month</td>
<td>0.1</td>
<td>0.4</td>
<td>0.3</td>
<td>0.9</td>
</tr>
<tr>
<td>BI14 Precipitation of driest month</td>
<td>27.0</td>
<td>3.0</td>
<td>4.0</td>
<td>-</td>
</tr>
<tr>
<td>BI15 Precipitation seasonality (coefficient of variation)</td>
<td>3.4</td>
<td>0.7</td>
<td>1.8</td>
<td>12.5</td>
</tr>
<tr>
<td>BI16 Precipitation of wettest quarter</td>
<td>0.1</td>
<td>6.5</td>
<td>3.9</td>
<td>-</td>
</tr>
<tr>
<td>BI17 Precipitation of driest quarter</td>
<td>1.0</td>
<td>0.2</td>
<td>0.7</td>
<td>-</td>
</tr>
<tr>
<td>BI18 Precipitation of warmest quarter</td>
<td>5.7</td>
<td>5.9</td>
<td>14.3</td>
<td>26.6</td>
</tr>
<tr>
<td>BI19 Precipitation of coldest quarter</td>
<td>2.5</td>
<td>4.9</td>
<td>0.5</td>
<td>-</td>
</tr>
</tbody>
</table>

2.3.2 New environments for projections to New Zealand

There were some areas with new environments, where at least one variable had a value that was outside the range of the training data (Figure 2.4; Table 2.8). The same cells were concerned for models of A. cunninghamiana and S. actinophylla, with areas of new environments for all three species primarily located in the South Island, including the Southern Alps and the northwest of the island (Figure 2.4). Most of these cells with new environments were located within the area predicted suitable for the full set models. The variables that showed negative MESS values for A. cunninghamiana and S. actinophylla were BIO12 (annual precipitation) and BIO14 (precipitation of driest month) and to a lesser extent BIO17 (precipitation of driest quarter), and for P. guajava most importantly BIO17. For the customised and the two reduced sets, only a small area on the South Island’s west coast had new environments, which does not fall within the area predicted suitable, except for a few cells with the reduced set of A. cunninghamiana and the customised set of P. guajava.
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Figure 2.4: Areas of new environments for a) *A. cunninghamiana* and *S. actinophylla*; and b) *P. guajava*, with shades of grey indicating the areas with negative MESS values for models using the different variable sets. Note that while exact MESS values differ between *A. cunninghamiana* and *S. actinophylla*, the cells affected by negative MESS values were identical for the two species.

When comparing predictions of the reduced and customised sets, overlaps between models remained very similar if areas with negative MESS values were excluded in the calculations; but overlaps increased up to 15% when comparing predictions of the full set with the other three sets (Table 2.5).

Table 2.8: Number of cells that have negative values in MESS maps for total area (of 11,624 cells in New Zealand) and within area predicted suitable and in brackets percentage of total area or area predicted suitable that have negative MESS values.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>Total NZ</th>
<th>Predicted area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. cunninghamiana</em></td>
<td>Full set</td>
<td>511 (4.40%)</td>
<td>495 (19.76%)</td>
</tr>
<tr>
<td></td>
<td>Customised set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td></td>
<td>Reduced set</td>
<td>12 (0.10%)</td>
<td>2 (0.0014%)</td>
</tr>
<tr>
<td></td>
<td>Red. NIWA set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td>Full set</td>
<td>213 (1.83%)</td>
<td>213 (4.55%)</td>
</tr>
<tr>
<td></td>
<td>Customised set</td>
<td>171 (1.47%)</td>
<td>7 (0.20%)</td>
</tr>
<tr>
<td></td>
<td>Reduced set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td></td>
<td>Red. NIWA set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td>Full set</td>
<td>511 (4.40%)</td>
<td>511 (32.61%)</td>
</tr>
<tr>
<td></td>
<td>Customised set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td></td>
<td>Reduced set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td></td>
<td>Red. NIWA set</td>
<td>12 (0.10%)</td>
<td>0 (0%)</td>
</tr>
</tbody>
</table>
2.4 Discussion

Predictions between models calibrated with the four sets of variables differ; in particular, model predictions using the full set of variables show a larger potentially suitable area in New Zealand than predictions using the customised or reduced sets of variables. The models calibrated with the full set of variables have to be discarded based on their high values of suitability in unlikely areas (such as in alpine areas), which partially coincide with negative MESS values. This indicates that the models in all probability extrapolated the fitted response unrealistically at the extremes of some climate variables (Elith et al. 2010). This may be because the observed current species distributions do not provide information about how the species may respond in new environments, therefore such predictions are often erroneous as well as ecologically and statistically invalid (Fitzpatrick & Hargrove 2009). The variables that showed negative MESS values in this study were precipitation variables, and with most areas of new environments situated on the South Island’s west coast, this is not surprising, as this is an area with extraordinarily high rainfall of up to 12,884 mm per year, and even in the driest month as much as 830 mm. The models may have extrapolated the fitted response to such extremely high values as highly suitable, irrespective of the temperature values. Response curves of these variables support this assumption: after a decrease in suitability with medium-high precipitation values, they show continuously increasing suitability with very high precipitation values. This may also explain why in this study using fewer variables resulted in a smaller distribution (for predictions in New Zealand). The potential distribution in the training region, on the other hand, was smaller when more variables were included, which is in accordance to other studies (e.g. Beaumont et al. 2005; Rödder et al. 2009), where it was observed that inclusion of more climatic parameters results in a smaller predicted distribution because of tighter constraints. While the full set models had high AUC values, this may be because, as Jiménez-Valverde (2012) pointed out, the lower the proportionate area predicted as suitable, the higher the AUC, as more background data are predicted as absences. The results of this study confirm that high AUC values are not necessarily associated with more realistic models and thus should not be used as a sole measure of model performance.

Differences between the customised and the two reduced sets of variables models (which were similar, with correlations between 0.84-0.98) were less evident. The analysis of MESS maps indicated that these models contained only very few or no values outside the training data range: the customised set for P. guajava showed a small portion of 0.2% of the area predicted suitable that had new environments, and for A. cunninghamiana 0.0014% in case of the reduced set, which have to be treated with caution. Another important issue to consider, suggested by Jiménez-Valverde et
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\textit{al.} (2009), is whether predictor variables are conserved over time or different regions. Mantel tests showed moderate values of Pearson correlations between the Worldclim (global) and NIWA (New Zealand) climate variables. The highest correlation was found if using only a reduced set of variables (and, in contrast, a much lower correlation if using the reduced NIWA set comprising an equal number, but different variables), which may indicate that models calibrated with these variables are more transferable to New Zealand. Furthermore, the reduced set of variables avoids problems associated with multicollinearity, such as highly unstable results (Robertson \textit{et al.} 2001).

Under current climate, predictions across the four models projected similar spatial extents in the North Island, although the degree of suitability of a given area may differ between the models. However, even when excluding areas with negative MESS values from the calculation, overlaps between predictions for the full and the reduced set of models were only 71, 71 and 44\% for \textit{A. cunninghamiana}, \textit{P. guajava} and \textit{S. actinophylla} respectively. Therefore, it has to be noted that while extrapolation to new environments contributes to the differences between models, it is not the sole cause of discrepancies between models calibrated with different sets of variables. To include the right number of parameters in a model is important, because too many or too few can lead to incorrect predicted distributions (Beaumont \textit{et al.} 2005; Dupin \textit{et al.} 2011). It has been suggested elsewhere, that preliminary multicollinearity analyses and other steps to reduce dimensions of the model may help in selecting appropriate predictors (Jiménez-Valverde \textit{et al.} 2011). Exploring the map for regions with new environments indicates where the models are most uninformed (Elith \textit{et al.} 2010), and investigating correlation structures of predictor variables over different regions gives an indication of model transferability (Jiménez-Valverde \textit{et al.} 2009). This study showed that careful selection of variables and investigation into extrapolation are two essential steps for selecting more realistic models.

Species distribution models do not tell us if an invasive plant will realise its potential distribution, as this may depend on other factors than climate, such as dispersal, stochastic events, or biotic interactions (Jiménez-Valverde \textit{et al.} 2011). Instead, SDMs give us a preliminary understanding of the magnitude of the threat posed by new weeds, if model building and evaluation is well thought-out. This study shows that careful consideration of variable selection is vital to obtaining robust predictions. When extrapolating to new regions, areas with new environments have to be analysed critically, as such areas may result in high predicted suitability in highly unlikely areas. When a preliminary variable selection procedure was applied, models resulted in more realistic and smaller potential distributions for the three species in this study. Moreover, transferability to a new geographic region may be better justified using the reduced set of variables.
This study contributes for sound and conscious selection of predictor variables, which reduces uncertainty of modelled distributions. This is vital for taking appropriate management measures, particularly at an early stage of spread.
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2.5 References


Chapter 2: The effects of climate variable selection on predictions of alien plants’ distributions


Chapter 2: The effects of climate variable selection on predictions of alien plants’ distributions

CHAPTER 3

Potential spread of recently naturalised plants under climate change

Abstract

Climate change and biological invasions are major causes of biodiversity loss and may also have synergistic effects, such as range shifts of invaders due to changing climate. Species distribution models provide an important tool to assess how the threat of invasive species may change with altered temperature and precipitation regimes. In this study, potential distributions of three recently naturalised plant species in New Zealand were modelled (*Archontophoenix cunninghamiana*, *Psidium guajava* and *Schefflera actinophylla*), using four different general circulation models (CCCMA-CGCM3, CSIRO-Mk3.0, GFDL-CM2.0 and UKMO-HADCM3) with two emission scenarios (A2 and B1) each. Based on a maximum entropy approach, models were trained on global data using a small set of predictors. The models were projected to the country of interest, using climate models that had been statistically downscaled to New Zealand, in order to obtain high resolution predictions. This study provides evidence of the potential range expansion of these species, with potentially suitable habitat increasing by as much as 169% (*A. cunninghamiana*; with up to 115,805 km² of suitable habitat), 133% (*P. guajava*; 164,450 km²) and 208% (*S. actinophylla*; 31,257 km²) by the end of the century compared to the currently suitable habitat. The results show that while predictions vary depending on the chosen climate scenario, there is remarkable consistency amongst most climate models within the same emission scenario, with overlaps in areas of predicted presence ranging between 81-99.5% (excluding CSIRO-Mk3.0). By having a better understanding of how climate change will affect distribution of invasive plants, appropriate management measures can be taken.

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3.1 Introduction

Climate change and biological invasions are considered likely to be major causes of biodiversity loss over the coming decades (Peterson et al. 2008). Alien species impact on native species through competition, predation or grazing, diseases, hybridisation, and they can even transform entire ecosystems (Mack et al. 2000). While climate change and plant invasions have each been studied extensively, few studies have considered their combined and potentially synergistic impacts (Thuiller et al. 2007). However, climate change may also have an impact on biological invasions, such as affecting the spread and colonisation of habitats by invasive plants (Walther et al. 2009). As a result of climate change, the predicted ranges of species may increase, decrease or experience a shift, which will pose a great challenge to management strategies. Therefore, long-term management plans require predictions of invasive species behaviour under climate change conditions (Beaumont et al. 2009; Bradley et al. 2010).

With climate as the dominant factor influencing the distribution of plants (Woodward 1987), species distribution models are an important tool used to make predictions of a species’ potential occurrence based on their climatic requirements (Pearson & Dawson 2003; Beaumont et al. 2009). Amongst the broad range of applications of distribution modelling, numerous efforts have been made to predict the spread of invasive plants (e.g. Rouget et al. 2004; Thuiller et al. 2005b; Ebeling et al. 2008) and the effects of climate change on species distribution (e.g. Bergengren et al. 2001; Thuiller et al. 2005a). However, the combination of the effect of climate change on spread of invasive plants has received much less attention (e.g. Kriticos et al. 2005; Scott & Batchelor 2006), at least until very recently, when a raft of studies have emerged (e.g. Broennimann & Guisan 2008; Peterson et al. 2008; Beaumont et al. 2009; Parker-Allie et al. 2009; Wilson et al. 2009; Bourdôt et al. 2010; Bradley et al. 2010).

Predicting the potential range of an invasive species under climate change is useful as it helps understand how the threat posed by an invasive species might change (Jeschke & Strayer 2008; Beaumont et al. 2009). Whether an invasive species should be eradicated, contained in a certain area or controlled in some other way is decided based on the threat it is likely to pose in the future (Scott & Batchelor 2006).

While such studies are clearly useful, concerns have been raised as to the application of species distribution models to such questions, because they represent non-equilibrium situations and require extrapolation (Elith & Leathwick 2009). This study aims to provide reliable results by using a robust methodology: a model algorithm is employed that has repeatedly been shown to
perform well (Maxent) (Elith et al. 2006), using a small set of ecologically relevant predictors, which furthermore avoid extrapolation to values outside the range of the training data. Results from a range of possible climate change scenarios, downscaled to the region of interest in order to provide high resolution results, are compared and quantified. While some other studies investigate several climate scenarios (Peterson et al. 2008; Beaumont et al. 2009), they are usually restricted to a maximum of two climate models and two emission scenarios, and model outputs are often only qualitatively described (Wilson et al. 2009; Bradley et al. 2010), or if quantified, averaged (Peterson et al. 2008; Bourdôt et al. 2010).

There are many alien plant species in New Zealand (ten times the number of native species), although most of the naturalised species are still at an early stage of invasion (Lee et al. 2000): in order to become invasive, an alien plant must pass through various stages including transport and introduction to a new area, followed by establishment of a self-sustaining population and subsequent spread leading to potential impact (Blackburn et al. 2011). In many cases climate change may facilitate further invasions: species originating from warmer ranges may be able to increase their populations and expand to wider areas under climate change (Walther et al. 2009). In New Zealand, a predicted warming of 0.7-5.1°C degrees by 2090, combined with fewer frosts (Ministry for the Environment 2008) may enable subtropical or tropical alien species to establish or expand their ranges southwards. This paper investigates the potential distribution of three newly naturalised (sub-) tropical plant species (*Archontophoenix cunninghamiana*, *Psidium guajava* and *Schefflera actinophylla*) in New Zealand by the end of the century under different climate change scenarios. By selecting newly naturalised species for this study, predictive models provide information to land managers at a time when control of the species may still be effective (Jones et al. 2010). Specifically, the objective of this study was to assess how distributions may change by the end of the century and how predictions vary amongst different general circulation models (CCCMA-CGCM3, CSIRO-Mk3.0, GFDL-CM2.0 and UKMO-HADCM3) and emission scenarios (A2 and B1).

### 3.2 Methods

#### 3.2.1 Study species

The three selected newly naturalised plant species in New Zealand are: *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. et Drude, *Psidium guajava* L. and *Schefflera actinophylla* (Endl.) Harms. They have subtropical or tropical native ranges and are recorded as invasive in other parts of the world. Being woody, bird-dispersed species, and widely sold in nurseries, they are of concern as potential environmental weeds. Their current distributions in New Zealand are limited to
the northern North Island (Auckland, Northland): they may be climate-limited and have the potential to spread further south with a warming climate.

*Archontophoenix cunninghamiana* (bangalow palm; Arecaceae) is a native of eastern Australia and was introduced to New Zealand as an ornamental as early as 1898, but was not recorded as naturalised until 1992 (Cameron 2000). Studies in Brazil indicate that *A. cunninghamiana* can be very invasive (Christianini 2006). *Psidium guajava* (common guava; Myrtaceae) is a native of Central America (Mexico to northern South America), but has been introduced to most subtropical and tropical regions for its edible fruit (Randall 2007). In New Zealand it was first recorded as naturalised in 1965 (Sykes 1982), but has not spread extensively since. *Schefflera actinophylla* (Queensland umbrella tree; Araliaceae) is native to Australia and New Guinea, and was recorded as naturalised in New Zealand in 2005 (Wilcox 2005). *Schefflera actinophylla* can form large monospecific stands and is considered very invasive in the Pacific Islands (Randall 2007).

### 3.2.2 Occurrence and climate data

Occurrence data originate from the Global Biodiversity Information Facility (GBIF; [http://data.gbif.org/](http://data.gbif.org/)), Australia’s Virtual Herbarium (AVH; [http://avh.chah.org.au/](http://avh.chah.org.au/)), Tropicos ([http://www.tropicos.org/](http://www.tropicos.org/)), all retrieved in November 2010, and from the literature for *A. cunninghamiana* (Christianini 2006). After cleaning occurrence data (checking that the coordinates match the recorded country name, deleting incomplete records that did not provide enough information to assign coordinates and removing duplicates, Sheppard 2013; Chapter 2), 81 global records remained for *A. cunninghamiana*, 152 for *S. actinophylla* and 1741 for *P. guajava* (see Figure 2.1 in Chapter 2).

To train the model, current climate data from Worldclim in 2.5 arc minutes resolution across the globe were used ([http://worldclim.org/](http://worldclim.org/); Hijmans et al. 2005). The model was then applied to future climate (changes expected for 2080-2099, hereafter termed 2090), using New Zealand-specific climate layers provided by the National Institute of Water and Atmospheric Research (NIWA; layers accessed November 2010) in 0.05° resolution (i.e. 3 arc minutes; approximately 5 x 5 km). Of the many Atmosphere-Ocean General Circulation Models (GCM) the Intergovernmental Panel on Climate Change (IPCC) uses in their Fourth Assessment Report (AR4) ([IPCC 2007](http://www.ipcc.ch/)), 12 had been statistically downscaled to New Zealand by NIWA because they validated well in their 20th century simulations against current climate in the New Zealand and Southwest Pacific region (Ministry for the Environment 2008; Reisinger et al. 2010). Downscaling increases the coarse scale resolution of
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the GCM (Wiens et al. 2009), in particular to represent effects of New Zealand’s complex topography (Ministry for the Environment 2008). Of the 12 downscaled GCMs available, in this study four were chosen, namely the CCCMA-CGCM3, CSIRO-Mk3.0, GFDL-CM2.0 and UKMO-HADCM3 models (Table 3.1), to include a variety of different projected changes in temperature and precipitation (IPCC 2007). For each of these four GCMs, two SRES (special report on emission scenarios) emission scenarios were used, one (B1) at the lower and one (A2) at the upper but not the extreme ends of predicted future emissions. Mean global warming calculated from a multi-model ensemble amounts to 3.13°C for SRES A2 and 1.79°C for SRES B1 by 2080-99 (IPCC 2007).

Table 3.1: Climate change models. Average annual temperature changes (in °C) for 2080-2099 relative to 1980-1999 for the SRES A1B, A2 and B1 scenario, globally and downscaled to New Zealand (Ministry for the Environment 2008; Reisinger et al. 2010).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>CCCMA-CGCM3</td>
<td>Canadian Centre for Climate Modelling and Analysis</td>
<td>2.99</td>
<td>2.69</td>
<td>2.92</td>
<td>1.27</td>
</tr>
<tr>
<td>CSIRO-Mk3.0</td>
<td>CSIRO, Australia</td>
<td>1.84</td>
<td>1.13</td>
<td>1.65</td>
<td>0.60</td>
</tr>
<tr>
<td>GFDL-CM2.0</td>
<td>Geophysical Fluid Dynamics Laboratory, NOAA USA</td>
<td>2.83</td>
<td>1.96</td>
<td>2.53</td>
<td>1.14</td>
</tr>
<tr>
<td>UKMO-HADCM3</td>
<td>Hadley Centre for Climate Prediction and Research, Met Office UK</td>
<td>2.79</td>
<td>1.56</td>
<td>2.13</td>
<td>0.86</td>
</tr>
</tbody>
</table>

3.2.3 Modelling approach and evaluation

A maximum entropy approach was applied to model distributions, implemented in Maxent Version 3.3.3e (www.cs.princeton.edu/~schapire/maxent/; Phillips et al. 2006). Maxent estimates the probability distribution by finding the distribution that is most spread out or closest to uniform (i.e. of maximum entropy), while respecting a set of constraints representing the incomplete information (Phillips et al. 2006). Default settings used were: a convergence threshold of $10^{-5}$, maximum of 500 iterations, all feature types and ten thousand global background points. The logistic output was chosen as a suitability score that estimates the probability of presence, given a temporal and spatial scale of sampling that results in a 50% chance of the species being present in suitable areas (Elith et al. 2011).
Maxent has been consistently ranked amongst the highest performing species distribution models in various situations (Elith et al. 2006; Hernandez et al. 2006; Wilson et al. 2009). In particular, it provides reasonably good estimates of potential range shifts with climate change (Hijmans & Graham 2006). Furthermore, when a model fitted on current climate data is projected onto future climate data (a new environment), the software highlights areas of the predicted distribution that represent climate conditions not experienced in training the model. Predictions in areas with high levels of clamping (i.e. where variables outside the training range are encountered, and treated as if they are at the limit of the training range) must be treated with caution (Wilson et al. 2009).

A ten-fold cross-validation was applied to all model runs, and the average output was used to assess the distribution of the species. For all models the full set of available occurrence data was used; that is, presence-only data from native and introduced ranges (except from New Zealand), which is preferable, as the fitted niche is then expanded to include potential differences between native and introduced ranges (Broennimann & Guisan 2008).

Six bioclimatic variables were chosen following investigation of the influence of different sets of variables on models (Sheppard 2013; Chapter 2): maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), temperature annual range (BIO7), mean temperature of the wettest quarter (BIO8), precipitation seasonality (BIO15) and precipitation of the warmest quarter (BIO18). These variables are ecologically relevant, with BIO5 and 6 representing important information on temperature tolerance limits, BIO15 showing how evenly rainfall is distributed throughout the year, and BIO18 giving a proxy for dryness in summer (Ibañez et al. 2009). BIO7 and 8 were included, as they may provide additional information, with these two variables showing low correlations with the other four. For the NIWA layers under current climate, the chosen variables have Pearson correlations < 0.8 (calculated in a pairwise fashion; Sheppard 2013; Chapter 2).

The variables selected for the species distribution models in this Chapter are from the set referred to as ‘reduced NIWA set’ in Chapter 2. Although Chapter 2 suggests that the ‘reduced set’ may be a preferable selection, Chapter 3 uses the reduced NIWA set because this Chapter had been published prior to Chapter 2, which was subsequently extended to include the reduced set following reviewer comments. I consider the choice of variables in this Chapter to still be valid, as the climate variables are ecologically relevant and avoid extrapolation. Moreover, the two sets share four of the six variables used, and correlations between results of the reduced and reduced NIWA sets were very high in any case (> 0.9, see Table 2.5). To confirm that results from the two sets of variables would remain similar for models under climate change, I ran a model using the reduced set for one of the climate change scenarios (CCCMA-CGCM3 A2) for each species and compared the results to the model with the reduced NIWA set. This confirmed the high consistency of results between the two sets, with correlations of 0.86-0.89.
Models under current climate were evaluated using the area under the receiver operating curve statistic (AUC). An AUC value of 0.5 indicates models that are no better than random, whereas models with perfect predictive ability have an AUC approximating 1. For further evaluations a threshold was chosen: the value that maximises test sensitivity and specificity under the receiver operating curve, which has been shown to perform well (Liu et al. 2005). Omission error was defined to indicate optimal models if it was below or equal to 5% (Anderson et al. 2003), and was tested with a one-tailed binomial test to see if accuracy of the predictions is greater than expected by chance (at $\alpha = 0.05$).

Because species distribution models applied to climate change scenarios often need to extrapolate to values outside the training data, the multivariate environmental similarity surface (MESS) was considered, showing the similarity of a point (in predicted area) to a reference set of points (training data) in regard to the predictor variables. These values were investigated for extrapolation to the various future climate layers. Percentage of total area in New Zealand with negative MESS values (i.e. at least one variable has a value that is outside the range of the training data, Elith et al. 2010) was calculated, as well as percentage of area within predicted presence.

### 3.2.4 Predictions to future climate scenarios

For each of the three species, eight models were run (all combinations of the four different GCMs and two emission scenarios).

To calculate the potential increase in the invaded area under climate change, a threshold was applied to the model (as above). The fraction of suitable area was calculated as the number of cells with values above the threshold divided by the total number of cells in New Zealand. The proportional increase in area under the different climate change scenarios relative to current climate was calculated. The size of potentially suitable habitat in New Zealand was calculated for each scenario, with each suitable cell comprising an area of 23 km$^2$ (Tait et al. 2006).

Pearson correlation was used to compare outputs of different climate scenarios pairwise between models (Syphard & Franklin 2009), which is useful for data with a likelihood between 0 and 1. To test the null hypothesis that there is no significant difference between pairwise predictions of the models under current climate and any of the future climates, a two-tailed Wilcoxon signed rank test was performed in R (R Development Core Team 2011; version 2.14.2 for Windows). Further, using the threshold, the percentage of overlap in predicted area between the different climate models was calculated.
Chapter 3: Potential spread of recently naturalised plants under climate change

3.3 Results

3.3.1 Model evaluation

Test AUC was $\geq 0.9$ for all species (with *A. cunninghamiana* 0.982, *P. guajava* 0.898 and *S. actinophylla* 0.960), and omission error was at an acceptable level < 5% (*A. cunninghamiana* 3.8%, *P. guajava* 4.8% and *S. actinophylla* 3.5%) (Sheppard 2013; Chapter 2). The $P$-value for one-tailed exact binomial test of omission error (for all ten models) was always < 0.001. For several models, there were areas with new environments, where at least one variable had a value that is outside the range of the training data. For all species, 0-0.28% of the New Zealand area contained new environments (corresponding to a maximum of 33 cells with negative MESS values of the total 11,624 cells in New Zealand) with variation depending on the climate layers used: 0.10% under current climate, 0.17% and 0.08% for CSIRO-Mk3.0 for A2 and B1 respectively, 0.05% for GFDL-CM2.0 B1, 0.15% and 0.28% for UKMO-HADCM3 for A2 and B1 respectively and 0% for the remaining climate scenarios. However, there are no areas with new environments within the predicted area for *P. guajava* and *S. actinophylla*. For *A. cunninghamiana* new environments occupied 0.02% and 0.07% of the area (A2 and B1) only under the UKMO-HADCM3 model. These areas were located in the central west coast of the South Island.

3.3.2 Potential distribution under future climate

Compared with the currently suitable area, for each of the three species the potentially suitable area changes by 2090 (Figures 3.1-3.3). For *A. cunninghamiana* (Figure 3.1), there is an increase from 16% to 20-43% of the area (corresponding to 53,567-115,805 km$^2$; Figure 3.4). For *P. guajava* (Figure 3.2) and *S. actinophylla* (Figure 3.3) in the case of CSIRO-Mk3.0 B1 there was a minimal decrease in suitable habitat (2% and 6% respectively), but the other climate models and emission scenarios predict an increase from 26% to 40-62% (98,095-164,450 km$^2$) and from 4% to 7-12% respectively (16,882-31,257 km$^2$; Figure 3.4). The percentage of suitable area for each individual scenario, given as proportion of the country and as the increase in area compared to currently suitable area, is given in Table 3.2; and the suitable areas are shown in Figures 3.5-3.7.
Figure 3.1: Potential distribution of *A. cunninghamiana* with model predictions in the logistic output, for current climate and future climate (2090) with emission scenarios A2 (top row) and B1 (bottom row) and the four different GCMs.
Figure 3.2: Potential distribution of *P. guajava* with model predictions in the logistic output, for current climate and future climate (2090) with emission scenarios A2 (top row) and B1 (bottom row) and the four different GCMs.
Figure 3.3: Potential distribution of *S. actinophylla* with model predictions in the logistic output, for current climate and future climate (2090) with emission scenarios A2 (top row) and B1 (bottom row) and the four different GCMs.
Figure 3.4: Mean size of potentially suitable area in km$^2$ ± standard error (for ten cross validation models) for a) *A. cunninghamiana*, b) *P. guajava*, and c) *S. actinophylla*; under current climate (white bars, ‘0’) and for emission scenarios A2 and B1 and the different climate models: GCM1: CCCMA-CGCM3; 2: CSIRO-Mk3.0; 3: GFDL-CM2.0; 4: UKMO-HADCM3.

Table 3.2: Percentage of suitable habitat in New Zealand (mean ± standard error in %) for ten cross-validation models under the chosen threshold (top rows, in bold), and percentage of increase in suitable habitat compared to currently suitable habitat (mean ± standard error in %) (bottom rows).

<table>
<thead>
<tr>
<th>Species</th>
<th>Threshold</th>
<th>CCCMA-CGCM3 A2</th>
<th>CCCMA-CGCM3 B1</th>
<th>CSIRO-MK3.0 A2</th>
<th>CSIRO-MK3.0 B1</th>
<th>GFDL-CM2.0 A2</th>
<th>GFDL-CM2.0 B1</th>
<th>UKMO-HADCM3 A2</th>
<th>UKMO-HADCM3 B1</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. cunninghamiana</em></td>
<td>0.279</td>
<td>16.11 ± 0.78</td>
<td>43.32 ± 1.60</td>
<td>30.88 ± 1.50</td>
<td>28.05 ± 1.99</td>
<td>20.04 ± 1.16</td>
<td>41.59 ± 2.35</td>
<td>33.62 ± 1.61</td>
<td>37.78 ± 4.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td>0.250</td>
<td>26.40 ± 1.33</td>
<td>56.86 ± 1.77</td>
<td>36.69 ± 1.82</td>
<td>43.73 ± 2.13</td>
<td>25.97 ± 1.68</td>
<td>53.93 ± 1.83</td>
<td>39.19 ± 1.66</td>
<td>61.51 ± 1.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td>0.164</td>
<td>3.80 ± 0.03</td>
<td>11.47 ± 1.10</td>
<td>6.64 ± 0.35</td>
<td>6.31 ± 0.43</td>
<td>3.60 ± 0.11</td>
<td>11.47 ± 1.02</td>
<td>6.63 ± 0.46</td>
<td>11.69 ± 1.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
<td>A2</td>
<td>B1</td>
</tr>
</tbody>
</table>

58
The Wilcoxon paired test always gave significant differences \( (P < 0.001) \) in predictions between current and future climates. Predictions using CSIRO-Mk3.0 B1 showed the highest correlations with predictions under the current climate and GFDL-CM2.0 A2 the lowest (Table 3.3).

The current area that overlaps with the predicted area of the different climate change scenarios, i.e. the area that is predicted to be suitable now and remains suitable by the end of the century, is generally very high: for *A. cunninghamiana* it is \( 97.55 \pm 2.71\% \) (mean \( \pm \) standard deviation, \( n = 8 \)), for *P. guajava* it is \( 96.63 \pm 5.33\% \) and for *S. actinophylla* 94.94 \( \pm \) 0.24\% (Figures 3.5-3.7). In terms of how much of the total predicted areas under current and future climates overlap, the proportions range between 51-86\% (*A. cunninghamiana*), 58-85\% (*P. guajava*) and 47-99.5\% (*S. actinophylla*) (Table 3.3).

Table 3.3: Pearson correlations (values on upper right side) and percentage of overlap in predicted area (lower left side, shaded) for all three species. In each pairwise comparison, the top rows are values for *A. cunninghamiana*, middle rows for *P. guajava* and bottom rows for *S. actinophylla*.

<table>
<thead>
<tr>
<th></th>
<th>Current</th>
<th>CCCMA-CCGM3 A2</th>
<th>CCCMA-CCGM3 B1</th>
<th>CSIRO-Mk3.0 A2</th>
<th>CSIRO-Mk3.0 B1</th>
<th>GFDL-CM2.0 A2</th>
<th>GFDL-CM2.0 B1</th>
<th>UKMO-HADCM3 A2</th>
<th>UKMO-HADCM3 B1</th>
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<tbody>
<tr>
<td>Current</td>
<td>0.731</td>
<td>0.904</td>
<td>0.836</td>
<td>0.949</td>
<td>0.705</td>
<td>0.863</td>
<td>0.798</td>
<td>0.875</td>
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</tr>
<tr>
<td>0.851</td>
<td>0.922</td>
<td>0.895</td>
<td>0.939</td>
<td>0.852</td>
<td>0.928</td>
<td>0.859</td>
<td>0.914</td>
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</tr>
<tr>
<td>0.606</td>
<td>0.755</td>
<td>0.786</td>
<td>0.957</td>
<td>0.564</td>
<td>0.759</td>
<td>0.650</td>
<td>0.733</td>
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<tr>
<td>CCCMA-CGCM3</td>
<td>54.15</td>
<td>0.898</td>
<td>0.784</td>
<td>0.808</td>
<td>0.943</td>
<td>0.891</td>
<td>0.770</td>
<td>0.753</td>
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<tr>
<td>CGCM3</td>
<td>63.28</td>
<td>0.931</td>
<td>0.902</td>
<td>0.896</td>
<td>0.971</td>
<td>0.934</td>
<td>0.888</td>
<td>0.855</td>
<td></td>
</tr>
<tr>
<td>A2</td>
<td>47.92</td>
<td>0.721</td>
<td>0.666</td>
<td>0.600</td>
<td>0.944</td>
<td>0.723</td>
<td>0.858</td>
<td>0.671</td>
<td></td>
</tr>
<tr>
<td>CCCMA-CGCM3</td>
<td>68.51</td>
<td>0.817</td>
<td>0.932</td>
<td>0.889</td>
<td>0.967</td>
<td>0.896</td>
<td>0.838</td>
<td>0.859</td>
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<tr>
<td>CGCM3</td>
<td>80.13</td>
<td>0.921</td>
<td>0.936</td>
<td>0.927</td>
<td>0.974</td>
<td>0.879</td>
<td>0.890</td>
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<tr>
<td>B1</td>
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<td>0.921</td>
<td>0.765</td>
<td>0.966</td>
<td>0.754</td>
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<tr>
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<td>0.738</td>
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<td>0.775</td>
<td>0.814</td>
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<td>Mk3.0</td>
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<td>0.895</td>
<td>0.924</td>
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<td>0.905</td>
<td>0.914</td>
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<td>0.774</td>
<td>0.617</td>
<td>0.911</td>
<td>0.732</td>
<td>0.906</td>
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<td>0.902</td>
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<td>B1</td>
<td>99.52</td>
<td>0.559</td>
<td>0.762</td>
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<td>0.743</td>
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<tr>
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<td>0.921</td>
<td>0.791</td>
<td>0.768</td>
<td></td>
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<td>CM2.0</td>
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<td>0.895</td>
<td>0.860</td>
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<td>0.899</td>
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<td>0.907</td>
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<tr>
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<tr>
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<td>0.721</td>
<td>0.711</td>
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<td>UKMO-HADCM3</td>
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<td>82.64</td>
<td>88.37</td>
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<tr>
<td>HADCM3</td>
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<td>87.51</td>
<td>79.05</td>
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<td></td>
<td></td>
<td></td>
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<td>B1</td>
<td>69.42</td>
<td>71.97</td>
<td>95.71</td>
<td>71.29</td>
<td></td>
<td></td>
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</tbody>
</table>
Figure 3.5: Potential distribution of *A. cunninghamiana* with binary model predictions using the threshold that maximised test sensitivity and specificity, for future climate (2090) with emission scenarios A2 (top row) and B1 (bottom row) and the four different GCMs. Yellow habitat is suitable currently and remains suitable, while red habitat becomes suitable by 2090 and blue habitat are areas that are lost (only suitable now but not by 2090).
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Figure 3.6: Potential distribution of *P. guajava* with binary model predictions using the threshold that maximised test sensitivity and specificity, for future climate (2090) with emission scenarios A2 (top row) and B1 (bottom row) and the four different GCMs. Yellow habitat is suitable currently and remains suitable, while red habitat becomes suitable by 2090 and blue habitat are areas that are lost (only suitable now but not by 2090).
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3.3.3 Comparisons of different climate scenarios

Potentially suitable areas vary depending on climate scenario and is generally smaller for emission scenario B1 than emission scenario A2 (Figure 3.1-3.7). Results for the different climate models within an emission scenario are rather similar, with the exception of CSIRO-Mk3.0, which always shows smaller increases (Figure 3.4). Correlations between model outputs using different climate models and emission scenarios were usually high (Table 3.3). The highest correlations, i.e. climate models that created the most similar model outputs, were observed between CCCMA-CGCM3 and GFDL-CM2.0 models for the B1 emission scenario. Overlaps between different climate change scenarios range between 47-99%, depending on scenario and species (Table 3.3). Differences
between various future model predictions were, however, always significant with \( P < 0.001 \) (except \( P = 0.010 \) comparing CCCMA-CGCM3 B1 and CSIRO-Mk3.0 A2 for \( A. cunninghamiana \)).

### 3.4 Discussion

#### 3.4.1 Potential distribution under future climate

All three species have the potential to substantially increase their range by the end of the century. Across all models, suitable habitat for \( A. cunninghamiana \) is predicted to increase by as much as 24-169\% (average: 101\%) compared to potentially suitable habitat under current climate. For \( P. guajava \) and \( S. actinophylla \), with the exception of the slight decrease for CSIRO-Mk3.0 B1, increases of 38-133\% (\( P. guajava \); average: 70\%) and 66-208\% (\( S. actinophylla \); average: 112\%), compared to currently suitable habitat, are predicted. This difference between current and future distributions shows the benefits associated with controlling spread of an invasive plant (Kriticos et al. 2005). Watt et al. (2010) detailed in their study of another invasive plant in New Zealand how such predictions of potential distribution can aid the development of appropriate management systems. While the three species in this study are not considered very invasive at present, any prediction of invasiveness (such as based on plant traits and anthropogenic factors) has to take residence time and potential range into account (Wilson et al. 2007).

Overall, the models predict the suitable habitat for \( A. cunninghamiana \) and \( P. guajava \) to extend into many coastal areas by the end of the century, amounting up to 115,805 km\(^2\) and 164,450 km\(^2\) of suitable habitat in New Zealand. Interestingly the northernmost tip of New Zealand becomes less suitable for \( A. cunninghamiana \) by 2090 under the A2 emission scenario compared to current climate, which is not likely an effect of rising temperatures, as this is at a latitude near the southern limit of the species’ native range in Australia (Cameron 2000). With \( A. cunninghamiana \) being a rainforest species, it may rather be a consequence of changes in precipitation patterns, as the far north is projected to receive less rain in the future (Ministry for the Environment 2008). Accordingly, precipitation of the warmest quarter (BIO18) is the second most influential variable in the models (with an estimated contribution of 27\%, Sheppard 2013; Chapter 2). In contrast, for \( P. guajava \), this same area becomes even more suitable by the end of the century. Contrary to \( A. cunninghamiana \), reduced precipitation may not be a problem, as \( P. guajava \) is more drought tolerant (Hao et al. 2009), with BIO18 only contributing an estimated 15\% for this species. The east coast of the North Island, which is predicted to become highly suitable, especially for \( A. cunninghamiana \), has a warm climate, but precipitation may be the limiting factor under current conditions. While the annual mean rainfall is projected to further decrease in these areas, a seasonal
change is expected with projected increases in summer and autumn (Ministry for the Environment 2008), when rain is at its most limiting. The small area at Westport on the South Island’s west coast that often shows high suitability, even for S. actinophylla in case of some A2 scenarios, experiences higher mean annual temperatures than the surrounding area. Overall, S. actinophylla is not predicted to expand far south, with the size of the predicted suitable habitat amounting to no more than 31,257 km$^2$. This is probably because this species is the most tropical, being adapted to higher mean temperatures than the other two species modelled, and with its native range in climates with little seasonal variation in temperature. Accordingly, temperature annual range (BIO7) was an important predictor for this species (with an estimated contribution of 42%, Sheppard 2013; Chapter 2).

### 3.4.2 Comparisons of different climate scenarios

In this study, substantial increases in suitable areas are predicted, and while there seems to be significant variation depending on which climate model and emission scenario is used, they all show the same general patterns of which areas are suitable, only disagreeing on degree of suitability. Moreover, there is consistency within each emission scenario, especially if we exclude the CSIRO-Mk3.0 model, which corresponds to merely a 0.6°C (B1) or 1.65°C (A2) increase in temperature in New Zealand by the end of the century (Reisinger et al. 2010). Accordingly, another study also showed a comparatively smaller predicted increase in distribution of an invasive plant in New Zealand under this model (Watt et al. 2010). Comparing the other three GCMs, the area overlap (across the three species) is 81-99.5% for emission scenario A2 and 82-99.2% for B1.

Considering the differences between A2 and B1, the amount of carbon emitted in the future will evidently make a large difference. However, another study found considerably greater variation between the climate models than between the emission scenarios within a model (Bourdôt et al. 2010). Although the A2 emission scenario is at the higher range of emission scenarios considered by the IPCC (IPCC 2000), recent projections suggest that this may even be a conservative estimate of future emissions (Sokolov et al. 2009).

### 3.4.3 Model limitations

A poor model may result in misleading predicted distribution ranges (Beaumont et al. 2009). To avoid this, an algorithm was chosen, which has repeatedly been shown to perform well. The chosen set of variables also considerably influences results, and by using few ecologically relevant predictors confidence in the results is increased. On the contrary if too many variables were used, extrapolation
to new values was required, and this was associated with dubious predicted presence in highly unlikely areas (such as alpine areas, Sheppard 2013; Chapter 2).

While climatic conditions are the most important factor controlling distribution on a large spatial scale for the majority of species (Ebeling et al. 2008), factors other than climate, such as dispersal, disturbance, and competition will determine which areas are actually occupied by a species. These other factors may also be altered under future climates, and therefore we cannot tell if the species will realise its current or future potential distribution (Beaumont et al. 2009). For the species on which this study focused, dispersal to new locations will be facilitated by humans and birds: the study species are popular garden plants, and their seeds are dispersed by birds; a vector which will enable them to spread over wide areas (Williams et al. 2010). It also has been suggested elsewhere that ornamental species may spread faster (Wilson et al. 2007).

One issue with projections to future climates is the difficulty in evaluating the predicted distributions (Hijmans & Graham 2006). Unlike predictions under current conditions, which can be tested, for the future there are no observed data and therefore a direct assessment is impossible (Hijmans & Graham 2006). By avoiding extrapolation to new environments, potential issues such as highly unlikely predictions are minimised.

Finally there is uncertainty associated with future climates. Thus, the inclusion of different climate models and emission scenarios is essential for understanding the role of climate change on species invasions. One important aspect of climate change that is not incorporated in the models, is the increase in carbon dioxide, which may additionally benefit plants and thus the spread of new invasive plants.

Species distribution models give us a preliminary understanding of the magnitude of the threat posed. If viewed at appropriate scales, the predictions of species distribution models can provide an insight into probable futures that can be useful in conservation and resource management (Wiens et al. 2009).

3.4.4 Conclusions

The three species studied here all have the potential to increase their distribution substantially, with two of them (A. cunninghamiana and P. guajava) finding suitable habitat in large areas of the North Island and even some areas in the South Island. Results are remarkably consistent amongst most General Circulation Models with the exception of CSIRO-Mk3.0. They differ more between emission scenarios; while retaining general patterns of which regions will be suitable. If these plant species
are controlled now, while distributions remain small, costs will be much lower than if we wait to take action until they have spread widely.
3.5 References


Chapter 3: Potential spread of recently naturalised plants under climate change


CHAPTER 4

The effects of elevated temperature and CO$_2$ on the growth of three potentially invasive plants

Abstract

Climate change, comprising an increase in carbon dioxide levels coupled with elevated temperature, may favour invasive plants as they possess traits that will facilitate adaptation to a new climate. In particular, alien plants of subtropical or tropical origin introduced to a colder region, are expected to increase the number and size of their populations and spread further with climate change. Seedlings of three such woody alien species in New Zealand (Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla) were grown in environmental chambers under the combination of two temperature (23.7 and 26°C) and two CO$_2$ (450 and 900 ppm) regimes; simulating current conditions and conditions predicted by the end of the century. Total biomass of $S$. actinophylla was 45% higher and total leaf area 35% larger under double compared to current CO$_2$. Root/shoot ratio was higher under double CO$_2$ across all species, and the number of branches was increased for $P$. guajava. Elevated temperature had a significant effect on germination of $P$. guajava seeds. The only significant interactive effect of elevated temperature and double CO$_2$ was for height of $S$. actinophylla seedlings at the time of harvest. This study provides strong evidence of more vigorous growth of $S$. actinophylla under future conditions, particularly increased CO$_2$, while the other two species are predicted to maintain current growth rates. It is essential to investigate the threat posed by potentially invasive species under future environmental conditions, so that appropriate management actions can be taken and resources for management allocated most effectively.

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**Chapter 4: The effects of elevated temperature and CO$_2$ on the growth of three potentially invasive plants**

### 4.1 Introduction

Carbon dioxide levels and temperature are two major factors affecting plant growth, development and function (Morison & Lawlor 1999). Elevated CO$_2$ is expected to increase productivity of C3 plants by stimulating photosynthesis and inhibiting respiration (Rogers et al. 1994). Moreover, plants respond to elevated CO$_2$ by reducing stomatal conductance, which results in a reduced transpiration rate and an increase in the plant’s water use efficiency (Drake et al. 1997). Increasing temperature enhances rates of plant development up to a temperature optimum, above which rates decrease again (Trudgill et al. 2005).

Global atmospheric concentrations of CO$_2$ and other greenhouses gases are rapidly increasing as a result of human activities, which in turn increase global average air and ocean temperatures (IPCC 2007). Indeed, CO$_2$ levels are predicted to increase to 730-1020 ppm by the end of the century (IPCC 2007). A survey of 60 plant growth experiments, conducted in both chamber and natural environments, showed increased photosynthetic rates of on average 58% higher under elevated CO$_2$ compared to ambient CO$_2$ conditions (Drake et al. 1997). Temperature is predicted to increase globally on average by 1.1-6.4°C by the end of the century (IPCC 2007). Already, plants have been affected by the temperature increase of 0.74°C globally over the last century (IPCC 2007); with evidence of earlier occurrence of spring events in recent decades arising from a wide range of taxa and geographic locations (Walther 2004). While many studies have investigated effects of temperature and CO$_2$ separately, in particular effects of CO$_2$ on crop plants of economic importance, there are still many uncertainties about the combined effects of elevated temperature and CO$_2$ on plant growth (Yoon et al. 2009). However, because changes in temperature and CO$_2$ are likely to occur simultaneously, it is of particular interest to study the interaction of these two factors (Morison & Lawlor 1999). It is expected that increasing temperatures would increase responses to CO$_2$, because of the decreased ratio of photosynthesis to photorespiration and the decreased ratio of gross photosynthesis to dark respiration (Morison & Lawlor 1999). However, as indicated by the variable results of the temperature and CO$_2$ interaction on growth from different studies, biomass responses cannot be readily predicted from photosynthesis responses alone (Morison & Lawlor 1999).

Naturally, climate change will not affect all plant species to the same degree, with individual species positively and others negatively affected (Thuiller et al. 2007). One group in particular that has been suggested to benefit from climate change are invasive plants. The predicted change in abiotic conditions will provide opportunities for alien plants to expand into regions where previously they could not survive and reproduce (Walther et al. 2009). Invasive plants may also possess traits
that facilitate adaptation to the new climate: invasive plants often show rapid dispersal abilities (Dukes & Mooney 1999), they usually tolerate a wide range of climate conditions, and often do not depend on coevolved pollinators or seed dispersers (Vilà et al. 2007). The question of how invasive plant species respond to rising CO$_2$ presents a research gap, requiring a case-by-case analysis (Hovenden & Williams 2010). Predicting which invasive plants will benefit or suffer from elevated CO$_2$ is of immense practical, economic and strategic importance (Hovenden & Williams 2010). Generally, it is expected that invasive plants, often being faster-growing species, may benefit more from elevated CO$_2$ (Thuiller et al. 2007). Greater response to elevated CO$_2$ has indeed been observed in alien compared to native congeners, studied mostly for forbs and grasses and some vines (Dukes & Mooney 1999; Vilà et al. 2007; Song et al. 2010). Recent increases in CO$_2$, tested by growing plants in environmental chambers under CO$_2$ levels that existed at the beginning of the 20th century compared to current CO$_2$ levels, have already shown a far greater positive response to CO$_2$ in some invasive forbs than expected (Ziska 2003). However, it is difficult to separate species-specific effects from the group effects between native and invasive plants (Thuiller et al. 2007). Furthermore, little is known about the interactive effects of temperature and CO$_2$ on growth of invasive plants.

Gaining better knowledge on how climate change will affect plant invasions is of critical importance, as alien plant invasions can drive native population declines (Baider & Florens 2011), with a recent meta-analysis of 1041 field studies showing that alien plants significantly reduced the fitness of resident plant species by 41.7%; growth by 22.1%; species abundance by 43.5%; and diversity by 50.7% (Vilà et al. 2011). Invasive plants are a particular concern in New Zealand: a pool of 25,049 vascular alien plant species have been introduced to this country, of which 2146 have naturalised, representing 53% of the total species richness (Diez et al. 2009). It can be expected that with a change in climate, species originating from warmer areas will be able to increase their populations and also colonise new areas (Walther et al. 2009). In particular, this may be the case for subtropical alien plants currently occurring in northern New Zealand only.

This is one of few studies to investigate the combination of elevated temperature and CO$_2$ on invasive plants, and particularly on woody species as they are rapidly increasing in importance as major invaders globally (Richardson & Rejmánek 2011). The study species are three newly naturalised plant species in northern New Zealand (Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla), which, like many alien plants, currently have limited geographic spread and small populations (Williams & West). However, I would expect an increase in their population size and a spread further south with climate change, as has been predicted by species distribution models (Sheppard 2013; Chapter 3). Seedlings of the three species were grown...
in environmental chambers, simulating current temperature and CO₂ levels and conditions expected by the end of the century. My aim was to investigate if these three species grow more vigorously under elevated temperature and/or under double CO₂, and I hypothesised that double CO₂ would have a stronger effect in combination with elevated temperature.

4.2 Methods

4.2.1 Study species

Three newly naturalised alien plants in New Zealand were selected as study species: *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. et Drude (bangalow palm), *Psidium guajava* L. (common guava) and *Schefflera actinophylla* (Endl.) Harms (Queensland umbrella tree). All three species were chosen primarily because they originate from warmer subtropical or tropical native ranges and although currently limited to the northern part of the North Island (with a mean annual temperature of 14 to 16°C), they have the potential to widely expand their range with climate change (Sheppard 2013; Chapter 3). Woody species were selected, as they are rapidly increasing in importance as major invaders globally, with New Zealand having one of the largest numbers of invasive woody species (Richardson & Rejmánek 2011). The juvenile life stage is of interest in this study, as rapid growth at an early life stage is critical for establishment and colonisation of a new area, and thus the potential for outcompeting native species. The selected species are not dispersal-limited as they are both bird-dispersed, and thus able to spread over wide areas (Williams 2006; Jordaan et al. 2011), and widely sold in plant nurseries. Availability of plants in nurseries is a strong predictor of invasiveness (Dehnen-Schmutz et al. 2007). *Archontophoenix cunninghamiana* of the family Arecaceae is a native of Eastern Australia. It is of concern as it has been shown to be very invasive in Brazil (Christianini 2006) and, in New Zealand, occurs in similar habitats as the closely related New Zealand native palm *Rhopalostylis sapida* H. Wendl. et Drude (nikau). *Psidium guajava* of the Myrtaceae is a native of Central America. It has been introduced to most subtropical and tropical regions because of its edible fruit, and has become invasive in many countries (Randall 2007). *Schefflera actinophylla* of the family Araliaceae is native to Australia and New Guinea. This shade tolerant species can also grow as an epiphyte and is very invasive in the Pacific Islands (Randall 2007).

4.2.2 Experimental design

The experiment was conducted in environmental chambers (Contherm CAT 610 RHS, Contherm Scientific Limited, Lower Hutt, New Zealand), with an inner space of 63 x 51 x 63 cm. Fully factorial
combinations of four treatments, temperature (ambient/elevated) and CO₂ (current/double), were replicated three times. As only three environmental chambers were available, treatments were applied over four periods of time, with the experiment conducted in a Youden Square design (Table 4.1). This design is similar to the Latin Squares commonly used in environmental chamber experiments (Langhans & Tibbitts 1997), but having at least one missing column. In this case, time periods comprise a complete representation of all four treatments (i.e. a complete block design for the time period component design) and treatment combinations were balanced with respect to chambers (i.e. a balanced incomplete block design for the environmental chamber component design). The experiment was conducted from August 2010 to August 2011, each time period lasting ten weeks.

Table 4.1: Experimental design across four time periods and three environmental chamber units.

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<th>Chamber 1</th>
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<td>Period 2</td>
<td>T 2 CO₂₁</td>
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<tr>
<td>Period 3</td>
<td>T 1 CO₂₂</td>
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<td>Period 4</td>
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T = Temperature; T 1/CO₂₁ = ambient/current values; T 2/CO₂₂ = elevated/double values. Future conditions are highlighted in bold.

Ambient temperature level was chosen to simulate Auckland’s current February (i.e. Austral summer) temperatures. A diurnal cycle was applied with 16 hours daytime and eight hours nighttime. Daytime temperature was set at 23.7°C, night-time at 15.8°C (mean daily maximum/minimum temperature in February, measured at the Auckland Owairaka station 36.900°S, 174.733°E at 41 m a.s.l., calculated from data over 25 years in the 1971 to 2000 period, National Institute of Water and Atmospheric Research 2013). For the future scenario, temperatures of 26 and 18.1°C were chosen, simulating the most likely increase of + 2.3°C for Auckland’s summer temperatures by 2090 (Ministry for the Environment 2008). The same increase in temperature was chosen for night- and daytime, as it is currently assumed that the increase will be the same for maximum and minimum temperatures (B. Mullan, National Institute of Water and Atmospheric Research, personal communication).

Due to technical difficulties of lowering CO₂ in the environmental chambers below indoor ambient levels (usually ranging from 400 to 500 ppm), CO₂ was set at 450 ppm for the current scenario, that is somewhat above the 396 ppm globally in March 2013 (National Oceanic and Atmospheric Administration 2013), and at a future double CO₂ scenario, that is 900 ppm. This is a
likely scenario, as atmospheric CO$_2$ concentrations estimates for 2100 were calculated by the Bern carbon cycle to be 836 ppm, or if simulated by coupled climate-carbon cycle models the value ranges between 730 to 1020 ppm by 2100 (IPCC 2007).

Humidity was set at 78.3%, which is equal to the mean humidity in February at 9am at Auckland’s Owairaka station (see above for climate station details). A light intensity of 120 µE m$^{-2}$s$^{-1}$ was chosen, using Philips Alto 18W cool white bulbs. Using an approximate conversion factor of 4.57 this results in approximately 550 µmol m$^{-2}$s$^{-1}$ PPF (photosynthetic photon flux) (Langhans & Tibbitts 1997).

Typical fluctuations of the set parameters as indicated by the manufacturer are ± 0.3°C for temperature, ± 5% for humidity and ± 30 ppm for CO$_2$. To measure accuracy, these parameters were monitored throughout the course of the experiment every ten minutes with an integrated PLCS5 microprocessor control unit. Temperature was measured by a solid state temperature sensor; humidity by a capacitive sensor probe; and CO$_2$ by an INFRA-RED detector. The data log showed that all mean values of temperature, humidity and CO$_2$ were within the typical fluctuations indicated by the manufacturer. Although there were significant differences in humidity among the chambers during each time period, all means were between 77.8-78.2%. There were significant differences among chambers in temperature, although fluctuations were also small (means ranging from 0.03°C lower to 0.07°C higher than the setting). Carbon dioxide fluctuated more with means in each time period differing between 6-20 ppm amongst chambers. Technical issues (malfunctioning solenoids) during the first three weeks of Period 1 meant that CO$_2$ cylinders were detached from Chambers 1 and 2, resulting in ambient CO$_2$ concentrations of 450-550 ppm (instead of the set 450 ppm). Technical issues were resolved and CO$_2$ levels were maintained as set for the final seven weeks of Period 1.

For each time period, four seedlings of each of the three species (A. cunninghamiana, P. guajava and S. actinophylla) were randomly chosen for each environmental chamber (12 seedlings per chamber, 48 across the whole experiment). Seedling height ranged from 15 to 30 cm (Figure 4.1). These seedlings were re-potted a week before applying treatments, planting them into individual 1 L round plastic pots (12.5 cm diameter by 10 cm height), with plastic saucers placed underneath. Pots were filled with Potpower™ potting mix (Debco, Melbourne, Australia).
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The 12 seedlings were randomly positioned within each environmental chamber for each time period (Figure 4.2). Seedlings were nine to 12 months old and obtained from North Island nurseries: New Zealand Palm Co, New Plymouth (A. cunninghamiana); Plantlife Propagators, Ashhurst and Lyndale, Auckland (P. guajava); and Kerikeri Plant Production, Kerikeri (S. actinophylla). During the experiment a few plant pest infestations occurred, which were manually removed and thus controlled successfully soon after detection. Pots were watered three times a week with 0.04 L (i.e. 3.25 mm) of water, accumulating to 42.25 mm a month, only two thirds of the 65 mm rainfall usual for February. However, within the environmental chamber the plants were kept moist without water accumulating in the saucers underneath the pots.

Figure 4.1: Typical seedlings at the start of the experiment: a) A. cunninghamiana; b) P. guajava; and c) S. actinophylla (individuals above from Period 1).

Figure 4.2: Seedling arrangement in environmental chambers (example from Chamber 2 in Period 1).
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The effect of temperature and CO$_2$ on seed germination was also tested for the three species. Seeds were imported from Australia (A. cunninghamiana, Seed Horticultural Ltd, Lower Dyraaba, New South Wales; P. guajava, Ole Lantana’s Seed Store Ltd, Toowoomba East, Queensland; S. actinophylla, Harvest Seeds and Native Plants Ltd, Sydney, New South Wales). For P. guajava and S. actinophylla, 15 seeds of each species were sown in a Petri dish on moist filter paper. Ten seeds of A. cunninghamiana were grown in a Petri dish in potting mix. One Petri dish of each species was placed in each environmental chamber. Due to unavailability of seeds, the seed germination experiment was only carried out in Periods 2 to 4.

4.2.3 Growth measurements

For all plants, height was measured and the number of leaves counted at the beginning of the experiment and thereafter every two weeks. Due to difficulties of measuring stem height of palm seedlings, height was defined as the distance from the soil to the leaf blade (i.e. stem plus petiole), choosing the leaf that maximises this distance. For P. guajava the distance from soil to the tip of the highest branch was chosen, and for S. actinophylla the maximum distance from soil to petiole. For P. guajava, the number of branches was counted (counted as a new branch if it exceeded 3 cm). At the end of the experiment, root and shoot (stem and leaves separately) biomass was harvested, dried in the oven at 70°C for 48 hours, and dry mass determined. Total biomass as well as root/shoot ratio was additionally calculated. Leaf area for all species was measured by photocopying the removed leaves, weighing the extracted pieces of paper and comparing to known paper mass. Specific leaf area (SLA) was determined by dividing leaf area by leaf mass. For the germination experiment, germination of seeds was recorded three times a week, with seeds recorded as germinated if the radicle exceeded 2 mm.

4.2.4 Data analysis

Data analysis was carried out in SAS statistical software (SAS Institute Inc., Cary NC, USA, version 9.2 for Windows). Graphs were produced using R (R Development Core Team 2012, version 2.14.2 for Windows).

The environmental chamber formed the experimental unit, as only one of the four treatment combinations can be assigned to a chamber at any given time. To achieve three replicates the experiment was conducted in four time periods using all three chambers during each. Since environmental chambers and time periods are not in themselves of interest, these were regarded as block factors and therefore were treated as random effects. Destructive one-off measurement data
such as biomass (root, shoot, and total), root/shoot ratio, leaf area and SLA were analysed based on a linear mixed model approach with temperature, CO\textsubscript{2} and species as the fixed effects. Restricted maximum likelihood (REML) was used to fit the linear mixed model to the data, because it gives more precise estimates of the means for balanced incomplete block designs. Type III hypothesis tests for the significance of each of the fixed effects and all two-way and three-way interactions were performed. Thereafter pairwise comparisons of means were performed for those main effects and interactions that were found to be statistically significant ($P < 0.05$) in the Type III hypothesis tests. The Tukey-Kramer method was used to adjust $P$-values. The standard error of the difference (SED) between means is reported for all significant pairwise comparisons. Means are referred to as Least Squares Means (LSMs), that is, the average predicted values for the response variable at each level of selected factors, averaged over all the levels of the other factors. Root/shoot ratio and SLA were log-transformed before analysis; therefore the LSMs generated by the model were on the log-scale. The difference between means was also converted back to its original units, giving the ratio between the two means, and the lower and upper 95% confidence limits around the ratio were calculated.

Height was analysed in a similar manner, however the fixed effects part of the model additionally included time (i.e. the weeks at which fortnightly measurements were made) and the random effects part of the model was extended to include a term (plant ID) to account for the correlation between repeated height measurements on each plant. As the variation between chambers was negligible this term was dropped from the random effects part of the model with the simpler model providing a better fit. As different plants, both within and between species, entered the study with different basal height, the baseline height (i.e. height at week zero) was fitted as a covariate in the model.

For number of leaves, a generalised linear mixed model approach was used to analyse the data. The data were assumed to follow a Poisson distribution and the model was fitted using a log-link function. As for height, the fixed effects part of the model additionally included time, the random effects part of the model was extended to include plant ID, but again dropping the chamber effect as variation was negligible, and the baseline number of leaves was fitted as a covariate in the model. A residual marginal pseudo-likelihood technique was used for the estimation of variances. Type III hypothesis tests for the significance of each of the fixed effects and all two-, three- and four-way interactions were performed, and pairwise comparisons of means for those effects found to be statistically significant. As the LSMs and standard errors generated by the model were on the natural log-scale, the difference between means was also converted back to its original units, giving the ratio.
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The lower and upper 95% confidence limits around the ratio were calculated instead of back-transforming the SED to the original units (because it follows the asymmetric Poisson distribution). The number of branches was also analysed in this way, although without the fixed effect species, as this variable was measured for \textit{P. guajava} only.

Seed germination was analysed using a linear mixed model, with time period and environmental chamber as random effects; and temperature, CO\textsubscript{2}, species (two levels only as \textit{A. cunninghamiana} did not germinate) and time (days after sowing seeds) as fixed effects. The proportion of germinated seeds was analysed using an arcsine square root transformation, where proportions of 0 and 1 were replaced by 1/4\(n\) and 1-1/4\(n\) respectively (with \(n = 15\)).

4.3 Results

4.3.1 Effects of temperature and CO\textsubscript{2} on biomass and leaf area

As results for root and shoot biomass analysed separately followed the same trends as total biomass, only statistics for total biomass are shown, with significant effects of CO\textsubscript{2}, species, and their interaction (Table 4.2). Pairwise comparisons of biomass between CO\textsubscript{2} levels for each species separately showed that only for \textit{S. actinophylla} biomass was significantly higher at double CO\textsubscript{2} levels compared to current CO\textsubscript{2} levels (Figure 4.3a), with a difference between LSMs of 4.22 ± 0.83 g (\(P < 0.001\)). There were no significant effects of temperature alone or the interaction between temperature and CO\textsubscript{2} on biomass for any of the plant species.

| Table 4.2: Type III tests of fixed effects for total biomass, root/shoot ratio, leaf area and SLA. |
|-----------------|------------------|-----------------|--------|--------|------------------|------------------|
| Effect          | Total biomass    | Root/shoot ratio| Leaf area | SLA    |
|                 | \(F\) | \(P\) | \(F\) | \(P\) | \(F\) | \(P\) | \(F\) | \(P\) |
| Temperature (T) | 0.06  | 0.803 | 0.11  | 0.752 | 0.55  | 0.458 | 0.01  | 0.941 |
| CO\textsubscript{2} | 9.75  | 0.002 ** | 7.03  | 0.042 * | 5.15  | 0.025 * | 0.37  | 0.581 |
| Species         | 77.1  | <0.001 *** | 84.8  | <0.001 *** | 164   | <0.001 *** | 1.19  | 0.308 |
| T*CO\textsubscript{2} | 0.00  | 0.973 | 1.50  | 0.271 | 0.00  | 0.971 | 0.29  | 0.625 |
| T*species       | 0.63  | 0.537 | 1.23  | 0.295 | 1.66  | 0.195 | 1.21  | 0.302 |
| CO\textsubscript{2}*species | 0.07  | <0.001 *** | 1.98  | 0.142 | 9.66  | <0.001 *** | 1.20  | 0.305 |
| T*CO\textsubscript{2}*species | 1.62  | 0.201 | 0.07  | 0.931 | 0.14  | 0.870 | 3.64  | 0.029 * |

Significance levels: * \(P < 0.05\), ** \(P < 0.01\), *** \(P < 0.001\).
There was a significant effect of CO$_2$ on root/shoot ratio (Table 4.2; Figure 4.3b), with root/shoot ratio at double CO$_2$ levels being 1.16 (95% confidence interval 1.04-1.29, $P = 0.042$) larger than at current levels (i.e. there is more root biomass relative to shoot biomass at double CO$_2$ levels).

There were significant effects of CO$_2$, species, and their interaction for leaf area (Table 4.2). Pairwise comparisons for each species showed that only for *S. actinophylla* leaf area was significantly higher at double CO$_2$ levels compared to current CO$_2$ levels (Figure 4.3c), with a difference between LSMeans of 247.39 ± 53.11 cm$^2$ ($P < 0.001$). SLA was not affected by temperature, CO$_2$ or their interaction (Table 4.2).

**Figure 4.3:** a) Total biomass, b) back-transformed root/shoot ratio, and c) leaf area of the three species at current and double CO$_2$ levels; LSMeans with 95% confidence intervals. Open triangles indicate *S. actinophylla*, open squares *P. guajava* and closed circles *A. cunninghamiana*.

**4.3.2 Effects of temperature and CO$_2$ on height**

Effects of temperature and CO$_2$ on height of the species differed depending on species and the number of weeks since treatment application (Table 4.3; Figure 4.4). Within the same treatment combination, there were significant increases in height over weeks, as well as between weeks for different treatment combinations in the case of *P. guajava* and *S. actinophylla*. However, the only significant difference between treatments for the same week was for *S. actinophylla*, with mean height under the elevated temperature and double CO$_2$ treatment being 5.71 ± 1.29 cm larger than under the ambient, current treatment at week ten ($P = 0.014$).
### Table 4.3: Type III tests of fixed effects for height, number of leaves, and number of branches of *P. guajava*.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Height</th>
<th>Leaves</th>
<th>Branches</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>Den. DF</td>
<td>( F )</td>
</tr>
<tr>
<td>Basal size</td>
<td>1</td>
<td>131</td>
<td>286</td>
</tr>
<tr>
<td>CO(_2)</td>
<td>1</td>
<td>130</td>
<td>1.41</td>
</tr>
<tr>
<td>Temperature (T)</td>
<td>1</td>
<td>130</td>
<td>5.08</td>
</tr>
<tr>
<td>Weeks</td>
<td>4</td>
<td>528</td>
<td>215</td>
</tr>
<tr>
<td>Species</td>
<td>2</td>
<td>129</td>
<td>14.0</td>
</tr>
<tr>
<td>T*CO(_2)</td>
<td>1</td>
<td>130</td>
<td>0.03</td>
</tr>
<tr>
<td>CO(_2)*weeks</td>
<td>4</td>
<td>528</td>
<td>0.44</td>
</tr>
<tr>
<td>T*weeks</td>
<td>4</td>
<td>528</td>
<td>1.54</td>
</tr>
<tr>
<td>T*CO(_2)*weeks</td>
<td>4</td>
<td>528</td>
<td>1.06</td>
</tr>
<tr>
<td>CO(_2)*species</td>
<td>2</td>
<td>128</td>
<td>2.61</td>
</tr>
<tr>
<td>T*species</td>
<td>2</td>
<td>128</td>
<td>2.67</td>
</tr>
<tr>
<td>T*CO(_2)*species</td>
<td>2</td>
<td>128</td>
<td>3.96</td>
</tr>
<tr>
<td>Species*weeks</td>
<td>8</td>
<td>528</td>
<td>22.2</td>
</tr>
<tr>
<td>CO(_2)<em>species</em>weeks</td>
<td>8</td>
<td>528</td>
<td>1.13</td>
</tr>
<tr>
<td>T<em>species</em>weeks</td>
<td>8</td>
<td>528</td>
<td>2.27</td>
</tr>
</tbody>
</table>

DF = numerator degrees of freedom; Den. DF = denominator degrees of freedom. Basal size refers to basal height, number of leaves, or number of branches at the start of experiment. Significance levels: * \( P < 0.05 \), ** \( P < 0.01 \), *** \( P < 0.001 \).
4.3.3 Effects of temperature and CO$_2$ on number of leaves and branches

There were no significant effects of CO$_2$ or the interaction of CO$_2$ and temperature on the number of leaves. However, effects of temperature differed depending on species and weeks (Table 4.3; Figure 4.4). Within the same temperature level, there were several significant increases in the number of leaves over weeks, but only for $P. guajava$ and $S. actinophylla$. Between weeks, comparing different...
temperature levels, there were only a few significant differences for \textit{S. actinophylla}. However, there were no significant differences between treatments for the same week.

\textit{P. guajava} had significantly more branches under double compared to current CO\textsubscript{2} (Table 4.3; Figure 4.5): averaged over weeks there were 1.28 (95% confidence interval 1.06-1.53, \(P = 0.012\)) more branches under double CO\textsubscript{2} compared to current.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{image.png}
\caption{Number of branches of \textit{P. guajava} at current (solid line with open squares) and double (dashed line with open squares) CO\textsubscript{2} levels over ten weeks; LSMs with 95% confidence intervals.}
\end{figure}

\subsection*{4.3.4 Effects of temperature and CO\textsubscript{2} on seed germination}

While germination of \textit{A. cunninghamiana} failed completely, \textit{P. guajava} reached a very high germination rate by the time of harvest with 95.56 ± 1.57\% of seeds having germinated (mean ± standard error) compared to 77.78 ± 5.33\% for \textit{S. actinophylla}. While there was no significant effect of CO\textsubscript{2} or the interaction of temperature and CO\textsubscript{2}, significant effects of temperature depended on species and day, with many significant differences between days at the same as well as at different temperature levels (Table 4.4). However, if only comparing germination at the same day, for \textit{P. guajava}, under elevated temperature more seeds germinated compared to ambient temperature at days 16 and 18 (Figure 4.6), with 41.48\% (confidence interval, 18.57-66.54\%, \(P < 0.001\)) and 27.40\% (95% confidence interval 8.54-51.97\%, \(P = 0.060\)) higher germination respectively.
Table 4.4: Type III tests of fixed effects for seed germination.

<table>
<thead>
<tr>
<th>Effect</th>
<th>DF</th>
<th>Den. DF</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (T)</td>
<td>1</td>
<td>52.5</td>
<td>5.82</td>
<td>0.019 *</td>
</tr>
<tr>
<td>CO$_2$</td>
<td>1</td>
<td>52.5</td>
<td>3.48</td>
<td>0.068</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>206</td>
<td>75.9</td>
<td>&lt;0.001 ***</td>
</tr>
<tr>
<td>Day</td>
<td>20</td>
<td>206</td>
<td>70.5</td>
<td>&lt;0.001 ***</td>
</tr>
<tr>
<td>T*CO$_2$</td>
<td>1</td>
<td>52.5</td>
<td>2.69</td>
<td>0.107</td>
</tr>
<tr>
<td>T*species</td>
<td>1</td>
<td>206</td>
<td>10.7</td>
<td>0.001 **</td>
</tr>
<tr>
<td>CO$_2$*species</td>
<td>1</td>
<td>206</td>
<td>0.17</td>
<td>0.679</td>
</tr>
<tr>
<td>T*CO$_2$*species</td>
<td>1</td>
<td>206</td>
<td>0.03</td>
<td>0.866</td>
</tr>
<tr>
<td>T*day</td>
<td>20</td>
<td>206</td>
<td>2.09</td>
<td>0.006 **</td>
</tr>
<tr>
<td>CO$_2$*day</td>
<td>20</td>
<td>206</td>
<td>0.07</td>
<td>1.000</td>
</tr>
<tr>
<td>T*CO$_2$*day</td>
<td>20</td>
<td>206</td>
<td>0.12</td>
<td>1.000</td>
</tr>
<tr>
<td>Species*day</td>
<td>20</td>
<td>206</td>
<td>2.05</td>
<td>0.007 **</td>
</tr>
<tr>
<td>T<em>species</em>day</td>
<td>20</td>
<td>206</td>
<td>0.47</td>
<td>0.974</td>
</tr>
<tr>
<td>CO$_2$<em>species</em>day</td>
<td>20</td>
<td>206</td>
<td>0.22</td>
<td>1.000</td>
</tr>
<tr>
<td>T*CO$_2$<em>species</em>day</td>
<td>20</td>
<td>206</td>
<td>0.27</td>
<td>0.999</td>
</tr>
</tbody>
</table>

DF = numerator degrees of freedom; Den. DF = denominator degrees of freedom. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Figure 4.6: Germination of *P. guajava* at days 14-21 at ambient (bars in light shade of grey) and elevated (bars in dark shade of grey) temperature; LSMs with 95% confidence intervals. Significance levels: · $P < 0.1$, *** $P < 0.001$. 
4.4 Discussion

Elevated CO$_2$ resulted in more vigorous growth of *S. actinophylla*: seedlings grown under double CO$_2$ showed 68% higher root, 37% higher shoot and 45% higher total biomass compared to seedlings grown under current CO$_2$, as well as 35% larger total leaf area. This was not the case for *A. cunninghamiana* or *P. guajava*, for which no significant effects of CO$_2$ were observed. These results indicate that responses to increased CO$_2$ levels are species-specific, rather than alien plants as a group being able to take advantage. In general, C3 trees are expected to do well: a review of Free-Air CO$_2$ Enrichment (FACE) studies showed, that of the different functional groups of C3 plants, trees (mostly young, rapidly growing) experienced the highest increase in the light-saturated leaf photosynthetic rate (with an average of 47% compared to 31% across all functional groups) and the largest aboveground biomass production (with an average of 28% compared to 20% across all functional groups) (Ainsworth & Long 2005). However, Ziska (2003) suggested that the increase in CO$_2$ already experienced over the past century (from 284 to 380 ppm), has had a significantly stronger effect on stimulating biomass of invasive plants than the CO$_2$ increase expected by the end of this century (from 380 to 719 ppm in his study). Therefore, it is possible that *A. cunninghamiana* and *P. guajava* may already have increased growth under CO$_2$ levels of 450 ppm in the environmental chambers (which, in addition, is already slightly higher than the actual current CO$_2$ level of 396 ppm). In accordance with this, another study comparing two elevated CO$_2$ levels (500 and 650 ppm) found a significant increase in growth of an invasive plant compared to current levels, but no difference between 500 and 650 ppm (Hättenschwiler & Körner 2003), suggesting that initial CO$_2$ increases are the most influential for stimulating plant growth. In chamber studies, the effect of elevated CO$_2$ on biomass of trees may also be underestimated (Kallarackal & Roby 2012), possibly due to a pot effect restricting responses of plants to elevated CO$_2$ (Long et al. 2004).

Interestingly, root/shoot ratio across the three species was significantly higher under double compared to current CO$_2$; the species invested more in root biomass compared to shoot biomass. Other studies have also shown that below-ground biomass showed the strongest relative increase to higher CO$_2$; averaged over six herbaceous invasive species in the United States (Ziska 2003) and for crop species such as wild oat (O'Donnell & Adkins 2001) and potato (Fleisher et al. 2008). This might aid the plants in taking up more nutrients than they would be able to at ambient CO$_2$, especially if nutrients are limiting (Rogers et al. 1996; Luo et al. 2006), which could be the case in this study where no additional fertiliser was provided. *Psidium guajava* grew more individual branches under double CO$_2$, suggesting that varying levels of CO$_2$ may result in different plant morphologies, such as decreased dominance of apical buds in favour of growth at lateral buds in this study. Another study
showed that elevated CO$_2$ increased branching and suppressed apical dominance in *Pinus radiata* seedlings (Conroy *et al.* 1990). Generally branching has not widely been reported, but a review of six species studied in FACE experiments showed an average increase in branching of 25% under elevated CO$_2$ (Ainsworth & Long 2005).

I found a significant effect of combining elevated temperature with double CO$_2$ for only one species: *S. actinophylla*, at week ten (i.e. at the time of harvest). *Schefflera actinophylla* plants were on average taller if grown under both elevated temperature and double CO$_2$ compared to current conditions (ambient temperature and current CO$_2$). In theory, the increase in photosynthesis is expected to be greater when the enzyme Rubisco is limiting at high temperature, because the rate of carboxylation at Rubisco is increased and the oxygenation reaction is competitively inhibited, decreasing photorespiration (Long *et al.* 2004). Indeed, a review of FACE studies showed that across experiments, photosynthesis was stimulated more at higher compared to lower temperatures (Ainsworth & Long 2005). However, this may not necessarily translate into biomass responses (Morison & Lawlor 1999). Another study showed that even when finding a significant interactive effect of temperature and CO$_2$, such as in the case of a native and an invasive C3 grass, the increase in growth was less than expected, based on the sum of independently manipulated temperature and CO$_2$ treatments (Hely & Roxburgh 2005). The same held true for the significant difference in height of *S. actinophylla* at week ten in this study: while the increase was the largest in the elevated temperature and double CO$_2$ treatment, the increase was sub-additive. The lack of interactive effects on biomass or any other growth parameter may also be due to the generally small effects of temperature in this study. However, comparisons across weeks (such as e.g. comparing week eight with week four), showed for *S. actinophylla* and *P. guajava* considerably more pairwise comparisons of size at later weeks at elevated temperature compared to size at earlier weeks at ambient temperature were significant than the other way around. This indicates that seedlings under elevated temperature may have experienced a small positive growth response to warming.

While temperature generally appeared to be of less importance for growth of seedlings, it accelerated seed germination of *P. guajava*, as the number of germinated seeds was higher at days 16 and 18 after sowing under elevated temperature. Another study showed greater germination rate of *P. guajava* at 25 and 30°C compared to 20°C (Sugahara & Takaki 2004). Conversely, I found no significant effects on germination of seeds of *S. actinophylla*. However, a repeated experiment with larger sample sizes and thus statistical power may find significant results for this species as well, as average seed germination was 6-11% higher under elevated temperature from days 14 to 18 compared to ambient temperature.
Recent studies that found significant effects of temperature often used a higher increase in temperature for their treatments, such as 3-4°C (Hely & Roxburgh 2005; Verlinden & Nijs 2010; Lee 2011), or even as much as 10°C (Yoon et al. 2009); whereas the 2.3°C used in this study is comparatively small but more applicable to the predicted increase in New Zealand. I chose this increase to simulate the current best estimate of expected temperature increase; however if temperature increase proves to be at the upper end of the range of predictions, this may benefit these alien plants to a greater extent. Furthermore, for subtropical species to persist in colder climates, increases in minimum temperature and with it reduced frosts during winter will be more critical (Vilà et al. 2007). A further study should investigate the effects of elevated minimum temperature on growth of these species.

Individualistic responses to increased CO₂ and climate change may lead to changes in community composition (Engel et al. 2009). While overall warming frequently results in positive effects on growth of individual plants, this is not necessarily the case for productivity of native plant communities. Other studies showed no effect of elevated temperature on biomass of an experimental grassland community (Sheppard et al. 2012) or a Mediterranean shrubland (Filella et al. 2004). Moreover, elevated temperature sometimes resulted in reduced productivity of experimental grassland communities (Lemmens et al. 2006; De Boeck et al. 2008). This may render plant communities more vulnerable to invasion, especially if the alien species do not show reduced growth under elevated temperature (such as shown in this study), and thus have a competitive advantage. Accordingly, in a study in Belgium, an experimental temperature increase of 3°C resulted in contrasting responses of ten congeneric native-alien plant pairs: on average, the alien plants showed no response but the native plants showed a reduced total biomass with increased temperature (Verlinden & Nijs 2010). If a fast-growing plant, such as S. actinophylla, increased its leaf area (as in this study under double CO₂) and thus its cover in a natural environment, growth of other species may be suppressed, resulting in more asymmetric competition among individuals (Engel et al. 2009; Kallarackal & Roby 2012).

Being able to study the influence of temperature and CO₂ in the controlled conditions of an environmental chamber is of great advantage. However, these chambers have been criticised due to their technical limitations such as size restrictions and pot effects (Long et al. 2004). Responses of these species may vary in natural environments, and therefore, the results of this study should be interpreted in combination with results from field studies. However, a review comparing FACE and chamber studies on the effect of elevated CO₂ on crops has shown that results are mostly consistent, with both types of studies showing increased light-saturated photosynthesis, decreased stomatal...
conductance, increased shoot and root growth, and decreased SLA (Kimball et al. 2002). However, the extent of reduction of stomatal conductance and enhancement of root relative to shoot growth differed; with both having a stronger effect in FACE compared to chamber experiments (Kimball et al. 2002). Another comparative review across a larger range of species found that there were some quantitative differences, with a smaller average increase in light-saturated C3 photosynthesis in FACE studies than in chamber studies (Long et al. 2004). Average increase in productivity in FACE studies amounted to 20% compared to 30% in chamber studies (Long et al. 2004). Therefore, while the same trends in environmental chamber and field studies can be expected; each method has its own advantages depending on its application. In natural environments space limitation is not a factor, which enables larger plants to be grown and longer-term studies. Furthermore, plants can be grown in naturally occurring soil without restrictions on rooting volume (Long et al. 2004). On the other hand, FACE experiments experience larger fluctuations in CO$_2$, which may underestimate responses (Gifford 2004 and references therein). In this study, as I was interested in individual responses of three species at the seedling stage, an experiment in an environmental chamber was more applicable.

In summary, this study provides strong evidence that *S. actinophylla* will grow more vigorously under increased CO$_2$ levels. *Psidium guajava* germinates faster under elevated temperature, while for *A. cunninghamiana* there are no differences in growth comparing either temperature or CO$_2$ levels. Consequently, climate change is likely to have a neutral or positive effect on growth of these three alien species, and needs to be considered in management decisions and assessments of invasion potential. A better understanding of plant responses to changing environmental conditions is essential to prioritise management actions and allocate the limited resources to manage invasive plants most effectively.
4.5 References


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Chapter 4: The effects of elevated temperature and CO\textsubscript{2} on the growth of three potentially invasive plants


CHAPTER 5

The effect of drought on the growth of three potentially invasive plants

Abstract

As individual plants vary in their tolerance to drought, the predicted increase in drought events with climate change may result in shifts in competitive balance and with it unpredictable impacts on plant communities. If alien plant species are among those better able to withstand drought, they may increasingly displace native species. The aim of this study was to investigate drought tolerance of three potential new weeds in New Zealand, at an early stage of their spread: Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla. Seedlings of the three species were exposed to two different durations of drought (21 and 51 days) in a shadehouse experiment. Seedling growth and soil moisture was measured regularly during the drought and a subsequent recovery period. Mortality of all species was nil, and the shorter drought had no effect on the growth of any of the species. However, the longer drought had a negative effect on foliar biomass of A. cunninghamiana and on growth rates, foliar and total biomass of P. guajava. The high drought tolerance of A. cunninghamiana and particularly S. actinophylla shown in this study may be an important factor assisting their spread under climate change.

\[9^{\text{6}}\] The contents of this Chapter have been revised and are published as: Sheppard CS (in press) The effect of drought on growth of three potential new weeds in New Zealand. Plant Protection Quarterly.
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5.1 Introduction

Potential biodiversity loss caused by the combined impacts of climate change and biological invasions is predicted to occur in the coming decades (Sorte et al. 2012). Climate change predictions (using six different emission scenarios) estimate a likely increase in temperature of 1.1-6.4°C by the end of the century (IPCC 2007). Decreases in precipitation are likely in most subtropical land regions, and extreme weather events such as drought are expected to increase (IPCC 2007).

While gradual trends of climate change, such as increasing temperature and CO₂ levels, have been studied extensively (for meta-analyses summarising such findings see Parmesan & Yohe 2003; Ainsworth & Long 2005; Dieleman et al. 2012), there is a lack of research on the effects of extreme events associated with climate change (Jentsch et al. 2007). One such type of extreme event with potentially severe impacts is drought. In general, drought, defined as a period of high water stress, negatively affects plant growth. With water stress, plants wilt, and become physiologically inactive; ceasing to carry out functions such as photosynthesis and cell expansion, and eventually die (Lambers et al. 1998). However, species differ in their ability to tolerate low water potentials (Lambers et al. 1998). Engelbrecht & Kursar (2003) have proposed three main effects on species with regard to survival and growth in drought conditions: 1) little effect on both survival and growth; 2) little effect on survival, but strong effect on growth; and 3) strong effect on survival and intermediate effect on growth; with plants falling along a continuum of these three impact scenarios. Even within the same functional group of plants, great variation in plant responses to drought can be observed, such as that found by Engelbrecht & Kursar (2003) when survival and growth were measured for seedlings of 28 species of tropical woody plants. Drought resistance differs among successional strategies for woody saplings and among plants occupying habitats ranging from open to closed canopy (Matías et al. 2012). Principally, plants have adapted to drought by either avoiding or tolerating it (Lambers et al. 1998).

Because of physiological differences among plant species, individual species may therefore respond differently to climate change, so that shifts in competitive balance occur (Walther 2004). Overall, droughts have frequently been reported to decrease plant community biomass (e.g. Sheppard et al. 2012). However, it is also possible that aboveground productivity of a plant community remains constant in a drought due to the increase in biomass of a single species which offsets the loss of others (Gilgen et al. 2010). Drought tolerance is also correlated with some species distributions in regards to both local and regional water availability (Engelbrecht et al. 2007; Baltzer et al. 2008). Changes in precipitation patterns, such as associated with climate change, may thus have direct effects on community composition and ecosystem function (Engelbrecht et al. 2007).
Alien plants affect native plant communities negatively, by reducing fitness and growth of resident plant species, and by decreasing native species abundance and diversity (Vilà et al. 2011). While both climate change and biological invasions are important factors impacting on ecosystem structure and functioning, their combination may also act synergistically (Thuiller et al. 2007; Sorte et al. 2012). Climate change provides opportunities for alien plants to invade new areas where previously they could not survive (Walther et al. 2009). Furthermore, climate change may decrease the resistance of natural communities to invaders (Thuiller et al. 2007). Invasive plants may be favoured under climate change as they often possess traits that facilitate adaptation to climate change, such as tolerance to a wide range of climate conditions, rapid dispersal and a lack of dependence on co-evolved mutualists (Vilà et al. 2007). Invasive plants of an ornamental origin have often been selected for traits such as drought tolerance (Wilson et al. 2012). Several studies suggested that drought may affect native plant communities by facilitating or providing opportunities for alien species to invade (Jiménez et al. 2011; Sheppard et al. 2012). Conversely, a meta-analysis comparing responses to climate change of alien versus native species showed a trend for alien plants to respond more negatively to reduced precipitation (Sorte et al. 2012). Performance of alien plants under drought conditions thus remains uncertain.

While there are many alien plant species in New Zealand, few have reached their full potential range (Williams & West 2000). For New Zealand, a temperature increase of 0.7-5.1°C is predicted by the end of the century, with a best estimate of 2°C (Ministry for the Environment 2008). Precipitation patterns will change, as westerly winds are projected to increase in winter and spring, bringing more rainfall to the west of both main islands and drier conditions in the east and north. In summer and autumn however, decreasing westerly winds are projected to bring drier conditions to the west and increased precipitation to the east of the North Island (Ministry for the Environment 2008). These changing climatic conditions may enable recently naturalised plants from subtropical and tropical regions, currently limited to the northern part of New Zealand, to spread further. Three such species are the focus of this study: Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla. Species distribution models have indicated that these species have the potential to widely expand their ranges in New Zealand under climate change conditions (Sheppard 2013; Chapter 3), including to some regions in which drought is forecasted (such as the east of the North Island for A. cunninghamiana and P. guajava). To test the validity of such predictions, I investigated the growth responses of these species to drought in a shadehouse experiment. Seedlings were used as this is expected to be the life stage most sensitive to drought (Engelbrecht & Kursar 2003). The aim of this study was to test: 1) whether two different durations of drought (lasting 21 and 51 days) negatively affected survival and growth of seedlings of these three alien
Chapter 5: The effect of drought on the growth of three potentially invasive plants

plant species; and 2) whether seedlings were able to recover from possible growth reductions upon return to well watered conditions.

5.2 Methods

5.2.1 Study species

The study species were Archontophoenix cunninghamiana (H. Wendl.) H. Wendl. et Drude (bangalow palm), Psidium guajava L. (common guava) and Schefflera actinophylla (Endl.) Harms (Queensland umbrella tree). These species were chosen because they are of concern as potential weeds in New Zealand. While their distribution is currently limited to the northern part of the North Island (with a mean annual temperature of 14-16°C), they have the potential to expand their range with climate change (Sheppard 2013). Archontophoenix cunninghamiana of the family Arecaceae is a native of eastern Australia. In Brazil, A. cunninghamiana has been shown to be invasive (Christianini 2006). Psidium guajava of the Myrtaceae is a native of Central America, and has been introduced to most subtropical and tropical regions as a fruit tree and has become invasive in many countries (Randall 2007). Schefflera actinophylla of the family Araliaceae is a shade tolerant species native to Australia and New Guinea. It is very invasive in the Pacific Islands (Randall 2007).

5.2.2 Experimental design

The experiment was conducted in a shadehouse at The University of Auckland Tāmaki Campus in Auckland, New Zealand. Four treatments were applied to seedlings of the three study species; two levels of drought (drought I and drought II) and two control treatments (control I and control II). Eight seedlings of each of the three species were used for each of the four treatments, totalling 32 seedlings per species and 96 overall. The drought treatment plants were randomly arranged in 8 x 6 rows in one compartment of the shadehouse, the control treatment plants in another adjacent, identical compartment.

Seedlings were propagated from seed sown in November/December 2010. Seeds of the three species were imported from Australia; A. cunninghamiana seeds were obtained from Seed Horticultural, Lower Dyraaba, New South Wales; seeds of P. guajava from Ole Lantana’s Seed Store, Toowoomba East, Queensland; and seeds of S. actinophylla from Harvest Seeds and Native Plants, Sydney, New South Wales. After germination, seedlings of each species were replanted into 0.45 L plastic planting bags (PB%) filled with Potpower™ potting mix (Debco, Melbourne, Australia). They were then kept indoors at Tāmaki Campus until transferral to the shadehouse in December 2011.
The experiment was conducted May-July 2012. The seedlings (15-17 months old at that time) were repotted into individual 1 L round plastic pots (12.5 cm diameter x 10 cm height), completely filled with Potpower™ potting mix and watered to field capacity. *Psidium guajava* seedlings were suffering from a moderate infestation of two-spotted spider mites (*Tetranychus urticae*) throughout the experiment (across all treatments). The drought treatments were started on 8 May 2012 (day one). For the drought treated seedlings, water was withheld for either 21 days (Drought I) or 51 days (Drought II), while the control seedlings were watered every other day at 6 am for ten minutes using an automatic drip watering system, resulting in ca. 40 mm of water delivered to the seedlings. Immediately after the drought treatment ceased, pots were watered in the same manner as control pots to give them some time to recover (roughly half the time of the length of the drought period, i.e. 11 and 27 days for Drought I and II plants respectively). This was done to test the resilience of the plants; that is, if plants resumed positive growth rates after the drought event finished.

For the duration of the experiment, the daily minimum temperature experienced in the shadehouse was 3.5 ± 0.66°C, the daily maximum temperature was 22.1 ± 0.53°C, and the humidity around midday was 66.7 ± 2.86% (means ± standard errors, n = 19). Soil moisture in all pots was measured three times a week using a soil moisture probe (HydroSense Soil Water Measurement System, CD620/CS620, Campbell Scientific Inc, Logan, Utah, USA). As the probe is calibrated for typical agricultural soils, soil moisture in the potting mix used in this experiment was estimated by applying a calibration equation. The equation is adapted from S. Wyse (unpublished data) who performed the calibration with independent measurements of soil water content (with n = 36 samples) using Living Earth Organic potting mix, which is assumed to be sufficiently similar to the potting mix used in this study.

During the experiment, height and the number of leaves were measured repeatedly. Additionally, the number of leaflets for *S. actinophylla* was recorded, as this species has compound leaves. Plants were measured at the beginning of the experiment (day zero), subsequently on day nine, day 16, day 21 (the end of Drought I), and on day 30. Drought I and Control I plants were measured again upon harvest on day 32. Drought II and Control II continued to be measured on day 42 and 51 (the end of Drought II), on day 60 and 66 during recovery and upon harvest on day 78. Aboveground biomass (divided into foliar and stem) was determined, first as fresh (ca. one hour after cutting) and then dry biomass (after drying at 70°C for 48 hours).
5.2.3 Data analysis

Data analysis was carried out in R (R Development Core Team 2012, version 2.14.2 for Windows). Growth data for Drought I and Control I was analysed separately from Drought II and Control II as they included different time periods. Height data was analysed with ANOVA; the number of leaves with a generalised linear model with a Poisson distribution. Fixed effects included treatment and species, and initial height and initial number of leaves were included as covariates. For measurements during the recovery period, a second analysis was carried out using height/number of leaves at the end of the drought instead of the initial height/number of leaves. For Drought II, individual analyses for each species were carried out due to significant interactions of treatment and species. Relative growth rates per day were also analysed (as increase in height or number of leaves/leaflets per unit of height/leaves/leaflets per day).

Biomass was analysed with ANOVA using the fixed factors treatment (four levels) and species (three levels) and their interaction. Biomass was natural log-transformed before analysis, and for the foliar biomass it was log (x + 1) transformed due to some zero values. Tukey HSD tests ($\alpha$ = 0.05) were used to compare multiple means. As the interaction of species and treatment was significant for all but dry stem biomass, individual analyses for each species were performed. Moisture content (dry basis; ([total fresh biomass - total dry biomass] / total dry biomass) * 100) was analysed the same way without applying a transformation.

5.3 Results

5.3.1 Soil moisture

Average estimated soil moisture across the entire experiment in control pots was 51.36 ± 0.13% for *A. cunninghamiana*; 50.57 ± 0.14% for *P. guajava*; and 53.77 ± 0.11% for *S. actinophylla* (means ± standard errors, n = 336). In comparison, drought treatment pots at the end of the drought reached soil moisture levels of 25.51 ± 0.31% and 19.83 ± 0.42% for *A. cunninghamiana* (Drought I and Drought II respectively); 22.62 ± 0.51% and 18.09 ± 0.39% for *P. guajava*; and 25.30 ± 0.38% and 20.65 ± 0.38% for *S. actinophylla* (means ± standard errors, n = 8). At the end of the recovery periods, similar levels to control pots were reached again (Figure 5.1).
Chapter 5: The effect of drought on the growth of three potentially invasive plants

Figure 5.1: Estimated soil moisture [%] throughout the experiment for a) *A. cunninghamiana*, b) *P. guajava*, and c) *S. actinophylla*; means ± standard errors (*n* = 8). Closed triangles indicate Drought I, open triangles Drought II, closed circles Control I, open circles Control II treatments. Vertical lines indicate the end of Drought I (day 21) and Drought II (day 51).

5.3.2 Survival

All individuals of all species survived both Drought I and Drought II treatments. Figure 5.2 shows examples of seedlings of the different treatments.
Chapter 5: The effect of drought on the growth of three potentially invasive plants

Figure 5.2: Examples of treatments: a-c) plants immediately after Drought I; d-f) Drought II plants at harvest (after recovery period); and g-i) Control II plants at harvest. Left column (a,d,g) are A. cunninghamiana; middle column (b,e,h) P. guajava; and right column (c,f,i) S. actinophylla.
5.3.3 Plant growth

For the plants allocated to the shorter drought period (Drought I), there were no significant effects of treatment for height or number of leaves/leafletlets at any point during the drought or recovery period; neither at the end of the drought, nor at the end of the recovery period (Figures 5.3-5.4). Number of leaves differed among species at every point in time (all $P < 0.001$).

**Figure 5.3:** Growth over time indicated by the number of leaves (left column) and absolute height [cm] (right column) for a-b) A. cunninghamiana, c-d) P. guajava, and e-f) S. actinophylla; means ± standard errors ($n = 8$). Closed triangles indicate Drought I, open triangles Drought II, closed circles Control I, open circles Control II treatments. Vertical lines indicate the end of Drought I (day 21) and Drought II (day 51).
For Drought II, the interaction of species and treatment was significant for number of leaves and height. Individual analyses for each species showed that there were no significant effects of treatment at any point during the drought or recovery period for *A. cunninghamiana* and *S. actinophylla* (Figures 5.3-5.4).

![Figure 5.4: Growth over time as number of leaflets of *S. actinophylla*; means ± standard errors (n = 8). Closed triangles indicate Drought I, open triangles Drought II, closed circles Control I, open circles Control II treatments. Vertical lines indicate the end of Drought I (day 21) and Drought II (day 51).](image)

For *P. guajava* there were significant treatment effects of Drought II on height and number of leaves: from day nine onwards, control plants were already significantly larger than drought plants (*P* = 0.007 at day nine; *P* = 0.007 at day 16; *P* = 0.019 at day 21; *P* = 0.020 at day 30; *P* = 0.024 at day 42; and *P* = 0.015 at day 51, the end of Drought II). During recovery, control plants remained significantly larger than drought plants at day 60 (*P* = 0.003), day 66 (*P* = 0.003), and until harvest at day 78 (*P* = 0.003). If initial size at the end of the drought was taken into account as a covariate for the recovery period, however, significance of the difference between drought and control treatments decreased over time, from *P* = 0.016 (day 60), *P* = 0.029 (day 66) to not significant at day 78 (*P* = 0.100). For number of leaves of *P. guajava*, significantly fewer leaves in drought compared to control plants were observed on day 30 (*P* = 0.014), with differences remaining highly significant (*P* < 0.001) from day 42 onwards. Even when taking the number of leaves at the end of the drought into account as a covariate, drought plants had significantly fewer leaves compared to control plants with *P* = 0.005 at day 60 and *P* < 0.001 at days 66 and 78. Results were similar for relative growth rates (Table 5.1).
Table 5.1: Relative growth rates in cm cm$^{-1}$ day$^{-1}$ * 1000 for height and no. no. day$^{-1}$ * 1000 for leaves and leaflets; means ± standard errors. During drought the growth rates are for 21 days (Drought I) and 51 days (Drought II) respectively, during recovery for 11 days (Drought I) and 27 days (Drought II). Significantly lower growth rates in a drought treatment compared to the respective control are indicated.

<table>
<thead>
<tr>
<th>Plant</th>
<th>Height</th>
<th>No. leaves</th>
<th>No. leaflets</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. cunninghamiana</td>
<td>Drought I</td>
<td>Control I</td>
<td>Drought II</td>
</tr>
<tr>
<td></td>
<td>0.100 ± 0.435</td>
<td>1.293 ± 0.140</td>
<td>1.019 ± 0.342</td>
</tr>
<tr>
<td></td>
<td>1.488 ± 1.488</td>
<td>2.976 ± 1.948</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>P. guajava</td>
<td>Drought I</td>
<td>Control I</td>
<td>Drought II</td>
</tr>
<tr>
<td></td>
<td>0.746 ± 1.333</td>
<td>0.209 ± 0.987</td>
<td>-0.457 ± 0.806*</td>
</tr>
<tr>
<td>S. actinophylla</td>
<td>Drought I</td>
<td>Control I</td>
<td>Drought II</td>
</tr>
<tr>
<td></td>
<td>1.578 ± 0.907</td>
<td>3.220 ± 1.857</td>
<td>1.420 ± 0.611</td>
</tr>
<tr>
<td></td>
<td>-2.480 ± 1.786</td>
<td>-1.049 ± 1.848</td>
<td>-1.247 ± 0.405</td>
</tr>
<tr>
<td></td>
<td>0.991 ± 2.033</td>
<td>2.431 ± 1.633</td>
<td>0.502 ± 0.468</td>
</tr>
</tbody>
</table>

During recovery

<table>
<thead>
<tr>
<th>Plant</th>
<th>Height</th>
<th>No. leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. cunninghamiana</td>
<td>Drought I</td>
<td>Control I</td>
</tr>
<tr>
<td></td>
<td>0.840 ± 0.556</td>
<td>2.238 ± 0.974</td>
</tr>
<tr>
<td></td>
<td>2.841 ± 2.841</td>
<td>2.841 ± 2.841</td>
</tr>
<tr>
<td>P. guajava</td>
<td>Drought I</td>
<td>Control I</td>
</tr>
<tr>
<td></td>
<td>1.128 ± 1.041</td>
<td>1.308 ± 1.549</td>
</tr>
<tr>
<td>S. actinophylla</td>
<td>Drought I</td>
<td>Control I</td>
</tr>
<tr>
<td></td>
<td>0 ± 0</td>
<td>0.758 ± 0.758</td>
</tr>
<tr>
<td></td>
<td>-1.136 ± 1.136</td>
<td>0 ± 0</td>
</tr>
<tr>
<td></td>
<td>-1.470 ± 1.063</td>
<td>0 ± 0</td>
</tr>
</tbody>
</table>

Significance levels: * $P < 0.05$, ** $P < 0.01$.

5.3.4 Biomass

For A. cunninghamiana, biomass was significantly lower (Tukey HSD at $\alpha = 0.05$) when comparing Drought II to Control II plants for total fresh biomass (Figure 5.5), fresh and dry foliar biomass; and moisture content was also lower (Table 5.2). For P. guajava, Drought II resulted in significantly lower biomass than the other three treatments, for all biomass measures except for dry stem biomass, which was only significantly lower than Control II (Figure 5.5; Table 5.2). Additionally, for fresh foliar biomass and total fresh biomass, Drought I was significantly lower than Control II. Moisture content was significantly lower in Drought II plants compared to all other treatments, and significantly lower in Drought I compared to Control II. For S. actinophylla there were no significant effects on biomass.
However, moisture content of the plants upon harvest was higher in Drought II treatments compared to Control II.

![Graph showing biomass comparison](image_url)

**Figure 5.5**: Total aboveground biomass [g] of a) *A. cunninghamiana*, b) *P. guajava*, and c) *S. actinophylla*; means ± standard errors (n = 8). Shaded bars show dry biomass; white bars show fresh biomass. Dr I = Drought I; Co I = Control I; Dr II = Drought II; Co II = Control II. Significant differences between treatments are indicated by differing letters.

**Table 5.2**: Results of the ANOVA for individual species using the fixed factor treatment (four levels) for different measures of natural log-transformed biomass and moisture content.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total biomass</th>
<th>Foliar biomass</th>
<th>Stem biomass</th>
<th>Moisture content</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. cunninghamiana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fresh biomass</td>
<td>2.74</td>
<td>0.062</td>
<td>3.29</td>
<td>2.31</td>
<td>0.098</td>
<td></td>
</tr>
<tr>
<td>Dry biomass</td>
<td>2.27</td>
<td>0.102</td>
<td>2.80</td>
<td>0.058</td>
<td>0.176</td>
<td></td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fresh biomass</td>
<td>43.9</td>
<td>&lt;0.001</td>
<td>36.4</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry biomass</td>
<td>30.5</td>
<td>&lt;0.001</td>
<td>28.3</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.54</td>
<td>0.027</td>
</tr>
<tr>
<td>Fresh biomass</td>
<td>1.46</td>
<td>0.248</td>
<td>1.53</td>
<td>0.228</td>
<td>1.28</td>
<td>0.300</td>
</tr>
<tr>
<td>Dry biomass</td>
<td>1.11</td>
<td>0.363</td>
<td>0.56</td>
<td>0.644</td>
<td>1.60</td>
<td>0.211</td>
</tr>
</tbody>
</table>
5.4 Discussion

The shorter drought period in this study, lasting 21 days and resulting in estimated soil moisture of on average 22-26% in the drought pots (compared to 50-54% in control pots), did not have any significant effects on height, number of leaves or aboveground biomass of any of the three species in this study. However, the longer drought period, lasting 51 days (resulting in estimated soil moisture that averaged 18-21%) affected growth of the three species to different extents, in particular having a negative impact on growth and biomass of *P. guajava*. For this species, mean total dry biomass of the Drought II treatment was only 35.5% of the control biomass; in contrast the other two species showed higher drought tolerance, with biomass of *A. cunninghamiana* under the Drought II treatment amounting to 72.4% of the control biomass; and 80.7% for *S. actinophylla*. Fresh biomass and dry foliar biomass under the longer drought treatment was, however, significantly lower for *A. cunninghamiana* compared to control; indicating that there was also a small negative effect of drought on *A. cunninghamiana*. For *S. actinophylla*, not even fresh biomass showed any significant differences between treatments, and moisture content at harvest was in fact higher in drought plants compared to control, suggesting that this species is very resilient to drought conditions.

While I found no published study on drought tolerance of *A. cunninghamiana* or *S. actinophylla*, lower rates of stomatal conductance (i.e. lower water loss through transpiration) were recorded in *A. cunninghamiana* compared to two other palm species in a study in California (Downer & Hodel 2001), which may aid its drought tolerance. The apparent drought tolerance of *A. cunninghamiana* is nevertheless somewhat surprising, as it grows naturally on stream banks and gullies in rainforest and swampy areas of open forest (Jones 1996). *Schefflera actinophylla* is also a rainforest species inhabiting lowland swamps and exposed rocky outcrops. A study of seedlings of the congeneric *S. heptaphylla* in China showed that growth was not significantly higher if plants were irrigated during the dry season (Hau & Corlett 2003), suggesting adaptation to low water availability. The results of this study indicate that *A. cunninghamiana* and *S. actinophylla* appear to follow the first type of adaption to drought response proposed by Engelbrecht & Kursar (2003), being very drought tolerant and showing little effect of drought on survival or growth.

*Psidium guajava*, as a widely studied species due to its horticultural importance, has been previously referred to as drought tolerant (Hao *et al.* 2009). In my study, wilting was observed in *P. guajava*, only for two individuals after Drought I, but after Drought II all individuals were wilting strongly, with leaves drooping at more than a 45° angle, and leaves browning and subsequently being shed (personal observation). Another study on drought tolerance of *P. guajava* showed wilting occurring after 18 days of water stress (Hao *et al.* 2009). For the congeneric *P. cattleianum*,
defoliation occurred after ca. 27 days of drought including one two-day re-watering period after 15 days (Yazaki et al. 2010). Similarly, in this study differences in number of leaves between drought and control plants became apparent after 30 days of withheld watering. My results suggest that *P. guajava* may fall closest to the second adaptation to drought response (Engelbrecht & Kursar 2003), surviving well but with significant effects on growth, shedding leaves in order to survive.

While *P. guajava* was clearly affected more by drought than the other two species, there is also a possibility that this species may have been weakened by the moderate infestation of two-spotted spider mite that occurred during my experiment, resulting in two stressors for the seedlings to cope with. Moreover, as for the other two species, there was no mortality due to drought. This is consistent with a study of 28 tropical woody seedlings, which showed that reduced survival was not correlated with reductions in growth (Engelbrecht & Kursar 2003). There is also some indication that *P. guajava* was able to recover after the drought period: at the end of the recovery period new leaf growth was observed on two individuals. Additionally, differences in height between drought and control plants were not significant at the end of the recovery period, if initial size at the end of the drought was taken into account. This indicates that, given more time, the plants would probably recover completely. This assumption is also supported by the observation that three months after the end of the experiment, new *P. guajava* plants had re-grown from roots in half the pots that had been left standing (with very little water available), after the stems were cut off at the base upon harvest. Therefore, overall *P. guajava* still has considerable ability to withstand drought.

With drought sensitivity correlated with species distributions in relation to water availability (Engelbrecht et al. 2007; Baltzer et al. 2008), the results of this experiment would probably not have been predicted from the global distribution of these three species. An analysis of the distribution of these species using species occurrence records, as in Sheppard (2013) in relation to precipitation of the driest quarter (BIO18), showed for *A. cunninghamiana* a precipitation range of 6-1329 mm, with a median of 476 mm; for *P. guajava* a range of 3-1819 mm, with a median of 440 mm; and for *S. actinophylla* a range of 14-1400 mm, with a median of 537 mm. These median values seem to suggest that generally *S. actinophylla* occurs in the least drought stressed habitats. This is surprising considering the results of this study, where *S. actinophylla* did not show any signs of drought damage even after 51 days of no watering. In New Zealand, BIO18 values range across the whole country between 113-3602 mm, with a median of 309 mm, with the regions most at risk from invasion by these species having a median rainfall of 100-300 mm in the summer quarter. While these values are at the lower end compared to the global distribution, the results of my study suggest that the species may well be able to tolerate soil moisture deficits experienced during
summer on the east coast of the North Island (median of 50 days below the field capacity of the soil) (National Institute for Water and Atmospheric Research 2013).

Being able to cope so well with drought indicates that *A. cunninghamiana* and *S. actinophylla* have the potential to persist in mesic environments they have already invaded even with increasing occurrences of more frequent extreme events such as droughts in the future. If these species are better able to withstand such stress, they may be able to outcompete native species under such future conditions. For example, a preliminary study showed the potential of *A. cunninghamiana* to outcompete New Zealand’s only native palm, *Rhopalostylis sapida* (nikau), under current conditions in similar habitats (J. Sullivan, unpublished data). If *A. cunninghamiana* is able to maintain or increase its competitive advantage over the native palm (belongs to the same subtribe as *A. cunninghamiana*) under future climate change conditions and extreme events, this native palm may be gradually replaced.

This study investigated growth response to drought while all other factors were held constant. However, many factors may potentially interact with drought, and results in a field situation may therefore be different. Field studies should be carried out and results interpreted in combination with the results of this artificial environment study. Furthermore, the timing of a drought is another factor of importance, influencing whether a species may acclimate growth to drought conditions. Depending on the timing of a drought, different species may be in different development stages and therefore affected to a different extent by a drought (Gordon et al. 1999). With this study conducted during early winter, drought may have been easier to tolerate than when combined with high temperature, as warming increases water loss (Peñuelas et al. 2004). Interactions with other factors may also result in differential responses to drought. For example, Gordon et al. (1999) showed greater drought damage to one species compared to another under increased nitrogen supply. Furthermore, herbivory may weaken a plant, but in a field situation alien plants are generally expected to be less affected by natural enemies (i.e. enemy release hypothesis, Keane & Crawley 2002).

Under shadehouse conditions, *P. guajava* showed moderate tolerance, *A. cunninghamiana* high tolerance and *S. actinophylla* very high tolerance to drought conditions. This may contribute to the continuing persistence and potential spread of these species in New Zealand under future climate change, and if native species show lower drought tolerance, may assist the alien species in displacing such natives.
5.5 References

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CHAPTER 6

Effects of interspecific alien versus intraspecific native competition on growth of native woody plants

Abstract

The success of invasive plants and their impacts on community structure are commonly explained by referring to their supposed higher competitive ability. However, invasive plants do not consistently outperform native species; and the role of competition may also depend on the stage of the invasion process. This study investigated competitive effects of woody alien plant species at an early stage of invasion (*Archontophoenix cunninghamiana*, *Psidium guajava* and *Schefflera actinophylla*) on closely related New Zealand native species of similar life form (*Rhopalostylis sapida*, *Lophomyrtus bullata* and *Schefflera digitata* respectively) in a shadehouse experiment. Effects of interspecific competition were compared to the competitive effects from intraspecific competition among seedlings of the native species over a 65 week period. Mortality was low throughout the experiment except for *S. digitata*, which was subsequently excluded from the results. The other native species were affected by density-dependent competition, but performance was also influenced by competitor biostatus. The alien palm, *A. cunninghamiana*, had stronger competitive effects on the native palm, *R. sapida*, than intraspecific competition among *R. sapida* individuals. Also, *P. guajava* showed some stronger competitive effects on *L. bullata* than intraspecific competition among *L. bullata* individuals. These alien species displayed some traits often associated with invasive plants: *A. cunninghamiana* had higher relative growth rates, biomass production and specific leaf area compared to *R. sapida*, while *P. guajava* had the highest specific leaf area and *S. actinophylla* the largest biomass production. The high competitive ability of these newly naturalised species compared to native species may be an important factor influencing their establishment success and subsequent invasion potential.

7 The contents of this Chapter are submitted for publication as: Sheppard CS & Burns BR. Effects of interspecific alien versus intraspecific native competition on growth of native woody plants. Under review at Plant Ecology.
6.1 Introduction

Competition is recognised as an important factor in structuring plant communities, but its relative importance under different environmental conditions and the plant traits associated with competitive ability are debated (Bengtsson et al. 1994). Competitive ability can be defined as the ability to suppress other plants (competitive effect) or the ability to avoid or tolerate suppression (competitive response) (Goldberg & Landa 1991). When plants of the same or different species are competing, mean plant performance is expected to decline with increased plant density (Freckleton & Watkinson 2000). Competition is common among plants and influences performance of individuals, abundance of populations and distribution of plant species (Goldberg & Barton 1992; Bengtsson et al. 1994).

Classical competition theory predicts that intraspecific competition should be greater than interspecific competition because individuals within one species share highly similar resource requirements (Tilman 1982). Coexistence is possible due to niche partitioning, that is, differences in resource requirements of different species, or facilitation, that is, one species modifying the environment in a way that is beneficial for another species (Fridley 2001). However, experimental studies have not consistently found intraspecific competition to be stronger (Goldberg & Barton 1992). Among plants, it is mostly size differences rather than species differences that are responsible for asymmetry in competition for nutrients and light (Bengtsson et al. 1994). Such size-asymmetric competition (i.e. resource uptake among competitors depending on size with largest plants obtaining a disproportionate share of the resources) tends to occur in later development stages and at higher densities, when a limiting resource is depleted (Schwinning & Weiner 1998). Competition for light is almost always size asymmetric with small plants highly affected, in contrast to competition for below-ground resources where plants of all sizes are affected (Schwinning & Weiner 1998; Weiner 1990; Coomes & Allen 2007).

Plant invasions are considered a major threat to global biodiversity (van der Wal et al. 2008). Contrary to classical competition theory, interspecific competition between native and alien plants may exceed intraspecific competition between native plants. When an alien plant is introduced, competition for limited resources is one of the first interactions the plant has with the recipient community (Vilà & Weiner 2004). The eventual dominance of an invasive plant and its impacts on community structure are usually explained as reflecting its higher competitive ability (Callaway & Aschehoug 2000; Levine et al. 2003). A recent meta-analysis showed that invasive plants decrease fitness of native plant species by 41.7% (mean effect size); growth by 22.1%; abundance by 43.5%; and diversity by 50.7% (Vilà et al. 2011). Certain plant traits often found in invasive species such as
high relative growth rates (RGR), high specific leaf area (SLA) and phenotypic plasticity are thought to infer higher competitive ability and predict invasion success (Ordonez et al. 2010; van Kleunen et al. 2010; Davidson et al. 2011; Lamarque et al. 2011). The question of whether invasive plants consistently outperform native species is of great importance to conservation efforts and vital for informing management strategies to promote native species (Daehler 2003).

Different studies on alien versus native competition have not always led to consistent results. One meta-analysis showed an average reduction in biomass or size of 46.6% of a native species due to competition with an alien species, but only a 17.6% reduction of an alien species due to competition with a native species (Vilà & Weiner 2004). However, another review comparing native and invader performance showed that only in 13% of the studies did the invader consistently outperform the native species (Daehler 2003). Competitive ability of native and invasive species may therefore depend on the environment. Within a given environment, competitive interactions may change over time, as individuals modify the availability of resources; therefore it is important to investigate competitive interactions at several points in time (Mangla et al. 2011). The role of competition may also differ among alien plants at various stages of the invasion process, because the factors that determine if an alien plant establishes may be different to those that determine subsequent spread (Vilà & Weiner 2004). Typically, the question of whether alien species have higher competitive ability than native species has been investigated for invasive plants at the final stages of spread. However, competition should also be addressed at earlier stages, such as during introduction and establishment (Vilà & Weiner 2004).

The aim of this study was to investigate competitive effects of three alien woody species at an early stage of their invasion. *Archontophoenix cunninghamiana*, *Psidium guajava* and *Schefflera actinophylla* are recently naturalised alien species in New Zealand with currently small geographic ranges. However, species distribution modelling for these three species has indicated larger potential distributions (Sheppard 2013; Chapters 2 and 3). The selected species are not likely to be dispersal-limited, as they are widely sold in commercial nurseries and bird-dispersed, enabling them to spread easily (Williams 2006; Jordaan et al. 2011). Woody plant species were chosen, as they are increasingly being recognised as among the most serious environmental weeds (Richardson & Rejmánek 2011). I investigated the competitive effects of these alien species in differing densities on confamilial or congeneric native species of similar life form and ecological niche (interspecific competition), and compared it with the competitive effects from native individuals of the same species (intraspecific competition) in a shadehouse experiment. The native species paired with each of the alien species mentioned above were *Rhopalostylis sapida*, *Lophomyrtus bullata* and *Schefflera*
digitata, respectively. Because the chosen native species occupy similar niches to the alien species, if the alien species are more competitive this will result in large potential impacts (MacDougall et al. 2009). Although naturally an alien species invading a native community will compete with many resident species, pairwise experiments are a suitable starting point to investigate competitive ability among species as there are no indirect effects of the larger plant community that make results difficult to interpret (Goldberg & Scheiner 2001). Greenhouse experiments, by removing the variability of natural environments, allow us to measure a factor of interest in isolation, with the results enabling generation of hypotheses, which can then be further tested in the field (Freckleton & Watkinson 2000).

Therefore, I grew seedlings of the native species (target plants) in a shadehouse under the controlled conditions of a pot experiment alone and in competition with either one, four or eight seedlings of the native or the matched alien species (neighbours) and measured growth of the target individuals at five week intervals over 65 weeks. I addressed the following hypotheses in this study: i) higher density or biomass of neighbours results in decreased growth of target individuals; ii) competition from alien neighbours (interspecific) results in a stronger reduction in growth of target individuals than competition from native neighbours (intraspecific); and iii) alien plant neighbours show higher RGR, larger biomass production and higher SLA compared to native plant neighbours.

6.2 Methods

6.2.1 Study species

The first species pair is in the family Arecaceae. Archontophoenix cunninghamiana (H. Wendl.) H. Wendl. et Drude (bangalow palm), is a native of eastern Australia. As a popular garden plant in New Zealand, it naturalised in 1992 (Cameron 2000). Archontophoenix cunninghamiana has also become invasive in Brazil (Christianini 2006). It was paired with the only native (endemic) palm in New Zealand, Rhopalostylis sapida H. Wendl. et Drude (nikau), which belongs to the same subtribe (Archontophoenicinae). The alien species also lives in similar habitats as R. sapida, such as gullies, stream banks and swampy areas, in shaded areas and under the canopy (Jones 1996).

The second species pair is in the family Myrtaceae. Psidium guajava L. (common guava) is a native of Central America, which first naturalised in New Zealand on the Kermadec Islands in 1965 (Sykes 1982). It has been introduced to many tropical and subtropical regions of the world and has often become invasive (Randall 2007). The native species chosen to pair with P. guajava is Lophomyrtus bullata Burret (ramarama), as the most similar native Myrtaceae species to P. guajava
in morphology and ecology. *Psidium guajava* can grow in a wide range of habitats, including forest edges and shrubland where *L. bullata* occurs.

The third species pair is in the family Araliaceae. *Schefflera actinophylla* (Endl.) Harms (Queensland umbrella tree) is native to Australia and New Guinea and is a shade tolerant species that can also grow as an epiphyte. It naturalised in 2005 in New Zealand (Wilcox 2005) and is also invasive in the Pacific Islands (Randall 2007). *Schefflera digitata* J.R. Forst. et G. Forst. (pate) was chosen to pair with it as a native congener of *S. actinophylla*, with both species’ habitats mainly found in lowland forests.

### 6.2.2 Experimental design

The experiment was designed to investigate effects of alien species competition on the native species for the three plant pairs in order to assess potential impacts. However, additive designs in competition experiments only look at effects of species X on Y, resulting in confounding effects of species proportion and density (Gibson et al. 1999). To avoid this limitation in this experiment, I also compared competitive effects of native neighbours. Growth of one native target individual in the centre of a pot was measured. It was grown with no competition (control) and with one, four or eight neighbours, either of the native (intraspecific competition) or alien species (interspecific competition), giving seven treatments (Figure 6.1). Ten replicates of each treatment were used, giving 70 pots per species pair, and 210 pots overall. Across the entire experiment, 200 individuals of each of the three native species and 130 of each of the three alien species were used.

![Figure 6.1: Experimental treatments, with N indicating native and A alien individuals; N in bold indicates the target individual.](image)

The competition experiment took place in a shadehouse at Tāmaki Campus, The University of Auckland, in Auckland, New Zealand. The mean annual temperature in Auckland is 15.1°C (National Institute of Water and Atmospheric Research 2013). The experiment was conducted between October 2011 and January 2013, a total of 65 weeks. A randomised block design was used; with the blocks corresponding to five shadehouse compartments of 3 x 4 m. Pots were of 20 cm
diameter and 4.5 L volume. The surface area of a pot was 0.032 m$^2$, resulting in plant densities of 32 plants/m$^2$ (single target plant treatment); 64 plants/m$^2$ (target plant with one neighbour); 159 plants/m$^2$ (target plant with four neighbours); and 286 plants/m$^2$ (target plant with eight neighbours). Space between neighbouring pots was maintained at 20 cm to avoid competition for light from plants in other pots.

The seedlings used in this experiment were propagated from seed sown in November/December 2010, seedlings thus being almost one year old. Seeds of the three alien species had been imported from Australia: seeds of *A. cunninghamiana* were obtained from Seed Horticultural, Lower Dyraaba, New South Wales; seeds of *S. actinophylla* from Harvest Seeds and Native Plants, Sydney, New South Wales; and seeds of *P. guajava* from Ole Lantana’s Seed Store, Toowoomba East, Queensland. After germination, seedlings of each species were replanted into 0.45 L plastic planting bags (PB ¾) filled with Potpower™ potting mix (Debco, Melbourne, Australia). Due to germination failure of native seeds, seedlings of *S. digitata* and *L. bullata* were obtained from Oratia Native Plant Nursery, Auckland (seed collected January 2011), while seedlings of *R. sapida* were collected from a native forest site (Whitford, Auckland; March 2011).

One month after the start of the experiment, a two-spotted spider mite (*Tetranychus urticae*) infestation was discovered on *S. digitata*, which persisted throughout the experiment. The infestation affected most *S. digitata* and *P. guajava* plants, resulting in high mortality of *S. digitata* and reduced growth and leaf loss of *P. guajava*. Several attempts were made to control the spider mite infestation across all treatments. Initially, 15 ml Yates Mite Killer (containing 250 g/L fatty acids in the form of potassium salts) was applied to *S. digitata* at week five. Three days later a further application of 10 ml occurred. Thereafter, plants were regularly sprayed with 10-30 ml of Yates Mavrik (9.6 g/L tau-fluvalinate in the form of a suspension concentrate), repeating this every seven days. As this proved ineffective, biological control was attempted, releasing 1000 adult *Phytoseiulus persimilis* (Mite-E™, Bioforce Ltd, Karaka) at week 17 (February 2012), with another 1000 adults released a month later. At weeks five, 15 and 50 all pots were additionally sprayed with 5 ml Kohinor 350 (active ingredient 350 g/L imidacloprid in the form of an aqueous suspension concentrate), 4 g Agree WDG (a biological insecticide containing 25,000 ITU/mg *Bacillus thuringiensis* var. *azawai/kurtstaki* in the form of a water dispersable granule) and 15 ml Yates Fungicide (containing 500 g/L chlorothalonil in the form of a suspension concentrate), which removed other minor invertebrate infestations successfully. Towards the end of the experiment (at week 60), a leafroller infestation was detected, mainly affecting *P. guajava* and *L. bullata*. I attempted to control this infestation manually by removing leafroller individuals regularly.
To compensate for declining nutrient and mineral availability in the pots over the course of the experiment, all pots were regularly fertilised from week 50, using 75 ml Yates Thrive All Purpose plant food (containing nitrogen, phosphorus, potassium, iron and trace elements; NPK analysis: 12.4:3:6.2) and ca. 150 g sulphate of iron applied in 30 L of water across all pots. This was repeated at first every seven days, later every ten and then every 14 days until the end of the experiment.

6.2.3 Growth measurements

After the start of the experiment, individuals that died were replaced immediately until three weeks after transplanting (30 *S. digitata* and two *L. bullata* individuals). When first measurements were made after five weeks, dead plants were also replaced but assigned a new ID, thereafter dead individuals continued to be replaced every five weeks until week 35. For *S. digitata*, due to high mortality and unavailability of seedlings, last replacements were made at week ten.

The native target individuals in the middle of the pots were measured every five weeks throughout the experiment. The neighbour individuals were measured four times: at the start of the experiment (week zero), at week 15, week 35 and at harvest (week 65). For all species, height was measured (for *A. cunninghamiana* and *R. sapida*, this was defined as the maximum distance from ground to tip of a leaf; for *S. actinophylla* and *S. digitata* the distance from ground to apical bud; and for *P. guajava* and *L. bullata* the distance from ground to tip of the main stem), and the number of leaves (longer than 1 cm) was counted. As *A. cunninghamiana*, *R. sapida*, *S. actinophylla* and *S. digitata* have compound leaves, the total number of leaflets was also recorded. For *A. cunninghamiana* and *R. sapida*, stem diameter was measured 1 cm above ground level. For *P. guajava* and *L. bullata*, the number of branches that exceeded 3 cm in length was counted.

Aboveground biomass was harvested in January 2013 by cutting off stems at the soil level. For *A. cunninghamiana* and *R. sapida*, however, they were harvested at the base of stem, even if it was slightly below soil level, in order to include the entire shoot biomass. Leaf area for all species was measured by photographing all leaves (from a distance that resulted in a distortion small enough to be negligible) and analysing the area (cm²) with Image J software (Wayne Rasband National Institutes of Health, USA). Plant material (aboveground biomass) was dried at 70°C for 36 hours before weighing. Belowground biomass was not harvested because the intertwining roots among individuals could not have been accurately separated.
Chapter 6: Effects of interspecific alien vs intraspecific native competition on growth of native woody plants

6.2.4 Data analysis

Three different types of analyses were carried out. First, neighbour biomass was regressed against target biomass and RGR. Then linear mixed models and generalised linear models were used to detect significant differences of target growth over 65 weeks among the neighbour density and neighbour biostatus (identity) treatments. Finally differences in growth traits for the various neighbour species were analysed with linear mixed models. Due to high mortality of S. digitata, analyses could not be carried out for this species. I did not use a competition index, as different target species were not directly compared, and the merging of primary variables into an index inevitably results in some loss of detail and can often make the statistical qualities difficult to comprehend (Jolliffe 2000; Weigelt & Jolliffe 2003).

6.2.4.1 Effects of neighbour biomass on biomass and RGR of target individuals

The influence of neighbours’ biomass (irrespective of number of individuals) on biomass and RGR of target individuals was analysed in R (R Development Core Team 2013, version 3.0.0 for Windows). For this analysis, the single target plant without neighbours (control) was excluded. For the final harvest data, the effect of the biomass of neighbours on the biomass of the target individuals was analysed. Biomass of the target individual was natural log-transformed in order to meet model assumptions, and linear regressions were fitted with neighbour biomass as an independent variable, ‘biostatus’ (native/alien) as a dummy variable, and their interaction. Final regression models included only significant effects. If the interaction of neighbour biomass and biostatus was significant, two separate regressions were fitted for alien and native neighbours.

To investigate how competition may have changed over time, changes in target plant growth rates were investigated as a function of neighbour biomass at the beginning of several growth intervals (Ramseier & Weiner 2006). Although rarely recognised, measurements at several points in time are necessary to understand changing dynamics of species interaction (Gibson et al. 1999). Biomass of individuals was estimated by fitting regressions to determine a relationship between final biomass and height and number of leaves. Best fit was obtained with a linear model that used the natural log-transformed number of leaflets (leaves in the case of P. guajava and L. bullata) and natural log-transformed height to predict natural log-transformed biomass. For all species, the regression models were highly significant ($P < 0.001$) and resulted in adjusted $R^2$ between 0.7-1 (Table 6.1). From the estimated biomass, RGR was then calculated as $\text{RGR} = (\ln W2 – \ln W1) / (t2 - t1)$, with $t1$ and $t2$ indicating time points 1 and 2 and $W1$ and $W2$ indicating the estimated biomass at time points 1 and 2. Neighbour biomass at the start of an interval (either at zero, 15 or 35 weeks),
biostatus (i.e. alien or native), and their interaction were used as independent variables, and RGR of the target individuals as the dependent variable, calculated over the immediately following ten weeks. Final regression models included only significant effects, and regressions were fitted separately for native and alien neighbours if the interaction was significant.

Table 6.1: Linear regressions to estimate natural log-transformed biomass, using natural log-transformed height and natural log-transformed leaflets (leaves for P. guajava/L. bullata) as independent variables. Model coefficients, numerator (DF) and denominator degrees of freedom (Den. DF), F and R² values are indicated.

<table>
<thead>
<tr>
<th>Species</th>
<th>Intercept</th>
<th>Ln (height)</th>
<th>Ln (leaflets)</th>
<th>DF</th>
<th>Den. DF</th>
<th>F</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. sapida</td>
<td>-6.294</td>
<td>1.843</td>
<td>0.452</td>
<td>2</td>
<td>196</td>
<td>278 ***</td>
<td>0.737</td>
</tr>
<tr>
<td>A. cunninghamiana</td>
<td>-5.825</td>
<td>1.784</td>
<td>0.454</td>
<td>2</td>
<td>127</td>
<td>325 ***</td>
<td>0.834</td>
</tr>
<tr>
<td>L. bullata</td>
<td>-6.044</td>
<td>1.289</td>
<td>0.607</td>
<td>2</td>
<td>197</td>
<td>749 ***</td>
<td>0.883</td>
</tr>
<tr>
<td>P. guajava</td>
<td>-6.069</td>
<td>1.454</td>
<td>0.664</td>
<td>2</td>
<td>118</td>
<td>398 ***</td>
<td>0.869</td>
</tr>
<tr>
<td>S. actinophylla</td>
<td>-3.368</td>
<td>1.013</td>
<td>0.918</td>
<td>2</td>
<td>127</td>
<td>418 ***</td>
<td>0.866</td>
</tr>
</tbody>
</table>

Significance level: *** P < 0.001.

6.2.4.2 Effects of competition density treatments on growth of target individuals

The effect of neighbours as different density treatments (number of individuals per pot) on target individuals was analysed in SAS statistical software (SAS Institute Inc., Cary NC, USA, version 9.2 for Windows). Target individual biomass and leaf area were analysed based on a linear mixed model approach, using restricted maximum likelihood (REML) to fit the linear mixed model to the data. Type III hypothesis tests for the significance of each of the fixed effects and interactions were performed. Thereafter pairwise comparisons of means were performed for statistically significant effects (P < 0.05) in the Type III hypothesis tests, using the Tukey-Kramer method to adjust P-values. Analyses were carried out separately for R. sapida and L. bullata. Shadehouse block was treated as a random effect, ‘treatment’ (control, one native, one alien, four native, four alien, eight native, eight alien neighbours) as a fixed effect. Similar models were then built excluding the control (single target plant), so that a fully factorial design resulted with ‘biostatus’ (native/alien) and ‘density’ (one/four/eight individuals) and their interaction as fixed effects, to investigate overall effects of native versus alien neighbours and differing densities of neighbours. Biomass and leaf area were natural log-transformed before analysis to stabilise the variance.

Measurements of diameter of R. sapida over time were analysed using a similar approach, but with ‘weeks’ as an additional fixed effect included in the model and an additional random effect
to account for the correlation between repeated measurements of each plant (‘pot’). Diameter was natural log-transformed before analysis. For number of branches of *P. guajava* a generalised linear mixed model was fitted, assuming the response variable followed a Poisson distribution, with a log-link. A residual marginal pseudo-likelihood technique was used for the estimation of variances. A preliminary analysis at week zero confirmed that there were no initial significant differences in diameter or number of branches between treatments at the start of the experiment.

**6.2.4.3 Comparison of growth rates of neighbour species**

To compare RGR, biomass and SLA of the different neighbour species, one individual was randomly chosen from each pot with four and eight neighbours, in order to get an equal number of samples for the different density treatments (ten for each species). RGR was calculated for these individuals over the duration of the experiment (weeks zero to 65, using estimated biomass at week zero), and a linear mixed model was fitted, including ‘block’ as a random factor and ‘species’ and ‘density’ and their interaction as fixed factors. Similarly, separate models were fitted with natural log-transformed final biomass or SLA as the response variable.

**6.3 Results**

**6.3.1 Mortality**

Mortality throughout the experiment was low for all species except *S. digitata* (Figure 6.2), with the highest mortality rates occurring in high density conditions (Table 6.2). For *S. digitata*, by the time of harvest, only five target individuals and one neighbour individual had survived. This species was therefore excluded from further analysis.
Chapter 6: Effects of interspecific alien vs intraspecific native competition on growth of native woody plants

Figure 6.2: Number of dead *S. digitata* target individuals over the first 30 weeks across the seven treatments. Replacement of dead individuals stopped after week ten, and all remaining plants except six had died by week 30 (plus one more died at week 55). Green open circles indicate native neighbours, blue closed circles alien neighbours and grey circles no neighbours. Dash-dot lines are for one neighbour, dashed lines for four neighbours, and solid lines for eight or no neighbours.

Table 6.2: Mortality over the course of the experiment for the different species and treatments. The number of dead individuals is indicated both for target individuals (one individual per pot in each of the seven treatments) and neighbour individuals (one, four or eight individuals per pot depending on density treatment).

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>1 native</th>
<th>4 native</th>
<th>8 native</th>
<th>1 alien</th>
<th>4 alien</th>
<th>8 alien</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Target</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. sapida</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td><em>L. bullata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
<tr>
<td><em>S. digitata</em>†</td>
<td>13</td>
<td>18</td>
<td>16</td>
<td>25</td>
<td>16</td>
<td>28</td>
<td>29</td>
<td>145</td>
</tr>
<tr>
<td>Neighbours</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R. sapida</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td><em>A. cunninghamiana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td><em>L. bullata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td></td>
<td>9</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>10</td>
<td></td>
<td></td>
<td>12</td>
</tr>
<tr>
<td><em>S. digitata</em>†</td>
<td>19</td>
<td>73</td>
<td>183</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>275</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

† Note that individuals of this species that died were not replaced after week ten.

6.3.2 Effects of neighbour biomass on biomass and RGR of target individuals

Figure 6.3 shows examples of treatments at harvest. 
Figure 6.3: Examples of the different treatments at harvest (after 65 weeks): a-g) *R. sapida* target plants with a) no neighbours, b) one native, c) one alien, d) four native, e) four alien, g) eight alien neighbours; h) *S. digitata* target with no neighbours; i) one, j) four, and k) eight *S. actinophylla* neighbours (targets dead); l-r) *L. bullata* target plants with l) no neighbours, m) one native, n) one alien, o) four native, p) four alien, q) eight native, r) eight alien neighbours; s) example of a shadehouse compartment.

Final biomass of the neighbour species had a significant effect on final biomass of *R. sapida* target individuals, but biostatus (native/alien) and the interaction had no significant effects, and
therefore these were removed from the model (Figure 6.4a). There was no significant effect of neighbour biomass at the start of a growth interval on RGR of the target individual (calculated over ten weeks) for the intervals weeks zero to ten or weeks 15-25 for R. sapida (Figure 6.4b,c). However, for the last time interval (RGR over weeks 35-45), neighbour biomass had a significant effect (Figure 6.4d). Again, biostatus (native/alien) and the interaction were not significant and excluded from the final model.

Figure 6.4: Relationships between growth of R. sapida target individuals and neighbour biomass, shown for a) neighbour biomass versus natural log-transformed target biomass at week 65; b) neighbour biomass at week zero versus RGR of target over interval weeks zero to ten; c) neighbour biomass at week 15 versus RGR of target over interval weeks 15-25; and d) neighbour biomass at week 35 versus RGR of target over interval weeks 35-45. Open circles indicate native neighbours, closed circles alien neighbours. Only significant regressions are shown (solid lines: for both native and alien neighbours), with $F$ and $R^2$ values indicated; significance levels: * $P < 0.05$, *** $P < 0.001$.

Final neighbour biomass did not affect L. bullata final target biomass significantly (Figure 6.5a). For RGR of L. bullata target individuals over weeks zero to ten both neighbour biomass at
week zero and biostatus had significant effects but not their interaction, with RGR of target individuals estimated to be 0.0414 g/week higher for native compared to alien neighbours (Figure 6.5b). For RGR over weeks 15-25 the interaction between neighbour biomass and biostatus was significant and therefore separate regressions were fitted for native and alien neighbours. For both types of neighbours biomass at week 15 had a significant effect; however, for native neighbours the slope was positive, that is, neighbour biomass had a positive effect on target individual RGR (Figure 6.5c). Neighbour biomass at week 35 did not have a significant effect on target RGR over weeks 35-45 (Figure 6.5d).

Figure 6.5: Relationships between growth of L. bullata target individuals and neighbour biomass, shown for a) neighbour biomass versus natural log-transformed target biomass at week 65; b) neighbour biomass at week zero versus RGR of target over interval weeks zero to ten; c) neighbour biomass at week 15 versus RGR of target over interval weeks 15-25; and d) neighbour biomass at week 35 versus RGR of target over interval weeks 35-45. Open circles indicate native neighbours, closed circles alien neighbours. Only significant regressions are shown (dashed lines: for native neighbours only; solid lines: for alien neighbours only), with F and R² values indicated; significance levels: * P < 0.05, *** P < 0.001.
### 6.3.3 Effects of competition density treatments on growth of target individuals

#### 6.3.3.1 Effects of density at harvest

For *R. sapida*, treatment had a highly significant effect on target biomass ($F_{6,59} = 7.81, P < 0.001$). Post-hoc comparisons, however, showed that control target plants were only significantly larger than plants in the treatment with eight alien neighbours (Figure 6.6a). Plants in the treatment with eight alien neighbours were also significantly smaller than all the other treatments. For *R. sapida*, both biostatus and density of neighbours were significant factors affecting target biomass, but not their interaction (Table 6.3). Target plants with native neighbours had significantly larger biomass than plants with alien neighbours (Table 6.3). For density, post-hoc tests showed that target plants in treatments with eight neighbours were smaller than with one or four neighbours (both $P < 0.001$).

For *L. bullata*, treatment was also overall extremely significant ($F_{6,59} = 4.52, P < 0.001$) with control plants having significantly larger biomass than plants in the treatment with eight alien neighbours (Figure 6.6b). Other significant differences included target plants with eight alien neighbours having significantly lower biomass than with one native or one alien neighbour and target plants with eight native neighbours having lower biomass than with one native neighbour.

Looking at the effects of biostatus and density of neighbours, only density had a significant effect on target biomass (Table 6.3). Post-hoc tests showed that plants in treatments with eight neighbours ($P < 0.001$) and four neighbours ($P = 0.041$) had significantly lower biomass than with one neighbour, and treatments with eight neighbours had lower biomass than with four neighbours ($P = 0.048$).

#### Table 6.3

<table>
<thead>
<tr>
<th>Effect</th>
<th>DF</th>
<th>Den. DF</th>
<th>Biomass</th>
<th>Leaf area</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>R. sapida</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biostatus</td>
<td>1</td>
<td>50</td>
<td>8.87 **</td>
<td>0.75</td>
</tr>
<tr>
<td>Density</td>
<td>2</td>
<td>50</td>
<td>12.8 ***</td>
<td>9.12 ***</td>
</tr>
<tr>
<td>Biostatus*density</td>
<td>2</td>
<td>50</td>
<td>1.49</td>
<td>0.46</td>
</tr>
<tr>
<td><strong>L. bullata</strong></td>
<td></td>
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</tr>
<tr>
<td>Biostatus</td>
<td>1</td>
<td>50</td>
<td>2.55</td>
<td>2.65</td>
</tr>
<tr>
<td>Density</td>
<td>2</td>
<td>50</td>
<td>12.2 ***</td>
<td>12.8 ***</td>
</tr>
<tr>
<td>Biostatus*density</td>
<td>2</td>
<td>50</td>
<td>0.08</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Significance levels: ** $P < 0.01$, *** $P < 0.001$. 

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For leaf area, treatment was also a significant factor ($F_{6,59} = 3.74, P = 0.003$) affecting *R. sapida* target plants. Post-hoc tests showed that leaf area of plants with eight alien neighbours was significantly smaller than the control, four native or four alien neighbour treatments (Figure 6.6c). Considering effects of biostatus and density of neighbours on leaf area of *R. sapida*, only density had a significant effect (Table 6.3). *Rhopalostylis sapida* target plants with four neighbours had a significantly larger leaf area than plants with one neighbour ($P = 0.044$) and also compared to plants with eight neighbours ($P < 0.001$).

For *L. bullata*, treatment also had a significant effect on leaf area of target plants ($F_{6,59} = 4.64, P < 0.001$). Target plants with eight alien neighbours had a significantly smaller leaf area than target plants in the control, with one native or one alien neighbour (Figure 6.6d). Plants with eight native neighbours also had a significantly smaller leaf area than plants with one native neighbour. Density overall had a significant effect on leaf area of *L. bullata* (Table 6.3), with plants with eight neighbours...
having a significantly smaller leaf area than both plants with one neighbour \((P < 0.001)\) or four neighbours \((P = 0.020)\).

### 6.3.3.2 Effects of density over time

Treatment \((F_{6,59} = 6.84, P < 0.001)\), weeks \((F_{13,819} = 1152, P < 0.001)\) and their interaction \((F_{78,819} = 3.76, P < 0.001)\) had significant effects on diameter over time for *R. sapida* (Figure 6.7a). These were due to the plants with eight alien neighbours having a significantly smaller diameter compared to some or all of the other treatments from week 30 onwards (Figure 6.7a). For the models with biostatus, density and weeks, all fixed effects were significant, as were most interactions including the three-way interaction (Table 6.4). Post-hoc tests showed the same significant differences between treatments as shown in Figure 6.7a.

Over time, treatment \((F_{6,68} = 3.78, P = 0.003)\), weeks \((F_{13,819} = 226, P < 0.001)\) and their interaction \((F_{78,818} = 2.99, P < 0.001)\) all had significant effects on number of branches of *L. bullata* (Figure 6.7b). Post-hoc tests showed that significant differences among treatments were only found from week 55 onwards. At first target plants with eight alien neighbours were significantly smaller than the control, one native or one alien treatment. Later, the treatments with eight native or four alien neighbours were also significantly smaller than some other treatments (Figure 6.7b). While density and weeks were significant factors affecting number of branches over time, so was their interaction (Table 6.4). Within the same week, from week 35 onwards plants with eight neighbours had less branches than plants with one neighbour (week 35: \(P = 0.049\); week 40: \(P = 0.035\); week 45: \(P = 0.010\); week 50: \(P = 0.032\); weeks 55-65: \(P < 0.001\)).

### Table 6.4: Linear mixed models for natural log-transformed diameter of *R. sapida* and generalised linear mixed model with a Poisson distribution and log-link for number of branches of *L. bullata* (excluding controls). Numerator (DF) and denominator degrees of freedom (Den. DF) and F values are indicated.

<table>
<thead>
<tr>
<th>Effect</th>
<th><em>R. sapida</em></th>
<th><em>L. bullata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>Den. DF</td>
</tr>
<tr>
<td>Biostatus</td>
<td>1</td>
<td>50</td>
</tr>
<tr>
<td>Density</td>
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<td>50</td>
</tr>
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<td>50</td>
</tr>
<tr>
<td>Biostatus*weeks</td>
<td>13</td>
<td>702</td>
</tr>
<tr>
<td>Density*weeks</td>
<td>26</td>
<td>702</td>
</tr>
<tr>
<td>Biostatus<em>density</em>weeks</td>
<td>26</td>
<td>702</td>
</tr>
</tbody>
</table>

Significance levels: * \(P < 0.05\), ** \(P < 0.01\), *** \(P < 0.001\).
Figure 6.7: Back-transformed means ± 95% confidence intervals of a) diameter of *R. sapida*, and b) number of branches of *L. bullata* target individuals over time across the seven different treatments. Green open circles indicate native neighbours, blue closed circles alien neighbours and grey circles no neighbours. Dash-dot lines are for one neighbour, dashed lines for four neighbours, and solid lines for eight or no neighbours. Differing letters indicate what significant differences between treatments were found (*P* < 0.05): for diameter the treatment with eight alien neighbours was smaller than some other treatments from week 30 onwards (a: < control; b: < control, 1 native; c: < control, 1 native, 4 native; d: < control, 1 native, 4 native, 4 alien; and e: < all other treatments). For the number of branches some differences among treatments were found from week 55 onwards (a: 8 alien < control, 1 native, 1 alien; b: 8 native < control; c: 8 native < control, 1 native, 1 alien; d: 4 alien < control).

6.3.4 Comparison of growth rates of neighbour species

In testing for differences in RGR of neighbour individuals across species and densities, both species (*F*₄,1₃₁ = 65.9, *P* < 0.001) and density (*F*₂,₁₃₁ = 6.43, *P* = 0.002) had significant effects, but there was no significant interaction (*F*₈,₁₃₁ = 1.51, *P* = 0.160). Post-hoc tests showed several significant differences among species, with *L. bullata* showing the highest RGR (Figure 6.8a). Relative growth rates with
eight neighbours were smaller than with one neighbour ($P = 0.002$). For final biomass, again both species ($F_{4,131} = 101, P < 0.001$) and density ($F_{2,131} = 7.07, P = 0.001$) had significant effects, but not their interaction ($F_{8,131} = 1.91, P = 0.063$). *Scheflera actinophylla* had a larger final biomass than all other species, and several other pairwise comparisons also showed significant differences (Figure 6.8b). Biomass with eight neighbours was lower than with one neighbour ($P < 0.001$). For SLA, species had significant effects ($F_{4,131} = 44.7, P < 0.001$), but density was only marginally significant ($F_{2,131} = 2.97; P = 0.055$) and their interaction not significant ($F_{8,131} = 1.20, P = 0.304$). Post-hoc tests showed several significant differences among species, with *P. guajava* having the largest SLA (Figure 6.8c).

![Figure 6.8: Boxplots of neighbours a) RGR, b) final biomass, and c) SLA for the different species shown for pots with one, four and eight neighbours (*S. digitata* not shown due to high mortality). Differing letters indicate significant differences between species ($P < 0.05$).]
6.4 Discussion

6.4.1 Effects of high neighbour biomass or density on growth of target individuals

My results showed that density-dependent competition affected the target species under the given conditions of this experiment. The first hypothesis, stating that higher densities or biomass of neighbours will decrease target performance, is therefore supported. Reductions in performance were recorded for growth and also mortalities of both *L. bullata* and *S. digitata* appeared to be greater in higher density treatments.

For *R. sapida*, increasing neighbour biomass had a negative effect on final biomass of the target. Target RGR at different time intervals indicated that this effect only became apparent after 35 weeks of growth (only weak effect, but stronger at harvest). Similarly results for the effects of density showed that having eight neighbours (i.e. density of 286 plants/m$^2$) resulted in a significantly smaller biomass of target individuals compared to one neighbour (64 plants/m$^2$) or four neighbours (159 plants/m$^2$). However, target individuals grown in intermediate densities (four neighbours) were either not affected by competition (biomass) or even positively affected (leaf area). These results highlight the need to investigate competition at several densities, as plant density can alter the balance between competition and facilitation (Callaway & Walker 1997). Overall for this species, competition is relevant but it takes some time to take effect and occurs under high densities only.

For *L. bullata*, significant effects of neighbour biomass on target RGR suggested that competition was most influential at the early stages of the experiment. Conversely, negative effects of increased neighbour density were found for number of branches from week 35 onwards with reduced growth of target individuals in the high density (eight neighbours) treatments. At harvest, negative effects of competition were not only found for eight neighbours but also for four neighbours, showing that intermediate neighbour densities already affected growth of target plants. Overall for *L. bullata*, I found at least some negative effects of competition on target plant growth throughout the duration of the experiment. These results are not surprising, as competition frequently occurs among plants. A review of field studies showed that high neighbour abundance compared to low neighbour abundance resulted in at least some negative effects on individuals in 83% of the studies, while 10% found positive effects (Goldberg & Barton 1992).

6.4.2 Competitive effects of alien compared to native neighbours

The results largely supported my second hypothesis, stating that effects of competition from alien neighbours (interspecific competition) are stronger than effects from native neighbours.
(intraspecific competition). This was evident at least under high density; although results for *R. sapida* were more conclusive than for *L. bullata*. Effects of neighbour density showed smaller biomass, leaf area and diameter of *R. sapida* target plants grown with eight alien neighbours. High density competition is likely to be relevant in the field, where even higher densities of palm seedlings than used in this experiment have been found in the forest understory: e.g. 1069 *A. cunninghamiana* seedlings counted in one square metre in an Auckland forest (J. Sullivan, unpublished data), and comparable densities to this of *R. sapida* in the forest site where these seedlings were sourced (personal observation). Moreover, overall tests of neighbour biostatus were also significant as target individuals with native neighbours had higher biomass compared to alien neighbours. These results show that *A. cunninghamiana* had stronger competitive effects than *R. sapida*. However, as effects of neighbour identity were not significant when considering neighbour biomass, these results could be due to the alien neighbours’ larger growth rates rather than inherently stronger competitive effects. Indeed, a review of field studies of competition showed that per-individual competitive effects of different neighbours were mostly significant, whereas per-gram effects of different neighbours were not (Goldberg & Barton 1992). This would be expected if competition for light and nutrients is more dependent on plant size than on species identity (Bengtsson et al. 1994). Development of size hierarchies and eventual competitive displacement at high densities is usually caused by unequal light interception of large versus small plants (Schwinning & Weiner 1998). At a later stage in my experiment, when plant individuals were large enough to shade neighbouring plants, competition between *R. sapida* and *A. cunninghamiana* for light may have become more size-asymmetric (Schwinning & Weiner 1998; Weiner 1990). However, it is also possible that significant differences of effects of biomass between the two species were not detected simply due to a lack of statistical power in the biomass regressions.

In the early stages of the experiment with *L. bullata*, significant differences between the effects of neighbour biomass of alien versus native neighbours were found. This is unlikely to have been due to competition for light, as plants were small to begin with. Initially results suggested that neighbour biomass had a significant negative effect on RGR of target individuals, but RGR was on average reduced more by alien compared to native neighbours. While the competitive effect of alien neighbours remained similar for target RGR over weeks 15-25, for native neighbours this pattern reversed as native neighbour biomass at week 15 subsequently had a positive effect on growth of target plants over a ten week interval. Mangla et al. (2011) also showed changing competition patterns over time, with intraspecific competition dominant initially for native grasses, and interspecific competition from invasive grasses dominant at later stages. Principally it is possible that complex combinations of facilitation and competition, which can occur simultaneously within the
same plant community or even among the same individuals (Callaway & Walker 1997), could explain the variable and even contradictory effects of competition found for *L. bullata*. However, as statistically significant relationships between neighbour biomass and target RGR were rather weak, the observed facilitative effect of intraspecific competition could also have been a statistical artefact, particularly since such a positive relationship was not found in the density analyses (see Figure 6.6). Moreover, removing the data point with the highest leverage in the analysis further reduced the significance of the relationship, resulting in an only marginally significant positive effect of neighbour biomass. Competitive effects of alien neighbours were also found for density: target plants with eight alien neighbours had the lowest biomass, leaf area and smallest number of branches. However, differences compared to eight native neighbours were not significant.

For *S. digitata*, although I am unable to determine for a particular individual whether its death was caused by the spider mite infestation or by competition from neighbours, a trend towards higher mortality in four or eight alien neighbour treatments was detected at weeks five and ten (see Figure 6.3). If herbivores selectively feed on inferior competitors, this worsens negative effects of competition and thus accelerates competitive exclusion (Kim *et al.* 2013).

Many studies have shown superior competitive ability of an invasive over a native plant species (Kolb & Alpert 2003; Garcia-Serrano *et al.* 2007; Kawaletz *et al.* 2013; Gruntman *et al.* in press). However, a review of 16 studies assessing relative competitive performance of native versus invasive species showed that competitive performance often depended on environmental conditions; under high nutrient conditions native species never had an advantage (Daehler 2003). Although I did not compare plant growth in several environments, there was some variability in nutrient resource availability over the duration of my experiment. The species in this study were grown in potting mix with slow-release fertiliser (stated to last up to six months i.e. 26 weeks), but because for 50 weeks no additional fertiliser was added, the amount of resources available would have gradually decreased to low levels. The increased growth observed from week 50 to harvest (see Figure 6.7) when regular fertiliser additions were applied, can be explained by the higher availability of nutrients as well as the higher temperatures during that time (October-January). For competitive ability of *A. cunninghamiana* there was no evidence that competitive effect changed with resource availability, as measurements for diameter over time showed consistently smaller diameter in target plants with eight alien neighbours from week 30 onwards. However, for *P. guajava*, competitive ability may depend on resource availability: alien neighbour biomass had a significant effect on target RGR at week zero and 15, but not at week 35, which was a resource-poor period. Additionally,
the negative effect of eight alien neighbours on number of branches of target individuals only became significant at week 55 after fertilisation occurred.

6.4.3 Comparisons of RGR, biomass production and SLA between alien and native neighbours

My third hypothesis, suggesting that certain plant traits such as higher RGR, biomass production and larger SLA, are associated with alien species, was only partially confirmed by the results. As predicted, *A. cunninghamiana* had higher RGR, larger final biomass and higher SLA compared to *R. sapida*. However, *L. bullata* showed higher RGR measured over 65 weeks compared to *P. guajava* as well as all other species, although final biomass did not differ significantly between *L. bullata* and *P. guajava*. Specific leaf area of *P. guajava* was, however, larger than *L. bullata* and all other species. *Schefflera actinophylla* reached larger final biomass than all other species, but comparisons with *S. digitata* are missing due to high mortality of the latter species. For the three investigated traits, there was no significant interaction of species and density treatments; that is, the five species responded similarly in RGR, biomass and SLA to three different levels of density. For the three investigated traits, there was no significant interaction of species and density treatments; that is, the five species responded similarly in RGR, biomass and SLA to three different levels of density.

There have been conflicting results about which plant traits are associated with high competitive ability and with invasiveness. High biomass production in invasive compared to native species has been shown to result in higher competitive ability (Kawaletz et al. 2013). High RGR has frequently been associated with invasive woody plant success (Grotkopp & Rejmánek 2007; van Kleunen et al. 2010; Lamarque et al. 2011). Conversely, a study of 33 species in New Zealand did not find a positive relationship between seedling RGR and invasiveness in naturalised woody plants, that is, RGR did not predict the rate of spread following naturalisation (Bellingham et al. 2004). Greater SLA in invasive compared to non-invasive species has also been found in other studies (Burns & Winn 2006; Grotkopp & Rejmánek 2007; Ordóñez et al. 2010; but see Domènech & Vilà 2008). High SLA, that is, thinner leaves, allow a plant to intercept more light, resulting in faster growth especially in shaded conditions (Domènech & Vilà 2008). Conversely, New Zealand woody species tend to be adapted to low soil fertility, and thus invest more in leaf structure, resulting in lower SLA (Craine et al. 2006). Having higher RGR, biomass production and SLA compared to the native resident species is therefore likely to assist *A. cunninghamiana* in being a successful competitor and becoming invasive, although such plant traits are not a universal explanation of competitive ability and invasion success. However, because niche differences between *A. cunninghamiana* and *R. sapida* are small, the alien species is likely to have a large impact on the native species as it has higher fitness (MacDougall et al. 2009). For *P. guajava*, the comparatively low RGR and biomass observed in my experiment may be due to the infestation of this species by spider mites, which is likely to have reduced its performance. The species’ high SLA could have been a disadvantage in these conditions, as high SLA tends to make
leaves highly susceptible to herbivory (Ordonez et al. 2010). *Psidium guajava* individuals widely differed in their trait values. Such plasticity in performance could result in high competitive ability under a resource-rich environment, facilitating invasion in such environments, but result in equal or lower performance in resource-poor environments (Burns & Winn 2006). Indeed, although mean biomass did not differ between *P. guajava* and *L. bullata*, maximum biomass reached by a *P. guajava* individual was far higher than for *L. bullata*. Considering the traits of *S. actinophylla*, the high RGR and biomass together with the 100% survival are likely to result in high competitive ability of this species, but this will have to be further compared to native species in another study.

### 6.4.4 Conclusions

Competitive ability of these newly naturalised species will influence their establishment success and subsequent invasion potential. The native target species were shown to be affected by density-dependent competition. Moreover, this study suggests that *A. cunninghamiana* may outcompete *R. sapida* when they co-occur particularly at high densities; while *P. guajava* may have the potential to outcompete *L. bullata* under nutrient-rich conditions with low herbivore pressure. The three alien species also share some traits associated with competitive ability and invasiveness. Other factors such as life stage, abiotic conditions and indirect interactions will affect the roles of competition and facilitation in a plant community (Callaway & Walker 1997). Having demonstrated that competition is likely to be an important process affecting interactions between the studied alien-native species pairs, competition should now be further tested in the field where many other factors can influence competitive outcomes.
6.5 References


Chapter 6: Effects of interspecific alien vs intraspecific native competition on growth of native woody plants


CHAPTER 7

Performance of alien plants and their native relatives in sites of differing climates: a field validation of species distribution models

Abstract

Climate change may facilitate alien species invasion in new areas, particularly for alien species from warmer native ranges introduced to colder areas. Species distribution models are a useful tool to provide a first insight into the potential spread of invasive species, dependent on their climatic requirements, but they do not account for other factors potentially important for invasion success. Although conclusions from modelling approaches and experimental studies are generally similar, combining the two approaches has rarely been done. The aim of this study was to validate species distribution models by conducting field trials in sites of differing suitability. Three recently naturalised alien plants in New Zealand were used as study species (Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla): they originate from warmer native ranges, are woody bird-dispersed species and of concern as potential weeds. Seedlings of these three species were grown and seeds were sown in six sites across the country, differing both in climate and suitability (as predicted by the species distribution models). Seedling growth and survival were recorded over two summer and one winter seasons, and climate variables (temperature, precipitation, wind) were monitored hourly at each site. Additionally, alien seedling performance was compared to those of closely related native species (Rhopalostylis sapida, Lophomyrtus bullata and Schefflera digitata). Furthermore, half of the seedlings were sprayed with pesticide, to investigate whether enemy release may be an important factor influencing performance of these species. The results showed large differences in growth and survival of the alien species among the six sites. In the more suitable sites, performance was frequently higher compared to the native species. Minimum and maximum temperatures and precipitation influenced relative growth rates and survival. Leaf damage from invertebrate herbivory was low for both alien

8 The contents of this Chapter have been revised and are published as: Sheppard CS, Burns BR & Stanley MC (in press). Predicting plant invasions under climate change: are species distribution models validated by field trials? Global Change Biology. DOI: 10.1111/gcb.12531
and native seedlings. There were few significant effects of the pesticide treatment, suggesting that the alien species did not have an advantage over the native species because of release from natural enemies. For *P. guajava* and *S. actinophylla*, performance in the field and predicted suitability of species distribution models were highly correlated, but correlations were lower for *A. cunninghamiana*. The projected increase in minimum temperature and reduced frosts with climate change may provide more suitable habitats and thus may enable the spread of these species. Combining models and experimental approaches greatly improves confidence in assessing invasion risk. More robust predictions of potential spread of alien species under current and future climate will result in great benefits for invasive species management, particularly for early control of potential weeds.
Chapter 7: Performance of alien plants and their native relatives in differing climates: a field validation of SDMs

7.1 Introduction

Invasive species are one of the most serious threats to biodiversity (Lambertini et al. 2011). Invasive plants in particular have been shown to severely affect plant communities. A recent meta-analysis estimated that invasive plants reduced fitness of native plant communities on average by 41.7%; growth by 22.1%; species abundance by 43.5%; and diversity by 50.7% (Vilà et al. 2011).

Climate change may facilitate the invasion of alien species in new areas (Thuiller et al. 2007). Although climate change will affect species, communities and ecosystems in many ways, not all species will be affected to the same extent, favouring those species that better tolerate altered conditions such as warmer, drier environments (Thuiller et al. 2007). Moreover, climate change may indirectly affect species by altering competitive interactions (Walther 2004), which could change competitive outcomes to favour the colonising species over resident species. In particular however, climate change will affect the geographic ranges of species (Thuiller et al. 2007). At a large spatial scale, climate is the dominant factor influencing species distributions (Woodward 1987). Species distribution models (SDMs) are an important tool used to make predictions of a species’ potential distribution by relating occurrence data to environmental conditions (Elith & Leathwick 2009).

Additionally, predicting the potential range of an invasive species under climate change is useful as it helps to understand how the threat posed by an invasive species might change (Jeschke & Strayer 2008). Such models have frequently predicted range expansions for invasive plants (Kriticos et al. 2003; Bradley et al. 2010a; Kleinbauer et al. 2010; Sheppard 2013). Conversely, other studies have also shown range shifts or even contractions in suitable ranges (Peterson et al. 2008; Bradley et al. 2009; Bourdôt et al. 2012; Gallagher et al. 2013).

Although SDMs provide a useful first insight into the potential spread of invasive species, they do not account for other factors important in determining invasion success. Generally, three main factors may influence survival and growth of an invasive species in a particular site: availability of resources, natural enemies and the physical environment (abiotic factors, including climate as a major component) (Shea & Chesson 2002) with only the latter used in SDMs. For natural enemies as a factor, the enemy release hypothesis predicts that the success of invasive plants is due to decreased pressure from natural enemies in their introduced range (Keane & Crawley 2002). If natural enemies are an important factor influencing population growth, and they have a greater impact on native than alien species, then alien species should be able to benefit by increasing their population growth. Contrary to the enemy release hypothesis, several recent studies have found that invasive plants are impacted by herbivory to a similar or even greater extent than native plants (Chun et al. 2010; Carrillo-Gavilán et al. 2012; Dostál et al. 2013; Heard & Sax 2013). With regard to
resources, high resource availability may facilitate invasion (Davis et al. 2000). For example, a review by Daehler (2003) showed that although alien species generally did not have universally higher performance, they usually performed better under increased resource availability.

Conclusions on the impacts of climate change on plant invasions derived from modelling and experimental approaches are generally similar (Bradley et al. 2010b). However, I am aware of only two studies that have combined the two approaches (Ebeling et al. 2008; Pattison & Mack 2008). Ebeling et al. (2008) tested local adaptation to frost in a common garden experiment and used this data to evaluate potential Buddleja davidii distributions together with results from a SDM. Pattison & Mack (2008) however actually evaluated their predictions from a CLIMEX model with field trials, testing seed germination and plant growth rates within and beyond the current range of Triadica sebifera. Combining modelling and experimental approaches in such a way could greatly improve confidence in assessing invasion risk under climate change and provide more robust predictions for management (Bradley et al. 2010b).

In New Zealand, invasive plants are of particular concern, as 53% (2146 species) of the total vascular flora is represented by naturalised species (Diez et al. 2009). Lag phases of several decades are common for plant invasions in New Zealand, averaging 20-30 years from first naturalisation to spread (Aikio et al. 2010). With a pool of about 25,049 alien plant species growing in New Zealand gardens (Diez et al. 2009), it is of utmost importance to prevent those with known or suspected negative impacts on native flora and fauna from invading into the natural environment (Sullivan et al. 2005). Three recently naturalised species with currently limited spread were thus the focus of this study: Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla. These are subtropical or tropical species, and it is expected that species such as these that originate from warmer native ranges will be able to increase their populations and expand their distributions under climate change (Walther et al. 2009). The study focused on woody plant species because they are rapidly increasing in importance as invasive plants globally (Richardson & Rejmánek 2011). In New Zealand, half of all environmental weeds are trees and shrubs (Howell 2008). The selected species are widely sold in nurseries and are bird-dispersed, thus they are not likely to be dispersal-limited (Williams 2006; Jordaan et al. 2011). Bird-dispersed woody invasive plants should always be regarded as a great concern (Richardson & Rejmánek 2011).

New Zealand also provides a good study system because the country spans across a wide range of climatic conditions (34-47° latitude): from a warm subtropical climate in the far north (with a current annual mean temperature of 16°C) down to a cool temperate climate in the far south (with an annual mean temperature of 10°C) and severe alpine conditions in the inland mountains.
(National Institute of Water and Atmospheric Research 2013). Most areas of New Zealand experience annual precipitation between 600 and 1600 mm, spread throughout the year with a dry period during the summer (National Institute of Water and Atmospheric Research 2013). By the end of the century, a temperature increase of 0.7-5.1°C is predicted across a range of scenarios, with a best estimate of 2°C (Ministry for the Environment 2008), somewhat lower than the global estimates of 1.1-6.4°C (IPCC 2007).

In this study, I carried out field trials, based on the results of previously compiled species distribution models (Sheppard 2013; Chapter 3), to test the performance of the three alien species in sites predicted by the SDMs to be suitable, potentially suitable (under climate change conditions only) and unsuitable. Furthermore, performance of each of the alien species at these sites was compared to a closely related native species: Rhopalostylis sapida, Lophomyrtus bullata and Schefflera digitata. Seedlings were grown in six sites across the country for two summer and one winter seasons (18 months overall). Seedling establishment is a critical life stage for the success of an invasion (Gurevitch et al. 2008). To account for two other main factors determining invasion success, I tried insofar as was possible, to choose sites of similar soil nutrient conditions. To investigate if natural enemies may play a role, pesticide was applied to half the seedlings at each site in order to exclude herbivores.

I addressed the following questions in this study: i) How does survival and growth of the three alien species compare to native relatives? ii) How does climate influence survival and growth? iii) Is there any evidence for the enemy release hypothesis? iv) Does survival and growth at the six sites correspond with predictions from species distribution models?

### 7.2 Methods

#### 7.2.1 Study species

##### 7.2.1.1 Alien species

The three chosen alien species are recently naturalised woody plants in New Zealand from warmer native ranges. Although they currently have limited spread in the northern most part of the country (Auckland, Northland), they are predicted to increase their range substantially under climate change (Sheppard 2013; Chapter 3).

Archontophoenix cunninghamiana (H. Wendl.) H. Wendl. et Drude (bangalow palm) is a native of Eastern Australia in the family Arecaceae. It is a popular garden plant in New Zealand and
naturalised in 1992 (Cameron 2000). In Brazil, *A. cunninghamiana* has become invasive (Christianini 2006). *Psidium guajava* L. (common guava) of the family Myrtaceae is a native of Central America, which first naturalised in New Zealand in the Kermadec Islands in 1965 (Sykes 1982). Because of its edible fruit, it has been introduced to many tropical and subtropical regions of the world, where it often has become invasive (Randall 2007). *Schefflera actinophylla* (Endl.) Harms (Queensland umbrella tree) in the family Araliaceae is a native species of Australia and New Guinea. In New Zealand it naturalised recently, in 2005 (Wilcox 2005). It is a shade tolerant species that can also grow as an epiphyte, and this species is invasive in the Pacific Islands (Randall 2007).

### 7.2.1.2 Native species

To pair with each of the alien species, a closely related native species in the same family was chosen. The native species are endemic to New Zealand and are not weeds themselves in other countries, as confirmed by their absence from the Global Invasive Species database (Invasive Species Specialist Group 2013), the Pacific Island Ecosystems at Risk database (US Forest Service 2013) and the Global Compendium of Weeds (Randall 2007).

*Rhopalostylis sapida* H. Wendl. et Drude (nikau palm) is an endemic palm that occurs in coastal and lowland forests throughout the North Island and in the South Island as far south as Greymouth on the west coast and the Banks Peninsula on the east (Moore & Edgar 1970). *Rhopalostylis sapida* was chosen to pair with *A. cunninghamiana* as it is the only native palm species. Moreover, it belongs to the same subtribe (Archontophoenicinae) and lives in similar habitats as *A. cunninghamiana* (Cameron 2000). *Lophomyrtus bullata* Burret (ramarama) is a species of a genus endemic to New Zealand. Its habitat is coastal and lowland forest and shrubland, across the North Island and it is also scarcely distributed in the South Island down to 42° latitude (Allan 1961). *Lophomyrtus bullata* was chosen as a native congener to *P. guajava* because it is the species within the Myrtaceae that is most similar to *Psidium* in terms of ecology and morphology. *Schefflera digitata* J.R. Forst. et G. Forst. (pate) is widespread throughout the North, South and Stewart Islands, occurring in lowland to lower montane forests (Allan 1961). *Schefflera digitata* is used as a native congener to *S. actinophylla* because it belongs to the same genus and has very similar morphology.

### 7.2.2 Field sites

Six sites across New Zealand (Figure 7.1; Table 7.1) with differing climate (Table 7.2) were chosen as field sites for this study. The sites differed in their predicted habitat suitability for the alien species according to species distribution models (Table 7.3) (see Sheppard 2013; Chapter 3). Actual records of establishment, however, exist only from the Whangarei and Auckland regions. The native species’
distributions encompass all six sites, except the range of *L. bullata* may not extend as far south as Lincoln and Greymouth on the South Island. The site at Auckland had originally been set up at the Auckland University Tāmaki Campus, however, due to destruction of the entire site because of construction of a new building, a new field site had to be established at Unitec Institute of Technology (set up two months later than the other five sites).

**Figure 7.1:** Field sites (green triangles), located between 35-44° latitude, shown on a map of annual mean temperature (data from NIWA climate layers used in Chapters 2-3).
Table 7.1: Geographic location and predicted suitability of field sites according to SDMs (at selected threshold, see Chapter 3) for *A. cunninghamiana* (AC), *P. guajava* (PG) and *S. actinophylla* (SA) with ✓ indicating sites predicted suitable under current climate and climate change; (✓) predicted suitable under climate change conditions only (at least under some scenarios); and X predicted unsuitable under current climate and climate change (exact suitability values are given in Table 7.3).

<table>
<thead>
<tr>
<th>Field site</th>
<th>Coordinates</th>
<th>Altitude (m a.s.l.)</th>
<th>Location</th>
<th>AC</th>
<th>PG</th>
<th>SA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>North Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whangarei</td>
<td>174.465122 E, 35.654786 S</td>
<td>58</td>
<td>Private land, Kiripaka</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Auckland</td>
<td>174.705917 E, 36.876444 S</td>
<td>16</td>
<td>Unitec Institute of Technology, Auckland</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>Hastings</td>
<td>176.880226 E, 39.659496 S</td>
<td>32</td>
<td>Plant and Food Research, Havelock North</td>
<td>✓</td>
<td>✓</td>
<td>X</td>
</tr>
<tr>
<td><strong>South Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greymouth</td>
<td>171.183300 E, 42.499061 S</td>
<td>72</td>
<td>Private land, Greymouth</td>
<td>(✓)</td>
<td>✓</td>
<td>X</td>
</tr>
<tr>
<td>Nelson</td>
<td>173.103641 E, 41.337259 S</td>
<td>26</td>
<td>Private land, Brightwater</td>
<td>X</td>
<td>(✓)</td>
<td>X</td>
</tr>
<tr>
<td>Lincoln</td>
<td>172.476554 E, 43.640548 S</td>
<td>10</td>
<td>Landcare Research, Lincoln</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

Table 7.2: Climate at the field sites summarised by annual mean temperature [°C] and annual precipitation [mm]. Values of the six temperature (T) and precipitation variables (bioclimatic variables) included in the SDMs (see Chapter 3) being tested in the field trials are shown. Data extracted from the National Institute of Water and Atmospheric Research (NIWA) climate layers in 0.05° resolution (ca. 5 x 5 km), averaged over period 1980-1999 (‘current’ climate).

<table>
<thead>
<tr>
<th>Climate variable</th>
<th>Whangarei</th>
<th>Auckland</th>
<th>Hastings</th>
<th>Greymouth</th>
<th>Nelson</th>
<th>Lincoln</th>
</tr>
</thead>
<tbody>
<tr>
<td>BIO1 Annual mean temperature</td>
<td>15.3</td>
<td>15.0</td>
<td>12.0</td>
<td>12.0</td>
<td>12.7</td>
<td>11.7</td>
</tr>
<tr>
<td>BIO12 Annual precipitation</td>
<td>1549</td>
<td>1221</td>
<td>1465</td>
<td>2759</td>
<td>971</td>
<td>608</td>
</tr>
<tr>
<td>BIOS Max. T of warmest month</td>
<td>24</td>
<td>23</td>
<td>22</td>
<td>20</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>BIO6 Min. T of coldest month</td>
<td>7</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>BIO7 T annual range</td>
<td>17</td>
<td>16</td>
<td>20</td>
<td>17</td>
<td>20</td>
<td>21</td>
</tr>
<tr>
<td>BIO8 Mean T of wettest quarter</td>
<td>12</td>
<td>12</td>
<td>15</td>
<td>13</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>BIO15 Precipitation seasonality†</td>
<td>22</td>
<td>23</td>
<td>22</td>
<td>12</td>
<td>12</td>
<td>17</td>
</tr>
<tr>
<td>BIO18 Precipitation of warmest quarter</td>
<td>357</td>
<td>239</td>
<td>316</td>
<td>681</td>
<td>215</td>
<td>135</td>
</tr>
</tbody>
</table>

† Coefficient of variation = standard deviation / mean.
Table 7.3: Site suitability according to species distribution models. Suitability index ranging from 0 (completely unsuitable) to 1 (completely suitable), as indicated by the logistic output of Maxent models described in Sheppard (2013) and Chapter 3, for predictions under current climate and eight different climate change scenarios (see Chapter 3 for details of climate change scenarios). Suitable sites/scenarios highlighted in bold, with the following thresholds used to classify continuous suitability into binary predictions (suitable/unsuitable): 0.279 for *A. cunninghamiana*, 0.250 for *P. guajava* and 0.164 for *S. actinophylla* (see Chapters 2 and 3).

<table>
<thead>
<tr>
<th>Climate</th>
<th>Whangarei</th>
<th>Auckland</th>
<th>Hastings</th>
<th>Greymouth</th>
<th>Nelson</th>
<th>Lincoln</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. cunninghamiana</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Current climate</td>
<td>0.51</td>
<td>0.42</td>
<td>0.37</td>
<td>0.14</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>CCCMA-CGCM3 A2</td>
<td>0.39</td>
<td>0.37</td>
<td>0.60</td>
<td>0.48</td>
<td>0.12</td>
<td>0.16</td>
</tr>
<tr>
<td>CCCMA-CGCM3 B1</td>
<td>0.48</td>
<td>0.40</td>
<td>0.41</td>
<td>0.35</td>
<td>0.11</td>
<td>0.06</td>
</tr>
<tr>
<td>CSIRO-MK3.0 A2</td>
<td>0.42</td>
<td>0.35</td>
<td>0.49</td>
<td>0.22</td>
<td>0.04</td>
<td>0.13</td>
</tr>
<tr>
<td>CSIRO-MK3.0 B1</td>
<td>0.52</td>
<td>0.40</td>
<td>0.37</td>
<td>0.19</td>
<td>0.04</td>
<td>0.07</td>
</tr>
<tr>
<td>GFDL-CM2.0 A2</td>
<td>0.40</td>
<td>0.32</td>
<td>0.55</td>
<td>0.49</td>
<td>0.17</td>
<td>0.09</td>
</tr>
<tr>
<td>GFDL-CM2.0 B1</td>
<td>0.46</td>
<td>0.40</td>
<td>0.47</td>
<td>0.38</td>
<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td>UKMO-HADCM3 A2</td>
<td>0.43</td>
<td>0.41</td>
<td>0.33</td>
<td>0.33</td>
<td>0.18</td>
<td>0.12</td>
</tr>
<tr>
<td>UKMO-HADCM3 B1</td>
<td>0.50</td>
<td>0.47</td>
<td>0.27</td>
<td>0.32</td>
<td>0.20</td>
<td>0.11</td>
</tr>
<tr>
<td>Avg. climate change</td>
<td>0.45</td>
<td>0.39</td>
<td>0.44</td>
<td>0.35</td>
<td>0.12</td>
<td>0.10</td>
</tr>
</tbody>
</table>

| **P. guajava**               |           |          |          |           |        |         |
| Current climate              | 0.53      | 0.38     | 0.32     | 0.33      | 0.14   | 0.08    |
| CCCMA-CGCM3 A2               | 0.64      | 0.60     | 0.50     | 0.36      | 0.28   | 0.21    |
| CCCMA-CGCM3 B1               | 0.60      | 0.52     | 0.35     | 0.26      | 0.20   | 0.13    |
| CSIRO-MK3.0 A2               | 0.58      | 0.55     | 0.42     | 0.29      | 0.09   | 0.13    |
| CSIRO-MK3.0 B1               | 0.54      | 0.37     | 0.32     | 0.27      | 0.05   | 0.09    |
| GFDL-CM2.0 A2                | 0.59      | 0.54     | 0.51     | 0.37      | 0.30   | 0.20    |
| GFDL-CM2.0 B1                | 0.59      | 0.52     | 0.34     | 0.32      | 0.16   | 0.13    |
| UKMO-HADCM3 A2               | 0.58      | 0.60     | 0.33     | 0.34      | 0.30   | 0.25    |
| UKMO-HADCM3 B1               | 0.63      | 0.53     | 0.28     | 0.33      | 0.25   | 0.21    |
| Avg. climate change          | 0.59      | 0.53     | 0.38     | 0.32      | 0.20   | 0.17    |

| **S. actinophylla**          |           |          |          |           |        |         |
| Current climate              | 0.37      | 0.28     | 0.04     | 0.06      | 0.02   | 0.02    |
| CCCMA-CGCM3 A2               | 0.49      | 0.26     | 0.10     | 0.12      | 0.03   | 0.07    |
| CCCMA-CGCM3 B1               | 0.36      | 0.36     | 0.05     | 0.14      | 0.02   | 0.02    |
| CSIRO-MK3.0 A2               | 0.35      | 0.18     | 0.06     | 0.05      | 0.03   | 0.06    |
| CSIRO-MK3.0 B1               | 0.36      | 0.28     | 0.04     | 0.05      | 0.02   | 0.01    |
| GFDL-CM2.0 A2                | 0.27      | 0.26     | 0.06     | 0.13      | 0.03   | 0.03    |
| GFDL-CM2.0 B1                | 0.35      | 0.36     | 0.04     | 0.14      | 0.02   | 0.02    |
| UKMO-HADCM3 A2               | 0.34      | 0.29     | 0.06     | 0.06      | 0.03   | 0.02    |
| UKMO-HADCM3 B1               | 0.53      | 0.36     | 0.04     | 0.12      | 0.02   | 0.02    |
| Avg. climate change          | 0.38      | 0.29     | 0.06     | 0.10      | 0.03   | 0.03    |
As far as possible, sites with similar soil properties, surroundings and vegetation types were chosen: sites were located on open flat ground dominated by alien pasture grasses in peri-urban areas (except for Whangarei, which was in a rural area and on a slight slope). Soil samples were collected from each site and analysed at the Landcare Research Environmental Chemistry Laboratory in Palmerston North for moisture content, pH, mineral nitrogen, phosphorus, cation exchange capacity, exchangeable bases (calcium, magnesium, potassium, sodium) and base saturation.

### 7.2.3 Experimental design

A fully factorial experiment was set up including the factors: 1) site (six levels; sites described in Table 7.1); 2) pesticide application (yes/no); 3) species pair (three levels: *A. cunninghamiana* and *R. sapida*; *P. guajava* and *L. bullata*; *S. actinophylla* and *S. digitata*); and 4) species biostatus (native/alien); giving $6 \times 2 \times 3 \times 2 = 72$ treatment combinations with 12 replicates each. Thus, 144 seedlings were grown at each site (24 of each species), and 864 seedlings across all sites. At each site, seedlings were grown in a randomised block design. In two blocks seedlings were planted beneath 25-35% shadecloth (Cosio Industries Ltd, Auckland) set up 70 cm aboveground, with seedlings at least 0.5 m away from the block edge or neighbouring seedlings (Figures 7.2-7.3). The shadecloth was set up in order to construct similar light conditions across the six sites and to create more realistic forest understory conditions (where seedlings of these alien species might invade). Between the two blocks at each site a weather station was set up and seeds were sown in 20 x 20 cm (2 x 30 seeds for each species) squares of bare ground, which were marked but not confined (Figure 7.2). The weather stations used in the experiment were of the type iROX PRO-X2 (OS Technology AG/SA, Switzerland), recording climate variables hourly, with the temperature sensor set up 1.25 m aboveground (temperature accuracy ± 1°C), the rain gauge 0.7 m aboveground (rain accuracy ± 0.8 mm) and the anemometer 3 m aboveground (wind direction accuracy ± 11.25°).
Chapter 7: Performance of alien plants and their native relatives in differing climates: a field validation of SDMs

Figure 7.2: Set-up of the field sites, with X indicating individual seedlings (planted in a randomised block design), and S indicating seed plots (of 30 seeds each). Due to space restrictions, in Greymouth the two blocks were set up perpendicular to each other, while in Nelson the two blocks were set up lengthways.

Figure 7.3: Example of a field site (Whangarei).
The field sites were established between 13 October and 8 November 2011 (except for the new Auckland site, which was established 24 December 2011). The experiment took place over two growing seasons and one winter (18 months overall). To aid establishment and help acclimatise seedlings to UV (as seedlings had been grown indoors), 25 cm high green plastic sleeves were fitted around the seedlings for the first few months. All sleeves were removed in February 2012. At the time of planting, *A. cunninghamiana* and *R. sapida* seedlings had heights of 15-26 cm, *P. guajava* and *L. bullata* 4-23 cm, and *S. actinophylla* and *S. digitata* 1-11 cm.

At the time of establishment, the surrounding vegetation was already mown on most sites, however in Whangarei kikuyu grass (*Pennisetum clandestinum*) up to 1 m high was present, likely resulting in higher competition for the planted seedlings. However, when seedlings were planted, at all sites all other resident plants within 10 cm radius of each seedling were removed manually. During the experiment, resident plants inside the blocks were cut back regularly (every two to three months). At the end of the experiment (April 2013), a rough estimate of productivity and intensity of neighbouring competition for each site was assessed by harvesting, drying (for 72 hours at 70°C) and weighing six 20 x 20 cm samples of the aboveground biomass of this surrounding vegetation at each site (after ten weeks of growth since they had been cut back to soil level).

### 7.2.4 Seedling propagation and seed sourcing

Seedlings of the three alien species used in this experiment were propagated from seed sown in November/December 2010, seedlings thus being almost one year old at the start of the experiment. Seeds of the three alien species were imported from Australia: seeds of *A. cunninghamiana* were obtained from Seed Horticultural, Lower Dyraaba, New South Wales; seeds of *P. guajava* from Australian Seed, Shoalwater, Western Australia; and seeds of *S. actinophylla* from Harvest Seeds and Native Plants, Sydney, New South Wales. Germination success (in seed trays filled with Potpower™ potting mix [Debco, Melbourne, Australia] placed indoors, with limited light availability, but regularly watered) for 1001 seeds was 38% for *A. cunninghamiana* (first seeds germinated after 39 days; 75% of final germination after 65 days); 55% for *P. guajava* (first seeds after 27 days; 75% germinated after 175 days); and 64% for *S. actinophylla* (first seeds after 12 days; 75% after 35 days) (Figure 7.4). After germination, at least 500 seedlings of each species were replanted into 0.45 L plastic planting bags (PB ™) filled with Potpower™ potting mix. Seeds of the native species were obtained from North Island nurseries, however, germination of seeds of all three species failed completely. Therefore, seedlings of *S. digitata* and *L. bullata* were obtained from Oratia Native Plant Nursery, Auckland (seed collected January 2011). Seedlings of *R. sapida* were collected from a native forest site (Whitford, Auckland; collected March 2011). Before transplanting to the experimental sites,
seedling growth for all species was generally slow as they were kept indoors with limited light availability.

Figure 7.4: Seed germination (% seeds, n = 1001) of the three alien species over time.

Due to seasonal unavailability, it was difficult to obtain fresh seeds for the seed plots for most species and older seeds had to be used, which may have had reduced viability. For A. cunninghamiana, R. sapida and P. guajava, seeds were used that had been bought a year earlier for seedling propagation (details of source see above). Schefflera actinophylla seed was obtained from Ole Lantana’s Seed Store, Toowoomba East, Queensland, Australia, however the supplier was unsure about the collection date. Fresh seeds of L. bullata and S. digitata were obtained from New Zealand Tree Seeds, Rangiora. Seeds sown in the second growing season were sourced from Bay of Islands Subtropicals, Kerikeri (A. cunninghamiana); Australian Seed, Shoalwater, Western Australia, Australia (P. guajava); Royston Petri Seeds Pty Ltd, Mudgee, New South Wales, Australia (S. actinophylla); Egmont Seed Company Ltd, New Plymouth (R. sapida); and New Zealand Tree Seeds, Rangiora (S. digitata). For L. bullata, due to unavailability of fresh seed, seeds purchased a year earlier from New Zealand Tree Seeds were used.

7.2.5  Pesticide application

The seedlings receiving the pesticide treatment were sprayed immediately after establishment and subsequently approximately every two months using a combination of Kohinor 350 (active
ingredient 350 g/L imidacloprid in the form of an aqueous suspension concentrate), Agree WDG (a biological insecticide containing 25,000 ITU/mg *Bacillus thuringiensis* var. *azawai/kurtstaki* in the form of a water dispersable granule) and Yates Bravo Fungicide (active ingredient 500 g/L chlorothalonil in the form of a suspension concentrate). This mixture was applied in 2 L of water (containing 2 ml Kohinor 350, 2 g Agree WDG and 6 ml Yates Bravo Fungicide) at each field site, and from April 2012 onwards as plants grew larger in 3 L of water (containing 3 ml Kohinor 350, 3 g Agree WDG and 9 ml Yates Bravo Fungicide). The control seedlings were sprayed with water.

Prior to the experiment, I tested if the pesticide application had an effect on seedling growth in the absence of herbivores. Sixteen seedlings (not used in the main experiment) of each species were grown in environmental chambers in the absence of invertebrates. The environmental chambers were set at a day/night regime of 23.7/15.8°C for 16/8 hours (Auckland summer temperatures) and a light intensity of 120 µE/m²s (equals ca. 550 µmol/m²s). Half of the seedlings receiving the pesticide treatment were sprayed with the mixture described above once at the beginning of the experiment and again after seven weeks. The other half of the seedlings served as a control and these were sprayed with water. Height, number of leaves and number of leaflets (*A. cunninghamiana*, *R. sapida* and *Schefflera* species only) were measured at four points in time over 14 weeks. Data were analysed in SAS statistical software (SAS Institute Inc., Cary NC, USA, version 9.2 for Windows). For the response variable height a linear mixed model was fitted with pesticide treatment, species and weeks as fixed factors and plant ID as a random factor (to account for correlated measurements of the same plant over time), fitting initial size as a covariate. Number of leaves and leaflets were analysed with the same factors, but fitting a generalised linear model with a Poisson distribution and log-link. The results showed that for the three response variables the factors weeks, species and their interaction were always highly significant (P < 0.001). The factor pesticide treatment, however, was never significant (height: F$_{1,76} = 0.47$, P = 0.495; number of leaves: F$_{1,73} = 0.02$, P = 0.876; number of leaflets: F$_{1,48} = 0.61$, P = 0.438). The interaction of pesticide with weeks or species was also never significant. Given these results, it can be confidently assumed that the pesticide application did not affect growth rates of the seedlings in the main experiment.

7.2.6 Growth measurements

After establishment, plants were visited every two months during the growing season to record data (October, December, February, April) and to apply pesticide (see Figure 7.5 for examples of plant seedlings). During winter, sites were visited once in the middle of the winter (July; no pesticide applied). Surrounding herbaceous vegetation was cut down to soil level on each visit.
Heights of the seedlings were measured (for *A. cunninghamiana* and *R. sapida*, this was defined as the maximum distance from ground to tip of a leaf; for *P. guajava* and *L. bullata* the distance from ground to tip of the stem; and for *S. actinophylla* and *S. digitata* the distance from ground to apical bud), and the number of leaves (longer than 1 cm) counted. As *A. cunninghamiana*, *R. sapida*, *S. actinophylla* and *S. digitata* have compound leaves, the total numbers of leaflets were also recorded. For *A. cunninghamiana* and *R. sapida*, stem diameters were also measured, 1 cm above ground level (spot marked on stem). For *P. guajava* and *L. bullata*, the numbers of branches were also counted, including all branches exceeding 3 cm length. Leaf herbivory damage was calculated as the percentage of leaves that showed damage (number of leaves with damage/total number of leaves) and the estimated average percent damage on damaged leaves. Multiplying the two measurements gave the estimated proportions of invertebrate leaf damage per plant individual. The numbers of germinated seeds were also counted on each visit.

**Figure 7.5:** Examples of seedlings at the end of Summer 1 in Auckland: a) *A. cunninghamiana*; b) *P. guajava*; c) *S. actinophylla*; d) *R. sapida*; e) *L. bullata*; and f) *S. digitata*.  

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On each visit (except in winter, July 2012), dead individuals (arising from failed transplanting or unsuitable weather conditions) were replaced if necessary (but assigned a new plant ID). Replacement of dead *S. digitata* individuals was stopped at the end of the first growing season due to unavailability of seedlings. Following Winter 1, new plant seedlings were established as required at the start of the second growing season (29 September to 15 October 2012). In some sites this resulted in a mixture of plants established in the first and second growing seasons (this was noted as an additional factor to investigate in the data analysis). Final replacements of dead individuals were made in December 2012. New seeds were also sown in October, but this time only 2 x 25 for each species at each site.

During the course of the experiment, several unforeseen problems with vertebrate browsing occurred. Upon my visit to Hastings in February 2012, I found high mortality due to pukeko (purple swamphen, *Porphyrio porphyrio*) pulling out plants (42 dead individuals; with pukeko the clearly identifiable cause in most cases). In July 2012, escaped domestic cattle (*Bos taurus*) browsed on the plants in Whangarei, removing most *A. cunninghamiana* and *R. sapida* individuals and some *S. actinophylla*, while others were partially damaged from browsing. Furthermore, rabbits (*Oryctolagus cuniculus*) caused major browsing problems in Hastings and Whangarei. After the first occurrence I tried to exclude the rabbits from the field sites by fencing off the plot using fishing line and wire. I also attempted to deter the rabbits by application of Treepel (an organic deterrent made from eggs) to the seedlings, however, both measures were unsuccessful. Although I repeatedly replanted seedlings, in the second growing season all *A. cunninghamiana* and *R. sapida* individuals in Whangarei were lost to rabbit browsing, and in Hastings all plant individuals were lost except 14 *S. actinophylla* individuals (with some of the remaining individuals suffering from partial browsing damage).

Biomass of the surviving individuals was harvested between 20 April and 5 May 2013, divided into shoot and root biomass. Leaf area for all species was measured by photographing all leaves (from a distance of 31 cm, resulting in a distortion small enough to be negligible) and analysing the area (cm$^2$) with Image J software (Wayne Rasband National Institutes of Health, USA). Plant material was dried at 70°C for 36 hours.

Because of the unexpected browsing damage and the resulting loss of data, the experiment was continued on a smaller scale for another winter in the three North Island sites (Whangarei, Auckland, Hastings). This time, 12 seedlings of each of the three alien plant species were used (no pesticide treatment, no native relatives) in each of the three sites, completely randomised in one block only. Seedlings were planted 20-28 April 2013 and harvested 30 August to 2 September 2013.
(after 18 weeks of growth). As there were no *A. cunninghamiana* seedlings available from my own plant propagation, the seedlings of this species were sourced from a local forest site this species has invaded (St John’s College bush, Auckland; collected January 2013). To avoid rabbit browsing, the shadecloth was this time also set up on the sides of the plots to enclose the seedlings.

### 7.2.7 Data analysis

All data were either analysed in SAS statistical software (SAS Institute Inc., Cary NC, USA, version 9.2 for Windows) or R (R Development Core Team, 2013, v 3.0.0 for Windows), and all graphs were produced in R.

#### 7.2.7.1 Climate data

Mean daily minimum, mean daily maximum and total precipitation values were calculated for each month over the duration of the experiment. A Kolmogorov-Smirnov test was carried out in R for each climate variable at each location to investigate if distributions of my weather data differ from long-term averages.

#### 7.2.7.2 Soil property and surrounding vegetation data

Soil properties were classified according to Blakemore *et al.* (1987), but not further analysed (as only one sample per site was taken). Surrounding vegetation was analysed in R using ANOVA, with natural log-transformed biomass as the response variable and site as the predictor variable. Post-hoc tests were performed using the Tukey-Kramer method to determine differences between individual sites.

#### 7.2.7.3 Mortality data

For mortality data (a binary variable with ‘0’ for alive and ‘1’ for dead) an analysis was attempted using a number of generalised linear mixed effects models with binomial distributions and a logit-link in SAS, however no appropriate model could be fitted that achieved model convergence. Therefore, only the proportion of dead individuals is reported for each season, calculated by summing up the recorded mortality on each visit divided by the number of individuals on each visit.

#### 7.2.7.4 Final harvest data

Biomass and leaf area data were analysed in SAS based on a linear mixed model approach, using restricted maximum likelihood (REML) to fit the linear mixed model to the data. Type II hypothesis tests for the significance of each of the fixed effects and interactions were performed. Thereafter
pairwise comparisons of means were performed for statistically significant effects ($P < 0.05$) in the Type II hypothesis tests, using the Tukey-Kramer method to adjust $P$-values. Fixed effects included site (six levels), species pair (three levels), biostatus (two levels), pesticide (two levels) and random effects included block. However, as block was not significant this was removed from the model.

Because in the final harvest data there was a mix of seedlings planted in Summer 1 and Summer 2, an additional analysis was carried out separately for Summer 1 plants only to see if results would differ. The response variables root, shoot and total biomass, root/shoot ratio, leaf area and specific leaf area (SLA) were all natural log-transformed before analysis to meet the assumptions of the model.

### 7.2.7.5 Growth over time data

Growth data from measurements over time were divided into three seasons, each six months long: Summer 1 (October 2011-April 2012), Winter 1 (April 2012-October 2012) and Summer 2 (October 2012-April 2013). Data were then analysed separately for the three seasons in SAS, because during winter mortality was very high. To analyse growth over time, shoot biomass of the seedlings at the various points in time was estimated by fitting linear regressions to determine a relationship between final biomass (natural log-transformed) and growth measures (height, diameter, number of leaves/leaflets; depending on the species’ growth type and best model fit). For all species, the regression models were highly significant ($P < 0.001$) and resulted in adjusted $R^2$ between 0.7-1 (Table 7.4).

**Table 7.4**: Linear regressions to estimate natural log-transformed shoot biomass, using the independent variables: natural log-transformed height (for all species); natural log-transformed number of leaves (for *P. guajava* and *L. bullata*); number of leaflets (for *S. actinophylla* and *S. digitata*); natural log-transformed diameter (for *A. cunninghamiana* and *R. sapida*); and natural log-transformed number of branches (for *P. guajava*). Model coefficients, degrees of freedom (DF), $F$ and $R^2$ values are indicated.

<table>
<thead>
<tr>
<th>Species</th>
<th>Intercept</th>
<th>Ln (height)</th>
<th>Ln (leaves) / leaflets</th>
<th>Ln (diameter / branches)</th>
<th>DF</th>
<th>$F$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. cunninghamiana</em></td>
<td>-4.666</td>
<td>0.427</td>
<td>2.046</td>
<td>2, 73</td>
<td>615</td>
<td>***</td>
<td>0.942</td>
</tr>
<tr>
<td><em>R. sapida</em></td>
<td>-4.106</td>
<td>0.476</td>
<td>1.456</td>
<td>2, 41</td>
<td>119</td>
<td>***</td>
<td>0.846</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td>-5.425</td>
<td>1.526</td>
<td>0.189</td>
<td>3, 118</td>
<td>346</td>
<td>***</td>
<td>0.895</td>
</tr>
<tr>
<td><em>L. bullata</em></td>
<td>-5.621</td>
<td>1.231</td>
<td>0.646</td>
<td>2, 116</td>
<td>1185</td>
<td>***</td>
<td>0.953</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td>-1.366</td>
<td>0.846</td>
<td>0.040</td>
<td>2, 129</td>
<td>205</td>
<td>***</td>
<td>0.757</td>
</tr>
<tr>
<td><em>S. digitata</em></td>
<td>-3.833</td>
<td>1.507</td>
<td>0.020</td>
<td>2, 31</td>
<td>133</td>
<td>***</td>
<td>0.889</td>
</tr>
</tbody>
</table>

Significance level: *** $P < 0.001$. 

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Estimated shoot biomass was analysed based on a linear mixed model approach, using restricted maximum likelihood (REML) to fit the linear mixed model to the data. Type II hypothesis tests for the significance of each of the fixed effects and interactions were performed. Thereafter pairwise comparisons of means were performed for statistically significant effects ($P < 0.05$) in the Type II hypothesis tests, using the Tukey-Kramer method to adjust $P$-values. Fixed effects included site (six levels), species pair (three levels), biostatus (two levels) and pesticide (two levels). Random effects included ‘block’ and a new term to account for the correlation between repeated measurements on each seedling: ‘plant’, nested within block. Month (three repeated measurements for the summer months, two for the winter) was also included as a random factor (as month was not primarily of interest). Because initial sizes frequently differed, estimated initial shoot biomass was included as a covariate in the model. Biomass was natural log-transformed before analysis to meet the assumptions of the model.

7.2.7.6 Winter 2 harvest data

The continuation of the experiment for an extra winter on a smaller scale resulted in a simpler design: a completely balanced factorial design with the factors site (two levels, as no individuals survived in Hastings) and species (three levels, alien species only) and their interaction. This data was analysed in R using ANOVA. The response variables total biomass, leaf area, root/shoot ratio and SLA were analysed, with all variables log-transformed except root/shoot ratio to meet the assumptions of the model. Initial analyses of height, diameter, number of leaves and branches showed that there were no differences in these growth measures between sites at the time of planting. Relative growth rates of shoot biomass over the 18 week period were also calculated, with initial shoot biomass estimated by fitting linear regressions to determine a relationship between final shoot biomass (natural log-transformed) and growth measures (regressions fitted specific to this extra winter data).

7.2.7.7 Herbivory damage

Leaf herbivory damage was analysed in SAS with a linear mixed model including the same factors as for the analysis of estimated shoot biomass described above. Initial damage was however not included as a covariate, as it was mostly zero. Herbivory damage was arcsine square root transformed to meet the assumptions of the model.

7.2.7.8 RGR/mortality versus climate

To investigate if climate variables had significant effects on relative growth rate (RGR) of the species, further analyses were carried out. I calculated RGR of estimated shoot biomass over each time interval as $\text{RGR} = (\ln W_2 - \ln W_1) / (t_2 - t_1)$, with $t_1$ and $t_2$ indicating time points 1 and 2 and $W_1$ and
W2 indicating estimated shoot biomass at points 1 and 2. Time was given as number of days between measurements (which varied between 33-94 days). For the same time interval, minimum and maximum temperature (average daily minimum and maximum) and precipitation (total) were calculated from the hourly recordings of weather data.

Analyses were carried out for each species pair separately in SAS, to investigate if minimum temperature, maximum temperature and precipitation had an effect on RGR, and whether that effect differed among the native and alien species. Linear mixed models were fitted. RGR was the response variable, and biostatus, minimum temperature, maximum temperature, precipitation and the interaction of biostatus with each of the three climate variables were the predictor variables. Random effects included block and plant nested in block; although these effects were removed if not significant to provide better model fit. Type II tests of each of the fixed effects were carried out. The solution statement in SAS was used to estimate the slopes and significance of each effect. Initial investigations showed that the pesticide treatment had very minimal effects on RGR and therefore was not included in the final models. The same analysis was then carried out for the response variable mortality, but a generalised linear mixed effects model was used with a binomial distribution and a logit-link. The same fixed effects were included as above, although the random effect block was removed as it was not significant.

7.2.7.9 Growth/mortality versus predicted suitability

Simple regression models were used to examine the relationship between growth/mortality at the various sites and predicted suitability (cf. Pattison & Mack 2008). This analysis was carried out in R. Biomass and leaf area were used as the response variables and predicted suitability (according to SDMs, current climate, see Table 7.3) was the predictor variable. Furthermore, for estimated shoot biomass over time an average value for each site was calculated to use as a response variable: the Least Square Means (LSMs) from the previously conducted analyses (separately for Summer 1, 2 and Winter 1) were used, averaging the LSMs over Summer 1 and 2 (except for A. cunninghamiana and R. sapida in Whangarei and Hastings where only data from Summer 1 was available). These values were subsequently averaged with the LSMs from Winter 1 (in order to give summer and winter growth rates equal weight). If the seedlings did not survive over winter (as was the case in Hastings, Nelson and Lincoln), the LSM for winter was assigned a zero. Finally for the response variable mortality, the number of surviving individuals divided by the total number of individuals (NA values excluded) was calculated for each season (giving an estimate of survivorship), then averaged across seasons in the same manner as for growth.
Chapter 7: Performance of alien plants and their native relatives in differing climates: a field validation of SDMs

7.3 Results

7.3.1 Climate data

The monthly temperature averages and precipitation totals for each site for the duration of the experiment, and how they compare to long-term averages, are shown in Figure 7.6. Kolmogorov-Smirnov tests showed that maximum temperature during the experiment was greater (at \( P < 0.05 \); Whangarei \( D_{21} = 0.41 \); Auckland \( D_{21} = 0.64 \); Greymouth \( D_{17} = 0.61 \); Nelson \( D_{17} = 0.50 \); Lincoln \( D_{17} = 0.56 \)) compared to long-term averages at all sites except Hastings \( D_{21} = 0.32 \). Furthermore, precipitation differed from long-term observations in Whangarei \( D_{21} = 0.45 \), Auckland \( D_{21} = 0.41 \), Hastings \( D_{21} = 0.50 \) and Nelson \( D_{17} = 0.50 \), but not in Greymouth \( D_{17} = 0.39 \) and Lincoln \( D_{17} = 0.39 \). There were no significant differences between minimum temperature as measured during my experiment and long-term observations (Whangarei \( D_{21} = 0.18 \); Auckland \( D_{21} = 0.18 \); Greymouth \( D_{17} = 0 \); Nelson \( D_{17} = 0.17 \); Lincoln \( D_{17} = 0.11 \)), but there was a trend towards lower minimum temperatures in Hastings \( D_{21} = 0.32; P = 0.010 \). Extreme weather events that occurred during the duration of the experiment include a deluge in December 2011 in Nelson, with Nelson experiencing the wettest summer on record in that summer (National Institute of Water and Atmospheric Research 2013). In summer 2012/2013, a drought occurred, with most parts of the North Island being extremely dry (National Institute of Water and Atmospheric Research 2013). From December 2012 to March 2013, Whangarei experienced only 45% of the long-term average precipitation; Auckland 42%; Hastings 19%; Lincoln 76%, whereas Greymouth and Nelson experienced near normal precipitation with 88% and 106%. While winter 2012 was colder than usual (in the first half), winter 2013 was milder (National Institute of Water and Atmospheric Research 2013). Of the six study sites, Hastings experienced the highest number of frost nights and lowest temperatures reached during winter (Table 7.5). In most sites, seedlings experienced partial or complete frost damage (Figure 7.7).

Average wind speeds were 5.0 km/h in Whangarei (ranging between 0-26.4 km/h); 2.1 km/h in Auckland (0-12.7 km/h); 3.1 km/h in Hastings (0-22.9 km/h); 4.6 km/h in Greymouth (0-29.6 km/h); 3.4 km/h in Nelson (0-23.3 km/h); and 4.6 km/h in Lincoln (0-18.7 km/h).
Figure 7.6: Monthly weather data summaries for the six field sites: a) Whangarei; b) Auckland; c) Hastings; d) Greymouth; e) Nelson; and f) Lincoln. Average daily minimum and maximum temperature (closed circles) and precipitation (grey bars) as measured at the field sites, and long-term average extracted from data provided by the National Institute of Water and Atmospheric Research (NIWA) climate layers (open circles and white bars), in 0.05° resolution (ca. 5 x 5 km), averaged over period 1980-1999 (‘current’ climate).
Chapter 7: Performance of alien plants and their native relatives in differing climates: a field validation of SDMs

Table 7.5: Number of frost nights (temperature below 0°C) and absolute minimum temperature [°C] measured at the six sites in Winter 1 and 2.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. nights</td>
<td>Absolute min.</td>
</tr>
<tr>
<td>Whangarei</td>
<td>2</td>
<td>- 0.8</td>
</tr>
<tr>
<td>Auckland</td>
<td>8</td>
<td>- 1.9</td>
</tr>
<tr>
<td>Hastings</td>
<td>58</td>
<td>- 5.8</td>
</tr>
<tr>
<td>Greymouth</td>
<td>0</td>
<td>+ 0.5</td>
</tr>
<tr>
<td>Nelson</td>
<td>13</td>
<td>- 2.2</td>
</tr>
<tr>
<td>Lincoln</td>
<td>31</td>
<td>- 6.2</td>
</tr>
</tbody>
</table>

Figure 7.7: Examples of seedlings of the alien species with frost damage in Winter 1: a) *A. cunninghamiana*, b) *P. guajava*, and c) *S. actinophylla* with partial frost damage (examples from Auckland); d) *A. cunninghamiana*, e) *P. guajava*, and f) *S. actinophylla* with complete frost damage (examples from Hastings).
7.3.2 Soil property and surrounding vegetation data

The six field sites had similar soil properties, with the exception of Greymouth, which was strongly acidic and generally had low to very low nutrient availability, with mineral nitrogen levels 5-14 times lower compared to the other sites. The other five sites had a moderately to slightly acid pH, high calcium, medium magnesium and low sodium content, a medium cation exchange capacity and a medium to high base saturation. Phosphorus and potassium varied more across sites; from (very) low phosphorus in Hastings and Greymouth to very high in Auckland and Nelson, and very low potassium in Greymouth and Auckland to very high in Lincoln (classifications after Blakemore et al. 1987) (Table 7.6).

Table 7.6: Soil properties of field sites: water content, pH, mineral nitrogen (nitrate \([\text{NO}_3^-]\), ammonium \([\text{NH}_4^+]\)), phosphorus (P), exchangeable bases (calcium [Ca], magnesium [Mg], potassium [K], sodium [Na]), cation exchange capacity (CEC) and base saturation (Base sat.).

<table>
<thead>
<tr>
<th>Field site</th>
<th>Water content [%]</th>
<th>pH</th>
<th>NO(_3^-) [mg/kg]</th>
<th>NH(_4^+) [mg/kg]</th>
<th>P [mg/kg]</th>
<th>Ca [cmol (+)/kg]</th>
<th>Mg [cmol (+)/kg]</th>
<th>K [cmol (+)/kg]</th>
<th>Na [cmol (+)/kg]</th>
<th>CEC [cmol (+)/kg]</th>
<th>Base sat. [%]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whangarei</td>
<td>56.7</td>
<td>5.7</td>
<td>12.9</td>
<td>&lt;0.1</td>
<td>11</td>
<td>9.66</td>
<td>2.78</td>
<td>1.15</td>
<td>0.14</td>
<td>22.7</td>
<td>61</td>
</tr>
<tr>
<td>Auckland</td>
<td>53.6</td>
<td>5.9</td>
<td>8.6</td>
<td>0.2</td>
<td>63</td>
<td>12.0</td>
<td>1.46</td>
<td>0.21</td>
<td>0.25</td>
<td>27.3</td>
<td>51</td>
</tr>
<tr>
<td>Hastings</td>
<td>34.9</td>
<td>6.2</td>
<td>4.8</td>
<td>1.5</td>
<td>9</td>
<td>10.9</td>
<td>2.60</td>
<td>1.22</td>
<td>0.10</td>
<td>20.2</td>
<td>74</td>
</tr>
<tr>
<td>Greymouth</td>
<td>48.1</td>
<td>5.2</td>
<td>0.5</td>
<td>0.8</td>
<td>11</td>
<td>3.35</td>
<td>0.36</td>
<td>0.08</td>
<td>0.15</td>
<td>17.6</td>
<td>22</td>
</tr>
<tr>
<td>Nelson</td>
<td>42.1</td>
<td>6.1</td>
<td>4.8</td>
<td>5.0</td>
<td>87</td>
<td>13.4</td>
<td>2.48</td>
<td>0.62</td>
<td>0.06</td>
<td>22.3</td>
<td>74</td>
</tr>
<tr>
<td>Lincoln</td>
<td>40.6</td>
<td>6.2</td>
<td>6.1</td>
<td>12.5</td>
<td>31</td>
<td>11.3</td>
<td>2.54</td>
<td>1.30</td>
<td>0.20</td>
<td>22.0</td>
<td>69</td>
</tr>
</tbody>
</table>

Dry matter production of the vegetation surrounding the seedlings on each site over ten weeks was: 566.71 ± 118.06 g/m\(^2\) (Whangarei); 343.13 ± 35.96 g/m\(^2\) (Auckland); 218.21 ± 32.32 g/m\(^2\) (Hastings); 304.88 ± 35.15 g/m\(^2\) (Greymouth); 218.50 ± 24.74 g/m\(^2\) (Nelson); and 173.92 ± 13.22 g/m\(^2\) (Lincoln; means ± standard errors). The ANOVA indicated that there were significant differences between sites \((F_{5,30} = 8.35, P < 0.001)\). Post-hoc tests (at \(P < 0.05\)) showed that Whangarei had significantly larger biomass production compared to Lincoln, Hastings and Nelson, and Auckland had larger biomass production compared to Lincoln.

7.3.3 Mortality data

Mortality during summer was generally low for all three alien species in all six sites (Table 7.7). However, by the end of Winter 1 no alien seedlings had survived in Hastings or Lincoln, and in Nelson only three \(P.\ guajava\) survived. Furthermore, for \(S.\ actinophylla\), all individuals in Auckland
and half the individuals in Greymouth died (although they were still alive in July 2012, they were dead by October 2012). However, in both Whangarei and Auckland, all individuals of all three species survived the second winter (Winter 2), with no frost damage (except on a few leaves on three *S. actinophylla* individuals in Auckland). In Hastings, as in the previous winter, all seedlings of all species appeared dead as they experienced severe frost damage: the leaves of all species were completely frost damaged, as well as the stems of *S. actinophylla*. However, for *A. cunninghamiana* the stems retained a green base (in nine out of 12 seedlings), which might have enabled them to recover in spring.

### Table 7.7: Seedling mortality [%] and in brackets number of samples for the various seasons. Dead individuals are given as the proportion of total counts over three visits (summers, total count 72), two visits (Winter 1 and in Auckland Summer 1, total count 48) or one visit (harvest) only (Winter 2, total count 12). Lower counts or NA values are due to missing values because of other causes of death (pukeko, cattle, rabbits) or non-replacement of seedlings.

<table>
<thead>
<tr>
<th>Site</th>
<th>Season</th>
<th><em>A. cunninghamiana</em></th>
<th><em>R. sapida</em></th>
<th><em>P. guajava</em></th>
<th><em>L. bullata</em></th>
<th><em>S. actinophylla</em></th>
<th><em>S. digitata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Whangarei</td>
<td>Summer 1</td>
<td>1.4 (72)</td>
<td>4.2 (72)</td>
<td>0 (72)</td>
<td>18.1 (72)</td>
<td>0 (72)</td>
<td>20.8 (72)</td>
</tr>
<tr>
<td></td>
<td>Winter 1</td>
<td>0 (8)</td>
<td>0 (15)</td>
<td>0 (48)</td>
<td>0 (48)</td>
<td>0 (28)</td>
<td>0.02 (45)</td>
</tr>
<tr>
<td></td>
<td>Summer 2</td>
<td>NA</td>
<td>NA</td>
<td>0 (69)</td>
<td>0 (72)</td>
<td>0 (72)</td>
<td>14.0 (57)</td>
</tr>
<tr>
<td></td>
<td>Winter 2</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0.02 (45)</td>
</tr>
<tr>
<td>Auckland</td>
<td>Summer 1</td>
<td>0.02 (48)</td>
<td>0 (48)</td>
<td>0 (48)</td>
<td>4.2 (48)</td>
<td>0 (48)</td>
<td>14.0 (57)</td>
</tr>
<tr>
<td></td>
<td>Winter 1</td>
<td>24.4 (45)</td>
<td>40.0 (45)</td>
<td>0 (48)</td>
<td>0 (48)</td>
<td>50.0 (48)</td>
<td>58.3 (48)</td>
</tr>
<tr>
<td></td>
<td>Summer 2</td>
<td>7.4 (68)</td>
<td>17.9 (67)</td>
<td>0 (72)</td>
<td>4.3 (70)</td>
<td>0 (72)</td>
<td>20.4 (49)</td>
</tr>
<tr>
<td></td>
<td>Winter 2</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0.02 (45)</td>
</tr>
<tr>
<td>Hastings</td>
<td>Summer 1</td>
<td>0.02 (60)</td>
<td>0 (65)</td>
<td>9.5 (63)</td>
<td>8.5 (71)</td>
<td>3.1 (65)</td>
<td>7.0 (71)</td>
</tr>
<tr>
<td></td>
<td>Winter 1</td>
<td>72.7 (33)</td>
<td>70.6 (34)</td>
<td>100 (24)</td>
<td>39.1 (46)</td>
<td>100 (24)</td>
<td>63.9 (36)</td>
</tr>
<tr>
<td></td>
<td>Summer 2</td>
<td>0 (12)</td>
<td>0 (12)</td>
<td>0 (37)</td>
<td>0 (25)</td>
<td>0 (58)</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>Winter 2</td>
<td>100? (12)†</td>
<td>100 (12)</td>
<td>100 (12)</td>
<td>100 (12)</td>
<td>100 (12)</td>
<td>100 (12)</td>
</tr>
<tr>
<td>Greymouth</td>
<td>Summer 1</td>
<td>0 (72)</td>
<td>4.2 (72)</td>
<td>0 (72)</td>
<td>2.8 (72)</td>
<td>1.4 (72)</td>
<td>29.4 (68)</td>
</tr>
<tr>
<td></td>
<td>Winter 1</td>
<td>0 (48)</td>
<td>4.2 (48)</td>
<td>12.5 (48)</td>
<td>0 (48)</td>
<td>28.9 (45)</td>
<td>5.4 (37)</td>
</tr>
<tr>
<td></td>
<td>Summer 2</td>
<td>11.1 (63)</td>
<td>2.8 (72)</td>
<td>0 (72)</td>
<td>0 (72)</td>
<td>1.4 (72)</td>
<td>3.9 (51)</td>
</tr>
<tr>
<td>Nelson</td>
<td>Summer 1</td>
<td>1.4 (72)</td>
<td>1.4 (72)</td>
<td>0 (72)</td>
<td>0 (72)</td>
<td>0 (72)</td>
<td>9.7 (72)</td>
</tr>
<tr>
<td></td>
<td>Winter 1</td>
<td>100 (24)</td>
<td>75.0 (32)</td>
<td>77.8 (27)</td>
<td>0 (48)</td>
<td>100 (24)</td>
<td>34.1 (41)</td>
</tr>
<tr>
<td></td>
<td>Summer 2</td>
<td>7.1 (70)</td>
<td>39.3 (56)</td>
<td>0 (72)</td>
<td>2.9 (70)</td>
<td>1.5 (68)</td>
<td>36.4 (22)</td>
</tr>
<tr>
<td>Lincoln</td>
<td>Summer 1</td>
<td>4.2 (72)</td>
<td>20.8 (72)</td>
<td>1.4 (72)</td>
<td>5.6 (72)</td>
<td>0 (72)</td>
<td>31.4 (70)</td>
</tr>
<tr>
<td></td>
<td>Winter 1</td>
<td>100 (24)</td>
<td>100 (24)</td>
<td>100 (24)</td>
<td>42.5 (40)</td>
<td>100 (24)</td>
<td>75.0 (28)</td>
</tr>
<tr>
<td></td>
<td>Summer 2</td>
<td>4.2 (72)</td>
<td>24.2 (66)</td>
<td>0 (72)</td>
<td>2.8 (72)</td>
<td>1.4 (72)</td>
<td>50.0 (2)</td>
</tr>
</tbody>
</table>

† Uncertain whether seedlings were entirely dead.
Chapter 7: Performance of alien plants and their native relatives in differing climates: a field validation of SDMs

Compared to mortality of the native species, *A. cunninghamiana* survival in Auckland in winter and Summer 2, in Nelson in Summer 2 and in Lincoln in both summers was much higher than for *R. sapida* (Table 7.7). In Hastings, Nelson and Lincoln all *R. sapida* individuals had died by the end of Winter 1, as for *A. cunninghamiana*. *Lophomyrtus bullata* showed high mortality in Whangarei in Summer 1, but contrary to *P. guajava* in Winter 1 this species had a few surviving individuals in Lincoln and Hastings, and all individuals survived in Nelson. Unlike *S. actinophylla*, *S. digitata* generally showed high mortality in Summer 1 (and Summer 2, provided there were any remaining individuals). In Winter 1, in Hastings and Lincoln the *S. digitata* seedlings died, but almost half survived in Nelson.

7.3.4 Final harvest data

Site, pair, biostatus and their interactions had significant effects on total biomass (Table 7.8). Post-hoc tests showed that for the three species pairs the alien species had larger biomass than the native species in Whangarei and Auckland, and *P. guajava* was additionally larger than the native, *L. bullata*, in Lincoln (Figure 7.8). There were significant differences among sites in alien species’ biomass, with the largest seedling biomasses found in Whangarei and Auckland (Figure 7.8). For effects of pesticide, post-hoc tests only showed that there was a trend towards pesticide-treated *L. bullata* and *P. guajava* seedlings having larger biomass in Auckland (*P* = 0.063). Results for the analysis of shoot and root biomass were very similar to total biomass and therefore are not further reported.

If only looking at the data from seedlings planted in Summer 1, the same interactions were significant for total biomass as mentioned above for all plants. If they could be estimated, the same pairwise differences remained significant, with one exception: for the *Schefflera* pair in Whangarei, the difference between biomass of the alien and native species was not significant for Summer 1 seedlings only.
Table 7.8: Linear models of natural log-transformed total biomass, root/shoot ratio, leaf area and SLA. Numerator degrees of freedom (DF), denominator degrees of freedom (Den. DF) and $F$-values are indicated.

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>Den. DF</th>
<th>Total biomass</th>
<th>Root/shoot ratio</th>
<th>Leaf area</th>
<th>SLA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>5</td>
<td>475</td>
<td>170 ***</td>
<td>39.7 ***</td>
<td>116 ***</td>
<td>89.9 ***</td>
</tr>
<tr>
<td>Pair</td>
<td>2</td>
<td>475</td>
<td>72.6 ***</td>
<td>38.6 ***</td>
<td>58.1 ***</td>
<td>58.7 ***</td>
</tr>
<tr>
<td>Site*pair</td>
<td>7</td>
<td>475</td>
<td>16.4 ***</td>
<td>9.30 ***</td>
<td>8.33 ***</td>
<td>4.18 ***</td>
</tr>
<tr>
<td>Biostatus</td>
<td>1</td>
<td>475</td>
<td>173 ***</td>
<td>12.9 ***</td>
<td>64.2 ***</td>
<td>208 ***</td>
</tr>
<tr>
<td>Site*biostatus</td>
<td>4</td>
<td>475</td>
<td>22.8 ***</td>
<td>8.65 ***</td>
<td>24.7 ***</td>
<td>2.95</td>
</tr>
<tr>
<td>Pair*biostatus</td>
<td>2</td>
<td>475</td>
<td>0.25</td>
<td>184 ***</td>
<td>0.38</td>
<td>4.31</td>
</tr>
<tr>
<td>Site<em>pair</em>biostatus</td>
<td>6</td>
<td>475</td>
<td>4.60 ***</td>
<td>9.84 ***</td>
<td>4.88 ***</td>
<td>3.88 ***</td>
</tr>
<tr>
<td>Pesticide</td>
<td>1</td>
<td>475</td>
<td>0.25</td>
<td>3.30</td>
<td>1.43</td>
<td>1.85</td>
</tr>
<tr>
<td>Site*pesticide</td>
<td>5</td>
<td>475</td>
<td>0.90</td>
<td>0.50</td>
<td>0.82</td>
<td>1.43</td>
</tr>
<tr>
<td>Pair*pesticide</td>
<td>2</td>
<td>475</td>
<td>4.82 **</td>
<td>0.49</td>
<td>3.40 *</td>
<td>0.62</td>
</tr>
<tr>
<td>Site<em>pair</em>pesticide</td>
<td>7</td>
<td>475</td>
<td>2.03 *</td>
<td>0.56</td>
<td>1.52</td>
<td>1.00</td>
</tr>
<tr>
<td>Biostatus*pesticide</td>
<td>1</td>
<td>475</td>
<td>0.62</td>
<td>4.08 *</td>
<td>0.66</td>
<td>0.02</td>
</tr>
<tr>
<td>Site<em>biostatus</em>pesticide</td>
<td>4</td>
<td>475</td>
<td>0.88</td>
<td>0.58</td>
<td>1.35</td>
<td>0.45</td>
</tr>
<tr>
<td>Pair<em>biostatus</em>pesticide</td>
<td>2</td>
<td>475</td>
<td>0.01</td>
<td>0.59</td>
<td>0.06</td>
<td>1.69</td>
</tr>
<tr>
<td>Site<em>pair</em>biostatus*pesticide</td>
<td>6</td>
<td>475</td>
<td>0.53</td>
<td>0.71</td>
<td>0.10</td>
<td>1.64</td>
</tr>
</tbody>
</table>

Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.  

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Figure 7.8: Total biomass; back-transformed LSMs ± 95% confidence intervals of a) the A. cunninghamiana and R. sapida species pair, b) the P. guajava and L. bullata species pair, and c) the S. actinophylla and S. digitata species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Significant differences ($P < 0.05$) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). Some results are missing for Whangarei and Hastings due to rabbit browsing. Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).

Differences in root/shoot ratio also depended on site, pair and biostatus (Table 7.8). While P. guajava had a higher root/shoot ratio compared to L. bullata in most sites, conversely R. sapida had a higher root/shoot ratio than A. cunninghamiana (Figure 7.9). No differences in root/shoot ratio were found for the Schefflera species. Differences among sites for the alien species varied depending on species, but frequently tended towards higher root/shoot ratios in more unsuitable sites (Figure 7.9). Post-hoc tests further showed that when pesticide was applied, native species had a lower root/shoot ratio compared to alien species ($P = 0.002$). Considering seedlings planted in Summer 1
only, results remained qualitatively the same where they could be compared, except that the effect of pesticide was no longer significant.

![Figure 7.9: Root/shoot ratio; back-transformed LSMs ± 95% confidence intervals of a) the A. cunninghamiana and R. sapida species pair, b) the P. guajava and L. bullata species pair, and c) the S. actinophylla and S. digitata species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance level: *** $P < 0.001$. Significant differences ($P < 0.05$) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). Some results are missing for Whangarei and Hastings due to rabbit browsing. Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).](image)

The three-way interaction of site, pair and biostatus was also significant for leaf area (Table 7.8). Post-hoc tests showed that leaf areas of P. guajava and S. actinophylla were significantly larger compared to their native relatives in some of the sites (Figure 7.10). For the alien species, Whangarei and Auckland had higher leaf areas than some of the other sites (Figure 7.10). Although the pair by
pesticide interaction was significant (Table 7.8), post-hoc tests showed no significant differences of pesticide on leaf area within one species pair. For seedlings planted in Summer 1 only, results remained the same, except that the difference in leaf area for the *Schefflera* species in Whangarei was no longer significant.

**Figure 7.10:** Leaf area; back-transformed LSMs ± 95% confidence intervals of a) the *A. cunninghamiana* and *R. sapida* species pair, b) the *P. guajava* and *L. bullata* species pair, and c) the *S. actinophylla* and *S. digitata* species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance levels: * $P < 0.05$, *** $P < 0.001$. Significant differences ($P < 0.05$) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). Some results are missing for Whangarei and Hastings due to rabbit browsing. Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).

For SLA, post-hoc tests for the significant site by pair by biostatus interaction (Table 7.8) showed that SLA was frequently larger in the alien compared to the native species, particularly for
the $P. \text{guajava}$ and $L. \text{bullata}$ species pair (Figure 7.11). There were also differences among sites for the alien species, with Greymouth showing the largest SLA (Figure 7.11). Results remained qualitatively the same if considering data from seedlings planted in Summer 1 only.

Figure 7.11: Specific leaf area (SLA); back-transformed LSMs ± 95% confidence intervals of a) the $A. \text{cunninghamiana}$ and $R. \text{sapida}$ species pair, b) the $P. \text{guajava}$ and $L. \text{bullata}$ species pair, and c) the $S. \text{actinophylla}$ and $S. \text{digitata}$ species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance levels: * $P < 0.05$, *** $P < 0.001$. Significant differences ($P < 0.05$) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). Some results are missing for Whangarei and Hastings due to rabbit browsing. Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).
7.3.5 Growth over time data

Estimated shoot biomass differed depending on site, pair and biostatus for both summers (Table 7.9). Post-hoc tests showed that the alien species were often significantly larger compared to the native species in many sites in Summer 1, and always in Whangarei and Auckland (Figure 7.12). In Summer 2, only *P. guajava* was larger than *L. bullata* in Whangarei (Figure 7.13). Furthermore, the native species were sometimes larger than the alien species in Greymouth and Nelson for Summer 2. There were also differences among locations for the alien species, with Whangarei and Auckland having larger biomasses than the other sites, particularly in Summer 2.

Pesticide had a significant effect in Summer 1, depending on site and pair (Table 7.9). Post-hoc tests showed that the only significant difference of interest was that for the *P. guajava* and *L. bullata* species pair, mean biomass of plants in Auckland without pesticide treatment was only half of the biomass of the pesticide treated plants (ratio of 0.54, with 95% confidence interval 0.41-0.72). For Summer 2, although pesticide had a significant effect depending on site, pair and type (Table 7.9), post-hoc tests showed no significant differences within a site within species.

**Table 7.9:** Linear mixed models of natural log-transformed estimated shoot biomass over time for the three seasons. Numerator degrees of freedom (DF), denominator degrees of freedom (Den. DF) and F-values are indicated.

<table>
<thead>
<tr>
<th></th>
<th>DF</th>
<th>Den. DF</th>
<th>Summer 1</th>
<th>DF</th>
<th>Den. DF</th>
<th>Summer 2</th>
<th>DF</th>
<th>Den. DF</th>
<th>Winter 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial biomass</td>
<td>1</td>
<td>1085</td>
<td>166 ***</td>
<td>1</td>
<td>599</td>
<td>1009 ***</td>
<td>1</td>
<td>324</td>
<td>616 ***</td>
</tr>
<tr>
<td>Site</td>
<td>5</td>
<td>6.26</td>
<td>29.2 ***</td>
<td>5</td>
<td>591</td>
<td>102 ***</td>
<td>2</td>
<td>331</td>
<td>18.4 ***</td>
</tr>
<tr>
<td>Pair</td>
<td>2</td>
<td>757</td>
<td>81.2 ***</td>
<td>2</td>
<td>574</td>
<td>98.8 ***</td>
<td>2</td>
<td>333</td>
<td>7.74 ***</td>
</tr>
<tr>
<td>Site*pair</td>
<td>10</td>
<td>769</td>
<td>11.5 ***</td>
<td>9</td>
<td>627</td>
<td>10.6 ***</td>
<td>4</td>
<td>341</td>
<td>1.93</td>
</tr>
<tr>
<td>Biostatus</td>
<td>1</td>
<td>807</td>
<td>142 ***</td>
<td>1</td>
<td>573</td>
<td>0.10</td>
<td>1</td>
<td>328</td>
<td>1.06</td>
</tr>
<tr>
<td>Site*biostatus</td>
<td>5</td>
<td>776</td>
<td>20.6 ***</td>
<td>5</td>
<td>633</td>
<td>16.8 ***</td>
<td>2</td>
<td>332</td>
<td>11.2 ***</td>
</tr>
<tr>
<td>Pair*biostatus</td>
<td>2</td>
<td>853</td>
<td>14.4 ***</td>
<td>2</td>
<td>579</td>
<td>15.2 ***</td>
<td>2</td>
<td>334</td>
<td>27.3 ***</td>
</tr>
<tr>
<td>Site<em>pair</em>biostatus</td>
<td>10</td>
<td>786</td>
<td>10.2 ***</td>
<td>7</td>
<td>625</td>
<td>4.12 ***</td>
<td>4</td>
<td>342</td>
<td>5.32 ***</td>
</tr>
<tr>
<td>Pesticide</td>
<td>1</td>
<td>748</td>
<td>4.66 *</td>
<td>1</td>
<td>565</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site*pesticide</td>
<td>5</td>
<td>765</td>
<td>2.04</td>
<td>5</td>
<td>586</td>
<td>3.06 **</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pair*pesticide</td>
<td>2</td>
<td>752</td>
<td>1.30</td>
<td>2</td>
<td>569</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site<em>pair</em>pesticide</td>
<td>10</td>
<td>771</td>
<td>1.89 *</td>
<td>8</td>
<td>592</td>
<td>3.04 **</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biostatus*pesticide</td>
<td>1</td>
<td>759</td>
<td>0.15</td>
<td>1</td>
<td>572</td>
<td>1.51</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site<em>biostatus</em>pesticide</td>
<td>5</td>
<td>778</td>
<td>0.77</td>
<td>5</td>
<td>629</td>
<td>3.52 **</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pair<em>biostatus</em>pesticide</td>
<td>2</td>
<td>764</td>
<td>0.25</td>
<td>2</td>
<td>574</td>
<td>1.16</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site<em>pair</em>biostatus*pesticide</td>
<td>10</td>
<td>786</td>
<td>1.04</td>
<td>6</td>
<td>577</td>
<td>2.54 *</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significance levels: * P < 0.05, ** P < 0.01, *** P < 0.001.
Figure 7.12: Estimated shoot biomass over Summer 1; back-transformed LSMs ± 95% confidence intervals of a) the *A. cunninghamiana* and *R. sapida* species pair, b) the *P. guajava* and *L. bullata* species pair, and c) the *S. actinophylla* and *S. digitata* species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance levels: ** $P < 0.01$, *** $P < 0.001$. Significant differences ($P < 0.05$) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).
Figure 7.13: Estimated shoot biomass over Summer 2; back-transformed LSMs ± 95% confidence intervals of a) the *A. cunninghamiana* and *R. sapida* species pair, b) the *P. guajava* and *L. bullata* species pair, and c) the *S. actinophylla* and *S. digitata* species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance levels: * P < 0.05, ** P < 0.01, *** P < 0.001. Significant differences (P < 0.05) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). For *A. cunninghamiana* and *R. sapida* results are missing for Whangarei and Hastings due to rabbit browsing. Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).

As the alien species died in Hastings, Nelson and Lincoln, only data from Whangarei, Auckland and Greymouth were analysed for the winter period. Estimated shoot biomass differed depending on site, pair and biostatus (Table 7.9), with the only significant difference between alien and native seedlings being that *S. digitata* had larger biomass in Auckland compared to *S. actinophylla* (all seedlings of this species had died by the end of winter in any case). Biomass in Whangarei was larger than the other two sites for *P. guajava* only (Figure 7.14).
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Figure 7.14: Estimated shoot biomass over Winter 1; back-transformed LSMs ± 95% confidence intervals of a) the *A. cunninghamiana* and *R. sapida* species pair, b) the *P. guajava* and *L. bullata* species pair, and c) the *S. actinophylla* and *S. digitata* species pair. Significant differences between alien and native species within sites are indicated by asterisks; significance level: *** $P < 0.001$. Significant differences ($P < 0.05$) between sites for the alien species only are indicated by differing lower case letters (not shown for native species as of secondary interest). Most species are missing in Hastings, Nelson and Lincoln due to mortality. Right hand y-axis shows predicted suitability of the sites according to SDMs under current climate (solid line) and average future climate (dashed line).

7.3.6 Winter 2 harvest data

Relative growth rates (shoot biomass) over the 18 weeks of Winter 2 were positive for *A. cunninghamiana* and *P. guajava* in Whangarei and Auckland (where all seedlings had survived), but negative for *S. actinophylla* (Table 7.10). RGR, final biomass, leaf area, root/shoot ratio and SLA did not differ between Whangarei and Auckland seedlings for *A. cunninghamiana* and *P. guajava* (Table
7.10). However, for *S. actinophylla*, seedlings in Whangarei showed larger RGR, larger leaf area and smaller root/shoot ratios compared to seedlings in Auckland.

**Table 7.10:** Growth over Winter 2. ANOVAs of estimated RGR of shoot biomass, natural log-transformed total biomass, root/shoot ratio, natural log-transformed leaf area and natural log-transformed SLA; *F*-values are indicated. Below means ± standard errors for each species are given for each site; significant differences between sites within species are indicated by differing lower case letters.

<table>
<thead>
<tr>
<th></th>
<th>RGR [g/day *1000]</th>
<th>Total biomass [g]</th>
<th>Root/shoot ratio</th>
<th>Leaf area [cm²]</th>
<th>SLA [cm²/g]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site*species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. cunninghamiana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whangarei</td>
<td>4.40 ± 0.55</td>
<td>1.79 ± 0.19</td>
<td>0.47 ± 0.02</td>
<td>97.85 ± 9.43</td>
<td>173.41 ± 6.89</td>
</tr>
<tr>
<td>Auckland</td>
<td>6.47 ± 0.54</td>
<td>1.71 ± 0.16</td>
<td>0.38 ± 0.03</td>
<td>88.80 ± 6.68</td>
<td>161.32 ± 6.35</td>
</tr>
<tr>
<td>(Hastings)†</td>
<td>(3.22 ± 0.83)</td>
<td>(1.02 ± 0.13)</td>
<td>(0.41 ± 0.04)</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td><em>P. guajava</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whangarei</td>
<td>1.00 ± 0.44</td>
<td>12.24 ± 1.15</td>
<td>0.60 ± 0.04</td>
<td>439.79 ± 22.85</td>
<td>116.52 ± 3.72</td>
</tr>
<tr>
<td>Auckland</td>
<td>1.25 ± 0.49</td>
<td>14.18 ± 1.66</td>
<td>0.66 ± 0.03</td>
<td>465.96 ± 40.47</td>
<td>122.72 ± 5.22</td>
</tr>
<tr>
<td><em>S. actinophylla</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whangarei</td>
<td>-3.03 ± 0.76</td>
<td>12.16 ± 0.89</td>
<td>0.63 ± 0.07</td>
<td>454.70 ± 43.55</td>
<td>142.53 ± 12.40</td>
</tr>
<tr>
<td>Auckland</td>
<td>-6.46 ± 0.55</td>
<td>10.90 ± 1.57</td>
<td>0.94 ± 0.08</td>
<td>275.93 ± 34.27</td>
<td>148.80 ± 5.62</td>
</tr>
</tbody>
</table>

Significance levels: * *P* < 0.05, *** *P* < 0.001.
† Hastings data for *A. cunninghamiana* was not included in the analysis, as uncertain if seedlings were alive.

### 7.3.7 Herbivory damage

Leaf herbivory damage was generally low for all species in most sites (Table 7.11), with many individuals not showing any damage at all. In rare cases, however, up to 50% of the leaf area was affected. Of the six species in this study, *P. guajava* was the species most affected by herbivory.
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Table 7.11: Herbivory damage [%] of each species in the treatment with and without pesticide, for Summer 1 and 2 averaged across all sites (with three measurements each); means ± standard errors.

<table>
<thead>
<tr>
<th>Species</th>
<th>Summer 1 With pesticide</th>
<th>Summer 1 No pesticide</th>
<th>Summer 2 With pesticide</th>
<th>Summer 2 No pesticide</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. cunninghamiana</td>
<td>0.36 ± 0.257</td>
<td>0.45 ± 0.188</td>
<td>0.00 ± 0.005</td>
<td>0.01 ± 0.009</td>
</tr>
<tr>
<td>R. sapida</td>
<td>0.69 ± 0.240</td>
<td>1.01 ± 0.428</td>
<td>0.09 ± 0.031</td>
<td>0.17 ± 0.041</td>
</tr>
<tr>
<td>P. guajava</td>
<td>1.66 ± 0.233</td>
<td>1.25 ± 0.167</td>
<td>0.64 ± 0.104</td>
<td>1.32 ± 0.244</td>
</tr>
<tr>
<td>L. bullata</td>
<td>0.19 ± 0.132</td>
<td>0.21 ± 0.076</td>
<td>0.07 ± 0.037</td>
<td>0.10 ± 0.050</td>
</tr>
<tr>
<td>S. actinophylla</td>
<td>0.86 ± 0.089</td>
<td>1.60 ± 0.145</td>
<td>0.04 ± 0.013</td>
<td>0.02 ± 0.009</td>
</tr>
<tr>
<td>S. digitata</td>
<td>0.91 ± 0.125</td>
<td>0.81 ± 0.111</td>
<td>0.22 ± 0.070</td>
<td>0.24 ± 0.127</td>
</tr>
</tbody>
</table>

The statistical analysis showed that for both Summer 1 and 2, herbivory damage depended on site, pair and biostatus (Table 7.12). Post-hoc tests showed that within site and species pair, the only difference between herbivory damage of alien and native species found were for the P. guajava and L. bullata species pair: for Summer 1, in Whangarei ($P = 0.008$), Auckland, Greymouth and Lincoln (all $P < 0.001$), P. guajava experienced higher herbivory damage compared to L. bullata. Similarly for Summer 2, herbivory damage on P. guajava was higher compared to L. bullata in Whangarei, Auckland, Lincoln (all $P < 0.001$) and tended to be higher in Nelson ($P = 0.053$).

For some species, herbivory damage differed among locations: during Summer 1, for P. guajava, herbivory damage in Auckland was higher than in Hastings ($P = 0.007$) or Lincoln ($P = 0.009$). During Summer 2, P. guajava experienced higher herbivory damage in Whangarei, Auckland and Lincoln than in Hastings, Greymouth and Nelson (all $P < 0.001$ except Auckland-Nelson $P = 0.007$ and Lincoln-Nelson $P = 0.010$). Rhopalostylis sapida experienced higher herbivory damage in Whangarei than in Auckland ($P = 0.002$), Greymouth ($P < 0.001$) and Lincoln ($P < 0.001$) in Summer 1. Schefflera actinophylla had higher herbivory damage in Whangarei ($P < 0.001$) and Hastings ($P = 0.014$) than in Auckland, and it was also higher in Whangarei than Greymouth ($P = 0.014$). There were no differences among sites for A. cunninghamiana, L. bullata or S. digitata in either summer season, and no differences for R. sapida and S. actinophylla in Summer 2.

The significant interaction of pair, biostatus and pesticide in Summer 1 (Table 7.12) showed, that S. actinophylla seedlings that had not been treated with pesticide had higher herbivory damage compared to those treated with pesticide ($P = 0.006$). The significant effect of pesticide in Summer 2 was due to plants treated with pesticide on average having 0.19% (95% confidence interval 0.14-0.24%) damage compared to 0.35% (95% confidence interval 0.24-0.46%) on plants without pesticide treatment.
Table 7.12: Linear mixed models of arcsine square root transformed leaf herbivory damage. Numerator degrees of freedom (DF), denominator degrees of freedom (Den. DF) and $F$-values are indicated.

<table>
<thead>
<tr>
<th>Factor</th>
<th>DF</th>
<th>Den. DF</th>
<th>Summer 1</th>
<th>DF</th>
<th>Den. DF</th>
<th>Summer 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>5</td>
<td>6.29</td>
<td>9.57 ***</td>
<td>5</td>
<td>6.72</td>
<td>9.14 ***</td>
</tr>
<tr>
<td>Pair</td>
<td>2</td>
<td>761</td>
<td>85.3 ***</td>
<td>2</td>
<td>621</td>
<td>57.5 ***</td>
</tr>
<tr>
<td>Site*pair</td>
<td>10</td>
<td>785</td>
<td>4.32 ***</td>
<td>9</td>
<td>705</td>
<td>5.03 ***</td>
</tr>
<tr>
<td>Biostatus</td>
<td>1</td>
<td>770</td>
<td>52.1 ***</td>
<td>1</td>
<td>631</td>
<td>46.2 ***</td>
</tr>
<tr>
<td>Site*biostatus</td>
<td>5</td>
<td>794</td>
<td>1.64</td>
<td>5</td>
<td>723</td>
<td>6.21 ***</td>
</tr>
<tr>
<td>Pair*biostatus</td>
<td>2</td>
<td>776</td>
<td>50.7 ***</td>
<td>2</td>
<td>638</td>
<td>79.7 ***</td>
</tr>
<tr>
<td>Site<em>pair</em>biostatus</td>
<td>10</td>
<td>804</td>
<td>2.74 ***</td>
<td>7</td>
<td>707</td>
<td>3.76 ***</td>
</tr>
<tr>
<td>Pesticide</td>
<td>1</td>
<td>758</td>
<td>3.65 *</td>
<td>1</td>
<td>610</td>
<td>3.34 *</td>
</tr>
<tr>
<td>Site*pesticide</td>
<td>5</td>
<td>780</td>
<td>0.26</td>
<td>5</td>
<td>644</td>
<td>0.45</td>
</tr>
<tr>
<td>Pair*pesticide</td>
<td>2</td>
<td>763</td>
<td>2.94 *</td>
<td>2</td>
<td>617</td>
<td>1.86</td>
</tr>
<tr>
<td>Site<em>pair</em>pesticide</td>
<td>10</td>
<td>787</td>
<td>0.56</td>
<td>8</td>
<td>656</td>
<td>0.86</td>
</tr>
<tr>
<td>Biostatus*pesticide</td>
<td>1</td>
<td>773</td>
<td>1.13</td>
<td>1</td>
<td>625</td>
<td>0.84</td>
</tr>
<tr>
<td>Site<em>biostatus</em>pesticide</td>
<td>5</td>
<td>796</td>
<td>0.20</td>
<td>5</td>
<td>719</td>
<td>0.94</td>
</tr>
<tr>
<td>Pair<em>biostatus</em>pesticide</td>
<td>2</td>
<td>778</td>
<td>4.48 *</td>
<td>2</td>
<td>631</td>
<td>1.44</td>
</tr>
<tr>
<td>Site<em>pair</em>biostatus*pesticide</td>
<td>10</td>
<td>806</td>
<td>0.44</td>
<td>6</td>
<td>646</td>
<td>1.69</td>
</tr>
</tbody>
</table>

Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

7.3.8 Seed germination

Almost no seeds sown in the experiment germinated and the small amount of data collected was not analysed further. It is uncertain whether seeds failed to germinate due to reduced viability, seed predation or unsuitable germination conditions. The only seeds that germinated in Summer 1 were for *P. guajava*; in Summer 2 no seeds of any alien or native species germinated. In Summer 1, at least one of the total of 60 seeds of *P. guajava* germinated in all sites: 3.3% germination in Whangarei; 21.7% germination in Auckland (additionally, 15% germination at the old Auckland site before its destruction); 18.3% germination in Hastings; 30% germination in Greymouth; 40% germination in Nelson; and 1.7% germination in Lincoln.

7.3.9 RGR/mortality versus climate

For all species pairs, increasing minimum temperature always had a significant positive effect on RGR of shoot biomass, whereas increasing maximum temperature had a negative effect (Table 7.13). Increasing precipitation had a negative effect on RGR of the *A. cunninghamiana* and *R. sapida* species pair. However, the only instances where effects differed among the alien and native species
were where effects of minimum temperature were slightly weaker for *P. guajava*; and increasing precipitation had a significant positive effect for *S. actinophylla*.

For mortality of the *A. cunninghamiana* and *R. sapida* species pair, increased minimum temperature decreased mortality, and there was a trend for this effect to be stronger for *A. cunninghamiana* (Table 7.13). Increased precipitation also decreased mortality of this species pair. For the *P. guajava* and *L. bullata* pair, increasing minimum temperature had a positive effect on mortality, while increasing maximum temperature and precipitation decreased mortality for both species, but the effects were stronger for *P. guajava* (Table 7.13). For the *Schefflera* species pair, increased minimum temperature decreased mortality of *S. actinophylla* only (Table 7.13). Increasing maximum temperature decreased mortality of both species, while increased precipitation decreased mortality of *S. digitata* but increased mortality for *S. actinophylla*.

**Table 7.13:** Parameter estimates from linear mixed effects models of climate variables versus RGR (estimated biomass in g/day * 1000) and generalised linear mixed effects models, with a binomial distribution and logit-link, of climate variables versus mortality, for each of the three species pairs. Parameter estimates are shown for effects of minimum temperature (T min), maximum temperature (T max) and precipitation; and for the climate variable’s interaction with the dummy variable ‘biostatus’, with parameter estimates given for the alien species group. Significant effects (P < 0.05) are highlighted in bold.

<table>
<thead>
<tr>
<th>Factor</th>
<th>A. cunninghamiana / R. sapida</th>
<th>P. guajava / L. bullata</th>
<th>S. actinophylla / S. digitata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>P-value</td>
<td>Estimate</td>
</tr>
<tr>
<td>RGR</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T min</td>
<td>1.609</td>
<td>&lt;0.001</td>
<td>4.242</td>
</tr>
<tr>
<td>alien</td>
<td>0.467</td>
<td>0.123</td>
<td>-0.840</td>
</tr>
<tr>
<td>T max</td>
<td>-0.660</td>
<td>0.002</td>
<td>-1.240</td>
</tr>
<tr>
<td>alien</td>
<td>-0.210</td>
<td>0.478</td>
<td>0.630</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-0.0045</td>
<td>0.035</td>
<td>0.0019</td>
</tr>
<tr>
<td>alien</td>
<td>-0.0042</td>
<td>0.164</td>
<td>0.0068</td>
</tr>
<tr>
<td>Mortality</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T min</td>
<td>-0.216</td>
<td>0.002</td>
<td>0.451</td>
</tr>
<tr>
<td>alien</td>
<td>-0.217</td>
<td>0.064</td>
<td>-0.263</td>
</tr>
<tr>
<td>T max</td>
<td>-0.074</td>
<td>0.302</td>
<td>-0.696</td>
</tr>
<tr>
<td>alien</td>
<td>-0.047</td>
<td>0.694</td>
<td>-1.275</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-0.0018</td>
<td>0.027</td>
<td>-0.0079</td>
</tr>
<tr>
<td>alien</td>
<td>0.0010</td>
<td>0.438</td>
<td>-0.0116</td>
</tr>
</tbody>
</table>
7.3.10 Growth/mortality versus predicted suitability

Although correlations between predicted suitability of SDMs and final harvest measures (biomass, leaf area) were near 0.5 for all species, the models were not significant (but a strong trend was found for *S. actinophylla*). Growth over time and survival correlated poorly with predicted suitability for *A. cunninghamiana*, while $R^2$ for *P. guajava* and *S. actinophylla* models ranged between 0.5-0.8 and models were all significant or at least showing a strong trend (Table 7.14). If regressions were fitted for *A. cunninghamiana* and *P. guajava* excluding the site Hastings, models were drastically improved, with all models significant except for survival of *A. cunninghamiana* (Table 7.14).

Table 7.14: Simple linear regressions of final biomass and leaf area, estimated shoot biomass over time and survival versus predicted suitability. Adjusted $R^2$, degrees of freedom (DF), $F$ and $P$ values shown. For *A. cunninghamiana* and *P. guajava* models excluding Hastings (H.) are also shown (due to the lower minimum temperatures at this site compared to the long-term average and missing data from Summer 2 due to rabbits).

<table>
<thead>
<tr>
<th></th>
<th>A. cunninghamiana</th>
<th>P. guajava</th>
<th>S. actinophylla</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R^2$</td>
<td>DF</td>
<td>$F$</td>
</tr>
<tr>
<td><strong>Final harvest:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>0.694†</td>
<td>2, 1</td>
<td>4.39</td>
</tr>
<tr>
<td>Leaf area</td>
<td>0.586</td>
<td>1, 2</td>
<td>5.25</td>
</tr>
<tr>
<td><strong>Over time:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.124</td>
<td>1, 4</td>
<td>1.71</td>
</tr>
<tr>
<td>Without H.</td>
<td>0.951†</td>
<td>2, 2</td>
<td>40.1</td>
</tr>
<tr>
<td><strong>Survival:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.268</td>
<td>1, 4</td>
<td>2.83</td>
</tr>
<tr>
<td>Without H.</td>
<td>0.408</td>
<td>1, 3</td>
<td>3.75</td>
</tr>
</tbody>
</table>

† Quadratic models.

7.4 Discussion

7.4.1 How do survival and growth of the three alien species compare to native relatives?

The results clearly showed that there were differences in survival and growth between the three alien and three native species and among the six sites. During the two summer seasons, mortality for all three alien species was low (4% for *A. cunninghamiana* and 1% for both *P. guajava* and *S. actinophylla* across the two summers and all sites) and lower compared to the native species (11% for *R. sapida*, 4% for *L. bullata* and 22% *S. digitata*). During winter, however, the three alien species
did not survive in the three coldest sites (Hastings, Nelson, Lincoln), and additionally for *Schefflera actinophylla* half the seedlings in Greymouth and all seedlings in the ‘suitable’ site of Auckland also died (in Winter 1 only). The three native species distributions’ generally extend as far south as Nelson and Greymouth, with Lincoln being outside the range of *L. bullata* and on the very edge of the range of *R. sapida* (Allan 1961; Moore & Edgar 1970), yet all the native species died in Hastings and Lincoln (except for a few *L. bullata*). *Rhopalostylis sapida* seedlings also died in Nelson, whereas all seedlings of *L. bullata* and about half of *S. digitata* survived. This unexpected high winter mortality of the native species could be due to seed/seedling sourcing from Auckland populations, whereas if the seeds had been sourced from regional populations, they might have shown local adaptation (e.g. Leimu & Fischer 2008). This could, however, also apply to the alien species: Park *et al.* (2012) for example found differences in cold hardiness among introduced populations of *Triadica sebifera*.

The alien species had higher biomasses and leaf areas in the suitable sites of Whangarei and Auckland (where they already have naturalised) compared to the native species, but differences in the other sites were mostly not significant. For seedling growth rates over the various seasons, differences between the alien and native species were more pronounced in Summer 1, with higher shoot biomass of the alien species compared to the native relatives found in many sites. Subsequently in Winter 1 and Summer 2 most differences disappeared, except for higher growth rates of *P. guajava* in Whangarei. The native species occasionally performed better; in Winter 1 for the *Schefflera* pair in Auckland and in Summer 2 in Nelson (*L. bullata* and *S. digitata* – although the latter had a very high mortality rate during Summer 2 compared to the alien species). Although high growth rates are often associated with successful invasive trees (Lamarque *et al.* 2011), another study found no differences in the average growth rates of invasive and native woody species when comparing seedling establishment in forest communities (Gurevitch *et al.* 2008). Moreover, a review of performance comparisons of alien and co-occurring native species showed that the native species usually had equal or higher performance in at least some growing conditions (Daehler 2003). Unlike the other two species pairs, for the *A. cunninghamiana* and *R. sapida* species pair, the native palm never performed better than the alien (in any of the sites). Germination and survival of *A. cunninghamiana* has previously been studied in Brazil, where this species has invaded Atlantic rainforest fragments: comparisons with a native palm, *Euterpe edulis*, showed 68% germination success for the alien and 30% for the native species, and persistence of germinated seeds through to seedlings was far higher for the alien species, with 30% seedling survival after one year for *A. cunninghamiana* compared to 3.5% for *E. edulis* (Mengardo *et al.* 2012). Although seed germination
could not be assessed in this study, in terms of survival across all seasons and sites 52% (166 compared to 109) more individual native palm species seedlings died in this study.

High SLA has also been shown to be associated with woody invasive plant species (Grotkopp & Rejmánek 2007). In this study, the alien species generally had higher SLA, although differences were not always significant. A review of 4473 species showed that alien plants had on average 15% higher SLA compared to native species (Ordonez et al. 2010). In this study, SLA of *A. cunninghamiana* was on average (across all sites) 10% higher compared to the native comparison species, 35% higher for *P. guajava* and 17% higher for *S. actinophylla*. Building low SLA leaves needs more investment per unit area, and with New Zealand woody species adapted to low soil fertility, they tend to invest more in leaf structure, resulting in lower SLA (Craine et al. 2006).

Seed germination could not be assessed accurately in this study, because of the uncertainty of whether lack of germination was due to climatic constraints, the seed not being viable or predation of seed. A further trial would have to reassess seed germination using a similar design to Pattison & Mack (2008) to prevent seed predation, and seed viability would need to be tested. However, the seed trials did show that during summer, *P. guajava* was able to germinate in all six sites, although germination success differed among sites. Naturally in the sites where seedlings did not survive the winter, successful germination is of no consequence.

### 7.4.2 How does climate influence survival and growth?

Differences between the highest biomass production (either in Whangarei or Auckland) and the lowest biomass production (in Greymouth) were considerable: total biomass was six, 11 or even 19 times higher (*A. cunninghamiana*, *S. actinophylla* and *P. guajava* respectively). Minimum temperature, maximum temperature and precipitation were associated with RGR of shoot biomass and with mortality. In particular, increasing minimum temperature had a strong effect on RGR of the *P. guajava* and *L. bullata* and RGR and survival of the *S. actinophylla* and *S. digitata* species pairs. The actual contributions of minimum versus maximum temperature have to be interpreted with some caution as these two variables are correlated (Pearson correlation of 0.8). This could explain the unexpected positive effect of increasing minimum temperature on mortality of the *P. guajava* and *L. bullata* species pair (that is, the higher minimum temperature, the higher the mortality, although the effect was weaker for the alien species), contrary to the strong negative effect of increasing maximum temperature found for this species pair. I found some evidence that the alien species were more strongly linked to climate measures: although few differences were found for RGR of shoot biomass (but increasing precipitation increased shoot biomass of *S. actinophylla*), minimum
temperature had a stronger effect on height of *A. cunninghamiana* and number of leaves of *S. actinophylla* and maximum temperature a stronger effect on leaves of *P. guajava* compared to their native relatives (data not shown). Increasing minimum or maximum temperature or precipitation also generally decreased mortality.

The three alien species are likely to have low frost tolerance because they originate from subtropical or tropical native ranges. The global occurrence data for the three species (as used in Chapter 3) showed that the bioclimatic variable BIO6 (minimum temperature of the coldest month) for *A. cunninghamiana* ranged from 3.5-12.8°C (5th-95th percentile) with a mean of 7.4°C; for *P. guajava* from 6.8-21.4°C with a mean of 14.8°C; and for *S. actinophylla* from 8.9-20.8°C with a mean of 14.8°C. The first half of winter 2012 was colder than usual in New Zealand (National Institute of Water and Atmospheric Research 2013). The average minimum temperature of the coldest month I recorded for Hastings was -1°C, and 1°C for Lincoln and Nelson, well outside the range the species occur globally (5°C for the three remaining sites, see Figure 7.6). For *P. guajava*, freezing tolerance has been experimentally tested in the lab in a study by Hao *et al.* (2009): leaf tissue freezing tolerance was -2.3 and -2.7°C for two cultivars, or -4.2 and -4.6°C if they had been going through a cold acclimation regime. This is consistent with the observed rare survival in Nelson, where an absolute minimum temperature of -2.2°C was recorded, and 100% survival in Auckland with an absolute minimum temperature of -1.9°C. There was some evidence that both *P. guajava* and *S. actinophylla* could recover from frost damage (personal observation): the three surviving *P. guajava* individuals in Nelson that had dropped all leaves during winter showed new spring growth, and one *S. actinophylla* that I considered to be dead after the winter season in Auckland produced new leaves the following summer. Therefore, all three alien species were able to tolerate partial frost damage. Nevertheless, for subtropical species to persist in colder climates, increases in minimum temperature and the associated reduced frost occurrences during winter will be critical (Vilà *et al.* 2007). This was demonstrated by *S. actinophylla* in Auckland, as a colder than usual winter (Winter 1) led to 100% mortality, whereas a milder winter at the same site resulted in 100% survival (1°C difference between average minimum temperatures during winter). Thus, a small change in climate and particularly minimum temperature can have a substantial effect on persistence of such alien species.

Low precipitation could be another limitation for growth and survival of the plant seedlings. Summer 2 was extremely dry in most parts of the North Island (National Institute of Water and Atmospheric Research 2013). As of 1 March 2013, many parts of the country had extremely dry soils, with extreme soil moisture deficit (> 130 mm of deficit) evident in most parts of the North Island and
some parts of the South Island, including Whangarei, Auckland, Hastings and Lincoln (National Institute of Water and Atmospheric Research 2013). Drought damage was only clearly visible on *S. digitata* (personal observation), particularly in Whangarei (with nine individuals dead from drought) and Auckland (11 individuals). Conversely, *P. guajava* and *S. actinophylla* appeared to be highly drought tolerant, with nil mortality for *P. guajava* and only one dead individual each for *S. actinophylla* in the three South Island sites. Results from the experimental drought responses in Chapter 5 are consistent with the high drought tolerance of *S. actinophylla* observed during the field experiment, while *P. guajava* was better able to withstand drought in the field than would have been expected from the shadehouse experiment. Such tolerance of extreme weather events, as predicted to occur more frequently with climate change (IPCC 2007), may be important for invasion success: if a drought damages the resident community, this may provide opportunities to invade (Diez et al. 2012; Sheppard et al. 2012). Additionally, unlike the alien species, *S. digitata* also did not cope well with flood: in the first couple of months after establishment of the Auckland field site, heavy rainfalls flooded the site temporarily (personal observation), which led to 92% mortality of this species recorded in February 2012.

**7.4.3 Is there any evidence for the enemy release hypothesis?**

If the enemy release hypothesis holds true, the native species should benefit more from exclusion of natural enemies, resulting in greater competitive ability (Keane & Crawley 2002). Thus, if there is support for the enemy release hypothesis, the pesticide treatment in this study should have benefitted growth of the native species more compared to the alien species. I found very little evidence for this in my results: the only significant difference of the pesticide by biostatus interaction was that pesticide-treated native species had a lower root/shoot ratio compared to alien species, which may suggest that the native species were able to produce more shoot biomass compared to the alien species when natural enemies were excluded. Herbivory damage was on average lower in pesticide-treated seedlings in Summer 2, showing the effectiveness of the pesticide application.

Although *A. cunninghamiana* and *S. actinophylla* experienced little herbivory damage, their native relatives were similarly unaffected. Moreover, although pesticide-treated *S. actinophylla* seedlings in Summer 1 had lower herbivory damage compared to non-treated plants, this did not translate into higher shoot biomass. Therefore, for these two species the alien species did not have an advantage due to release from natural enemies in this field setting. Although many studies have provided support for the enemy release hypothesis (e.g. Wolfe 2002; DeWalt et al. 2004; Cappuccino & Carpenter 2005; Vilà et al. 2005), recent studies have found similar damage on alien and native
species (Chun et al. 2010; Carrillo-Gavilán et al. 2012; Dostál et al. 2013). In terms of vertebrate browsing, the alien and native species within a pair were generally equally affected, but S. actinophylla was the only species that survived rabbit attacks in Hastings. Although herbivory has been identified as the primary cause of seedling mortality in natural populations (Moles & Westoby 2004), from the observed damage levels in this study, I conclude that invertebrate herbivory is unlikely to be an important constraint for growth of these alien species. Conversely vertebrate herbivory had severe effects in these anthropogenic environments (although browsing by cattle, pukeko and rabbits, in particular, would be less likely to occur inside a forest understory).

For the P. guajava and L. bullata species pair, the seedlings not treated with pesticide had lower final biomass and shoot biomass in Summer 1 in Auckland. Differences may have been more apparent in this site because the diversity of insect herbivores and intensity of herbivory tend to increase with temperature (Bale et al. 2002). Psidium guajava did not benefit from enemy release, moreover this species was generally affected more by herbivory compared to the native relative. These two species are the least related of the three alien-native species pairs, with different leaf anatomy. The higher SLA of P. guajava leaves compared to L. bullata may be one reason this species was more susceptible to herbivory (Ordonez et al. 2010). In their study, Heard & Sax (2013) also found that alien species were more affected by herbivory, and they suggested that this may facilitate coexistence in a community, as it offsets the higher competitive ability of the alien species. However, the low levels of invertebrate herbivory (on average <2% of the leaf area) observed in this study are unlikely to severely affect species performance and persistence.

7.4.4 Does survival and growth at the six sites correspond with predictions from species distribution models?

Performance in the field and predicted suitability of the species distribution models were highly correlated for growth and survival of S. actinophylla and P. guajava, but correlations were lower for A. cunninghamiana. Measures of biomass and leaf area for this latter species, however, were only available for four data points (due to rabbit browsing), making it difficult to show any relationships. Moreover, for shoot biomass over time, if the Hastings site was excluded, the models drastically improved. The high predicted suitability in Hastings in the SDMs (suitability 0.37 under current climate) was indeed not reflected in the performance of the seedlings in the field trials. However, the temperature and precipitation measured for the duration of this study differed widely from the long-term average used in the SDMs. As previously mentioned, the first half of Winter 1 was colder than usual (National Institute of Water and Atmospheric Research 2013), and this was very evident in June 2012 in Hastings (with an average daily minimum temperature of -1°C compared to 3°C later
in July and August). Such a sudden onset of winter would have been difficult for the seedlings to cope with. Although Winter 2 started milder, minimum temperatures for both winters were on average 2°C lower than the long-term average (averaged over the three winter months). Even with the cold start to Winter 1 being a region-wide occurrence, comparisons with records from a NIWA weather station show that regional winter temperatures in Hastings were overall slightly warmer in these two years than the long-term average (National Institute of Water and Atmospheric Research 2013). My particular field site thus had a cooler microclimate, and the possibility of successful establishment at different sites in the region cannot be excluded for *A. cunninghamiana* and *P. guajava*. In addition, the much lower growth rates in Hastings in Summer 2 compared to Summer 1 are most likely due to the problems caused by rabbit browsing. Similarly, for *S. actinophylla* (the most tropical species) in Summer 2, somewhat lower than expected growth rates in Whangarei (the warmest site) are likely due to half the *S. actinophylla* seedlings experiencing damage from cattle browsing. The high growth rates generally observed in Whangarei for all three alien species, in spite of the high productivity of neighbouring herbaceous vegetation, indicate that climate had a stronger effect on growth compared to competition from resident species.

The high rates of survival in Greymouth clearly supported the prediction that this site may provide suitable habitat for *A. cunninghamiana* and *P. guajava*, and surprisingly, to a lesser extent, even for *S. actinophylla*. However, the observation that the growth rates were much lower in this site may reflect nutrient availability rather than climate. Although I attempted to choose sites of similar soil nutrient conditions, the difficulty of obtaining a field site on the South Island’s west coast meant, that I had to use a site of different soil conditions compared to the remaining field sites. The particular field site chosen is not necessarily representative of the region. According to the Land Environments of New Zealand (LENZ), the west coast region around Greymouth in general is classified as type M, which has high natural fertility, or as type O, which has moderate to low fertility (Leathwick et al. 2002). The Greymouth field site in this study however had very little mineral nitrogen available (1.3 mg/kg), 5-14 times less than the other field sites, and also very low base saturation with low amounts of calcium, magnesium and potassium. Mineral nitrogen is usually the primary nutrient limiting plant growth: a global meta-analysis showed an average plant growth response of 29% to nitrogen addition (LeBauer & Treseder 2008). Although high SLA is usually associated with resource-rich environments (Reich et al. 1992), despite the low nutrient availability the seedlings at the Greymouth site had high SLA, possibly reflecting the high precipitation at this site. In evergreen shrubs and trees, increasing precipitation was correlated with decreasing leaf mass per area in a global data set (LMA; equals increasing SLA) (Wright et al. 2004). High root/shoot ratio is also a trait associated with resource-poor environments (Chapin et al. 1993). Despite the generally
much higher root/shoot ratio of *R. sapida* compared to *A. cunninghamiana*, this species did not perform better than the alien counterpart, even in the nutrient-poor site of Greymouth.

The only other study that has attempted a similar field validation of species distribution models (Pattison & Mack 2008) found no significant relationship between RGR of *Triadica sebifera* seedlings and suitability predicted by their CLIMEX model. CLIMEX is a process-based niche model that integrates modelled population responses to climate to create a series of annual indices, which are combined into an overall measure of favourableness (Sutherst *et al.* 2007). Pattison & Mack (2008), however, did find a significant positive correlation between seed germination and predicted suitability, although the correlation was higher between seed germination and mean daily minimum temperature. They additionally investigated competition, which was assessed in a separate study for my species (see Chapter 6). Generally, in my study the results of the SDMs and field trials, with the above mentioned exceptions and their possible explanations, are mostly consistent. Of course such field validations of SDMs are complicated because different factors and plant traits may be determining the frequency of invasive plants at the regional versus the local scale (Speek *et al.* 2011). While the SDMs were built using regional temperature and precipitation, the field trials monitored local climate (which may be quite different, as shown for Hastings). Moreover, opportunities for invasion may differ for a given invasive species from year to year as environmental conditions vary (Gurevitch *et al.* 2008), as demonstrated in this study by *S. actinophylla* performance in Auckland. To take some of this variation into account, as much as was feasible, this study was carried out over two summers, and for the three North Island sites, two winters.

Finally, the question remains of what effect climate change is likely to have on the three alien study species? The results of the field trials suggest that the three study species are currently able to persist in a wide range of temperature and precipitation conditions, as long as minimum temperatures do not drop below a certain level and frost nights are rare. A temperature increase of 0.7-5.1°C by the end of the century (Ministry for the Environment 2008) is therefore likely to lift some of the limitations to establishment due to cold sensitivity of the study species. Particularly, as even a modest change in mean temperature can lead to large reductions in the frequency of frost occurrence (Ministry for the Environment 2008). According to the SDMs, predicted suitability for *S. actinophylla* will remain similar in the six sites of this study. However, the field trials indicated that with increases in minimum temperature current limitations to its establishment due to cold snaps should disappear: a 1°C difference between average minimum temperatures in Auckland in Winter 1 compared to Winter 2 made all the difference to its survival. For the predicted suitability increases of *A. cunninghamiana*, in particular in Greymouth, this seems likely from my observed survival rates.
in the field. For *P. guajava*, Auckland is predicted to become even more suitable. Considering the high growth rates, biomass production and survival compared to their native relatives already observed in the currently suitable sites, with climate change these alien species may be able to increase in abundance, potentially outcompeting native species.

### 7.4.5 Conclusions

Considerable differences in growth and survival among the six sites support the assumption that climate is a dominant factor for performance of the alien species in this study. In the more suitable sites, performance of the alien species was frequently higher compared to the native species. Minimum and maximum temperature and precipitation influenced growth and survival of the seedlings. Conversely, invertebrate herbivory had negligible effects on seedling growth. Results from the SDMs correlated with survival and growth of seedlings in the field trials. This demonstrates that combining the results from climate based models with field trials growing the alien species within and beyond predicted ranges will give more reliable predictions of an invasive plant’s potential spread (Pattison & Mack 2008). Moreover, invasion risk under climate change may be assessed with higher confidence. This in turn will result in great benefits in the SDMs application in invasive species management. Here I showed that three alien subtropical species may become increasingly invasive with climate change. If such potentially invasive species can be controlled at an early stage of their naturalisation, this will be a cost-effective way to mitigate potentially large impacts.
Chapter 7: Performance of alien plants and their native relatives in differing climates: a field validation of SDMs

7.5 References


CHAPTER 8

General discussion
8.1 Research summary

Climate change and plant invasions have each been studied extensively, but few studies have considered their combined and potentially synergistic impacts. Climate change may provide opportunities for alien plants to expand into regions where they previously could not survive and reproduce. The aim of my PhD thesis was to investigate if such species from warmer native ranges, recently naturalised in New Zealand, may become more invasive under climate change, using Archontophoenix cunninghamiana, Psidium guajava and Schefflera actinophylla as model species.

To predict potential range expansions of these species, I applied species distribution models (SDMs), which have become a popular (and often the only feasible) tool to provide a first insight into the risk alien plants may pose in the future. To build appropriate models (using a maximum entropy algorithm; ‘Maxent’), I first investigated the implications of selecting different sets of climate variables (Chapter 2). Comparing the results of the SDMs including various sets of climate variables showed that if too many predictors were included, extrapolation to novel environments was required. As a consequence, highly unlikely predictions in some areas occurred, whereas reduced sets of variables resulted in more realistic predicted distributions. Therefore, using a reduced set of predictors, I compiled models to predict the potential distributions of the three model species under current climate and under a range of climate change scenarios (Chapter 3). These models indicated that the study species are likely to expand their range by the end of the century by on average (across eight climate change scenarios) 101% (A. cunninghamiana), 70% (P. guajava) and 112% (S. actinophylla).

Under experimentally manipulated elevated temperature and doubled CO₂, I then investigated growth rates of the three model species in environmental chambers (Chapter 4). This experiment showed that growth of S. actinophylla under doubled CO₂ was more vigorous compared to current CO₂, resulting in 45% higher biomass. There was no effect of CO₂ on biomass of the other two species, but root/shoot ratio was higher under doubled CO₂ across all species, and branching was increased for P. guajava. Effects of a 2.3°C temperature increase (as predicted for 2090) on seedling growth were generally small, however, P. guajava seeds germinated faster. I also studied drought responses in a shadehouse experiment (Chapter 5). The three species showed high drought tolerance, with no significant effects of a three week drought (resulting in estimated soil moisture of 22-26%) on growth of any of the species. A longer seven week drought (soil moisture 18-21%) reduced biomass significantly only for P. guajava, but there was no mortality.
Furthermore, I investigated the effects of competition of the alien species on closely related native species; and compared competitive effects to intraspecific competition among the native species (Chapter 6). Effects of competition from *A. cunninghamiana*, particularly under high densities, on a closely related native species, *Rhopalostyli sapida*, were stronger compared to intraspecific competition among the native species. *Psidium guajava* also showed some stronger competitive effects on *Lophomyrtus bullata* than intraspecific competition among *L. bullata* individuals. However, results were less conclusive for this species, with competitive effects of the alien and the native species often similar. For *S. actinophylla*, competitive effects could not be assessed, due to high mortality of the native species, *Schefflera digitata*.

Finally, to validate the SDMs, I conducted field trials to test whether the alien species would perform as predicted in suitable, potentially suitable and unsuitable habitats (as identified by the models): I grew seedlings in six sites across the country and measured their growth and survival in two-month intervals over 18 months (Chapter 7). Climate at the field sites was monitored, and I compared performance of the alien species to closely related native species. Additionally, I investigated the role of natural enemies, by applying a pesticide treatment to half of the seedlings. The field trials showed high performance of the alien plants in the sites identified as suitable. Growth and survival were frequently higher in the suitable sites compared to the native species and high even during a severe drought in summer 2013. However, severe frosts in three of the sites caused seedling mortality during winter. Leaf herbivory was low throughout, and there was no evidence for the enemy release hypothesis. Measures of shoot biomass and survival generally correlated well with predicted suitability of the SDMs (under current climate), confirming that the models have identified areas at risk from invasion. The projected increase in minimum temperature and reduced frosts under climate change conditions may allow increased seedling survival and growth in sites predicted to be suitable.

The combined results from the models, field trials and controlled environment experiments confirm the potential of the model species to maintain or increase their performance under future climate change, providing evidence of their potential invasiveness. By having higher confidence in the potential risk of newly naturalised plants and where they may spread, we can aid management decisions that lead to greater cost effectiveness: resources can be prioritised and allocated effectively, to control alien plants at an earlier stage of their naturalisation.
8.2 Potential invasiveness: success at establishment and spread

Having been transported and introduced to New Zealand for horticulture, the three model species, as with the majority of naturalised alien plants, have escaped from cultivation (Hulme et al. 2008). They are at an early stage of the invasion process, with few known occurrence records outside of cultivation (although only limited information on their distribution exists; e.g. 40 herbarium records for *A. cunninghamiana*; 16 for *P. guajava*; and four for *S. actinophylla* from the Auckland and Northland regions; New Zealand National Herbarium Network 2011). To continue to naturalise, and eventually enter the spread stage of the invasion process, they will need to overcome various barriers (see Figure 1.1 in Chapter 1; Blackburn et al. 2011). Some of these they have already overcome, having naturalised at least locally.

Propagule pressure, a key factor for successful establishment, was not investigated in this study, as species were selected on the basis that dispersal should not be a limitation (all being bird-dispersed and widely sold in nurseries). It is thus the abiotic factors, and in particular climate, which are likely to pose a major barrier to spread of these species away from their initial establishment sites. Additionally, biotic factors, such as competition from native species and presence of natural enemies, may also affect spread at a more local scale. Specific traits may assist the species to succeed in their new range. These factors are discussed below and synthesised in Table 8.1; and the influence of climate change is assessed, as well as the potential impacts on native species.
Table 8.1: Synthesis of results indicating invasion potential for the three model alien species.

<table>
<thead>
<tr>
<th></th>
<th>A. cunninghamiana</th>
<th>P. guajava</th>
<th>S. actinophylla</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average predicted spread by 2090 under climate change (Chapter 3)</td>
<td>101% increase 82,000 km² suitable</td>
<td>70% increase 114,000 km² suitable</td>
<td>112% increase 20,000 km² suitable</td>
</tr>
<tr>
<td>Drought tolerance (Chapters 5+7)</td>
<td>High</td>
<td>Medium-high</td>
<td>High</td>
</tr>
<tr>
<td>Minimum cold tolerance (Chapter 7)</td>
<td>5.7°C avg. winter temp. 8 frost nights</td>
<td>5.7°C avg. winter temp. 8 frost nights</td>
<td>6.7°C avg. winter temp. 2 frost nights</td>
</tr>
<tr>
<td>Performance under increased minimum temperature (Chapter 7)</td>
<td>Increased survival and growth</td>
<td>Increased growth</td>
<td>Increased survival and growth</td>
</tr>
<tr>
<td>Performance under increased maximum temperature (Chapters 4+7)</td>
<td>Equal or decreased growth</td>
<td>Increased survival and seed germination, equal or decreased growth</td>
<td>Increased survival, equal or decreased growth</td>
</tr>
<tr>
<td>Performance under elevated CO₂ (Chapter 4)</td>
<td>No change</td>
<td>No change</td>
<td>Increased biomass</td>
</tr>
<tr>
<td>Susceptibility to invertebrate herbivory (Chapters 6+7)</td>
<td>Low</td>
<td>Medium</td>
<td>Low</td>
</tr>
<tr>
<td>Traits (Chapters 6+7)</td>
<td>High RGR High biomass High survival High SLA Seed germination ?</td>
<td>At times high RGR At times high biomass High survival High SLA High seed germination</td>
<td>High RGR High biomass High survival High SLA Seed germination ?</td>
</tr>
<tr>
<td>Competitive effects (Chapter 6)</td>
<td>Strong</td>
<td>Medium</td>
<td>?</td>
</tr>
<tr>
<td>Invasiveness elsewhere (Chapter 1)</td>
<td>Brazil only</td>
<td>Widespread</td>
<td>Tropical islands, Florida</td>
</tr>
<tr>
<td>Other attributes (Chapter 1 and observations from Chapters 4-7)</td>
<td>Bird-dispersed Shade tolerant</td>
<td>Bird-dispersed Can re-sprout from cut stumps</td>
<td>Bird-dispersed Shade tolerant Can re-sprout from cut stumps Can grow as epiphyte</td>
</tr>
<tr>
<td>Invasion potential</td>
<td>High</td>
<td>High</td>
<td>High (under climate change only)</td>
</tr>
</tbody>
</table>

8.2.1 Climate

Species distribution modelling using six bioclimatic variables showed that, at least for A. cunninghamiana and P. guajava, there is considerably more suitable habitat in New Zealand compared to where these species currently occur, indicating that they do not yet occupy their full potential range. Moreover, a substantial increase in suitable habitat is predicted under climate change. Increasing potential ranges under climate change have been found for other invasive trees such as Robinia pseudacacia in Austria (Kleinbauer et al. 2010), Acacia nilotica in Australia (Kriticos et al. 2003) or Tamarix spp. in the Northwestern United States (Kerns et al. 2009). Regional
decreases in suitability, as found in some other studies (e.g. Bradley et al. 2009; Kriticos et al. 2011) were only rarely predicted for the study species: for example, the far north is predicted to become less suitable for *A. cunninghamiana* under some climate change scenarios. I hypothesised that this was associated with the reduced precipitation projected for that region becoming a limiting factor (Ministry for the Environment 2008). However, interpreting this finding together with the results from the field trials, particularly the high survivorship during the severe drought in summer 2013, indicates that expecting potential range reductions due to reduced precipitation may be a conservative assumption. Although a few seedlings died in Auckland, survival was higher compared to the native relative, and no visible drought damage was observed on surviving seedlings. Moreover, the results from the experimental drought treatments in the shadehouse confirmed the high drought tolerance of *A. cunninghamiana*. It has been suggested that changes in precipitation during specific seasons appear to be a particularly important predictor of plant invasion (Bradley et al. 2010). Moreover, a meta-analysis showed that invasive species tended towards more negative responses to decreased precipitation compared to native species (Sorte et al. 2013). However, for the three study species this is unlikely to be the case: the experimental drought study showed 100% survival for all three species, and although growth of *P. guajava* was severely affected by the longer drought, comparisons with performance in the field indicated that in a more natural environment the species was highly tolerant of drought (tolerating extreme soil moisture deficits of > 130 mm; National Institute of Water and Atmospheric Research 2013).

For the subtropical species in this study, decreased mortality due to increasing minimum temperatures and decreasing frost occurrences appeared more critical (Vilà et al. 2007). Frost conditions may result in the formation of ice crystals within or between cells, which can cause physical damage, leading to either tissue-specific damage or mortality (Inouye 2000). Severe frosts did indeed result in 100% mortality of the seedlings in the field trials, although *A. cunninghamiana* and *P. guajava* were able to tolerate occasional temperatures below freezing and partial frost damage. The inclusion of various sites and seasons in the field trials showed key responses to climate: for example, a 1°C difference in average minimum temperatures between two winters at the same site (Auckland) increased survival from 0% to 100% for *S. actinophylla*. Cold tolerance of the three species is estimated to lie somewhere between an average winter minimum temperature of 3.0-5.7°C with infrequent frost nights for *A. cunninghamiana* and *P. guajava*; and 5.7-6.7°C with rare frost nights for *S. actinophylla*. It is evident from the field trials that the predicted temperature increase of 0.7-5.1°C by the end of the century and reduced frost occurrence (particularly considering that even a modest change in mean temperature can lead to large reductions in the
frequency of frost occurrence; Ministry for the Environment 2008), will result in more suitable habitats in New Zealand for the three species, as predicted by the SDMs.

Increasing temperature and heat waves associated with climate change (Ministry for the Environment 2008) are unlikely to be a limitation for the three species: originating from warmer native ranges, they are expected to be adapted to such conditions (Vilà et al. 2007). The field trials showed very low mortality during summer when temperatures were at their maximum; and increasing maximum temperature was correlated with reduced mortality of P. guajava and the Schefflera species. Increasing maximum temperatures may reduce relative growth rates, although this equally affected the native species. Furthermore, the environmental chamber experiment confirmed that the species were able to maintain their growth rates under summer temperatures such as those expected in Auckland by the end of the century. Additionally, elevated CO₂ greatly increased biomass of S. actinophylla, while the other two species maintained constant biomass. Combining elevated temperature and CO₂ significantly enhanced height of S. actinophylla only. Accordingly, a meta-analysis of temperature and CO₂ manipulation experiments of plants (not separated into native versus invasive plant species) showed that the combined treatment of elevated temperature and CO₂ usually resulted in less than additive effects (Dieleman et al. 2012). Although this study did not test responses of native species, a recent meta-analysis showed that generally increasing CO₂ benefitted terrestrial invasive plant species more than native species (Sorte et al. 2013).

Climate is the dominant factor influencing plant distributions on large spatial scales (Woodward 1987). On a smaller spatial scale, other factors may limit the distributions of plant species. Thus, the results from SDMs should indicate the maximum possible extent of the range, that is, an overestimation of the suitable range. On the contrary, survival outside the range predicted to be suitable (under current climate), such as was the case for A. cunninghamiana and to a lesser extent for S. actinophylla in Greymouth, would suggest an underestimation of the potentially suitable range by the SDMs. However, modelling studies have shown that even after 200 years, invasive woody species (Lonicera japonica, Triadica sebifera) have not reached equilibrium with climate: they have not yet colonised all areas predicted to be suitable (Pattison & Mack 2008; Beans et al. 2012). Therefore, although by the end of the century as much as 115,805 km² (A. cunninghamiana; worst case climate change scenario, 43% of New Zealand’s area), 164,450 km² (P. guajava; 62%) and 31,257 km² (S. actinophylla; 12%) are predicted to become suitable habitats for the three species in New Zealand, the residence times of these species might not be long enough to reach these full potential ranges. Assuming average spread rates of 2-42 km/year (nearest neighbour
to furthest neighbour), as calculated for 100 alien plant species in New Zealand (Aikio et al. 2010), spread from Auckland to Hastings could take anything from as little as eight years to as long as 180 years, for example. Higher rates of spread would probably reflect human mediated dispersal, such as increased planting effort. Colonisation is unlikely unless there is propagule pressure for geographically separated areas (e.g. South Island): people might decide to plant these species in their gardens, if the climate becomes mild enough. Planting alien horticultural species, which are invasive elsewhere, in marginal climates should indeed be discouraged, as this may result in further range expansion (Beans et al. 2012). The sale of plants in nurseries beyond their range aids the spread of garden plants. For example, in Europe native species are sold in commercial nurseries on average 1000 km further north than their natural range limit, which was proposed to give them “a head start on climate change” (Van Der Veken et al. 2008).

While some studies have shown that anthropogenic influences are more important in determining alien plant distributions (Hulme 2009; Marini et al. 2012), for subtropical species to spread southwards in New Zealand (i.e. towards higher latitudes) climate is very likely the key limiting factor. Other studies have highlighted the importance of climate and the influence of climate change on alien species from warmer native regions. For example, in the eastern Otago region of New Zealand, alien species richness in native forests could mainly be explained by regional climate and land cover variables: warm, dry and small forest fragments had higher numbers of alien species (whereas local soil and stand structure variables had much smaller effects on alien species richness; Ohlemuller et al. 2006). Another study showed that neophyte (i.e. alien species introduced after 1500) species richness could largely be explained by mean annual temperature and the extent of urban areas; but temperature increase had a stronger effect than ongoing urbanisation on the potential increase in neophyte species richness in Switzerland (Nobis et al. 2009). Because many areas in Austria are currently only slightly too cool, climate change will greatly enhance invasion success of Ambrosia artemisiifolia (Essl et al. 2009). Furthermore, climate change, and in particular the lengthening of the growing season and reduced frosts, has allowed evergreen alien ornamental broad-leaved species to colonise forest areas in southern Switzerland (Walther 2002). In particular, similar to the invasion of A. cunninghamiana in New Zealand, another palm species, Trachycarpus fortunei, is invading southern Switzerland (Walther et al. 2007). This species has successfully colonised deciduous forests, having established as the northernmost palm population. Although T. fortunei has been cultivated in that region for decades, it has not been able to establish until recent climate change resulted in continuously warmer and shorter winter seasons (Walther et al. 2007). Walther et al. (2007) suggest that, as palms have been used as effective bioindicators of warm climates in the palaeobotanical literature, they may also be useful as bioindicators of current climate
change. Hence, the recent naturalisation of *A. cunninghamiana* and its future spread may be indicative of ongoing climate change. Similarly, there are a few other naturalised palm species in New Zealand (*Howea belmoreana, Howea forsteriana, Livistona australis, Phoenix canariensis, Syagrus romanzoffiana, Trachycarpus fortunei, Washingtonia robusta*), most of which have only naturalised in the last decade (New Zealand Plant Conservation Network 2013).

### 8.2.2 Biotic factors

Establishment success of alien plants in a particular community may be hindered by biotic resistance: this includes competition from resident plant species and the presence of natural enemies (Levine *et al*. 2004). Although results from a meta-analysis showed that biotic resistance significantly reduced alien seedling establishment and performance, biotic resistance is unlikely to completely repel invaders (Levine *et al*. 2004). Biotic factors were not the main focus of this thesis, but the various experiments gave some evidence that biotic resistance is generally unlikely to limit invasion success of the three study species. Planting of the seedlings in the field trials in communities of competitive pasture grasses with an aboveground biomass productivity of 170-570 g/m² (ten weeks growth) was highly successful. The frequently higher performance of the alien compared to the native species, observed both in the competition and field experiments (discussed in more detail in the section below) may allow them not only to establish, but to potentially outcompete resident native species.

Other than the direct effects of climate change on plant growth and distributions discussed above, climate change may also have indirect effects by altering species interactions (Thomas 2010). An important question, not directly addressed in this study, is whether relative performance and competitive interactions will remain the same under climate change conditions. Evidence from the few studies addressing this question is not conclusive: a meta-analysis of climate change effects (temperature, CO₂, precipitation) on performance of alien and native species showed that alien and native species generally responded similarly to the projected changes in climate (Sorte *et al*. 2013). However, Sorte *et al*. (2013) suggested that if the current trend was for alien species to outperform native species, then this will not be altered under climate change. Furthermore, one study experimentally addressing competitive interactions under elevated temperature for three herbaceous invasive species in Europe showed that climate warming did not alter competitive balance between alien-native species pairs (Verlinden *et al*. 2013). Competitive rankings between 14 invasive alien-native species pairs were also not altered by elevated CO₂ concentrations, however, the relative success of the alien species increased because native species had on average a reduced competitive response under elevated CO₂ (Manea & Leishman 2011). Extreme events such as droughts associated with climate change could also affect biotic interactions, as they may weaken
native resident species, providing more opportunities to invade (Diez et al. 2012; Sheppard et al. 2012).

The presence of natural enemies can provide biotic resistance to invasion, while their absence can greatly contribute to invasion success: it is frequently suggested that invasive species succeed in their new range because of the absence of their specialist enemies (i.e. the enemy release hypothesis; Keane & Crawley 2002). In the field trials, I quantified the extent of leaf herbivory and tested its effect on seedling performance to determine whether there was any evidence for enemy release. Although levels of leaf herbivory damage were usually low, there was no support for the enemy release hypothesis, as the native species were equally unaffected. Nevertheless, it appears to be unlikely that the establishment of A. cunninghamiana and S. actinophylla will be limited by natural enemies: not only did they experience very little herbivory damage in all six field sites, but also in the shadehouse environment, in conditions where invertebrate herbivores frequently thrive. Both species were unaffected by an outbreak of spider mites and leafrollers. The only herbivores observed to favour S. actinophylla were aphids and scale insects (in the shadehouse environment), but even in their presence, performance of the seedlings was not visibly reduced (personal observation). Conversely, the congeneric native species, S. digitata, was highly susceptible to spider mite attack (Tetranychus urticae Koch; a globally occurring horticultural pest originally described from Europe), resulting in almost 100% mortality of the seedlings. A review of 63 studies suggested that there may be opposing effects of native and alien herbivores (including vertebrates, molluscs and insects) on plant invasions: while native herbivores provide biotic resistance, alien herbivores would facilitate invasions, by disproportionally reducing the abundance of native species (Parker et al. 2006). The observed response to spider mites in the two Schefflera species is consistent with this theory.

For Psidium guajava I found evidence that this species was attacked more, not less, by herbivores than its native counterpart. However, the levels of leaf herbivory observed in the field trials were unlikely to severely reduce its performance. Conversely, the species was severely affected by the spider mite infestation in the shadehouse environment, although unlike S. digitata, this did not lead to mortality, but instead reduced growth and leaf shedding. Psidium guajava was also favoured by leafrollers, both in the field and the shadehouse environments; therefore this species seems susceptible to a variety of generalist herbivores. Even though there was still some evidence for higher competitive effects of the alien neighbours on growth of native target plants compared to native neighbours, it is highly likely that without the presence of natural enemies, P. guajava could have been much more competitive. Although high SLA may favour this species in terms of fast
growth, it may render it highly susceptible to herbivory (Ordonez et al. 2010). In India, 80 species of insects and mites have been reported to attack *P. guajava* (Mani & Krishnamoorthy 2007). Thus, in certain conditions, and perhaps particularly under low nutrient availability and in the presence of natural enemies, invasion of *P. guajava* may be unsuccessful in spite of a suitable climate. Moreover, increasing temperatures due to climate change will also affect development, survival, range and abundance of insect herbivores (Bale et al. 2002). However, the high growth rates of seedlings in Whangarei and Auckland, in spite of frequently experiencing higher leaf herbivory compared to the other sites, indicate that the benefits of increased temperature on growth rates may more than offset the damage from increased herbivory.

### 8.2.3 Traits of the alien species

Besides the biotic and abiotic conditions that provide opportunities for invasion (‘niche opportunities’; Shea & Chesson 2002), alien species may often share traits that make them successful invaders: invasive species have been shown to differ from native species in traits related to physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness (van Kleunen et al. 2010).

Although there are no traits that universally predict invasion success, high growth rates and biomass production are traits often associated with woody invasive species (Grotkopp & Rejmánek 2007; Lamarque et al. 2011). In this study, the field trials frequently showed higher biomass production of the alien compared to the native species, at least in the climatically suitable sites. Magnitudes of differences amounted to as much as 2.4 times higher biomass for *A. cunninghamiana* compared to *R. sapida*; while for *P. guajava* and *S. actinophylla* maximum biomass production was more than six-fold compared to their native counterparts. *Schefflera actinophylla* obtained the largest biomass in the competition experiment but it was a native species, *L. bullata*, which had the fastest relative growth rates. Thus, while generally *A. cunninghamiana* and *S. actinophylla* had higher growth rates and biomass production compared to their native counterparts, a potential advantage of *P. guajava* over *L. bullata* is much more context-dependent: in warm climates and under low herbivore pressure, its biomass production was larger by several orders of magnitudes (compared to other conditions and compared to the native relative). Therefore, the availability of sites that allow vigorous growth of this species, such as observed in Whangarei, are likely to increase with climate change.

High rates of survival have also been associated with invasive woody species success (Lamarque et al. 2011). Conversely, Bellingham et al. (2004) did not find that relative growth rates
and survival predicted invasiveness (measured as the rate of geographic spread) of naturalised woody species in New Zealand. For the three model species in my study, rates of survival were very high except when temperatures dropped below their respective cold tolerance (see above). The seedlings survived a wide range of conditions both in the field and in the artificial environments, including drought, flood, competition and herbivory. Alien seedling survival was much higher than for the native species (except for *L. bullata*, which was more tolerant to a wider range of conditions compared to the other two native species). Another trait that many invasive species share is high specific leaf area (SLA), allowing a plant to intercept more light and thus enabling faster growth (Grotkopp & Rejmánek 2007; Ordonez *et al.* 2010). This study showed that the alien species had higher SLA compared to the native species, both in the shadehouse (competition experiment) and field (although differences were not always significant). Moreover, SLAs measured in the environmental chamber experiment across all treatments were frequently even higher than observed in the competition and field experiments (on average 165 cm$^2$/g for *A. cunninghamiana*, 168 cm$^2$/g for *P. guajava* and 178 cm$^2$/g for *S. actinophylla*).

Seed germination rates may also be higher in invasive woody species compared to native species (Lamarque *et al.* 2011). The germination stage is critical in plant life history; and the ability to germinate rapidly under a wide range of environmental conditions is thus important for invasive species success (Beckmann *et al.* 2011). In this study, germination of native seeds was never successful, either when sown indoors in seed trays and potting mix under well watered conditions, or out in the field in natural soil under a range of climatic conditions. Germination rates of the alien species indoors were high (38-64%), and even higher in the environmental chambers (75% *S. actinophylla*; 95% *P. guajava*), but lower in field conditions (*P. guajava* only, 2-40%). In the artificial settings, the first seeds germinated 11 days (environmental chambers) or 12 days (indoors) after sowing for *S. actinophylla*; 14 days (environmental chambers) or 27 days (indoors) for *P. guajava*; and 46 days (indoors) for *A. cunninghamiana*. Climate change is expected to have an important effect on plant regeneration from seed, because temperature and water supply are critical for seed germination (Walck *et al.* 2011). Temperature increased rates of germination of *P. guajava*. Palm seeds generally take a long time to germinate, but although I kept monitoring the *R. sapida* seed trays for a year, no germination occurred for this species. An unpublished experiment comparing germination of *A. cunninghamiana* with *R. sapida* yielded a 24% germination success in *A. cunninghamiana*, with germination occurring within a few months, and 1% germination success in *R. sapida*, with germination taking > 18 months (J. Sullivan, unpublished data). The differences in seed germination between the alien and native species could be a result of an introduction bias: it has been shown that cultivated alien species germinated earlier and more successfully compared to
related native species in Switzerland (Chrobock et al. 2011). Although this study provided evidence that *P. guajava* can germinate in a wide range of both natural and artificial environments, unfortunately evidence of germination for *A. cunninghamiana* and *S. actinophylla* seeds in the field setting is missing. Another study should therefore repeat a seed trial to determine the influence of climate, using an improved design, where seed viability is tested and the role of seed predation investigated. For example, rats have been reported to eat the seeds of *P. guajava* (West 1996), which could be a major limitation for recruitment of this species, although at least some seeds successfully germinated in all six field sites in this study.

### 8.2.4 Impacts

The most common mechanism by which alien plants impact on native species is through competition (Levine et al. 2003). The competition experiment showed support for the hypothesis that effects of competition from alien neighbours (interspecific competition) are stronger than effects of native neighbours (intraspecific competition). This was more evident under high density, and more evident for *A. cunninghamiana*. Therefore, in a native forest site such as St John’s College bush in Meadowbank, Auckland (where the species has widely naturalised; Cameron 2000), these results imply that within a few decades, this forest may be dominated by alien instead of native palms, if control efforts are not continued.

Martin et al. (2009) compiled a global list of invasive plants which have been shown to invade intact forest communities. These species are shade tolerant and include proportionally more woody species. Such invasions are a slower process than invasions on disturbed sites, but they lead to potentially severe and long-term impacts (Martin et al. 2009). This list includes *S. actinophylla*, and although *A. cunninghamiana* as a ‘new’ invasive species was not mentioned, this species is likely to belong to this group as well. *Psidium guajava*, however, is intolerant of deep shade, and it is therefore unlikely to invade undisturbed forest. However, other natural ecosystems may be at risk from invasion by this species. *Psidium guajava* has elsewhere been observed to have adverse impacts in both agricultural and natural habitats, such as on the Galapagos Islands, where it is widely replacing native highland vegetation (Tye 2001). As in the Galapagos Islands, adverse impacts in New Zealand may therefore not only be restricted to forest edges and disturbed areas, but could include a range of rare open ecosystems that contain low-growing vegetation (see list of Williams et al. 2007).

Generally, a review of pairwise experiments showed that the presence of alien species reduced biomass or size of native species on average by nearly 50% (Vilà & Weiner 2004). Moreover,
a meta-analysis of field studies showed that invasive plants severely reduced fitness, growth, species abundance and diversity of native plant communities (Vilà et al. 2011). Although the study by Vilà et al. (2011) did not find a significant difference in impact between island and mainland ecosystems, Pyšek et al. (2012) found that invasive plants are far more likely to cause significant impacts on species richness on islands compared to the mainland. The high amount of endemism in New Zealand would be of particular concern, including the three endemic species used in this study. Conversely, introductions of alien plants do not always have significant impacts on plant communities, even in New Zealand (e.g. Meffin et al. 2010). However, robust quantitative assessments of impacts of alien plants have been undertaken for fewer than 200 species globally (Hulme et al. 2013). In order to control alien species at an early stage of their invasion, we cannot afford to wait until impacts are visible. Rather, if we have sufficient reason to suggest an alien species may become a problem, such as because of its traits, higher performance compared to native species and suitable climate in the recipient region (see Table 8.1), it is more cost-effective to act early.

8.3 Management implications

8.3.1 Management of the three study species in New Zealand

To synthesise, climatic conditions are important for the establishment and potential spread of the three alien species, although they are able to survive under a wide range of conditions, including severe droughts, as long as minimum temperatures do not drop below their cold tolerance, and frost nights are rare or infrequent. Biotic resistance is unlikely to be important, but natural enemies may be a limiting factor for P. guajava under some conditions. The three species share some traits that may contribute to their invasiveness, such as high growth rates, SLA and biomass production, high rates of survival and seed germination. They have the potential to impact on native species, primarily through competition. Thus, they appear to have both the attributes to become invasive, and the recipient region (i.e. New Zealand) appears to provide the biotic and abiotic conditions that offer opportunities to invade. With climate change, suitable habitat is predicted to further increase in New Zealand, and survival and growth rates of the species are likely to either remain constant or increase.

With the several independent lines of evidence from the models, controlled environment experiments and field trials indicating the potential invasiveness of these species (Table 8.1), I recommend that management action is taken now to prevent their spread. Concerning the Auckland region, I would advise the Auckland Council to move these three species from the ‘Research Plants’
category to the ‘Surveillance Pest Plants’ category (prohibited from sale, propagation, distribution and exhibition) in the next version of their Regional Pest Management Strategy. This is considered most crucial for *A. cunninghamiana*, due to its tolerance of a wide range of climatic conditions and its universally higher performance compared to *R. sapida*, as the only native palm species in New Zealand. This study has provided evidence that the risk of *A. cunninghamiana* outcompeting the native palm is relatively high, and its spread could result in the gradual replacement of *R. sapida*.

Ideally, for *P. guajava*, another assessment would be undertaken to further test the hypotheses about the role of nutrient availability, natural enemies and seed predation on its performance. However, this species clearly has the potential to grow vigorously under current conditions at least in the warmest regions of the country. Although it is less likely that species such as *L. bullata* will be directly outcompeted and intact forests are unlikely to be invaded, other more open natural ecosystems may be at risk, as once established this species may become very persistent due to its ability to tolerate and recover from various stresses and re-grow from cut stumps.

*Schefflera actinophylla* is at a very early stage of invasion in New Zealand, but also the species with the most tropical origins. It is not surprising therefore, that the SDMs and field trials indicate that even Auckland is only marginally suitable for this species under current climate. However, this study clearly showed the immense potential for this species to be highly invasive once climatic limitations are lifted. Characteristics that facilitate its invasion potential are: tolerance of a wide range of frost-free climate conditions; extremely high survival rates; high biomass production; positive response to elevated CO$_2$; ability to recover from mammal herbivory (cattle, rabbits); shade tolerance; and being able to re-grow from cut stumps and stem fragments. Although management action could possibly be delayed for a few decades for *S. actinophylla*, we have the rare opportunity to detain an invasion with potentially severe impacts and even total control may be achieved.

To prevent further spread of these species outside Auckland, the Northland Regional Council needs to be alerted to consider banning the legal sale and planting of the species as well. Additionally, more southern regional councils, in areas that were shown to be suitable, need to be made aware of the potential invasion risk of these species, so that possible infestations can be controlled early. As these species have not naturalised in these regions yet, they should be listed as ‘Total Control Pest Plants’, that is, plants for which eradication is a feasible aim. The data contained in this thesis can be used to conduct cost-benefit analyses for inclusion of these species in their respective regional pest management strategies. Furthermore, these species could be considered for inclusion in the National Pest Plant Accord to ban them from sale nationwide.
The pool of about 25,049 alien species in New Zealand (Diez et al. 2009) will include many other such subtropical woody species. Given that it is impractical to carry out a thorough empirical assessment of potential invasiveness for every one of them, how should they be managed? Prohibiting all such species from sale on the precautionary principle is likely to meet with much resistance. However, if there is any indication that a species may show invasive behaviour, such as: being invasive elsewhere, tolerating a range of climate conditions, resistance to herbivores, sharing traits likely to assist its spread, and if a species appears likely to have an impact on native species, preventative action should be seriously considered. In general, it is certainly more cost-effective (and ecologically sound) to prohibit a few too many species from sale compared to managing widespread invasions with potentially severe impacts. Moreover, encouraging the public to plant native species, instead of the alien, will be highly beneficial not only for native fauna and restoration attempts, but also in averting negative impacts associated with plant invasions.

8.3.2 Management of new weeds under climate change

Climate change poses great challenges for the management of invasive trees and shrubs (Richardson & Rejmánek 2011). Although traditionally the ‘typical weeds’ were early successional herbaceous species adapted to disturbance, and studies on these still dominate the literature (Martin et al. 2009), the importance of woody invasive species is increasingly being recognised (Richardson & Rejmánek 2011). Moreover, the traditional assumption that undisturbed environments such as forests are not invasible is being challenged; with alien, shade tolerant, and frequently woody, species observed to invade undisturbed forest communities (Martin et al. 2009). Among the currently listed invasive woody species, those originating from temperate regions dominate (Richardson & Rejmánek 2011), but climate change is likely to affect this trend: the potential threat of subtropical alien woody species due to climate change needs to be considered across temperate regions globally. Efforts to combat plant invasions have largely been reactive, that is, a new species becomes invasive, and subsequently a plan is developed to manage it (Thuiller et al. 2007). With limited resources available and an ever-increasing number of potential weeds, it is crucial that more preventative management is taken.

Bradley et al. (2010) suggested that experimental studies should be used to directly test predictions gained from modelling studies, an approach that was taken in this study. The increased confidence in the model predictions greatly benefits management of invasive plants (Bradley et al. 2010). Naturally, the pool of alien species is too large to make it feasible to carry out such a thorough assessment for each and every one of them. However, the results of this comprehensive study on the potential invasiveness of three subtropical woody alien species clearly show that there
is need for concern about this ‘new’ group of potential weeds. Moreover, it is critical to include climate change into weed risk assessments. In Australia, a report was carried out for 41 sleeper weeds, assessing their potential distributions under climate change (Scott et al. 2008). For some species Scott et al. (2008) also carried out environmental chamber studies to further inform and develop the models (process-based, i.e. CLIMEX). This showed a general predicted shift southwards (Scott et al. 2008). The results were used to give management recommendations and to direct future research. It is imperative that such reports should be conducted globally. Although the application of species distribution models to climate change and invasive species has been criticised, this study and others show that SDMs do have an important role to play: SDMs are the easiest, fastest and cheapest way of assessing potential invasion risk. However, I have highlighted in Chapter 2 that careful model building and evaluation is essential. Araújo & Peterson (2012) suggested that criticism of SDMs has often been misplaced, resulting from confusion between what the models actually show versus what people desire they would show. Predictions of potential distributions of invasive species should be considered as risk maps, with overprediction being a desirable property (Jiménez-Valverde et al. 2011). Theory, experimental studies and field trials can be used to further guide the assessment of invasion risk in various locations and context, as undertaken in this study.

One major challenge for the management of invasive plants is that even if scientists have demonstrated that certain alien species have negative impacts on native species, communities or ecosystems, the species might still be valued by at least some groups of society, such as garden-lovers for ornamental plants (Simberloff et al. 2013). Moreover, it is difficult to convince the public of the importance of early control of potentially invasive species, because people will only perceive an impact, if both the alien species and its impact are clearly visible (Simberloff et al. 2013). Increasing awareness of plant invasions is essential, in particular among the horticulture industry, as they have the capability to prevent many future invasions (Bradley et al. 2012). A major problem with addressing climate change is that its effects are usually ‘slow’ and therefore go unnoticed. Thus, widely publicising scientific evidence for the impacts of plant invasions and climate change to both land managers and the general public is essential to mitigate negative impacts of these two important drivers of global change.

As stated in the report by McGlone & Walker (2011) on the ‘Potential effects of climate change on New Zealand’s terrestrial biodiversity and policy recommendations for mitigation, adaptation and research’, “the arrival of new weeds and increased invasiveness of existing weeds is one of the most troubling likely consequences of climate change”. It is time to start acting on it.
8.4 Future research

Effective management of invasive plants in the 21st century necessitates a better understanding of invasion risk under global change (Bradley et al. 2010). Interactions between climate change and plant invasions are complex, and additionally complicated by biotic interactions (Thuiller et al. 2007). The dominant drivers of global change and plant responses will vary with location and invasive species under consideration, making it difficult to generalise the impact of global change on plant invasions (Bradley et al. 2010). Thus, more species-specific assessments are necessary, combining multiple factors of global change and forecasting methods (Bradley et al. 2010). Validating of models with field trials such as done by Pattison & Mack (2008) and in Chapter 7 is very rare. Although this thesis includes a thorough assessment of potential invasiveness under climate change, by necessity, the study had to be limited to three species. Similar assessments should be carried out for a larger group of alien plants, in order for generalisations to be drawn. In particular, little is known about the invasion ecology of most of the 622 woody invasive species globally (Richardson & Rejmánek 2011). The importance of early successional species in invasion ecology may be overstated, and generalisations from such research may not apply to invasions into forests (Martin et al. 2009). Therefore, more research focus needs to be on the group of woody invaders, particularly for environmental weeds that have the potential to invade undisturbed environments.

To address management of new weeds as a consequence of climate change in New Zealand, a report needs to be compiled to assess potential invasion risk, similar to the report on sleeper weeds in Australia mentioned above (Scott et al. 2008). As a minimum, such a report should include SDMs under current and future climate change scenarios, and a literature search of alien species’ invasive behaviour elsewhere. For the high risk species emerging from such a study, additional experiments could be conducted to test seed germination, growth rates and survival. The results of the report should be used to prioritise weed control and surveillance efforts.

To further extend a thorough assessment of potential invasiveness, tests in several microhabitats in each (potentially) suitable region would be beneficial because patterns of invasion are likely to vary substantially with local site conditions. With exception of the SDMs, this study only considered the seed and seedling life stages (but more seed germination trials are necessary). This is justified because early developmental stages are more sensitive to climate than adult stages; and seedling establishment is a critical life stage for the success of an invasion (Gurevitch et al. 2008; Walck et al. 2011). Yet, further assessment of the effects of climate change on adult plants, including effects on phenology and reproductive output, would be useful. There are other drivers of global change, which were not explicitly considered in this study. Future research should investigate the
-role of these drivers, in particular nitrogen deposition and land use change, and the interactions with multiple drivers of global change. Moreover, potential distribution models could be extended to overlay with area of high conservation value such as reserves (see e.g. Gallagher et al. 2010) and patterns of dispersal could be integrated into models (see e.g. Smolik et al. 2010; Crossman et al. 2011).

This study greatly contributes to the understanding of plant invasions under climate change. However, it seems as if science has only just begun to scratch the surface of the complex interactions of these two factors. More research needs to be conducted, both in New Zealand and globally, and its results need to inform policies and weed management strategies. This is critical in order to mitigate negative impacts of single and multiple drivers of global change on biodiversity.
8.5 References


