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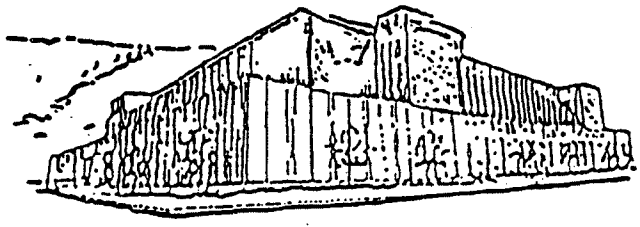
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**Ecological Restoration after Removal of Exotic Conifer Plantations  
in Argentine Patagonia's Nahuel Huapi National Park**

By

Marion E. Hourdequin

A.B. Princeton University

Presented in partial fulfillment of the requirements for the

Degree of Master of Science

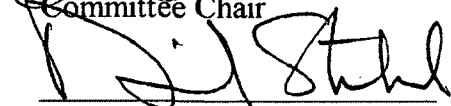
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Ecological Restoration after Removal of Exotic Conifer Plantations in Argentine Patagonia's Nahuel Huapi National Park (106 pp.)

Director: Carol A. Brewer, Ph.D. 

Early this century, humans brought a variety of North American and European plants to Argentine Patagonia. In Nahuel Huapi National Park (NHNP), many exotic conifers were introduced, including ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*). Recently, however, land managers in the Argentine national park service (Administracion de Parques Nacionales) have recognized that these exotic trees have the potential to invade native plant communities, threaten biodiversity, and change ecosystem structure and function.

To address this problem, the park service began clearcutting NHNP's exotic conifer plantations in the 1980s, with the intent of reestablishing native trees at these sites. Thus far, native trees have largely failed in clearcut sites; however many clearcuts are regenerating with exotic conifers. In this study I examined potential barriers to native tree success in clearcut sites and investigated the possibility that a native vine (*Mutisia spinosa*) limits reinvasion of clearcuts by exotic trees.

In field experiments, I tested the effects of proximity to shrubs, protection from herbivory (cages), and shade on seedlings of three species of native trees (*Nothofagus dombeyi*, *Austrocedrus chilensis*, and *Lomatia hirsuta*). One year after planting, seedlings near shrubs were in better condition than those in the open. In addition, cages had a positive effect on seedling condition for all three species, although *A. chilensis* and *N. dombeyi* appeared more susceptible to browsing than *L. hirsuta*. Shade, which I hypothesized might improve seedling condition by protecting plants from excessive solar radiation, had no statistically significant effects on either growth or condition.

I also examined soil nutrients and measured microclimatic variables in clearcut sites. Microclimatic data weakly supported the hypothesis that excessive light can stress seedlings. Soil data showed a trend toward lower nutrient levels in clearcuts, but the mechanisms and biological significance of this pattern are not known. Examination of the relationship between exotic conifers (*P. ponderosa* and *P. menziesii*) and *Mutisia spinosa* suggested that the native vine may slow growth of exotic trees, but is unlikely to prevent reinvasion. The data presented here provide a foundation for future research and improvement of restoration techniques after exotic conifer plantations have been clearcut.

## Acknowledgements

Many people assisted with this project, and my hope is that many others will carry this work forward into the future, since much remains to learn about conifer invasions and ecological restoration in Argentine Patagonia. I am particularly grateful to have had the intellectual, logistical and personal support of my thesis advisor, Dr. Carol Brewer, who was a consistent advocate, a fastidious editor, and a caring mentor. My committee members, past and present, also shaped my intellectual growth and progress during graduate school, so my thanks to Dr. Paul Alaback, Dr. Andrew Sheldon, Dr. Cathy Zabinski, Dr. Ray Callaway, Dr. Doug Emlen, Dr. Steve Siebert, and Dr. Richard Hutto. I also particularly appreciate the generous assistance of Dr. Tom de Luca with the soils component of this thesis.

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During my tenure at University of Montana, I was supported by a National Science Foundation Graduate Fellowship, which gave me the flexibility to pursue my own interests and provided ample financial support. I am deeply grateful for this.

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# CHAPTER 1

## Exotic Conifers and Native Forests in Northern Patagonia

### INTRODUCTION

Exotic conifers pose a threat to native biodiversity in Patagonia. Various species of pines (*Pinus spp.*) as well as Douglas fir, maples and other non-native trees were planted in northern Patagonia's Nahuel Huapi National Park beginning in the early part of the twentieth century. These trees have begun, in many cases, to naturalize, spreading beyond the boundaries of plantations and into native vegetation. The story of exotic trees in Patagonia is not entirely new – we have witnessed similar invasions in South Africa, New Zealand and Australia – however, the spread of non-native trees in this region of South America is at an early stage, and may be more easily controlled than late-stage invasions that exist elsewhere (Hobbs & Humphries 1995). To effectively control invasions will require both biological knowledge and social and political will. In the biological realm, our ability to design an effective conservation and restoration plan for the area will be assisted by an examination of pine invasions elsewhere throughout the world, an understanding of the ecology of plant invasions more generally, and a specific look at the ecology of both native and exotic trees in Argentine Patagonia.

### I. BIOLOGICAL INVASIONS AND PINES

Biological invasions have long been of interest to ecologists. As early as 1872, Charles Darwin remarked on the spread of European cardoon into Argentinean grasslands (Mack 1985), and less than a century later, Charles Elton produced a classic text, *The Ecology of Invasions by Animals and Plants*, focusing exclusively on this key topic. The theoretical importance of biological invasions is widely-touted (e.g., Mack 1985), as the introduction of new species provides the opportunity to examine central ecological

questions about competition, facilitation, community structure, and whether individual species 'matter' in ecological communities (Ramakrishnan & Vitousek 1989). In addition, invasions by exotic species offer an angle from which to investigate the role of chance, timing and stochasticity in population growth (Crawley 1989). Physiological ecologists have used exotic species to examine plant-environment interactions (Beerling 1985 citing Harris 1967), and for evolutionary ecologists, invasions provide systems in which to study processes of genetic change and adaptation.

In recent years, the importance of studying exotic species has grown dramatically, as we have realized that biological invasions are not simply interesting; today, these invasions pose a major threat to biodiversity worldwide (M. Soule, personal communication). From zebra mussels in the Great Lakes to knapweed in the Intermountain Western United States, exotic species now command the attention not only of ecologists, but of public land managers, private landowners and the general public.

Biological invasions have drawn increasing attention to the interconnections among animals, plants and abiotic processes. For example, in the U.S. Northern Rocky Mountains, the accidental introduction of an exotic disease, white pine blister rust, has wreaked havoc on populations of whitebark pine (*Pinus albicaulis* Engelm.). In some areas, infection levels reach 90% or more (Kendall 1992). This, in turn, has led to reduced crops of pine nuts, an important food source for red squirrels, Clark's nutcrackers and grizzly bears. The consequences of reduced pine nut production have not yet been fully elucidated; however it is clear that bears alter their foraging behavior and movement patterns in response to poor whitebark seed crops (Mattson et al. 1992). Thus the implications of a single exotic disease can be widespread and far-reaching.

While ecosystems in the Northern Rockies adjust to a major decline in whitebark pine, a key high elevation tree species, ecological communities in many parts of the

Southern Hemisphere are experiencing a massive increase in populations belonging to this same genus, *Pinus*. A recent review by Richardson, Williams and Hobbs (1994) reports that sixteen species of pine have become invasive in parts of the Southern Hemisphere. Included in this list are *Pinus ponderosa* Laws. and *Pinus contorta* Dougl., two species native to the northwestern United States.

To date, most work on pine invasions has focused on New Zealand, South Africa and Australia, where European colonization occurred relatively early, and where pines were introduced as long as 300 years ago (Kruger et al. 1989). In most of South America, European settlement occurred later, and invasions by exotic plants are correspondingly at an earlier stage. Although Monterey pine (*Pinus radiata* D. Don) has been widely planted in Chile, and many species of pine have been planted across the Andes in Argentine Patagonia, to date few large-scale invasions have been reported in southern South America. In part, the slow spread may reflect the recent introduction of these new species (Richardson et al. 1994) rather than their inability to invade Chilean and Argentine landscapes. Time lags commonly characterize biological invasions and can occur between initial introduction and the commencement of spread, as well as between a initial slow rate of spread and a later acceleration in population growth (Kowarik 1995).

In areas where pine invasions do occur, the ecological consequences can be significant. In South Africa, for example, *Pinus pinaster* Ait. has invaded 3256 km<sup>2</sup>, primarily in natural fynbos shrubland (Richardson et al. 1994). Pines in this region often form dense thickets, and their invasion has resulted in local extinction of endemic plants (Richardson et al. 1994). In addition, areas with dense pine stands are susceptible to more intense fires and reduced levels of runoff as compared to native vegetation (Richardson et al. 1996).

In New Zealand, similar effects have been found. Where pines have invaded tussock grasslands, native vegetation is often suppressed and changes occur in secondary

succession (Richardson et al. 1994). Pines also affect hydrologic regimes: In New Zealand, watersheds with pine plantations have been found to have lower low flows and lower annual flows than native forest or grassland pastures (Dons 1987, Fahey & Jackson 1997). Finally, pines can affect nutrient cycling (Richardson et al. 1994). Changes in nutrient cycles often occur as a consequence of plant invasions; other examples include alternations in nitrogen cycling caused by the invasive evergreen tree *Myrica faya* Ait., which colonizes volcanic areas in Hawai'i (Vitousek and Walker 1989).

Evidence from throughout the Southern Hemisphere indicates that invasions by exotic pines can alter nutrient cycling, slow decompositional processes, change vegetation structure, affect community composition and alter animal habitat availability (Richardson et al. 1994). In general, invading trees are likely to have significant effects on ecological processes due to their large size, long lives and ability to alter structural characteristics of a landscape. However, the spread of exotic herbs, shrubs, birds and a variety of other animals also shapes today's ecosystems. The scientific community has acknowledged and addressed this issue by developing a SCOPE program on biological invasions, which has spawned a variety of theoretical and empirical studies that provide a framework for understanding (Drake et al. 1989).

## **II. KEY QUESTIONS IN BIOLOGICAL INVASIONS RESEARCH**

As discussed earlier, research in plant invasions spans a variety of ecological scales, from genetics and physiology to ecosystem processes. However a few key organizing questions emerge from the literature and can be used to frame research on pine invasions generally, and exotic conifers in Argentine Patagonia more specifically.

### *What characteristics make a plant a good invader?*

Much recent work has been dedicated to this question. In the late 1980s, ecologists answered this question from an anecdotal perspective, picking out common features among known invaders. Ashton and Mitchell (1989), for example, list vegetative reproduction, rapid reproduction and dispersal by humans as three key traits determining the invasiveness of aquatic plants. Noble (1989) following Baker (1965) adds that the 'ideal plant invader' would be plastic, perennial, many-seeded and self-compatible, and would grow rapidly, flower early, disperse well, compete well, and germinate well under a wide range of conditions. Formidable requirements for a plant! Both Noble (1989) and Baker (1965) note that all of these characteristics are unlikely to be found in a single species – rather the picture they paint provides a gestalt model of what traits one might expect in a good weed.

More recently, characterization of the traits common to successful invaders has grown more sophisticated. Discriminant analysis has gained popularity as a method for developing predictive models of invasion. Rejmanek and Richardson (1996), for example, used this technique to select the key characteristics determining pines' invasive ability. Of ten initial traits, only three – seed mass (low), juvenile period (short) and interval between seed crops (short) – were found to significantly differentiate between invasive and non-invasive species of pines (Rejmanek and Richardson 1996).

These advances may assist in predicting which species are generally more likely to spread in new environments. However Noble (1989) points out that lists of traits are not enough: "The properties of the invaded habitat are a critical determinant of the likely success of any invader," thus we must take not only the invader, but the invaded ecosystem into account.

*What characteristics make an ecosystem susceptible to invasion? What makes an ecosystem resistant to invasion?*

Fox and Fox (1986) offer series of hypotheses for evaluating community invasibility. These authors focus on resource availability and community attributes as factors determining a community's susceptibility to invasion (Fig. 1). In this model, disturbance can shift resource availability, creating a change in the types of resources available or a flush in particular resources (Fox and Fox 1986). Such shifts and changes can provide an opportunity for new colonizers to establish within the community (Fox and Fox 1986).

The idea that disturbances facilitates invasion has been widely supported by correlative data showing that invasions are almost always coincident with changes in natural disturbance regimes (Richardson et al. 1994, Fox and Fox 1986), however only a few experimental studies have directly examined how disturbance influences the invasion process. Hobbs (1989) conducted experiments in Western Australian shrubland and heath habitats to study how mechanical soil disturbance and fertilization affected survival and growth of an exotic grass and an exotic herb. His results showed that disturbance increased the success of invaders, and that nutrient supplementation further enhanced this effect (Hobbs 1989).

More recently, Burke and Grime (1996) examined invasibility of British limestone grasslands. In this study, seeds of fifty-four native plant species were sown into plots where they were locally absent (although the species were native to the region). Disturbance, fertility and patch size were all manipulated. Results again showed disturbance to be a key factor, particularly when accompanied by an increase in resources (Burke and Grime 1996).

With regard to pine invasions, evidence suggests that disturbance is a key factor as well: "Invaded grasslands in Australia, New Zealand and South Africa invariably have a

history of perturbation" (Richardson et al. 1994). Fire and large herbivores are two examples of disturbances that may facilitate invasion. Fire can both clear vegetation and change resource availability, while large herbivores may trample, fertilize the soil with their manure, and selectively alter vegetative composition. In Argentine Patagonia, for example, the success of pine and Douglas fir invasions may partly rest on the history of livestock grazing in grasslands as well as the influence exotic deer on understory structure and composition in forests (Veblen et al. 1989, Veblen et al. 1992).

In some ecosystems, the disturbance-invasion relationship may involve feedback mechanisms. Under this scenario, disturbance initially facilitates invasion, then the invading organisms catalyze further disturbance, which in turn promotes further invasion. Hughes et al. (1991) provide an example from Hawai'i, where exotic grasses increase fire frequency to the detriment of natives and to the benefit of the invaders. Since the invading grasses are adapted to fire, they quickly recover and flourish after a blaze, whereas the natives decline.

A similar scenario may occur in conifer-invaded areas. A number of North American conifers, such as lodgepole pine (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*), frequently experience fire in their native ranges and can thrive after these disturbances. Although lodgepole pine's thin bark does not protect it from fire-induced mortality, this species has serotinous cones that release seeds when exposed to heat, thus lodgepole pine often recruits successfully after fire (Kershaw et al. 1998). Ponderosa pine, on the other hand, has a thick bark and can survive low intensity fires (Kershaw et al. 1998). When pines invade new ecosystems where fire was previously infrequent, they may increase fire susceptibility or intensity (Richardson et al. 1996), and if native plant species are not adapted to fire, the invasion-induced change in disturbance regime may place natives at a disadvantage.



Disturbance and resource availability clearly play important roles in the invasion process. However, they are not the only influences on invasibility. Other factors that may affect community invasibility include species richness, habitat type, structural diversity, and rate of recovery from disturbance (Fox and Fox 1986, Richardson et al. 1994). In general, resistance to pine invasion appears to increase from sparsely-vegetated dunes to grassland to shrubland to forest (Richardson et al. 1994). Richardson et al. (1994) also suggest that in addition to vegetation structure, actual *species composition* may influence the potential for pine invasion. In South African fynbos, areas with the native shrub *Protea nitida* Miller appear to resist invasion, in part due to the shrub's association with C4 grasses which may "impose a biotic barrier to invading pines" (Richardson et al. 1994).

As we have seen, a variety of deterministic factors influence the likelihood of invasion. However recent work has also shown that the invasion process is not entirely deterministic. A particular species may be introduced on multiple occasions, and succeed only once. This may either result from fluctuations in the weather or other factors that control invasibility or arise simply due to chance (Crawley 1989).

#### ***What are the roles of chance and timing in biological invasions?***

Richardson et al. (1994) note that most pine invasions occur in areas where these trees have been cultivated historically. A long history of cultivation provides a plant many opportunities for dispersal, establishment and spread. The 'exposure time' of a species to a new ecosystem can affect the probability that a plant will, by chance, arrive at suitable sites for survival and growth (Kowarik 1995). In addition, changes in precipitation and other factors may make a given area suitable for establishment in one year, but unsuitable in another (Kowarik 1995). Therefore the longer that a plant is present in a region, the more likely it is to establish independent populations (Kowarik 1995). Similarly, the probability of establishment increases with the number of times a plant is introduced (Crawley 1989).

The increase in establishment with exposure time can be thought of as analogous to buying a series of lottery tickets over one's lifetime rather than one ticket on a single day: the more often one plays, the more likely she'll win.

Of course, the probability of winning the lottery also depends on the odds on a given day. On some days, the odds of winning are poor, while on other days the chances are better. Similarly, the timing of species introductions has a direct effect on the likelihood of successful establishment. For example, establishment may be much more likely at an early stage of succession than a late one. Thus the timing of introduction relative to disturbances and subsequent succession may play a key role in invasion success or failure (Crawley 1989).

The interplay between invasions and timing has received detailed attention in relatively few cases. In general we lack the knowledge and ability to incorporate timing into models of species invasions in any meaningful way (Crawley 1989). Chance, on the other hand, can be incorporated by introducing stochasticity into invasion models (Crawley 1989).

### *What methods are available for control of biological invasions?*

Given the widespread effects of biological invasions, governments and land management agencies have realized that descriptive and predictive studies are not enough to address the problem. Thus, a significant body of applied research has recently emerged focusing on control measures for exotic species. In addition, control programs have been implemented in many areas to limit the spread of exotic plants and restore native flora.

A number of different methods have been developed to control exotic plants, though few have been fully effective or without significant secondary consequences. The primary means of control today involve physical methods, chemical methods and biocontrol, and they usually focus on removing undesired species, with less emphasis on

promoting growth of native or desirable plants (Hobbs & Humphries 1995). Hobbs and Humphries (1995) critique the narrowness of this approach, calling for "a shift in emphasis from an individual species approach to an ecosystem and socioeconomic approach, and a shift in emphasis from control to prevention." Their point is well-taken, as it is extremely difficult to control invasions once they reach an advanced stage. In many cases, however, exotic plants receive little attention until the problem is severe and widespread.

Furthermore, Hobbs and Humphries (1995) point out that current control techniques are far from magic bullets: the side-effects of herbicides are little studied and poorly understood, the development of biocontrol agents is expensive and time-consuming (and often unsuccessful), and mechanical removal is extremely labor-intensive and generally not feasible over large areas.

The spread of biological invasions can be much better controlled if intervention occurs early (during the lag phase of population growth), and if an "integrated management" plan is enacted, considering not only the invader, but the invaded ecosystem as well as human social and economic factors (Hobbs & Humphries 1995). Such a plan would involve prioritization of areas for conservation or production (of crops, for example) as well as an evaluation of the current status of these areas and their levels of disturbance (Hobbs & Humphries 1995). Ideally, the plan would also incorporate at least a rough consideration of the spatial dynamics of biological invasions. Such consideration would identify corridors along which spread might occur, potential barriers to invasion, and the areas of the landscape most and least susceptible to colonization by exotics.

A truly integrated approach would also consider the human role in biological invasions. Since most invasions are associated with disturbance, and humans are a major source of ecological disturbance, an understanding of how, where, when and why human activities are affecting the landscape will be crucial to effective planning (Hobbs &

Humphries 1995) – however this broad approach is rarely taken by ecologists working on biological invasions.

In Argentine Patagonia, control of conifer invasions will require not only an understanding of the region's ecology, but consideration of the social and economic factors that first led people to plant non-native trees, and the factors that encourage continued planting today. Some of the incentives are economic: land is inexpensive in Patagonia and pines grow rapidly there, providing a relatively rapid return on the investment of planting trees (Schlichter and Laclau 1998). In addition, exotic conifer plantations are being encouraged and subsidized by European organizations interested in tree planting as a means to sequester carbon dioxide and counter global climate change (Schlichter and Laclau 1998). Finally, at a smaller scale, many people may not recognize that certain conifer species are exotic and that they have the potential to become invasive. Such individuals may plant exotic conifers as ornamentals or windbreaks in their yards without realizing that these species potentially threaten native biodiversity in the region.

Educational programs and public dialogue are needed to increase consciousness about exotic plants in Argentine Patagonia, to understand social and economic motivations for planting exotics, and to make informed decisions about the future of the region. Such efforts will require interagency cooperation as well as citizen involvement. As Hobbs and Humphries (1995) write, "It can happen that agricultural or range scientists promote the use of species for which other scientists are developing weed-control measures." To avoid this situation in Patagonia will require partnerships between the Argentine national park service (Parques Nacionales) and the national agricultural agency (Instituto Nacional de Tecnologia Agropecuaria). In addition, further scientific study and monitoring are needed to more clearly define the potential for invasion and the potential strategies for managing invasions.

In Argentine Patagonia, integrated management of conifer invasions would entail a comprehensive assessment, which would include: 1) identification of exotic conifer plantations and other plantings (e.g., ornamental, windbreaks); 2) inventory of spread beyond planted areas; 3) evaluation of varying susceptibilities to invasion, depending on climate, disturbance regime and other factors; 4) examination of the spatial arrangement of current exotic tree distributions and control of spatial spread; 5) prioritization of areas for protection; and 6) identification of measures to control and prevent spread, and to minimize ecosystem invasibility. As discussed earlier, such an assessment would need to take place in a socioeconomic context: why are people choosing to establish pine plantations (what are the economic incentives)? do people view exotic trees as a problem (and why or why not)? what are people willing to do to help control invasion? how much will control measures cost?

Control of biological invasions is a daunting task; however a broad and contextual approach is much more likely to succeed than a narrow, post-hoc attack with chemicals, bulldozers or laboratory-bred insects. And a crucial part of this contextual approach involves ecological restoration and an understanding of native plant communities and their functioning.

***How can native ecosystems be restored after invasion? Some background about native trees in Argentine Patagonia...***

This is clearly a crucial question for biological conservation, and a question upon which this thesis is centered. However, relatively little research exists in this area, and governments, citizens and land management agencies throughout the world are struggling to construct effective restoration plans without the benefit of significant experience in this area. Undoubtedly, our ability to restore native ecosystems will improve as we gain increased knowledge about the functioning of complex natural systems.

Perhaps one of the most important components of a restoration plan involves an understanding of the native ecosystem and its functioning prior to disturbance and invasion. In the mesic forests of Argentine Patagonia where my research took place, three tree species dominate the forest: *Nothofagus dombeyi*, *Austrocedrus chilensis*, and *Lomatia hirsuta*. Following is some basic autecological information about each.

*Nothofagus dombeyi* is the largest South American representative of the Southern Beech family, or Nothofagaceae, and can grow to 50 meters in height. It is an evergreen broadleaved tree, and its native range extends from 38°30' to 44° South latitude in Argentina (Veblen et al. 1996). *N. dombeyi* ranges over a variety of soil types, and can grow where soils are well-drained or sometimes saturated with water (Veblen et al. 1996). The tree is monoecious, flowers in austral spring, and produces mature fruits throughout the summer (Veblen et al. 1996). Seeds are dispersed primarily by gravity and wind, and *N. dombeyi* does not maintain a long-lived seed bank – instead seeds germinate in the year following their production (Veblen et al. 1996). *Nothofagus dombeyi* is relatively shade-intolerant and requires disturbances, such as treefall gaps, for regeneration (Veblen et al. 1996). However it is unusual to see *N. dombeyi* growing in very open areas or areas outside the forest (M. Hourdequin, personal observation). The tree requires a moderately moist environment, and usually grows in areas with more than 1200 mm of rainfall per year (Veblen 1989).

*Austrocedrus chilensis*, a member of the Cupressaceae, has scaly juniper-like leaves and grows in a wide range of environmental conditions. In the western part of its Argentinian range, *A. chilensis* grows with *N. dombeyi* in mesic forest, where annual rainfall reaches up to 1700 mm (Veblen et al. 1995). However, *Austrocedrus* also extends eastward to the edge of the steppe, which receives only about 500 mm of precipitation per year (Veblen et al. 1995). On the eastern side of the Andes, the north-south range of *A. chilensis* extends from 36°30' to 43°35' South latitude. Like *N. dombeyi*, *A. chilensis*

lacks a seed bank (Gobbi & Schlichter 1998, citing Raffaele and Gobbi 1996) and seeds are dispersed by wind (Veblen et al. 1995). Shade and moisture are both important to young seedlings' development (Gobbi & Schlichter 1998), although in general *A. chilensis* is not highly shade-tolerant and requires large gaps in forested areas in order to regenerate (Gobbi & Schlichter 1998, citing Kitzberger 1995).

In mesic forests, large-scale disturbance as well as tree fall gaps can facilitate regeneration of *A. chilensis*. Infrequent, catastrophic fires in the *Nothofagus dombeyi*-*Austrocedrus chilensis* forest region can promote establishment of even-aged stands of both species (Veblen & Lorenz 1987, Veblen et al. 1995). Landslides can also provide an opportunity for *Austrocedrus* establishment. In drier climates further east, *A. chilensis* regeneration is more variable and probably depends on particularly moist years, the protection of nurse shrubs, or both (Veblen et al. 1995, Kitzberger et al. *in press*). In many areas, *A. chilensis* regeneration may be limited not only by climatic conditions, but by the effects of browsing by deer and livestock (Veblen et al. 1989, Veblen et al. 1995).

The autecology of *Lomatia hirsuta* has not been well-studied, and little literature is available relating to this species. *Lomatia* is a member of the Proteaceae and often grows as a large subcanopy shrub species. It has thick tough leaves and appears resistant to browsing, perhaps because of its tannin-rich leaves (Veblen et al. 1992). *Lomatia* often co-occurs with *Austrocedrus* in relatively open woodland environments (Veblen et al. 1989), which would suggest that the tree is more tolerant of xeric conditions than *Nothofagus* and other more mesic species. Little information is available on *Lomatia* regeneration, however the tree does have wind-dispersed seeds (M. Hourdequin, pers. obs.) and is capable of resprouting (Veblen et al. 1995).

Autecological information and an understanding of regeneration processes is important to control of conifer invasions in northern Patagonia, because successful control of exotics requires not only removal of the invader, but conservation and restoration of

native plant communities. This, in turn, requires knowledge of the ecological conditions that allow establishment and regeneration of native forest species.

#### IV. CONIFER INVASIONS IN NORTHERN PATAGONIA

Pines and Douglas fir were introduced to Nahuel Huapi National Park in the early part of the twentieth century, with the arrival of European immigrants to the area. The large island at the center of Lake Nahuel Huapi, Isla Victoria, was privately owned at the time, and many exotic plantations were established based on the vision of German forester Otto Alberti (Vallmitijana 1997). Afforestation with exotic trees continued into the 1930s, and many of these trees populate the island today. Species include ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), sequoia (*Sequoia sempervirens*), maple (*Acer spp.*), and a variety of fruit trees. Most of the plantings occur in areas previously forested with native trees, primarily coihue (*Nothofagus dombeyi*) and cipres (*Austrocedrus chilensis*).

Along with new plants, European settlers brought a variety of animals to Isla Victoria and the surrounding mesic forest region of northern Patagonia. Although domestic livestock have now been eliminated from the island, at least two species of exotic deer remain (*Dama dama* and *Axis axis*), and recent work has shown that deer have had a significant impact on forest community structure (Veblen et al. 1992).

The interactions between the exotic plants and animals has not been fully elucidated; however, it seems clear that deer significantly reduce recruitment of young trees and may therefore influence forest succession and stand replacement (Veblen et al. 1992). The effects of deer on recruitment of exotic trees has not been previously studied – however, field observations suggest that the exotic trees such as ponderosa pine and Douglas fir are not as heavily browsed as their native counterparts. Such differential



susceptibility to herbivory could have serious consequences for the persistence of native plant communities in the region.

In many areas, pines and Douglas firs have begun spreading beyond plantation boundaries and into native vegetation. The exotic conifers are wind dispersed, and their seeds may travel some distance (300m or more) with the strong Patagonian winds (Chauchard et al. 1988, Administracion de Parques Nacionales Argentina, hereafter A.P.N., 1988). If colonization occurs at many disparate locations, the invasion of these species could be extremely difficult to track and control.

The Argentine national park service is currently working to eliminate exotic conifers from parts of Nahuel Huapi National Park, and to restore native vegetation in these areas (A.P.N. 1988). The complex relationships among plants and animals, both native and exotic, will play a key role in determining the outcome of succession after exotic conifer species have been removed.

### *Invasions and ecological restoration in Argentine Patagonia*

The aim of this thesis is to begin to examine the factors controlling regeneration at sites where exotic conifers have been clearcut to make way for native species. In every case I observed, regeneration of native trees was poor or nonexistent at these sites (see Appendix for data summarizing woody plant regeneration). Native shrubs were often present, but many sites were also being recolonized by pines and Douglas fir. Restoration in this case must have two purposes: first, to prevent reinvasion and second, to reestablish native vegetation. Understanding environmentally-limiting factors to native tree survival, tracking patterns of succession, describing the abiotic environment, and studying community-level interactions between native and exotic plants will contribute to our understanding of Patagonian ecosystems and plant invasions, and ideally, will help improve our ability to conserve and restore native forests.

Chapter 2 addresses the central question with which this thesis is concerned: what factors are preventing native tree recolonization in clearcut conifer plantations? I first describe the patterns of succession in one clearcut on Isla Victoria, then present the results of two experiments analyzing the effects of shrubs, protection from herbivory, and shade on growth and survival of native tree seedlings. In addition, this chapter includes a discussion of microclimatic conditions in each of the experimental treatments, and how microclimate may affect establishment of native trees in clearcut areas. Finally, I present results of soil analyses in paired clearcut and forested sites on Isla Victoria and the nearby Huemul Peninsula (Fig. 2). The goal of this portion of the study was to identify similarities and differences between soil conditions in clearcuts and those in adjacent native forest. If afforestation by exotic trees and/or clearcutting negatively affect soil fertility, this may inhibit native plant regeneration.

In Chapter 3, I present the results of a brief study examining relationships between a native Patagonian vine, *Mutisia spinosa*, and exotic conifer seedlings regenerating in a clearcut on Isla Victoria. The purpose of this study was to investigate *Mutisia's* potential role as a native 'biocontrol' of ponderosa pine and Douglas fir. In addition, this chapter highlights the value of understanding community-level interactions between native and exotic plants.

Chapter 4 provides a discussion of my research, and of exotic conifer invasions generally, for an audience of nonscientists. The information presented overlaps significantly with the ideas discussed in Chapters 1-3, however, the language is less technical and data are described rather than presented formally.

Chapter 5 summarizes and concludes, providing a brief outline of the salient points of my thesis research and the potential for future work on this topic. This final chapter is followed by an Appendix, in which I present transect data from one site on Isla Victoria (3 separate locations within this site were surveyed) and from four sites on the Huemul

Peninsula. These data were collected primarily to provide the Argentine Park Service with baseline data to use in ongoing monitoring and evaluation of restoration efforts in clearcut conifer plantations; for this reason they are presented with only brief discussion and interpretation.

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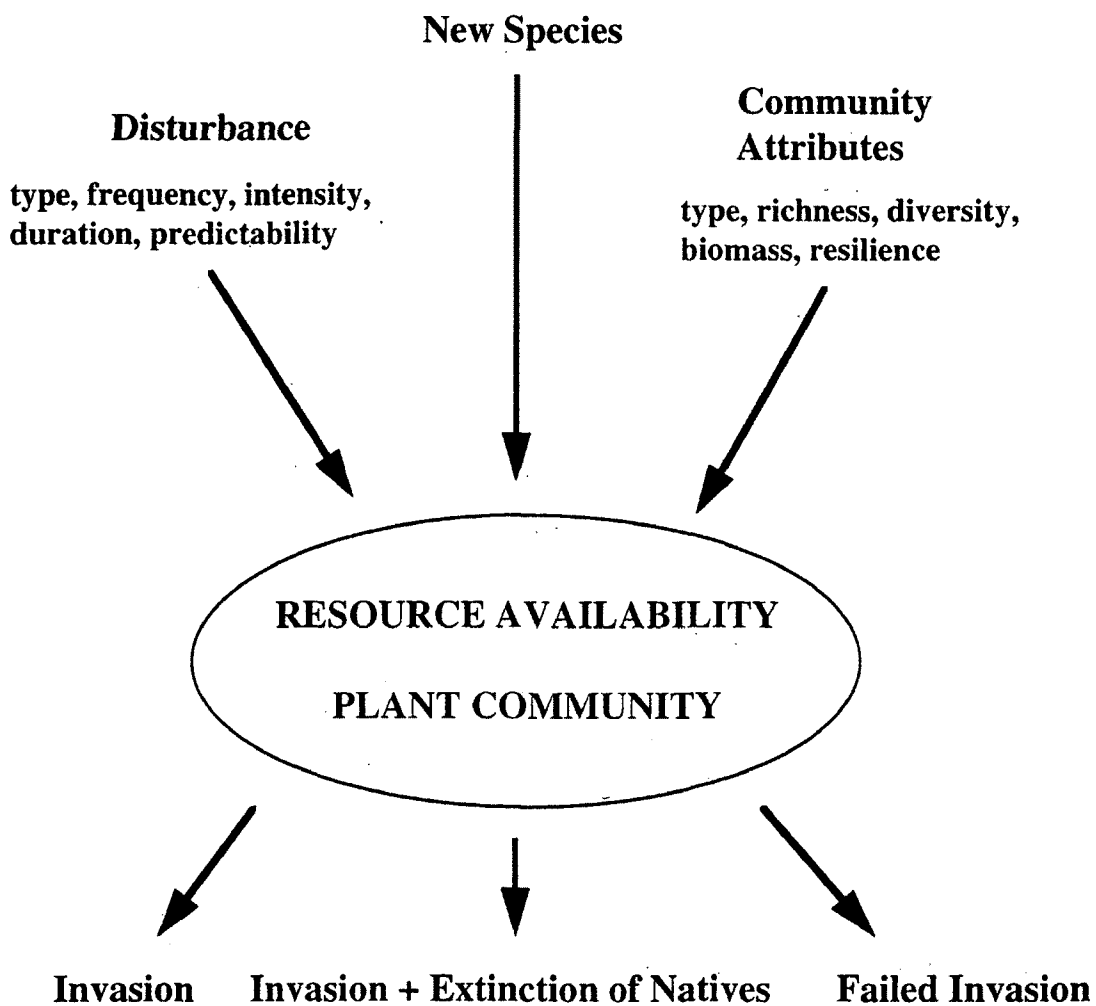
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Figure 1. Disturbance and community attributes each affect resource availability and the plant community, which in turn influence the outcomes of invasion. Redrawn from Fox and Fox (1986).



## CHAPTER 2

### Ecological Restoration after Removal of Exotic Conifers in Northern Patagonia: What Limits the Survival of Native Trees?

#### INTRODUCTION

In many parts of the world, the ecology and management of forest ecosystems have grown increasingly complex due to the introduction of new varieties and species of trees. Particularly in the Southern Hemisphere, exotic trees have been widely planted and naturalization of these species now threatens native plant communities in parts of New Zealand, South Africa and Australia (Richardson et al. 1994). Given the extent and speed with which humans are altering native forests, conservation biologists and land managers concerned with the maintenance of diverse, native plant and animal communities face many challenging research and management questions.

In Argentine Patagonia, exotic trees were introduced in large numbers at the beginning of the twentieth century, with the goal of discovering highly productive species for wood production (Vallmitjana 1997). In particular, a variety of North American conifers were brought to northern Patagonia, including ponderosa pine (*Pinus ponderosa* Dougl. ex Laws & Laws, Pinaceae) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco, Pinaceae) (Schlichter & Laclau 1998). Although these species continue to be planted throughout the region, there is growing concern about the ecological changes caused by afforestation with exotic conifers, and additionally, many scientists and land managers have acknowledged the potential for these species to invade native ecosystems.

Due to these concerns, the Argentine Park Service established a program to eliminate exotic tree plantations within Patagonia's Nahuel Huapi National Park. Many of the park's plantations have now been clearcut, with the goal of reestablishing native vegetation at these sites. However very little information exists regarding the effects of ponderosa pine and Douglas fir plantations on ecological factors such nutrient cycling, soil



properties, and seed banks, and we know even less about how clearcutting affects ecological processes in such areas (Schlichter & Laclau 1988).

Understanding ecological changes resulting from afforestation with exotic species, as well as from subsequent clearcutting, will be crucial in restoring native trees to former plantation sites. Site history, disturbance regime, abiotic conditions, seed rain and seed bank, native and exotic plant autecology, and plant-animal interactions may all affect the outcome of succession (Fig. 1). In addition, it is likely that many of these factors interact. For example, site history affects the abundance and diversity of species represented in the seed bank, and variation in susceptibility to herbivory will likely influence regeneration of native and exotic plants.

In Patagonia, succession in clearcut sites appears to differ significantly from plant community development in nearby native forests. Most of the clearcuts occur in areas surrounded by mixed temperate forest, dominated by *Nothofagus dombeyi* (Mirbel) Oerst. (Nothofagaceae), *Austrocedrus chilensis* (D. Don) Florin et Boutleje (Cupressaceae), and *Lomatia hirsuta* (Lam.) Diels ex Macbr. (Proteaceae) – however these species are absent or rare as colonists of former plantations. In contrast, although tree recruitment in adjacent native forests is spatially patchy, all three species regenerate (*N. dombeyi*, *A. chilensis*) or resprout (*L. hirsuta*) in the forest understorey (M. Hourdequin, pers. obs.). Interestingly, regeneration of *N. dombeyi* and *A. chilensis* in mesic forests appears to require disturbance (Veblen 1989, Gobbi et al. 1998), however these species were not observed colonizing large openings created by clearcuts. This pattern may be attributable to qualitative and quantitative differences between clearcuts and natural disturbances, such as landslides or treefalls. Studies with *A. chilensis* suggest that young seedlings need some protection from the sun and desiccation, though seedlings cannot regenerate where light levels are very low (Gobbi et al. 1998, Kitzberger et al. in press). Thus, while much of the forest understorey may be too dark to allow regeneration, light intensity in clearcuts

may be too high, creating a stressful environment for young seedlings.

Only a few studies have examined successional processes in Patagonian mesic forests, and little information exists regarding regeneration requirements and autecology of native trees. The primary objective of this study was to examine factors affecting plant succession in clearcut conifer plantations, with the goal of identifying barriers to the success of native trees. If limiting factors can be identified, restoration techniques can be adjusted accordingly. Here we focused on microsites, herbivory, and climatic conditions as potential influences on growth and survival of native seedlings and used an experimental approach to evaluate the success of *N. dombeyi*, *A. chilensis* and *L. hirsuta* seedlings under different experimental treatments.

### **Hypotheses**

1) *Shrubs may act as "nurse plants" for young tree seedlings.* Microsite conditions can play a key role in plant succession (Titus & Del Moral 1998). In desert ecosystems, for example, shrubs have been found to "nurse" young cacti, perhaps due to their moderating effects on environmental conditions (Franco & Nobel 1989). In Argentine Patagonia, recent work suggests that at least one native tree species, *A. chilensis*, may depend on nurse plants for regeneration in dry sites (Kitzberger et al. in press). We predicted that in clearcuts, variation in microclimatic variables, such as light, temperature, wind and relative humidity, would be moderated by the presence of shrubs. From this, we hypothesized that if such microclimatic buffering existed, it would promote survival of native tree seedlings by reducing the damaging effects of excessive solar radiation, high temperatures, and rapid evapotranspiration. Therefore we proposed that shrubs may facilitate regeneration of native trees, and that restoration may be more successful if seedlings are planted close to shrubs. We used a yearlong experiment to investigate this possibility.

2) *Shade treatments may ameliorate seedling survival if excess solar radiation is causing young trees physiological stress.* Because we suspected that exposure to high light intensities might be partly responsible for the poor survival of seedlings planted in recent clearcuts, we also conducted a short-term experiment examining the effects of shade on growth and survival of native tree seedlings. The experiment was conducted during the austral summer, when we expected that the influence of high light would be the greatest, because solar radiation is more intense and days are longer at this time of year.

3) *Protection from herbivory may improve native seedlings' growth and survival.* In addition to microclimatic conditions and plant-plant interactions, plant-animal interactions may influence successional processes in plant communities. In Argentine Patagonia, recent studies suggest that introduced deer have a significant effects on native plant composition and regeneration (Veblen et al. 1989, Veblen et al. 1992). At our study sites, deer sign was widely evident; we therefore examined the hypothesis that herbivory by large mammals limits growth and survival of native tree seedlings, and that exclusion of herbivores will increase regeneration success of native trees. We conducted experiments with all three dominant forest species and expected differences in growth and survival based on species-specific susceptibility to herbivory.

## **METHODS**

### **Study sites**

The study was conducted on Isla Victoria (approx. 40°53.47 S, 71°32.07 W) and the Huemul Peninsula in Nahuel Huapi National Park, Rio Negro and Neuquen, Argentina (Fig. 2). Native forest in the study area is composed primarily of *Nothofagus dombeyi* (Nothofagaceae), *Austrocedrus chilensis* (Cupressaceae) and *Lomatia hirsuta* (Proteaceae). The climate is temperate and mesic, with a mean summer temperature of 16°C and a mean winter temperature of 4.3°C (Chauchard et al. 1988). Average annual

rainfall is approximately 1640 mm, with 70% of rain falling during the winter months (May-September) (Chauchard et al. 1988). It should be noted, however that 1998 and 1999 were extremely dry years in the region, with precipitation far below normal levels. Soils in this region are derived primarily from volcanic rock and ash originating in the Andean Cordillera. The soils are permeable, erodible, and low in bioavailable phosphorus (Herrero undated, Mazzarino et al. 1998).

#### *Puerto Madera*

Puerto Madera is a former *P. ponderosa*/*P. menziesii* plantation, which was clearcut in stages between 1986 and 1994 (M. Mermoz, pers. comm.). Since the plantation was cut, some of the regenerating exotic conifers have been removed by hand-cutting. A portion of the site was replanted with native seedlings (*N. dombeyi*, *A. chilensis* and *L. hirsuta*) in May, 1998. This planting was used for experiments during summer 1999.

#### *Pampa Pseudotsuga*

Pampa Pseudotsuga, located in the northwestern region of Isla Victoria, was previously forested with *P. menziesii* and was clearcut in austral autumn, 1997. A portion of the clearcut was replanted with *N. dombeyi*, *A. chilensis* and *L. hirsuta* during the following spring, however few seedlings survived. In May, 1998, a second section of the site was replanted for experimental purposes, again using *N. dombeyi*, *A. chilensis* and *L. hirsuta*. Experimental treatments at this site commenced with planting in austral fall, 1998, and continued through austral summer, 1999.

### **Patterns of regeneration**

We examined patterns of regeneration by woody plants (trees and shrubs) in the experimental site at Puerto Madera. To describe successional vegetation, line transects were used to measure shrub and tree cover. For each clearcut, we located six 45-m parallel line transects, spaced 4 m apart. The precise starting point the transects was chosen randomly within an investigator-selected general area. Along each transect we recorded identity, location and length of the line intersected for each occurrence of shrub or tree (primarily seedlings) species. Transect data were summarized by calculating percent cover of each species and average height by species. We did not measure woody plant cover at Pampa Pseudotsuga because the clearcut was recent (cut in 1997), and the primary vegetative cover was herbaceous.

### **Growth and survival of native tree seedlings**

#### *Puerto Madera experiment: the effects of proximity to shrubs and herbivory*

To examine the effects of proximity to shrubs and herbivory on growth and survival of *N. dombeyi*, *A. chilensis* and *L. hirsuta*, we established a 48- by 90-m experimental grid within a ponderosa pine clearcut at Puerto Madera. Each 4- by 15-m section of the grid contained a "shrub" and "open" site. Shrub sites were within 50 cm of the base of a shrub measuring at least 50 cm in both height and width and were located on the shrub's southeast side (sheltered from afternoon sun and from the prevailing northwesterly wind). To each shrub and open site, we randomly assigned a seedling species and herbivory treatment (with or without a cage) to create a factorial experiment with shrub and cage treatments as factors.

Seedlings were planted in early May, 1998. Height and number of branches were measured at the time of planting. In 1999, we returned to the site and measured height, number of live and dead branches (*N. dombeyi* and *L. hirsuta* only), and width (*A.*

*chilensis* only) for each seedling. In addition we evaluated each seedling's condition on a scale from 0 (dead) to 3 (healthy, with more than 50% of branches showing active buds or green leaves) and quantified herbivory (number of branches browsed). Treatment effects on condition and growth were analyzed using two-way analyses of variance (ANOVAs) for each species, with microsite (shrub/open) and exposure to herbivory (caged/uncaged) as factors. Effects of microsite and cages on browsing were analyzed with nonparametric tests (Mann-Whitney U), because caged plants had zero values for herbivory, therefore the data violated the assumption of normality.

*Pampa Pseudotsuga experiment: the effect of shade*

To examine the effects of shade on survival and growth of native tree seedlings, we first established an experimental planting of *N. dombeyi*, *A. chilensis* and *L. hirsuta* in May 1998 at Pampa Pseudotsuga. Experimental trees were planted in a 54 X 24 m grid, with eighteen columns and eight rows spaced 3 m apart. The trees were planted in a regular order throughout the grid, however the eight-row structure created an alternating pattern in all directions (with no rows or columns of a single species).

In mid-February, 1999, we inventoried the seedlings, measured their height, number of live and dead branches (*N. dombeyi* and *L. hirsuta* only), and width (*A. chilensis* only), and assessed their condition (0 to 3). Only relatively healthy plants (from categories 2 and 3) were used for the shade experiment. From the included trees, we randomly selected half of the seedlings from each species for shade treatments (n=9 shaded plants for *N. dombeyi*, 6 for *A. chilensis* and 8 for *L. hirsuta*). Shade treatments were created using a simple metal frame covered with shade cloth.

The experimental time frame differed from the shrub/cage experiment described earlier. The shade experiment was conducted in austral summer and lasted approximately 7 weeks, at which point each seedling was remeasured and reassessed. Because data

violated the requirements of parametric tests, results were analyzed using Mann-Whitney U tests, with shade treatment as the factor.

### **Microclimatic measurements**

For all microclimatic data, three measurements were taken for each variable (temperature, light, and relative humidity), then averaged for analysis. Measurements occurred in austral summer, 1999.

#### *Puerto Madera*

To examine the relationship between microclimatic variables and tree seedling vigor, we randomly selected 8 individuals rated as "ones" (poor condition) and 8 rated as "threes" (good condition) for each species, then measured microclimate (light (PAR,  $\mu\text{mol}/\text{m}^2/\text{s}$ ), relative humidity (%), temperature ( $^{\circ}\text{C}$ ) and wind (m/s)) next to each individual plant in morning, midday and evening. We conducted measurements on two typical summer days (February 26 and March 13, 1999). We measured light (2/26 only), relative humidity, temperature, and wind (3/13 only). Measurements were made at the tallest point for each individual plant. Results were analyzed using seedling condition as the factor in one-way repeated-measure analyses of variance (ANOVAs), with each species analyzed separately.

To examine the differences between microclimatic conditions in "shrub" and "open" treatments, we randomly selected 7 "shrub" sites, then paired each "shrub" site with the nearest "open" treatment site. The paired design was used to minimize inter-site variation due to differences in slope, distance from forest edge, and other factors, and to strengthen our statistical power to detect differences between treatments.

We measured light (PAR,  $\mu\text{mol}/\text{m}^2/\text{s}$ ), temperature ( $^{\circ}\text{C}$ ) and relative humidity (%) for all pairs. Measurements were made at 25 cm above the soil surface for all plants, near midday, February 26, 1999, under a clear sky. Results were analyzed using paired t-tests.

### *Pampa Pseudotsuga*

Microclimatic data were collected at Pampa Pseudotsuga for two primary reasons: 1) to determine the level of shading provided by the experimental shade treatment, and 2) to determine whether the shade treatment resulted in significant changes in relative humidity or temperature as compared to open sites. We measured microclimatic variables (light (PAR,  $\mu\text{mol}/\text{m}^2/\text{s}$ ), temperature ( $^{\circ}\text{C}$ ) and relative humidity (%)) next to 24 randomly selected shaded plants (8 per species) and their nearest unshaded neighbors. The paired design was used to minimize inter-site differences unrelated to treatment.

All measurements were made on February 28, 1999, near midday. Although a single set of measurements fails to characterize the variation in microclimate over the course of the experiment, it did allow us to compare conditions between the shade and control treatments. Because the day was partly cloudy and light conditions varied, we used a paired sampling design, alternating measurements between shaded and open sites. Pairwise sampling helped control for the effects of temporal changes in ambient light, allowing us to compare relative light availability in the open and the shade treatments.

### **Soil analyses in clearcuts and adjacent forest**

At both experimental sites (Puerto Madera and Pampa Pseudotsuga), we collected soil samples from the clearcut area and adjacent native forest. We also collected soils from two clearcut sites on the Huemul Peninsula ("Rodal 4" and "Rodal 8) and from adjacent native forests. For each subsite (forest or clearcut), we sampled soils at 4-6



stratified random points along a 40 m transect, located approximately 20 m from the forest edge. At each sampling point, we collected four samples which were then pooled to create a composite sample.

Soils were collected to a depth of 15 cm. Samples were placed in plastic bags and transported to a laboratory at Universidad Nacional del Comahue in Bariloche, Argentina, where they were air dried. For all samples, the following analyses were performed: pH in water (Thomas 1996), pH in NaF (Blakemore et al. 1987), electrical conductivity (Blakemore et al. 1997), organic carbon (Nelson & Sommers 1996), total nitrogen (Bremner 1996), extractable phosphorus (Kuo 1996), exchangeable potassium (Knudsen et al. 1982), and exchangeable magnesium plus calcium (Lanyon & Heald 1982). In addition, volcanic material was estimated visually and rated on a scale from 0 to 4 (0=absent, 1=scarce, 2=intermediate, 3=abundant). Soil chemistry data were analyzed using nonparametric tests because the assumption of equal variances was violated for many of the variables, and in the case of volcanic ash, data were non-normally distributed.

### **Statistical analyses**

Results from all components of the study were analyzed with StatView for MacIntosh (SAS Institute, Cary, NC). Where t-tests were used, p-values represent the result of two-tailed tests unless otherwise indicated. Where Mann-Whitney U tests were used, statistics were not corrected for ties unless otherwise indicated. Diversity was calculated using Simpson's D ( $1/\sum P_i^2$ ), the inverse of the sum of the squared proportional abundance of each species (Begon et al. 1986). The theoretical maximum for D is equal to the species richness, S, and as community evenness declines, D declines (Begon et al. 1986).

## RESULTS

### Patterns of regeneration

The native vine, *Mutisia spinosa*, comprised more than half of woody plant cover at Puerto Madera (Fig. 4). The native shrub *Berberis darwinii* was the next most abundant, at approximately 10% cover; all the remaining species had cover values of less than 10%. The species regenerating in the clearcut included native shrubs (*Mutisia spinosa*, *Berberis darwinii*, *Berberis buxifolia*, *Diostea juncea*, *Schinus patagonicus*, *Ribes magellanicum*), exotic shrubs (*Rubus sp.*, *Rosa eglanteria*), exotic trees (*Pinus ponderosa*, *Pseudotsuga menziesii*), and one native tree seedling (*Luma apiculata*). Total richness was 11, with 4 exotic species and 7 native species. Because evenness was low, diversity as measured by Simpson's Index was only 1.92. Plants covered only 35% of the area surveyed; more than half of the clearcut was comprised of bare ground, stumps or woody debris that had not been colonized by plants.

### The effects of shrubs and herbivory on native tree seedlings (Puerto Madera)

#### *Condition and Proportion of Live Branches*

For all three species, average condition was higher for seedlings growing near shrubs than in the open (Fig. 5, 2-way ANOVAs,  $p=0.003$  for *N. dombeyi*,  $0.02$  for *L. hirsuta*, and  $<0.0001$  for *A. chilensis*). The presence of a cage had no significant effect on the condition of *N. dombeyi* or *L. hirsuta* (2-way ANOVAs,  $p=0.10$  for *N. dombeyi* and  $0.95$  for *L. hirsuta*); however the condition of *A. chilensis* was significantly better with cages than without (2-way ANOVA,  $p=0.005$ ).

The average proportion of live branches was higher for both *N. dombeyi* and *L. hirsuta* in the shrub treatment; however this effect was statistically significant only for *N. dombeyi* (Fig. 6, 2-way ANOVAs,  $p<0.001$  for *N. dombeyi* and  $0.09$  for *L. hirsuta*). The cage treatment had no effect on proportion of live branches for *L. hirsuta*. For *N.*

*dombeyi*, plants with cages had a higher proportion of live branches than unprotected plants (Fig. 6, 2-way ANOVA,  $p < 0.05$ ).

### *Growth*

Only *A. chilensis* exhibited significantly different growth responses to the experimental treatments. Growth of *A. chilensis* was significantly greater when cages were present (Fig. 7, 2-way ANOVA,  $p < 0.0001$ ) and in the absence of shrubs ( $p = 0.001$ ). All three species showed average negative growth under most treatments; the only exception was neutral to slightly positive growth for *A. chilensis* with cages.

### *Herbivory*

Where cages were intact and fully covered the experimental plants, seedlings showed no signs of browsing by deer (Fig. 8). A few cages were collapsed or knocked over; plants with collapsed or missing cages were excluded from the analyses.

Cages reduced browsing for all three species. In the absence of cages, 100% of *N. dombeyi* and *A. chilensis* seedlings were browsed, while 25% of uncaged *L. hirsuta* seedlings were browsed. At the individual plant level, cages affected the number of branches browsed for all three species (Mann-Whitney U, corrected for ties,  $p < 0.0001$  for *N. dombeyi* and *A. chilensis*,  $p = 0.03$  for *L. hirsuta*). However, uncaged seedlings showed inter-specific differences in the number and percent of branches affected by deer. For uncaged *N. dombeyi*, 59% of all branches were browsed, with an average of  $10.6 \pm 1.1$  (1 S.E.) browsed branches per plant. *A. chilensis* had only  $4.0 \pm 2.5$  browsed branches per plant, and *L. hirsuta* had a mean of  $0.24 \pm 0.11$  browsed branches, with only 2% of all branches showing signs of herbivory. (The percent of branches browsed was not calculated for *A. chilensis* due to difficulty in quantifying total branch number in this species.)

When both caged and uncaged seedlings were analyzed, the number of browsed branches did not differ for seedlings in shrub versus open sites (Mann-Whitney U, corrected for ties,  $p=0.3$  for *N. dombeyi*,  $0.4$  for *A. chilensis* and  $0.2$  for *L. hirsuta*). However, when caged plants were excluded, *L. hirsuta* near shrubs had significantly fewer branches browsed than plants in the open (Mann-Whitney U, corrected for ties,  $p=0.05$ ). The effect of shrubs was not significant for uncaged *N. dombeyi* or *A. chilensis* (Mann-Whitney U, corrected for ties,  $p=0.1$  for *N. dombeyi* and  $0.6$  for *A. chilensis*).

These results are corroborated by the distribution of browsed plants near shrubs versus in the open (Table 1). For *L. hirsuta*, all of the browsed seedlings were in the open (uncaged plants near shrubs were unaffected by deer). For *N. dombeyi* and *A. chilensis*, all uncaged seedlings were browsed, whether with or without shrubs.

#### **The effects of shade on seedling growth and condition (Pampa Pseudotsuga)**

Due to declines in seedling condition between planting and commencement of the experiment the following year, sample sizes were small ( $n=4$  shaded and  $4$  open seedlings for *N. dombeyi*,  $n=8$  and  $12$  for *A. chilensis*,  $n=8$  and  $9$  for *L. hirsuta*). When species were analyzed individually, the shade treatment had no significant effects on either growth (Mann-Whitney U,  $n=4$ ,  $p=0.06$  for *N. dombeyi*,  $n=8$  shaded and  $12$  for shade, open,  $p=0.2$  for *A. chilensis*, and  $0.2$  for *L. hirsuta*) or condition (Mann-Whitney U,  $p=0.08$  for *N. dombeyi*,  $0.9$  for *A. chilensis*, and  $0.08$  for *L. hirsuta*) for any of the three species.

Pooling the species for analysis revealed a significant effect of shade on growth (Mann-Whitney U,  $p=0.01$ ), but not condition (Mann-Whitney U,  $p=0.6$ )

The pattern of change in vertical height was similar for all three species. On average, shaded seedlings lost vertical height, and seedlings in the open had positive vertical growth (Fig. 9). The loss of height in some seedlings probably resulted from bending over and/or deer browsing of the tallest branches.

In contrast to the pattern in height, there was no consistent pattern in seedling condition for the three species (Fig. 10). For *A. chilensis*, mean change in condition was similar in the shade and in the open. For *N. dombeyi*, seedlings in the open had a greater decline in condition than those in the shade, while for *L. hirsuta*, the trend was reversed.

### **Microclimatic measurements**

#### *Puerto Madera*

Microclimatic conditions for experimental plants with high condition ratings (rated 3) differed in only a few cases from those with low condition ratings (rated 1) (Table 2). For *N. dombeyi*, temperature and wind differed significantly in the vicinity of high versus low condition seedlings. Microsites with seedlings in good condition had higher mean temperatures and lower mean wind speeds than microsites with seedlings in poor condition. Relative humidity and light were not significantly different for the two groups of *N. dombeyi* seedling microsites (Table 2). For *A. chilensis*, only light differed significantly between seedlings in high and low condition; temperature, relative humidity and wind were not significantly different. On average, *A. chilensis* seedlings in good condition were growing in sites with lower light levels than those in poor condition. None of the microclimatic variables differed between microsites for good and poor condition seedlings of *L. hirsuta*.

Paired comparisons of the shrub and open treatment sites at Puerto Madera revealed significant differences in temperature and light, but not relative humidity (paired t-tests,  $p < 0.05$  for temperature,  $p < 0.05$  for light,  $p = 0.1$  for relative humidity, Table 3). Mean temperature was higher near shrubs than at open microsites, while light levels were lower near shrubs than in the open (Table 3).

### *Pampa Pseudotsuga*

Paired comparisons of shaded and unshaded sites revealed significant differences in light, but not in temperature or relative humidity (Table 4, paired t-tests,  $p < 0.001$  for light,  $p = 0.6$  for temperature,  $p = 0.5$  for relative humidity). Mean light levels in the shade were only 15% of those in the open, with a mean value of  $113 \mu\text{mol}/\text{m}^2/\text{s}$  at shaded sites versus  $739 \mu\text{mol}/\text{m}^2/\text{s}$  in the open (Table 4).

### **Soils**

Nutrient levels, pH, conductivity and ash content varied from site to site, as did differences between the forest and clearcut habitat types (Fig. 11). Despite large intersite variation, forest/clearcut differences existed within certain sites for a number of variables (Table 5). For example, at both Puerto Madera and Pampa Pseudotsuga, soil pH was higher in forests than in clearcuts (Fig. 11). Conversely, pH was lower in forests than in the clearcut at Rodal 4.

For pH in sodium fluoride (Fieldes & Perrott 1966, cited in Flach et al. 1984), an indicator of amorphous material (i.e., material lacking crystalline structure, such as volcanic ash), three of the sites (Puerto Madera, Pampa Pseudotsuga and Rodal 4) had significantly higher values in clearcuts than in forest (Table 5, Fig. 11).

Where there were significant differences in nutrient levels between clearcuts and forest, nutrient levels were consistently lower in the clearcuts (Table 5, Fig. 11). In addition, conductivity was significantly lower in clearcuts than in forests at three of the four sites (Table 5). In addition to having lower mean nutrient levels, in many cases, clearcuts had significantly less variation in nutrient levels than forests (Table 6).

## DISCUSSION

Preventing invasion by *P. menziesii* and *P. ponderosa* in Argentine Patagonia requires removal of source populations such as plantations on Isla Victoria. Clearcutting exotic conifers arrests annual production and dispersal of seeds by mature trees, which in turn should slow spatial spread by non-native conifers. However, methods of plantation removal and subsequent restoration demand attention, because clearcut areas will not necessarily rebound to their original condition, and these sites potentially can be recolonized by exotic rather than native plants.

Succession in clearcut conifer plantations proceeds very differently than in nearby native forests. Transects at Puerto Madera indicated that very few native tree species were regenerating in the clearcut, although six native shrub species were present, along with two species of exotic shrubs. The recolonizing shrubs tended to be plants that tolerate xeric conditions and typically regenerate at the steppe-forest ecotone, rather than in the mesic forest surrounding the clearcut. This suggests that microclimatic conditions in clearcut conifer plantations may mimic those usually found in drier areas further east.

Both seed bank composition and seed rain may play important roles in succession (Kotanen 1996), however propagule availability was not examined in this study. Interestingly, the two exotic trees, *Pinus ponderosa* and *Pseudotsuga menziesii*, both have seed dormancy and accumulate soil seed banks, whereas at least two of the native species (*Nothofagus dombeyi* and *Austrocedrus chilensis*) lack this ability to store seeds (Raffaele & Gobbi 1996, Veblen et al. 1996). Although seeds set the stage for succession, other factors must limit native tree regeneration: even though Puerto Madera is surrounded by native forest, none of the three most common native tree species was found recolonizing the clearcut. In addition, restoration plantings with native trees have repeatedly failed in clearcut sites.

Our experimental results suggest that, at least during 1998-1999, the clearcuts at Puerto Madera and Pampa Pseudotsuga were stressful environments for native tree seedlings. At Pampa Pseudotsuga, only about one-third of the seedlings planted in 1998 were sufficiently healthy (condition > 1) for use in the shade experiment, and under all experimental treatments, condition declined over the course of the experiment. The poor survival of native trees in clearcut plantations may reflect both biotic processes, such as competition and herbivory, and abiotic factors, such as nutrient availability. Our data suggest that nurse shrubs and protection from herbivory may both affect regeneration of *N. dombeyi*, *A. chilensis* and *L. hirsuta* after exotic conifers are removed.

### **Shrub and Shade Effects on Seedling Condition and Growth**

At Puerto Madera, seedlings of all three species fared better near shrubs than in the open; however we cannot precisely determine *why* seedling condition was better in the presence of shrubs. It is possible that shrubs facilitate tree seedling survival by buffering microclimatic conditions and/or increasing soil water retention and organic matter, but another explanation is that shrubs get established in favorable microsites, which are also good places for tree seedlings to grow. In this latter scenario, open sites are those less favorable to plant growth; this is why they have not yet been colonized by shrubs, and why tree seedlings fare poorly there. Testing this latter hypothesis would require manipulation of shrubs, either through removal or planting.

The first explanation, that shrubs buffer microclimatic conditions, is addressed preliminarily by our data. At Puerto Madera, microclimatic measurements revealed differences in both light and temperature between the shrub and open treatments; relative humidity did not differ significantly. Our results suggest that shrubs block some solar radiation and may provide a warmer midday microclimate than open sites. The temperature difference should be interpreted cautiously, however, because temperature



differences between shrub and open sites may be depend on time of day and wind speed. Light differences are likely to vary in magnitude throughout the day, however, we would not expect changes in the direction of the effect. Additional measurements would provide a more complete description of how microclimatic conditions differ between sites near shrubs and those in the open. It is possible that both the presence and magnitude of microclimatic differences vary with season and weather conditions.

By themselves, microclimatic differences between shrub and open sites are not sufficient to account for differential growth and survival of seedlings at different microsites. If microclimatic conditions are responsible for the differences in seedling success that we observed, we would expect to see differences in light, temperature, wind or relative humidity for seedlings in good condition versus those doing poorly. Our data weakly confirmed this prediction, however differences were species-specific. For *A. chilensis*, light levels were lower near seedlings in good condition. For *N. dombeyi*, temperature was significantly higher and wind was significantly lower near good condition seedlings than poor condition seedlings.

At the time of our measurements, sites near shrubs had lower light levels and higher temperatures than open sites, and our data suggest that lower light levels (for *A. chilensis*) and higher temperatures (for *N. dombeyi*) positively affect seedling condition. In combination, these results support the hypothesis that microsites near shrubs may benefit seedlings through microclimatic effects.

For *A. chilensis*, our results suggest a possible mechanism for poor seedling condition: excess photoradiation may damage leaves, leading to physiological stress for young seedlings in clearcut sites. Work by Kitzberger (1995) supports the possibility that protection from excessive solar radiation enhances survival of *A. chilensis* seedlings. Measurements of light response curves are needed to test this hypothesis.

If high light negatively affects seedling survival in open microsites, then one would expect shade treatments to ameliorate the influences of high light on seedling condition. However we found the opposite result at Pampa Pseudotsuga, where shade did not significantly improve growth or survival. In fact, for all three species, seedlings in the shade treatment *declined* in height. In contrast, unshaded seedlings had positive vertical growth.

These contradictory results may be explained in part by the fact that shaded seedlings at Pampa Pseudotsuga received much less light than those at Puerto Madera. The shade treatment at Pampa Pseudotsuga allowed penetration of only 15% of the ambient light, while shrub microsites at Puerto Madera received 67% as much light as open sites. At low light levels, photosynthetic carbon fixation will increase as radiation increases; it is only when light levels exceed a plant's maximum photosynthetic capacity that photoinhibition and leaf damage are likely to occur (Osmond 1994).

Unfortunately little information exists on the light requirements of Patagonian tree species. For *N. dombeyi*, light response experiments found a low light compensation point (LCP) (13 and 20  $\mu\text{mol}/\text{m}^2/\text{s}$  for seedlings grown in the shade and in the sun, respectively) (Read and Hill 1985). In addition, at 800  $\mu\text{mol}/\text{m}^2/\text{s}$  or less, *N. dombeyi* seedlings reached their maximal photosynthetic capacity (Read and Hill 1985). Our light data suggest that on a typical sunny day, *N. dombeyi* seedlings growing near shrubs are well above the LCP, and at midday, light levels should be sufficient for *N. dombeyi* seedlings to reach maximal photosynthetic capacity (Table 3). At Pampa Pseudotsuga, both the open and shade treatments had light levels above the LCP for *N. dombeyi*, however on the day we conducted measurements (which was partly cloudy), light levels in the shade were well below those required for *N. dombeyi* to achieve maximal photosynthetic capacity. As stated above, this difference may partly explain the poor performance of shaded seedlings at Pampa Pseudotsuga.

A second explanation for different responses to shade and shrub treatments is that microsites near shrubs may differ from open sites not only in light availability, but in a variety of other ways. Shrubs may also affect temperature or other microclimatic variables, and sites near shrubs may have higher soil fertility or greater soil moisture. Unlike the shade treatment, which was designed to isolate a single variable, the shrub treatment at Puerto Madera leads less directly to a mechanistic explanation of plant response.

In addition, the shrub/herbivory experiment took place over the course of a year, while the shade experiment occurred during a single summer season. Both shrub and shade effects on seedling growth and survival may vary seasonally, therefore results of the two experiments are not strictly comparable. In addition, there may be a tradeoff between growth and survival. For example, seedlings in the shelter of shrubs may benefit at times by avoiding photodamage, but over the course of the year, lower light levels may reduce net photosynthesis and growth.

Our results suggest that experimentation with different levels of shade is needed to illuminate the response of each species to varying light levels, and the corresponding costs and benefits for growth and survival. In addition, a fuller understanding of the differences between shrub and open microsites, in conjunction with more autecological information about native seedlings, would clarify the mechanisms responsible for differential growth and survival at different sites. Long-term experiments, with frequent monitoring of seedling condition and growth would allow detection of seasonal changes in treatment effects, as well as changes in treatment effects over the course of a tree's life history. Finally, shrub removal or shrub addition experiments would help differentiate between the effects of shrubs, in and of themselves, and the effects of sites (since shrubs may simply be growing in favorable sites).

### **Cages and the Effects of Deer Browsing on Seedling Survival and Growth**

Cages, when intact, prevented deer browsing on all species. Susceptibility to herbivory differed on a species-specific basis. For those seedlings without cages, *N. dombeyi* had the highest number of browsed branches, followed by *A. chilensis* and *L. hirsuta*. *L. hirsuta* consistently had very little or no evidence of browsing, and the only plants that were browsed were those that were in the open without cages. Interestingly, none of the *L. hirsuta* seedlings near shrubs experienced any browsing, suggesting that shrubs were sufficient to deter herbivory on this species. The results from this experiment are consistent with other studies on herbivory in the region, which suggest that *Austrocedrus* and *Nothofagus* are frequently browsed, while *L. hirsuta* is relatively unpalatable (Veblen et al. 1989, Veblen et al. 1992, Relva & Veblen 1998).

Our results suggest that *A. chilensis* may be most strongly affected by browsing. For this species, both growth and condition were significantly higher in the presence of cages. In contrast, for *N. dombeyi* and *L. hirsuta*, cages had no significant effect on either variable. The low browsing levels on *L. hirsuta* imply that deer are not the primary factor preventing regeneration. On the other hand, for *A. chilensis* in areas of high deer density, protection from herbivory may be key to regeneration success. We observed deer, as well as pellets and bedding areas, in and around the clearcut at Puerto Madera, suggesting that the area is frequently used by large herbivores. We did not compare browse pressure between the clearcut and adjacent forest, however it would be interesting to know whether deer preferentially browse in open areas, or if conversely, they prefer areas of greater cover.

The experimental approach of this study complements previous descriptive research on herbivory in Argentine Patagonia (e.g., Relva & Veblen 1998). The experimental plot contained an equal number of seedlings for each of the three species, and the seedlings were randomly assigned to locations within the plot. Therefore the

results provide a look at browsers' preferences that is relatively unbiased by density, at least at the single-clearcut scale. Because animals may shift their food preferences as relative densities change (Newman et al. 1995), data are more difficult to interpret when plant densities are uncontrolled. Further studies of deer browsing and its affect on plant regeneration could manipulate species densities and examine herbivores' sensitivity to these changes.

### Soils

Our soil data show significant differences in soil pH, electrical conductivity, and some nutrients (K, Ca+Mg, N) between clearcuts and native forest at a number of sites. In most cases, nutrient levels in clearcuts were equivalent to or lower than those in forests. In addition, at many sites, heterogeneity in soil characteristics was reduced in clearcuts as compared to native forests. These results suggest that clearcuts have more uniform nutrient levels than native forests, and that particularly fertile microsites may be uncommon in clearcuts.

The differences in nitrogen levels between forests and clearcuts may be biologically-important, because nitrogen often limits plant growth in temperate forests (Tamm 1991; Mazzarino et al. 1998). Although only one site, Pampa Pseudotsuga, had statistically significant differences in soil nitrogen, mean nitrogen levels were lower in clearcuts than in adjacent forests at all sites. However, it is difficult to know whether lower nitrogen levels in clearcut sites limit regeneration of *N. dombeyi*, *A. chilensis* and *L. hirsuta*. Recent work shows that both *N. dombeyi* and *A. chilensis* have high nutrient-use efficiencies, as compared to evergreen species of the northern hemisphere and deciduous shrubs and trees of Patagonia (Mazzarino et al. 1998). In addition, Buamscha et al. (1998) found high nitrogen conservation ability in *A. chilensis*. Little information exists on nutrient use by *L. hirsuta*. To understand the role that nitrogen plays in succession

after removal of exotic conifers, additional information is needed on nitrogen mineralization (a measure of *available* nitrogen) and plant uptake and nitrogen use.

Phosphorus may also influence succession and native tree regeneration, since Patagonian soils have high P retention capacity (Mazzarino et al. 1998). Surprisingly, work in *Nothofagus pumilio* forests in the region suggests that although available phosphorus is low, nitrogen is the limiting nutrient (Mazzarino et al. 1998). In Patagonian forests generally, phosphorus deficiency may be ameliorated by mycorrhizal associations (Mazzarino et al. 1998). Two of the three native trees studied here are known to form mycorrhizal relationships – *N. dombeyi* (ectomycorrhizae) and *A. chilensis* (vesicular-arbuscular mycorrhizae) – which may assist phosphorous uptake by regenerating trees (Fontenla et al. 1991, Veblen et al. 1996, Mazzarino et al. 1998).

From our data, it is difficult to determine the biological consequences of soil nutrient availability in clearcut sites. In addition, we cannot determine whether differences between clearcuts and forests are primarily attributable to the history of afforestation, or to clearcutting and associated erosion (Schlichter and Laclau 1998) and leaching of nutrients. Research on this question is limited. One study on Patagonian conifer plantations found that up to fifty years of afforestation with exotic conifers does not affect pH (Schlichter and Laclau 1998 citing Broquen et al. 1993). Other research with *P. menziesii* indicates that afforestation of low fertility sites may not cause nutrient declines, whereas high fertility sites do show decreased nitrogen, organic matter and cation levels (Schlichter and Laclau 1998). Further work is needed to elucidate site-specific differences in nutrients, and in the effects of afforestation and subsequent clearcutting on soil characteristics.

## CONCLUSIONS

The results of these experiments suggest no simple path to ecological restoration

of post-plantation clearcut sites, however a number of key points emerge. First, in many cases the three tree species responded differently to experimental treatments. For example, *A. chilensis* appears to be most vulnerable to herbivory, and *L. hirsuta* the least vulnerable. Responses to microclimatic conditions and nutrient availability also are likely to differ from one species to another, thus any restoration program must take into account the unique ecology of the species being planted.

Second, the effects of proximity to shrubs may differ and be more complex than the effects of simple shade treatments. Other potential positive effects of shrubs include retention of water, microclimatic buffering, protection from herbivory and amelioration of soil conditions (Franco & Nobel 1989, Raffaele & Veblen 1998, Kitzberger in press). On the other hand, shrubs may compete with tree seedlings for water, light and nutrients, so many different conditions and interactions can affect the performance of tree seedlings planted near shrubs.

Third, responses to various restoration treatments may differ from site to site and year to year. Because these experiments took place in an extremely dry year, all seedlings were exposed to a major stressor of a significantly greater magnitude than usual. For many tree species, recruitment is episodic and depends on years with particular climatic conditions. Therefore in the absence of intensive post-planting care (e.g., watering, fertilization, protection from wind and water), restoration efforts are almost inevitably bound to fail in certain years. To compensate for the vagaries of natural climatic variation, it may be necessary to plant in a series of successive years, increasing the chances that at least one cohort will be relatively successful.

Finally, these experiments were conducted at only two sites, which were relatively close to one another. Intersite differences in soils, thermal regimes and precipitation may create different limiting factors at different sites. Because climate and precipitation in

northern Patagonia change dramatically over very short geographic distances, additional experimentation will be required to clarify how limiting factors vary from site to site.

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Table 1. Frequency of herbivory on seedlings in the shrub/cage experiment, Puerto Madera. Number with herbivory/total.

Species	Treatment			
	Open	Shrub, No Cage	Cage, No Shrub	Shrub & Cage
<i>N. dombeyi</i>	11/11	13/13	0/5	0/7
<i>L. hirsuta</i>	5/15	0/10	0/9	0/13
<i>A. chilensis</i>	8/8	13/13	0/11	0/13

Table 2. Results from repeated-measures analyses of variance for microclimatic differences between seedlings in good and poor condition, Puerto Madera.

	F-value	P-value
<b>Temperature</b>		
<i>N. dombeyi</i>	4.75	<0.05*
<i>A. chilensis</i>	0.42	0.5
<i>L. hirsuta</i>	2.27	0.2
<b>Relative Humidity</b>		
<i>N. dombeyi</i>	0.33	0.6
<i>A. chilensis</i>	2.18	0.2
<i>L. hirsuta</i>	0.89	0.4
<b>Wind</b>		
<i>N. dombeyi</i>	6.04	0.03*
<i>A. chilensis</i>	0.90	0.4
<i>L. hirsuta</i>	0.06	0.81
<b>Light</b>		
<i>N. dombeyi</i>	2.05	0.2
<i>A. chilensis</i>	8.19	0.01*
<i>L. hirsuta</i>	0.53	0.5

Table 3. Microclimatic data for open and shrub treatment, Puerto Madera. Data are means  $\pm$  1 S.E. N=7 measurements each near shrubs and in the open. P-values represent results of paired t-tests. A one-tailed test was used for light because we had the a priori expectation that light levels would be lower in the shrub sites than in the open; two-tailed tests were used for relative humidity and temperature. Measurements were taken at midday, on a sunny summer day.

Microclimatic Variable	Treatment		P-value
	Shrub	Open	
Light ( $\mu\text{mol}/\text{m}^2/\text{s}$ )	751.4 $\pm$ 197.1	1230.1 $\pm$ 30.4	<0.05*
Relative Humidity (%)	40.3 $\pm$ 1.0	39.3 $\pm$ 0.7	0.12
Temperature ( $^{\circ}\text{C}$ )	34.1 $\pm$ 0.5	32.1 $\pm$ 0.6	0.04*

Table 4. Microclimatic data for microsites with seedlings in the shade experiment, Pampa Pseudotsuga. Data are means  $\pm$  1 S.E.; n=24 measurements each in the shade and in the sun. P-values represent results of a two-tailed paired t-test. Measurements were taken near midday on a cloudy summer day.

Microclimatic Variable	Treatment		P-value
	Shade	Open	
Light ( $\mu\text{mol}/\text{m}^2/\text{s}$ )	113.1 $\pm$ 15.1	738.7 $\pm$ 166.2	<0.001
Relative Humidity (%)	45.6 $\pm$ 0.9	45.3 $\pm$ 0.8	0.51
Temperature ( $^{\circ}\text{C}$ )	23.8 $\pm$ 0.8	24.2 $\pm$ 0.5	0.61

Table 5. Results of tests for differences in soil characteristics between forest and clearcut sites. P-values and z-values indicate results of Mann-Whitney U tests for differences between clearcuts and forest; asterisks indicate significance at  $p < 0.05$ . Because for many variables there was an interaction between site and habitat type (forest clearcut), the pooled "all sites" data should be interpreted with caution.

Variable	Site	Z-value	P-value
pH H <sub>2</sub> O	All sites	-1.46	0.1
	PM	-2.56	0.01*
	PP	-2.72	0.007*
	R8	-0.58	0.6
	R4	-2.31	0.02*
pH NaF	All sites	-3.17	0.002*
	PM	-2.56	0.01*
	PP	-2.48	0.01*
	R8	-0.14	0.9
	R4	-2.02	0.04*
Electrical Conductivity	All sites	-2.72	0.007*
	PM	-2.56	0.01*
	PP	-2.56	0.01*
	R8	-0.58	0.56
	R4	-2.02	0.04*
Potassium	All sites	-1.61	0.1
	PM	-2.40	0.02*
	PP	-0.88	0.4
	R8	-0.73	0.5
	R4	-0.58	0.6

Table 5 continued.

Variable	Site	Z-value	P-value
Calcium + Magnesium	All sites	-2.46	0.01*
	PM	-2.24	0.03*
	PP	-2.88	0.004*
	R8	0.00	>0.9
	R4	-0.87	0.4
Phosphorus	All sites	-0.33	0.7
	PM	-0.56	0.6
	PP	-0.24	0.8
	R8	-1.16	0.3
	R4	-0.58	0.6
Organic Carbon	All sites	-0.95	0.3
	PM	-1.21	0.3
	PP	-1.92	0.05
	R8	-0.87	0.4
	R4	0.00	>0.9
Nitrogen	All sites	-2.26	0.02*
	PM	-1.76	0.08
	PP	-2.88	0.004*
	R8	-0.14	0.9
	R4	-1.44	0.15
Volcanic Material	All sites	-0.18	0.9
	PM	0.00	>0.9
	PP	-0.96	0.3
	R8	-1.16	0.3
	R4	-0.58	0.6



Table 6. Differences in soil heterogeneity between forests and clearcut sites. Variance ratios represent the F-statistic.

Measured Variable	Site	Variance Ratio (F/C)	P-value
pH H2O	All sites	3.7	0.007*
	PM	2.1	0.4
	PP	3.4	0.2
	R8	4.5	0.2
	R4	8.3	0.1
pH NaF	All sites	3.3	0.01*
	PM	2.2	0.4
	PP	8.2	0.04*
	R8	0.8	0.9
	R4	18.6	0.04*
Electrical Conductivity (mS/m)	All sites	22.2	<0.0001*
	PM	36.8	0.001*
	PP	1.9	0.5
	R8	26.5	0.02*
	R4	8.5	0.1
Potassium (cmol/kg)	All sites	4.3	0.003*
	PM	5.0	0.1
	PP	0.7	0.7
	R8	1.9	0.6
	R4	16.4	<0.05*

Table 6 continued.

Measured Variable	Site	Variance Ratio (F/C)	P-value
Calcium + Magnesium (cmol/kg)	All sites	7.3	<0.0001*
	PM	12.4	0.02*
	PP	13.9	0.01*
	R8	5.7	0.2
	R4	49.3	0.009*
Phosphorus (mg/kg)	All sites	1.3	0.5
	PM	0.6	0.6
	PP	4.7	0.1
	R8	0.2	0.2
	R4	5.4	0.2
Organic Carbon (g/kg)	All sites	2.0	0.1
	PM	2.7	0.3
	PP	1.9	0.5
	R8	6.1	0.2
	R4	0.7	0.8
Nitrogen (g/kg)	All sites	2.2	0.1
	PM	26.8	0.003*
	PP	1.6	0.6
	R8	2.9	0.4
	R4	10.1	0.1
Volcanic Material	All sites	2.0	0.1
	PM	1.0	>0.9
	PP	---	---
	R8	---	---
	R4	---	---

Figure 1. Factors affecting succession after exotic conifers are clearcut. Site history plays a key role in determining current conditions. Native forest sites in Nahuel Huapi National Park were converted to plantations early in the twentieth century, then clearcut beginning in the 1980s. The outcome of succession will be determined by site history, biotic and abiotic conditions, and human intervention. In addition, these factors interact (as suggested by the overlapping circles), so succession is a complex process, and significant ecological knowledge is necessary to effectively restore native forests.

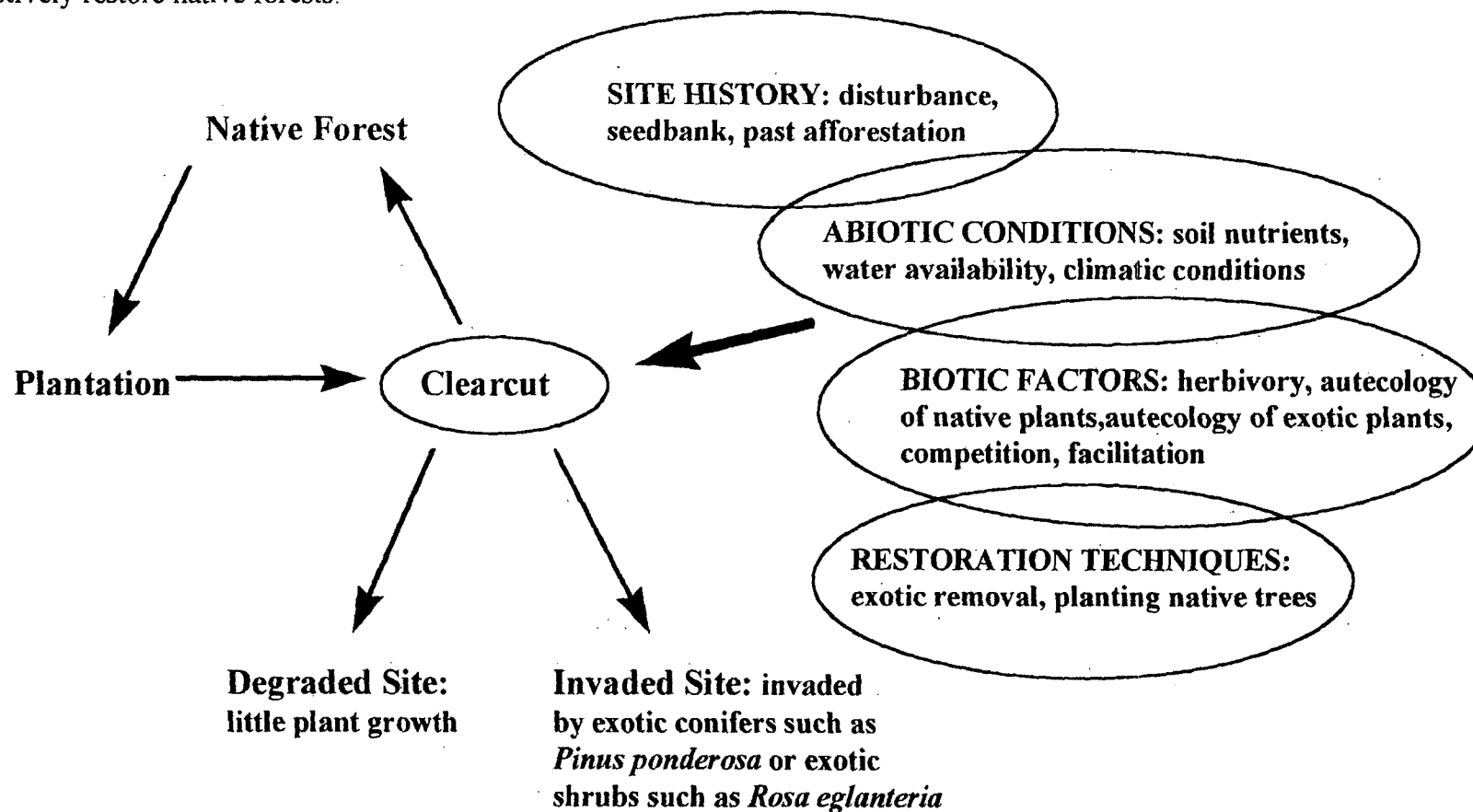


Figure 2. Study sites were located on Isla Victoria in the center of Nahuel Huapi Lake and the Huemul Peninsula area, on the north side of the lake.

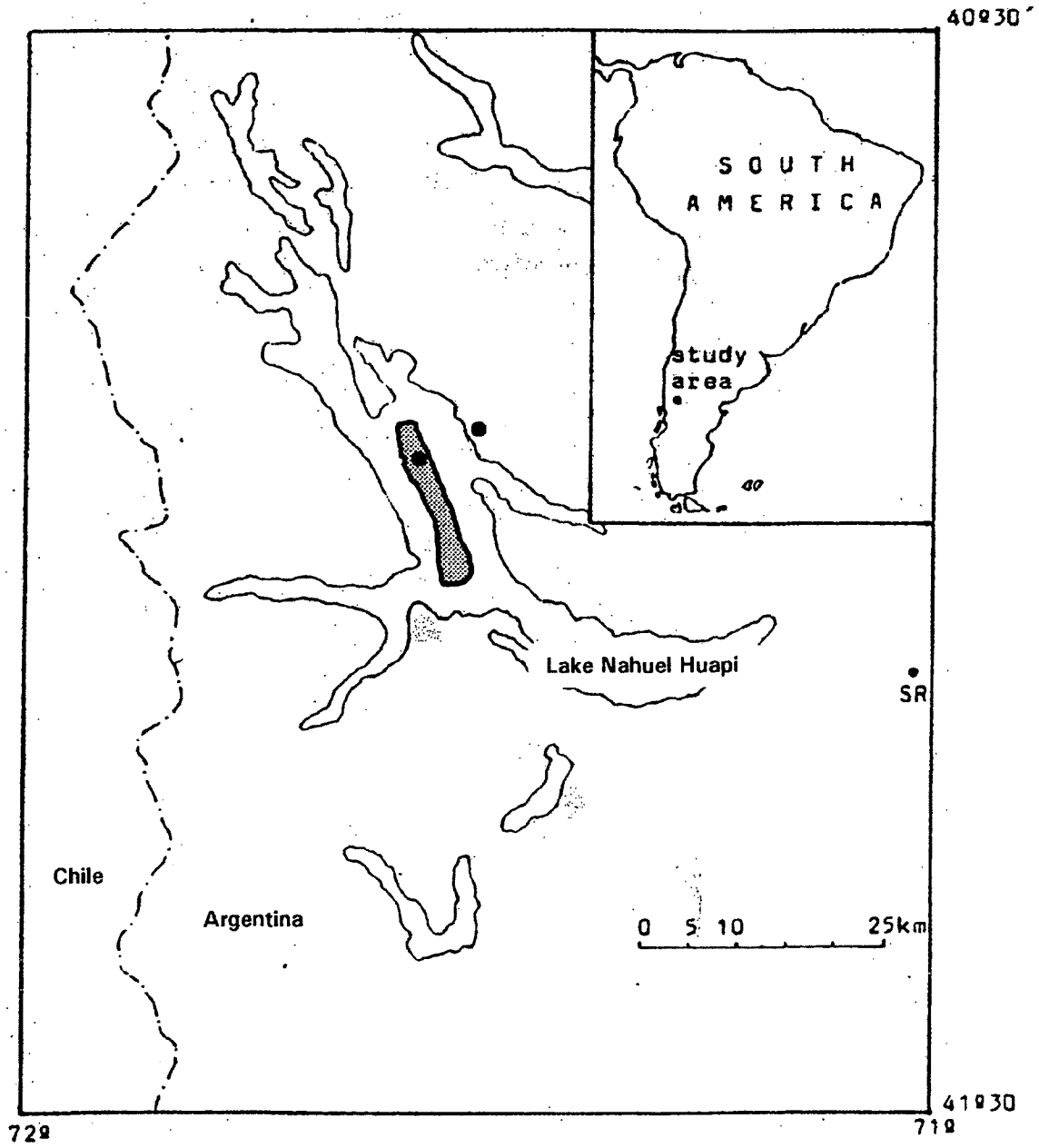


Figure 3. Planting pattern for shade experiment Pampa Pseudotsuga. Seedlings were spaced 3 m apart.  
 ND = *N. dombeyi*, AC = *A. chilensis*, LH = *L. hirsuta*

	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH
	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND
	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC
	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH
	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND
	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC
	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH
	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND	AC	LH	ND
Column	5	6	7	8	9	10	11	12	13	14	15	16	17	18

Figure 4. Percent cover in tree/shrub transects at Puerto Madera. Species are abbreviated as follows: MR = *Mutisia retusa*, BD = *Berberis darwinii*, PP = *Pinus ponderosa*, ST = stump, RE = *Rosa eglanteria*, DWD = downed woody debris, RSp. = *Rubus sp.*, BB = *Berberis buxifolia*, DJ = *Dioscorea juncea*, PM = *Pseudotsuga menziesii*, SP = *Schinus patagonicus*, RM = *Ribes magellanicum*, LA = *Luma apiculata*.

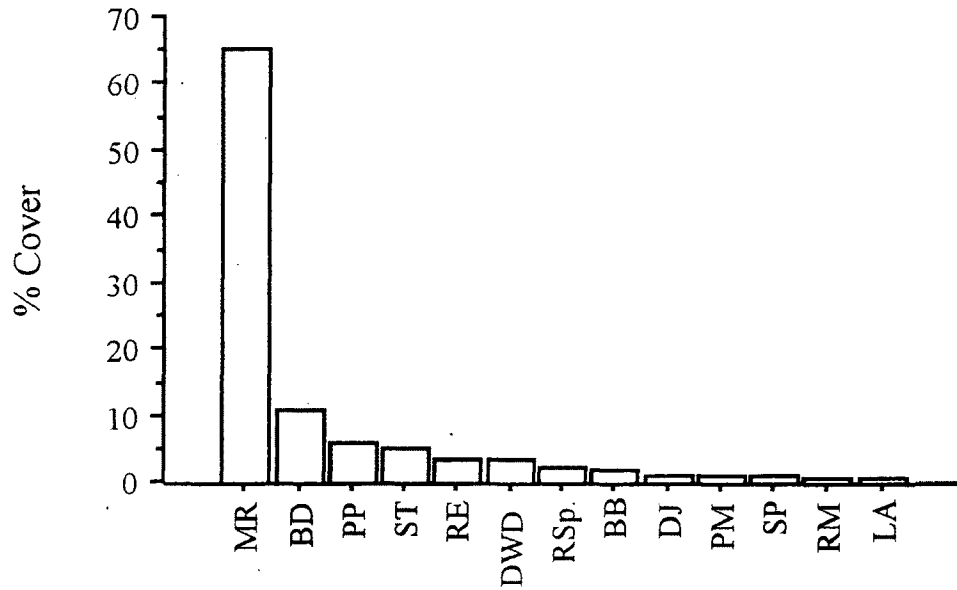


Figure 5. Seedling condition (rated 0 to 3, where 0 indicates dead seedlings and 3 indicates seedlings with 50% or more green leaves; see text for further explanation) under different experimental treatments at Puerto Madera. Data are means  $\pm$  1 S.E.

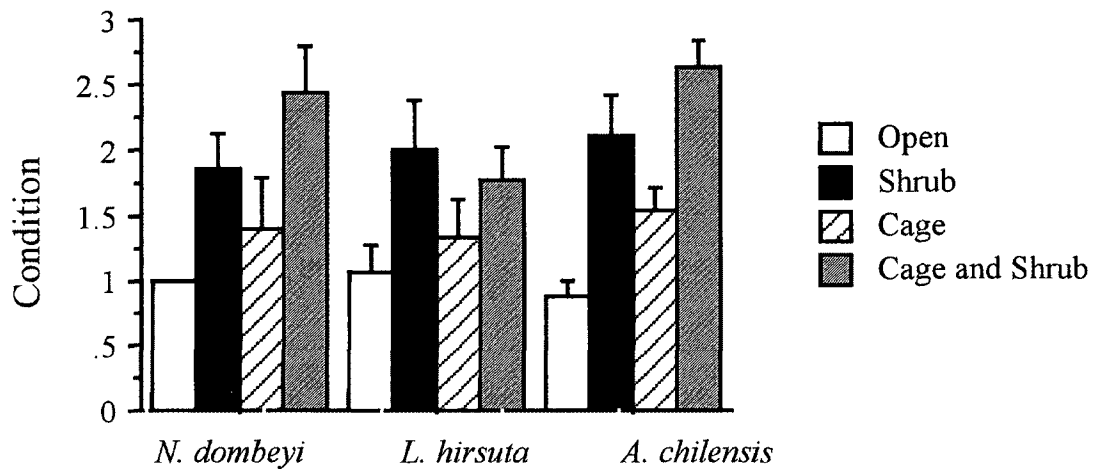


Figure 6. Proportion of branches with green leaves or active buds for *N. dombeyi* and *L. hirsuta* seedlings at Puerto Madera. Data are means  $\pm$  1 S.E.

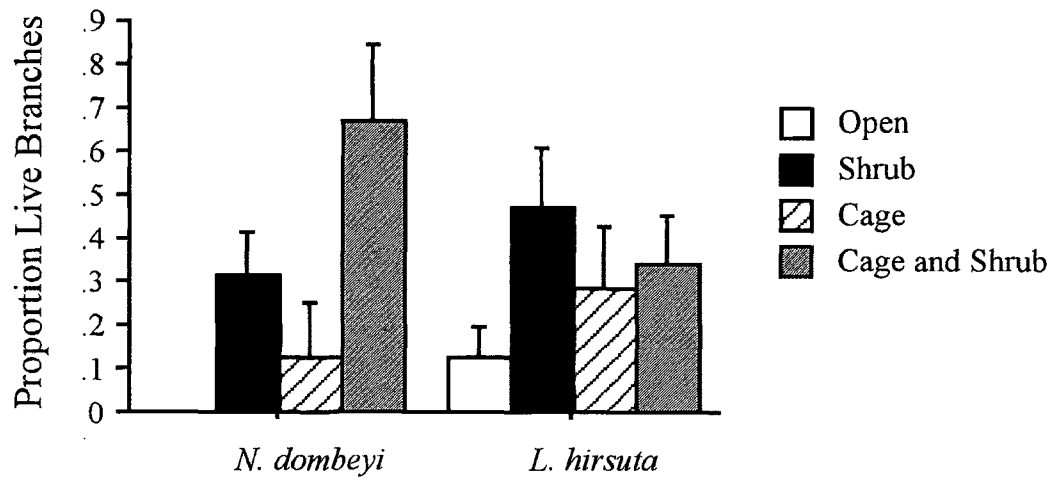




Figure 7. Change in height of seedlings under different experimental treatments at Puerto Madera. Data are means  $\pm$  1 S.E. Loss of height over the course of the experiment was probably caused by bending over and/or deer browsing of the tallest branches.

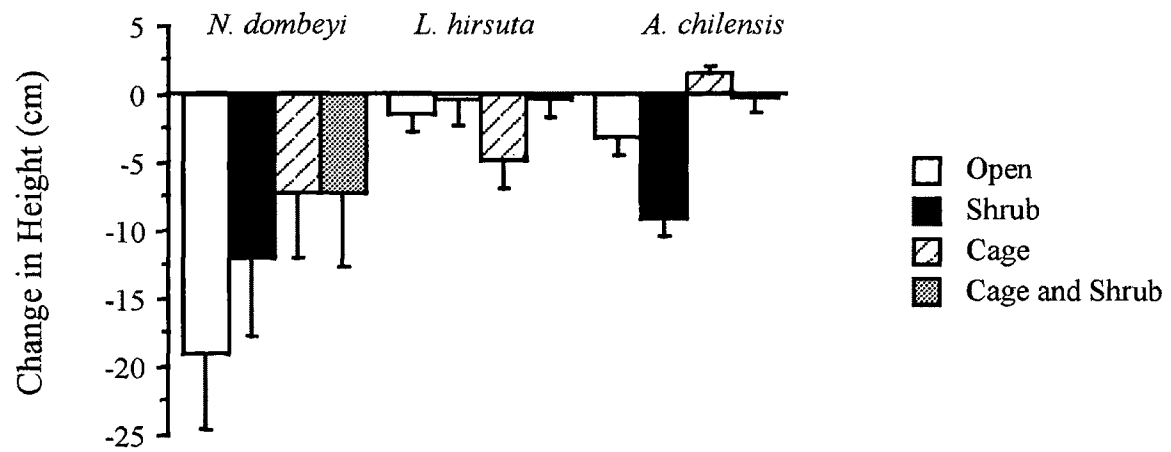


Figure 8. Number of branches showing evidence of browsing for seedlings in the shrub/cage experiment at Puerto Madera. Data are means  $\pm$  1 S.E. (Note that although we were unable to quantify the *total* number of branches for *A. chilensis*, it was possible to count the number of branches that were browsed.)

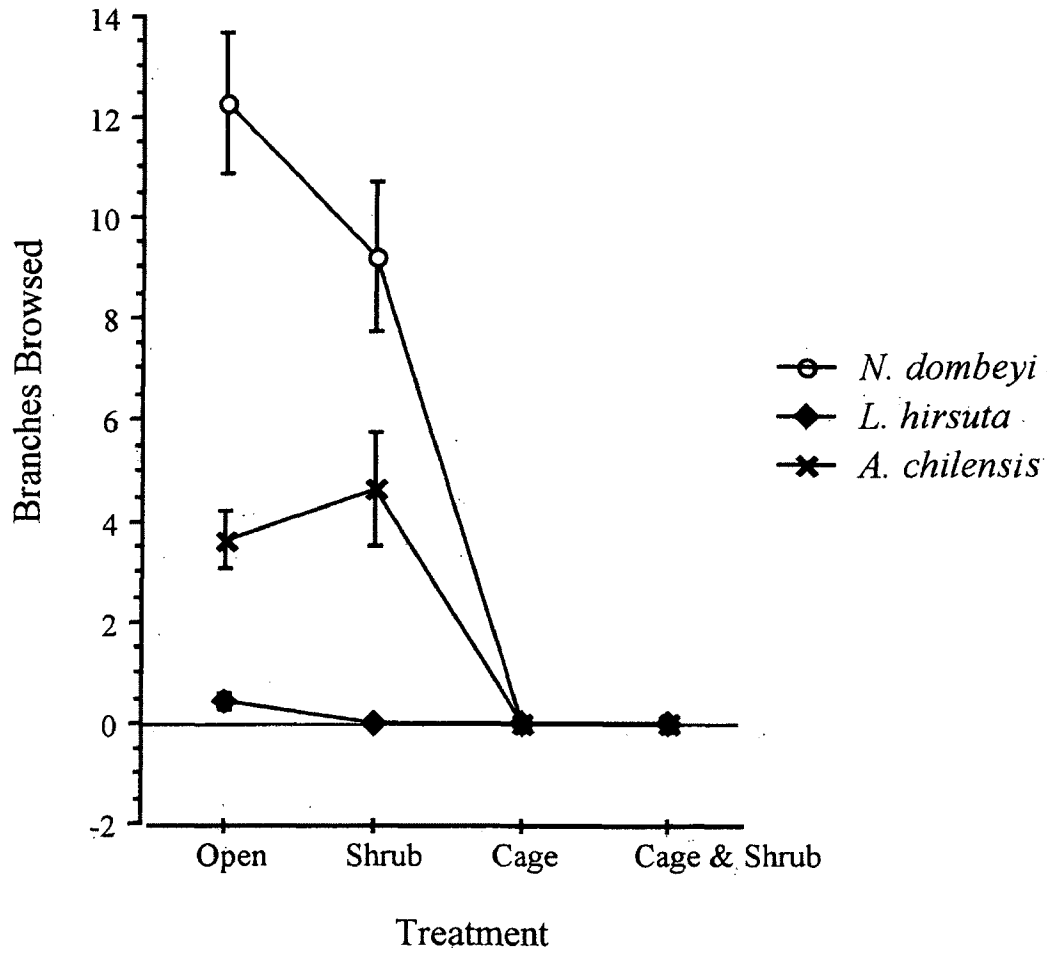


Figure 9. Change in height of seedlings under shade and open treatments at Pampa Pseudotsuga. Data are means  $\pm$  1 S.E. The loss of height in some seedlings is probably due to the tallest branches bending over and losing erectness.

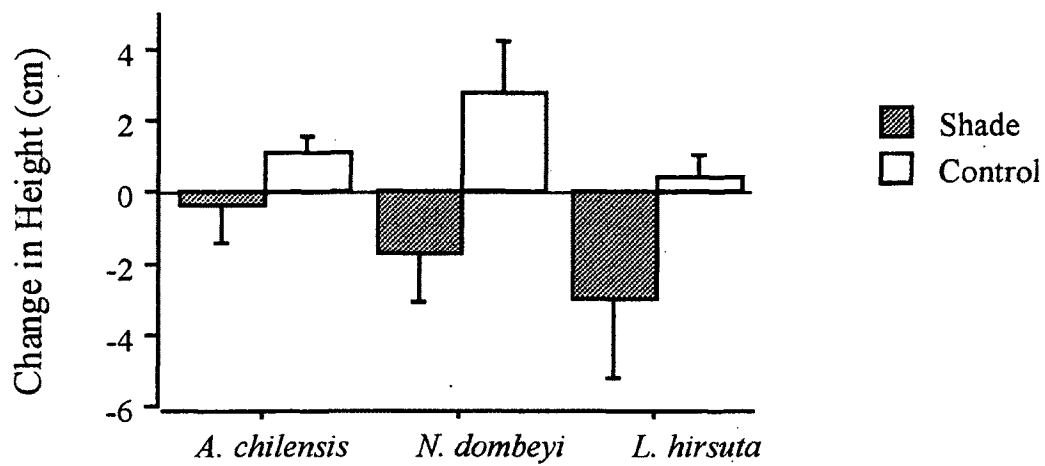


Figure 10. Change in seedling condition over the course of the shade experiment at Pampa Pseudotsuga. Data are means  $\pm$  1 S.E.

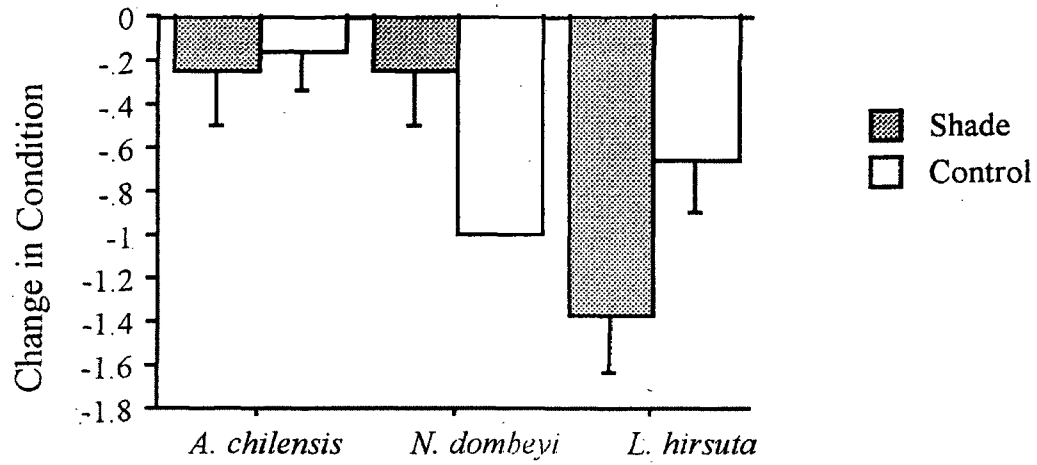


Figure 11. Soil pH, electrical conductivity, potassium, calcium and magnesium, organic carbon, nitrogen and volcanic ash content for four paired forest and clearcut sites. Data are means  $\pm$  1 S.E. (PM = Puerto Madera, PP = Pampa Pseudotsuga, R8 = Rodal 8, R4 = Rodal 4; F = forest, C = clearcut.)

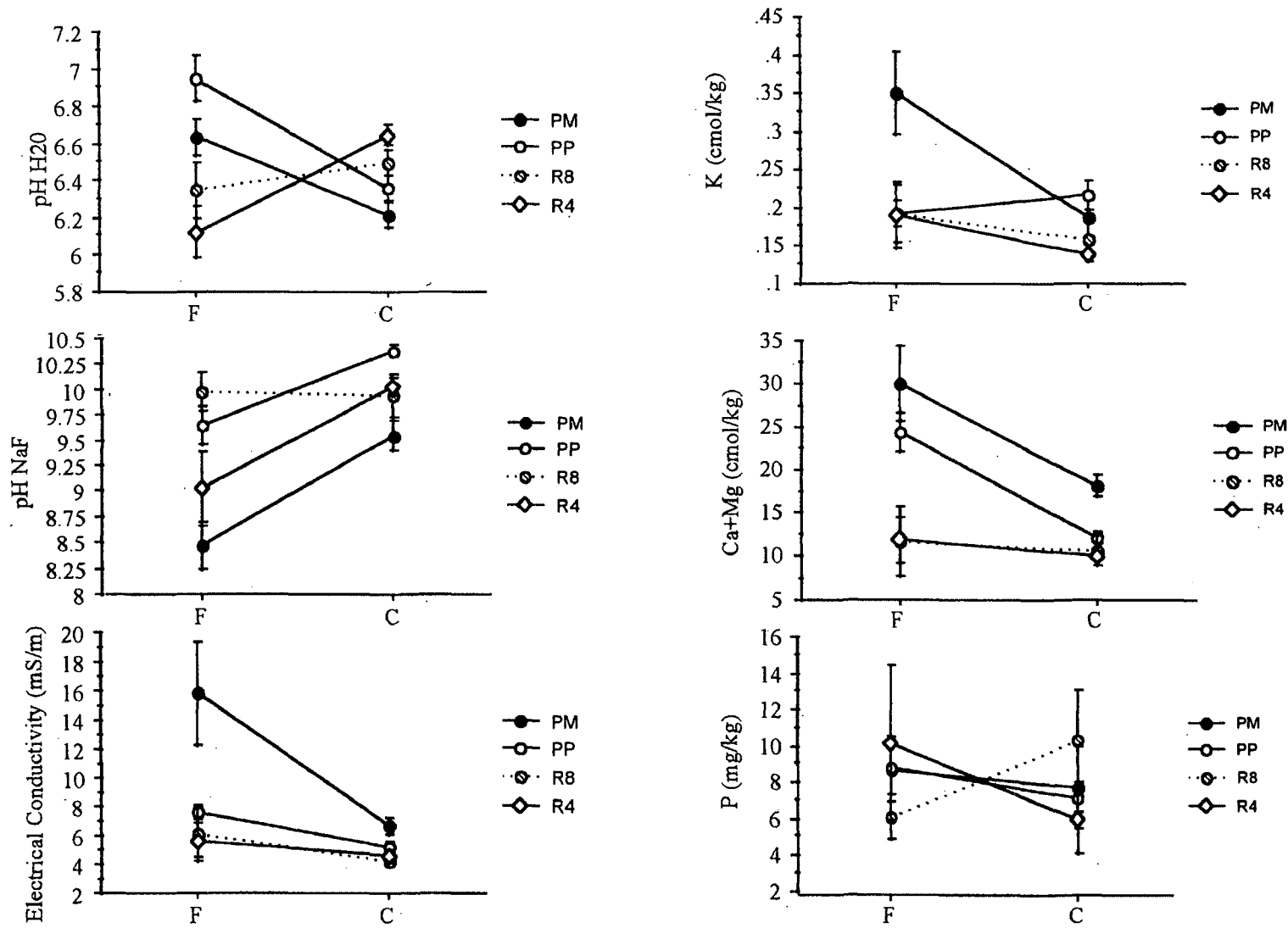
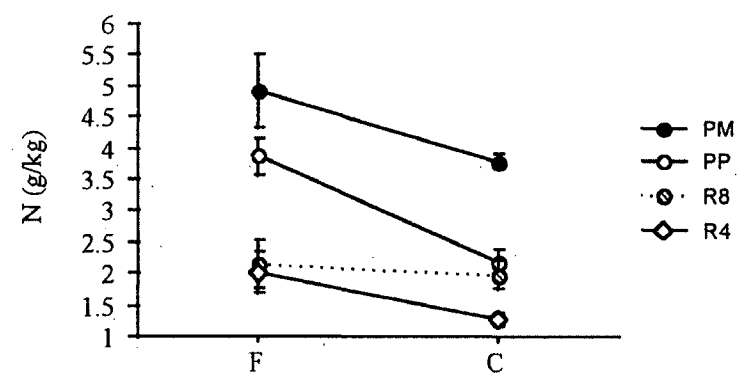
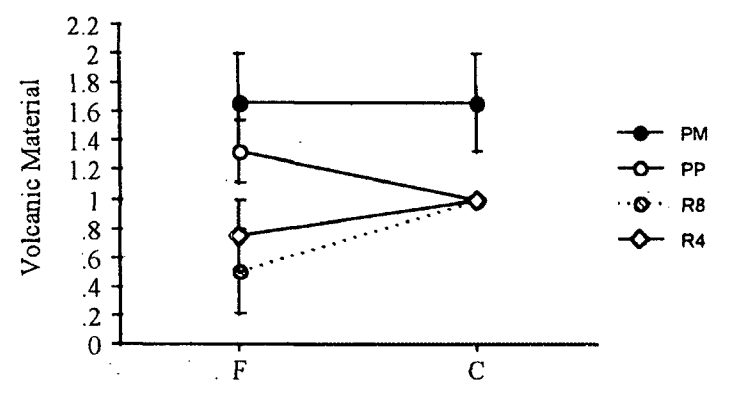
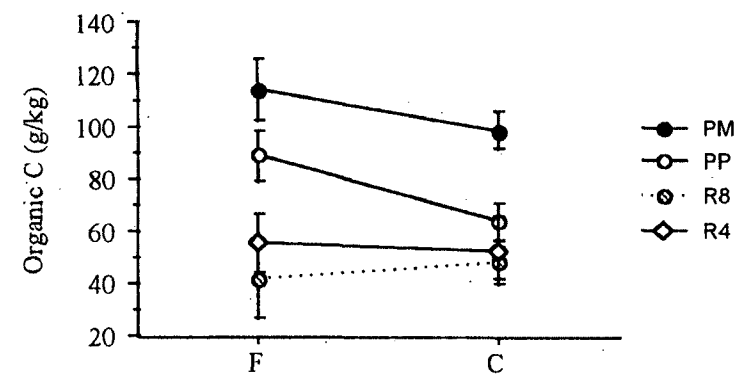


Figure 11 continued.



### CHAPTER 3

#### Plant Succession after Clearcutting of Exotic Conifers in Argentine Patagonia: Can A Native Vine (*Mutisia spinosa*) Slow Reinvasion?

##### INTRODUCTION

Invasions by exotic plants can trigger dramatic ecological changes. Consequences span multiple scales – exotics can affect the growth and diversity of native vegetation (vanWilgen & Richardson 1985, Richardson et al. 1989), modify nutrient cycles (Vitousek & Walker 1989, Davis & Lang 1991) and change disturbance regimes (Hughes et al. 1991). These changes, in turn, can affect native biodiversity, and in some cases, directly influence resource availability to human communities. In New Zealand, for example, Dons (1987) found significantly lower annual river flows in watersheds with exotic pines than in either grassland or native forest.

During the past century, exotic pines have been widely planted throughout the Southern Hemisphere. Australia, New Zealand, South Africa and Chile now all have substantial plantations of exotic pines (Richardson et al. 1994). Introduction of exotic conifers into Argentine Patagonia began later and invasions are less advanced than in many other areas, where the naturalization and spread of non-native trees have precipitated a variety of ecological changes.

The control of biological invasions is most effective when the invaded areas are relatively small and localized. Patterns of invasion often exhibit a "time lag," where the population of an exotic species persists at low levels for years or even decades before explosively growing in size and areal extent (Kowarik 1995). The spread of exotic conifers in Argentine Patagonia has thus far been relatively slow; however the region may be on the cusp of a rapid increase in the rate of invasion, suggesting that now is a crucial time for control.

Control methods for exotic species are still experimental and vary widely depending on the location and type of invading plant. Techniques for controlling invasive plants include cutting or hand-pulling, herbicide spraying, livestock grazing, burning, and biocontrol. In Patagonia's Nahuel Huapi National Park, land managers began a program in the 1980s to clearcut exotic tree plantations and restore native forest. The Patagonian control program, like many others, has met limited success: exotic trees are reinvading clearcut areas, while native trees have failed to colonize.

In addition to their limited effectiveness, many exotic control methods have ecological "side effects," – ranging from killing non-target plants (herbicides), soil disturbance (grazing and hand-pulling), and cascading effects of new species introductions (biocontrol).

Reducing these ecological side effects and finding more effective control methods for exotic plants will require a better understanding of both the invader and the invaded ecosystem. What characteristics make ecological communities resistant to invasion? What limits the spread of exotics?

Crawley (1986) cites three factors that limit invasion: lack of mutualists, competition, and natural enemies. In our study area in Argentine Patagonia, little research has addressed the role of these factors in preventing spread of exotic plants. At our study site, neither lack of mutualists such as mycorrhizae nor natural enemies such as herbivores appear to control growth of exotic conifers (*Pseudotsuga menziesii* (Mirb.) Franco and *Pinus ponderosa* Dougl. ex Laws. & Laws.). However we observed many conifer seedlings that were heavily colonized by a native vine, *Mutisia spinosa* Ruiz et Pavon (Asteraceae). In this study, we examined competitive interactions between exotic conifers and *M. spinosa* in areas where conifer plantations were clearcut to control the spread of these non-native trees into surrounding native plant communities.



## STUDY AREA

The study was conducted on Isla Victoria (approx. 40°53.47 S, 71°32.07 W) in Nahuel Huapi National Park, Rio Negro and Neuquen, Argentina. Native forest in the study area is primarily composed of *Nothofagus dombeyi* (Mirbel) Oerst. (Nothofagaceae), *Austrocedrus chilensis* (D. Don) Florin et Boutleje (Cupressaceae), and *Lomatia hirsuta* (Lam.) Diels ex Macbr. (Proteaceae). The climate is temperate and mesic. Mean summer temperature is 16 °C and a mean winter temperature is 4.3 °C (Chauchard et al. 1988). Average annual rainfall is approximately 1640 mm, with 70% of rain falling during the winter months (May-September) (Chauchard et al. 1988). Soils in this region are primarily derived from volcanic ash originating in the Andean Cordillera.

We worked in a clearcut that was previously forested with ponderosa pine and Douglas fir, both of which are exotic to South America. Slope at the site ranged from 4° to 17°, with a southeasterly aspect. The site was cut in stages between 1986 and 1996. Current vegetation on the site is a mixture of grasses, shrubs and exotic conifer seedlings, with major components of the successional vegetation including *Mutisia spinosa*, *Diostea juncea*, *Ribes magellanicum*, *Berberis darwinii*, *Berberis buxifolia*, and *Schinus patagonicus* (native), and *Pinus ponderosa*, *Pseudotsuga menziesii*, *Rosa eglanteria*, and *Rubus sp.* (exotic). Within the clearcut we observed no naturally-regenerating seedlings of the three dominant forest species.

*Mutisia spinosa* Ruiz et Pavon (Asteraceae) is a perennial rhizomatous vine which produces pink daisy-like flowers and small plumed seeds. The leaves are tough and appear resistant to both insect and mammalian herbivory (pers. obs.). At Puerto Madera, *M. spinosa* covered large areas, growing in clumps which appear to spread both outward and upward.

## METHODS

We used line transect methods to evaluate spatial associations between *M. spinosa* and each conifer species. We established a 48 m baseline that ran perpendicular to the long axis of the clearcut and roughly marked the transition between former Douglas fir and ponderosa pine plantation. The exact starting point for the baseline was randomly located. At 8 m intervals along this baseline, we established line transects running both 50 m upslope into the former ponderosa pine plantation and 50 m downslope into the former Douglas fir plantation. The descriptive data gathered using these line transects is presented elsewhere. For the purposes of this study, we divided the transects into 5 m sections and used species presence/absence data to examine spatial associations between *M. spinosa* and conifers at this spatial scale.

In order to examine *M. spinosa*-conifer interactions, we used a stratified-random design to locate starting points for eight belt transects parallel to the long axis of the clearcut, with four transect running uphill into areas formerly forested with ponderosa pine, and four running downhill into the area formerly planted with Douglas fir. Transects were 4m wide by 50m in length. In each transect we marked all Douglas fir and Ponderosa pine seedlings with aluminum tags and measured their heights. If the tree was in contact with a shrub or shrubs, we identified the shrub, measured its tallest point within the tree canopy, and estimated the percent of conifer branches "colonized" by the shrub.

In 1999, we returned and remeasured heights of the tagged trees, and again recorded the presence of shrubs and their colonization levels. We analyzed data with contingency tables using the chi-squared statistic (Zar 1984; for spatial association between *Mutisia* and conifer seedlings); t-tests (to compare height and growth with and without *Mutisia*); and regression (to relate initial conifer height to growth, with and without *Mutisia*). StatView for MacIntosh was used to conduct the analyses (SAS Institute, Inc., Cary, NC).

## RESULTS

Neither conifer species showed a significant spatial relationship with *M. spinosa* at the 5m scale ( $\chi^2=0.082$ ,  $0.064$  and  $p=0.77$ ,  $0.80$  for *Pinus ponderosa* and *Pseudotsuga menziesii*, respectively). The species distributions were independent of one another, suggesting that they co-occur primarily by chance, rather than responding to similar microsite conditions or actively facilitating or excluding one another at particular sites. We also examined the hypothesis that *Mutisia* preferentially grows on substrates provided by shrubs, stumps and downed woody debris. However no significant relationship between *Mutisia* and woody substrates was detected ( $\chi^2=0.02$ ,  $p=0.88$ ).

Conifer seedlings that were colonized by *M. spinosa* were significantly taller than those without the vine (Figure 1; 2-tailed t-test,  $t=2.08$ ,  $3.36$  and  $p=0.04$ ,  $0.001$  for *P. ponderosa* and *P. menziesii*, respectively). Although one possible explanation for this pattern is that *Mutisia* causes conifer seedlings to grow faster, our observations suggested instead that *Mutisia* colonizes conifer seedlings as they grow.

We found that seedlings with *M. spinosa* had a greater mean growth those without *M. spinosa*, though the result was not statistically significant (Figure 2;  $t=1.52$ ,  $1.69$  and  $p=0.13$ ,  $0.10$  for *P. ponderosa* and *P. menziesii*, respectively). If *M. spinosa* negatively affected conifer seedling growth, we would have expected opposite trends, thus these data suggest that *M. spinosa* has little effect on conifer growth. However, because of the relationship between *M. spinosa* colonization and original seedling height, we conducted additional analyses to examine the potential confounding effect of height.

Regressions using data on conifer height and growth (1998-1999) were highly significant for both species (Figure 3,  $p<0.0001$  for both species,  $r^2=0.825$ ,  $0.656$  for *P. ponderosa* and *P. menziesii*, respectively); taller seedlings grew faster than shorter ones, and growth rate increased linearly with original height. To examine *M. spinosa's* effect on conifer growth while controlling for height, we regressed height and growth separately for

seedlings with and without *M. spinosa*. For both species, the slope of the regression was significantly lower for trees with *M. spinosa* than those without (Table 1 and Figure 4;  $t=2.03$ ,  $p<0.05$  for *P. menziesii*,  $t=3.92$ ,  $p<0.0005$  for *P. ponderosa*). These results suggest that *M. spinosa* had a significant negative effect on the growth of both *P. menziesii* and *P. ponderosa*.

Multiple regression analysis of conifer growth versus seedling height and percent colonization by *M. spinosa* corroborated the conclusion that *M. spinosa* slows the growth of *P. menziesii*, although the results for *P. ponderosa* were equivocal (Table 2). As in the simple regression, height was highly significant for both species ( $p<0.0001$ ). However for Douglas fir, the level of colonization by *M. spinosa* in 1999 was also significant. Douglas fir showed a negative relationship between growth rate and 1999 percent colonization (regression coefficient =  $-0.261$ ,  $p=0.02$ ). In contrast, the level of colonization had no significant effect on vertical growth of ponderosa pine ( $p=0.92$  and  $0.45$  for percent colonization by *M. spinosa* in 1998 and 1999, respectively).

## DISCUSSION

Our results do not support the hypothesis that *M. spinosa* can prevent reinvasion by exotic conifers. In our two-year study, we observed no conifer mortality, and all of the trees in the study area, both with and without *M. spinosa*, grew taller. Douglas firs did grow significantly slower with *M. spinosa* than without it; however, the presence of *M. spinosa* did not significantly influence the growth of ponderosa pine. The source of this species-specific difference is unclear, however the slope of the regression lines showed similar patterns for both species. *M. spinosa* may have an effect on ponderosa pine but we perhaps lacked the power to detect it. A larger sample size or data from subsequent years might help further elucidate the relationship between *M. spinosa* and ponderosa pine.

Are the effects of *M. spinosa* on Douglas fir and ponderosa pine biologically significant? Using the height-growth regressions to predict growth with and without the vine, we would expect a 1 m tall Douglas fir to grow 51 cm/year without *M. spinosa* and 41 cm/year with it. Similarly, the regression would predict a 55 cm height increase for a 1 m tall ponderosa pine without *M. spinosa*, compared to 47 cm without the vine. Regardless of the slightly lower growth rates in the presence of *M. spinosa*, regeneration of Douglas fir and Ponderosa pine in clearcuts at Puerto Madera is proceeding at a rapid rate.

Our data suggest that the competitive effect of *M. spinosa* on exotic conifer growth is mild. Interestingly, however, the year in which the study was conducted corresponded with a fifty-year drought in the region. Thus the climatic conditions under which the study was conducted were anomalous. Continued monitoring of conifer-*M. spinosa* relationships at the site may reveal an interaction between competition and rainfall. Perhaps *M. spinosa* grows faster when rainfall is not limiting and has a stronger effect on conifer growth.

Although our work fails to establish support for *M. spinosa* as a "native biocontrol," this information about exotic-native plant interactions in Argentine Patagonia strengthens our knowledge of community structure in an invaded ecosystem. Through careful community level studies, we may be able to better understand what makes Patagonian plant communities invulnerable, and how to maintain native plant communities that can resist invasion.

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Table 1. Regression relating initial height of Douglas fir and ponderosa pine seedlings to vertical growth.

	Coefficient	Standard Error	T-value	P-value
<i>Pseudotsuga menziesii</i>				
Height (cm)				
with <i>Mutisia</i>	0.407	0.042	9.634	<0.0001
without <i>Mutisia</i>	0.512	0.032	16.256	<0.0001
<i>Pinus ponderosa</i>				
Height (cm)				
with <i>Mutisia</i>	0.408	0.071	5.716	<0.0001
without <i>Mutisia</i>	0.549	0.060	9.158	<0.0001

Table 2. Multiple regression relating growth to conifer starting height and percent colonization of conifer seedlings by *Mutisia* in 1998 and 1999.

	Coefficient	Standard Error	T-value	P-value
<i>Pseudotsuga menziesii</i>				
Height (cm)	0.482	0.035	13.820	<0.0001
Percent colonization (1998)	-0.172	0.109	-1.585	0.1186
Height (cm)	0.488	0.032	15.472	<0.0001
Percent colonization (1999)	-0.261	0.113	-2.313	0.0244
<i>Pinus ponderosa</i>				
Height (cm)	0.460	0.058	7.901	<0.0001
Percent colonization (1998)	0.013	0.125	0.106	0.9164
Height (cm)	0.441	0.056	7.848	<0.0001
Percent colonization (1999)	0.108	0.140	0.769	0.4458



Figure 1. Conifer height with and without *Mutisia*. Data are means  $\pm$  1 S.E.

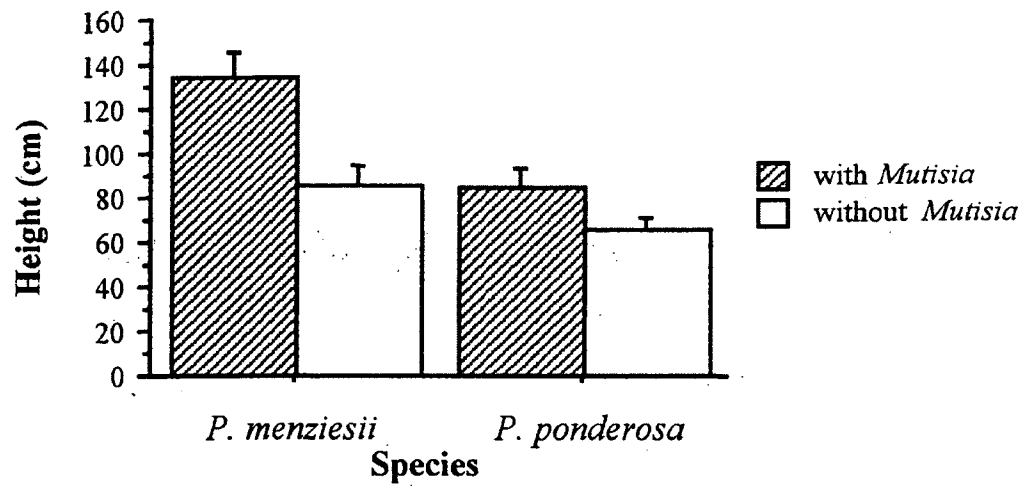


Figure 2. Growth with and without *Mutisia*. Data are means  $\pm$  1 S.E.

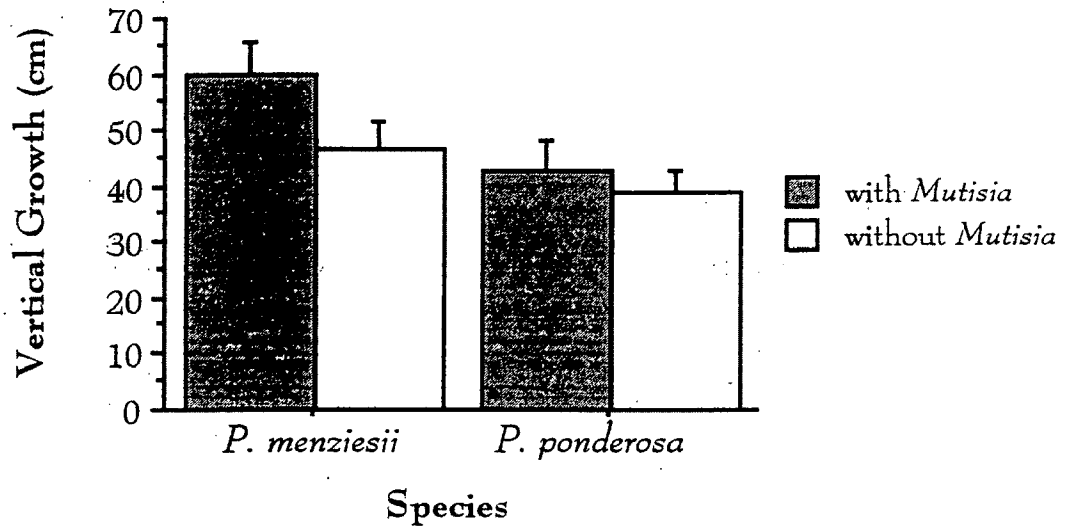


Figure 3. Relationship between conifer starting height and vertical growth. Closed circles represent *P. ponderosa*, open circles represent *P. menziesii*. Zero-intercepts were forced in the analyses.

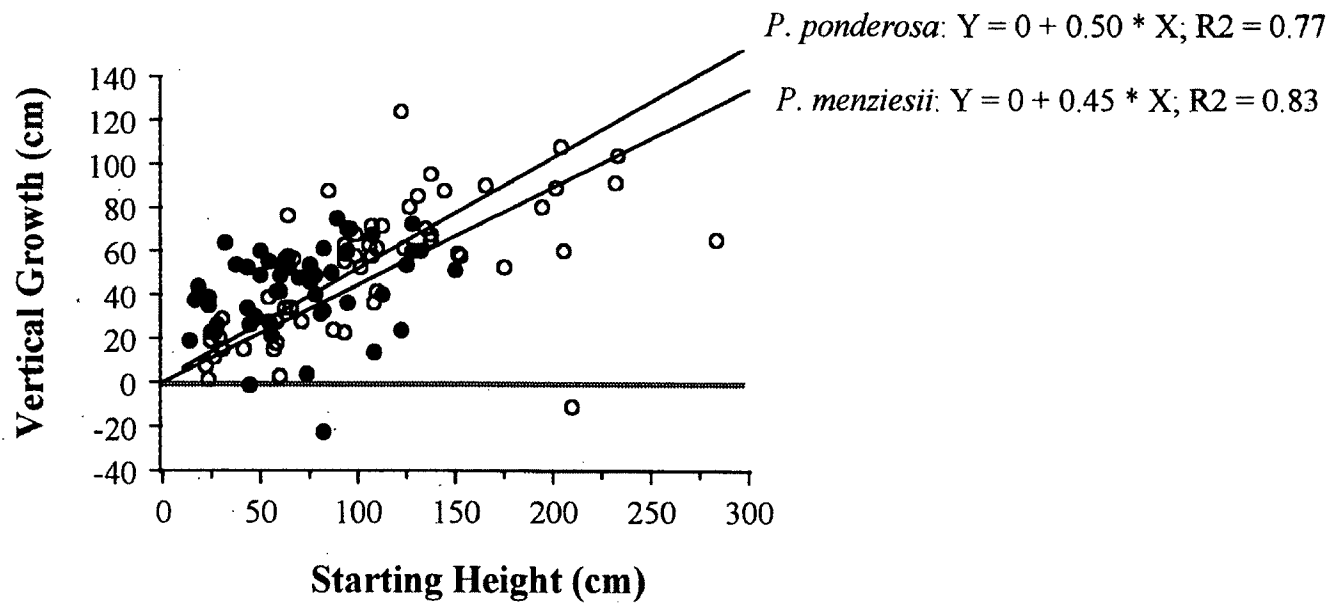
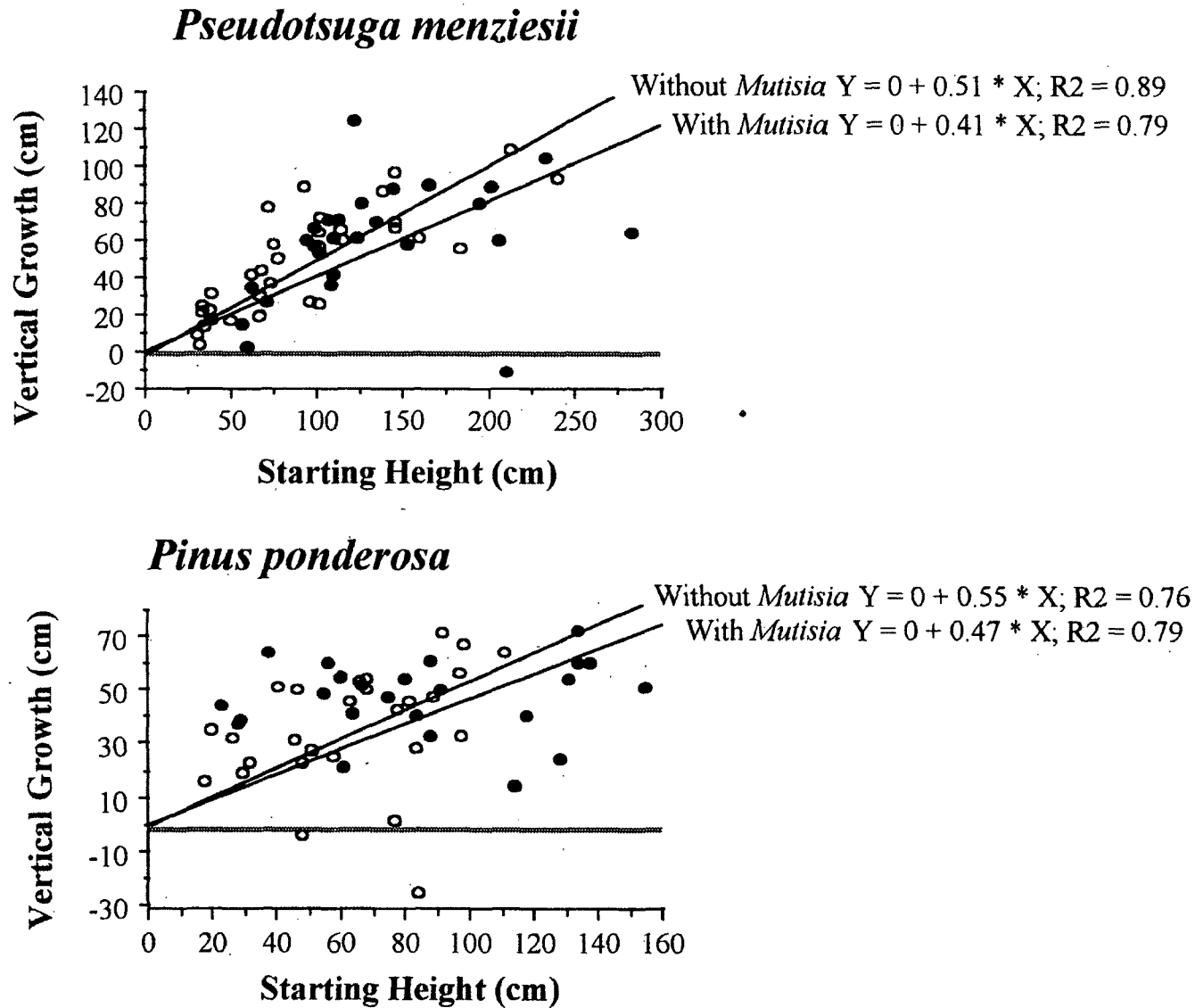


Figure 4. Relationship between starting height and growth for conifers with and without *Mutisia*. Open circles represent conifer seedlings with *Mutisia*; closed circles represent conifer seedlings without *Mutisia*. Zero-intercepts were forced in the analyses.



## CHAPTER 4

### Patagonia's Pines: Strangers Far From Home

The natural range of pines wraps around the globe in the Northern Hemisphere.<sup>1</sup> From Russia to Europe to North America, trees of the genus *Pinus* grow – often flourishing in places where other trees struggle: sandy soils, wind-blown mountain tops, or nutrient-poor sites. In North America, pines grow from coast to coast, but as we travel south through Mexico and into Central America, we reach the southern limit of pines' American range. The native range of pines ends somewhere before South America begins, and scientists don't yet understand exactly why. What blocked the migration of pines further southward?

Whatever the reason, pines and their relatives in the pine family – including Douglas fir, true firs, and spruce – never colonized the Southern Hemisphere on their own, except for a single Sumatran pine species whose range crosses the Equator.<sup>2</sup> However, during the past few centuries, many of these northern conifers have made the southward trek with human help.

With the advent of the colonial era, traffic in animal and plant species around the world grew at a rapid pace. Many settlers sought to make strange, new places more familiar by planting trees, shrubs and herbs from their far-away homes – and in this way, pines were introduced to New Zealand, Australia, Africa, and South America.<sup>3</sup> Many of these "exotic" trees flourished and were planted widely for timber.

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<sup>1</sup>Lanner, Ronald T. 1996. *Made for Each Other: A Symbiosis of Birds and Pines*. New York: Oxford University Press, 10. See also Mirov, Nicholas T. 1967. *The Genus Pinus* New York: Ronald Press.

<sup>2</sup> Ibid.

<sup>3</sup> Richardson, D.M., P.A. Williams, and R.J. Hobbs. 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography* 21: 511-527.

Although one might suspect that exotic trees would struggle in the face of new environmental conditions, in some regions of the Southern Hemisphere, exotic conifers actually grow *faster* than they did in their home ranges, and faster than their native counterparts.<sup>4</sup> Ecologists offer a number of explanations for this odd phenomenon – one of which is that organisms in new environments may find themselves free from the "natural enemies" that keep them in check at home.<sup>5</sup> Thus, while pines in North America struggle against bark beetles, fungal pathogens and a variety of other diseases and hungry herbivores, those in South America may remain relatively untroubled by such pests. This simple explanation probably fails to tell the whole story – however in many cases, it may be part of the puzzle.

Not only do exotic conifers sometimes grow faster than native species; at times they may outcompete them. In the South African fynbos shrublands, for example, introduced pines have spread throughout the native vegetation, creating a threat to native plant diversity.<sup>6</sup> Cases like these, where pines invade shrublands, are particularly serious from a conservation perspective because the invading trees can convert an ecosystem of one type into an entirely different one. Where trees replace shrubs, they change the structure of the plant canopy, and this can suppress growth of understory plants in invaded fynbos.<sup>7</sup> In addition, pines may compete with other plants for water, rapidly sucking moisture from the soil and releasing it into the atmosphere. Pines can also affect

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<sup>4</sup>Schlichter, T. and P. Laclau. 1998. Ecotono estepa-bosque y plantaciones forestales en la Patagonia norte. *Ecologia Austral* 8: 285-296.

<sup>5</sup>Williamson, M. 1996. *Biological Invasions*. London: Chapman & Hall, 68. See also: Gonda, H.E. 1998. Height-diameter and volume equations, growth intercept and needle length, site quality indicators, and yield equations for young ponderosa pine plantations in Neuquen, Patagonia, Argentina. Ph.D. Dissertation. Oregon State University, Corvallis, Oregon. 198 pp.

<sup>6</sup>Richardson, D.M., R.M. Cowling, and B.B. Lamont. 1996. Non-linearities, synergisms and plant extinctions in South African fynbos and Australian kwongan. *Biodiversity and Conservation* 5: 1035-1046.

<sup>7</sup>Richardson, Williams and Hobbs, 1994.

patterns of natural disturbance in the fynbos – for example, fire intensity may increase where invaders grow in thick stands.<sup>8</sup>

What's so significant about the spread of pines into new places? After all, don't plants and animals migrate naturally, expanding and contracting their ranges over time? The answer is yes – and any time a plant or animal population expands into a region for the first time, ecologists call it a "biological invasion."<sup>9</sup> In recent times, however, the term biological invasion has taken on new significance, since most invasions are catalyzed by human action. What's more, human-caused biological invasions today pose a major threat to biodiversity worldwide.<sup>10</sup> Many of us in the United States have direct experience with exotic plants or animals, many of which have begun to compete with native species, and in some cases, displace them. From purple loosestrife in Eastern wetlands to zebra mussels in the Great Lakes to spotted knapweed in the Rocky Mountain West, exotic species are bringing dramatic changes in landscapes and ecosystems across North America.

Our success in controlling exotic species and preventing loss of native biological diversity depends crucially on if and when we intervene. In areas like South Africa, invasion by exotic trees is at an advanced stage and is very expensive and challenging to control.<sup>11</sup> In other parts of the world, however, invasions are just beginning. Since problems are easiest to solve when they're small and localized, a special opportunity to take action and prevent further spread exists in places where exotic conifer invasions are at an early stage.

Argentine Patagonia is such a place. In this region of southern South America, pines and Douglas firs arrived with the settlement of Europeans in the early twentieth

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<sup>8</sup>Richardson, Cowling and Lamont, 1996.

<sup>9</sup>Mack, R.N. 1985. Invading plants: their potential contribution to population biology. Ch. 9 in *Studies on Plant Demography: A Festschrift for John L. Harper*. London: Academic Press.

<sup>10</sup>M. Soule, personal communication.

<sup>11</sup>Richardson, Williams and Hobbs, 1994. See also: Hobbs, R.J. and S.E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9: 761-770.

century, and many of the plantations begun at this time still stand today. For example, on Isla Victoria in Patagonia's Nahuel Huapi National Park, tourists can visit and view plantations that began before 1920 with the work of Otto Alberti, an ambitious German silviculturalist.<sup>12</sup>

Unfortunately, the enthusiasm of Alberti and his modern-day successors may pose a serious threat to native biodiversity in Patagonia. Throughout northern Patagonia, pines and Douglas firs continue to be planted for windbreaks, ornamentals, and for timber. And as these trees mature, their seeds are dispersed on stiff Patagonian winds. Douglas firs often thrive in the moister habitats, where native Southern Beech trees grow, while the pines flourish in more open, arid shrublands and steppe. In forested areas, pine regeneration is usually inhibited by the lack of direct sunlight these trees require to grow; however Douglas firs are more tolerant of shady conditions and can creep into the understory even in areas where the forest canopy is intact.

The social and economic incentives for planting exotic trees make the problem a difficult one. Pines grow quickly and offer an attractive option for people seeking to turn old pastures into financially-productive timberland. The complexities involved here will require careful consideration of the social costs and benefits of exotic conifers, as well as an assessment of the ecological costs of afforestation. Clearly, when exotic plants spread rampantly throughout a new ecosystem, there are usually many unintended and unanticipated consequences, often resulting in expensive and Sisyphean control strategies.

On private lands, the problem remains a thorny one. However in the national parks, where conservation of native ecosystems is a priority, the task is clearer. So in the early 1980s, the Argentine Park Service, recognizing the potential threats of invasion by

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<sup>12</sup>Vallmitjana, Ricardo. *Historias de Bariloche: Isla Victoria, Primera y Segunda Parte*. In *Todo Supermarkets Newsletter*, 1998. Original information from: Archiva Historico Regional Ricardo Vallimitjana, Cooperative de Electricidad Bariloche Ltda., Bariloche, Rio Negro, Argentina.



exotic conifers, began a program to remove the non-native trees and reestablish native forests in Nahuel Huapi National Park.<sup>13</sup>

This, however, was easier said than done. The Park Service program began by surveying the existing plantations within the park, assessing the spread of exotics beyond their original planting sites, and developing a plan to eliminate pines and Douglas firs and restore natural vegetation.<sup>14</sup> By the late 1980s, the cutting had begun, leaving swaths of bare ground ready to be planted with native trees, ready to return to forests of coihue, cipres and radial – trees that colonized this region of their own accord, without human help.<sup>15</sup>

Many of the clearcuts were planted with native species: the majestic coihue (*Nothofagus dombeyi*) of the Southern Beech family; cipres (*Austrocedrus chilensis*), which looks similar to a North American juniper; and radial (*Lomatia hirsuta*), a member of the Proteaceae, a family only found south of the equator. Unfortunately, the young seedlings did not fare well. When I began my ecological research in the park in 1998, a few recently-planted survivors were hanging on – but just barely. Their leaves were wilted and browned, and by the end of the summer, many of the young trees looked deathly thin and weak.

On the other hand, a number of the clearcuts I observed were beginning to fill with young pine and Douglas fir seedlings, which, by contrast, seemed to be doing quite well. Why were the exotics coming back, while the natives were faring so poorly?

As is commonly the case in ecology, the possible explanations are numerous. Perhaps the decades of pine forest changed the soil, making conditions unfavorable to

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<sup>13</sup>Monica Mermoz, Parques Nacionales Argentina, personal communication.

<sup>14</sup>Administracion de Parques Nacionales Argentina. 1988. Convenio entre la Administracion de Parques Nacionales y la Provincia de Rio Negro, Tema 1 - Proyecto de manejo silvicultural para la paulatina erradicacion de las especies forestales exoticas de Isla Victoria. Administracion de Parques Nacionales Argentina unpublished report, Bariloche, Argentina.

<sup>15</sup>Monica Mermoz, personal communication.

native trees. In some areas, pines have been shown to have an acidifying effect on soils.<sup>16</sup> Maybe the soil pH dropped to a level where native trees could not survive, or perhaps the soil microorganisms, or the availability of certain nutrients changed to the detriment of native species. On the other hand, it might not be the soils at all. It could be something as simple as seeds. Pines and Douglas firs have seeds that can remain viable in the soil for years, whereas at the two dominant Patagonian tree species, coihue and cipres, lack any period of "seed dormancy."<sup>17</sup> Instead, their seeds germinate in the year following their maturation – if it is a poor year for survival, too bad for them. In exotic conifer plantations, many years worth of pine and Douglas fir seeds probably accumulate under their parents, and when the parent trees are cut, this accumulated dormant "seed bank" kicks into gear, producing young trees to recolonize the area. The native trees, on the other hand, must depend on dispersal of their seeds from nearby trees into the clearcut, and these seeds have only one chance – they cannot wait for an ideal year to germinate. Again, the natives may be at a disadvantage.

A third explanation for the regeneration of exotics and the lack of natives in the clearcut areas has to do with environmental conditions. When trees are clearcut, there is a sudden and significant increase in sunlight reaching the soil surface. Temperatures rise and humidity drops. In addition, the area is more exposed to wind, increasing the danger of desiccation for young plants. Ecological physiologists use light meters, thermometers and wind gauges to measure these microenvironmental changes, but no special instrument is necessary to feel the difference between standing in the forest shade and stepping into the baking sun on a warm summer day in Patagonia. The sun in this region may be

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<sup>16</sup>Davis, M.R.; and M.H. Lang. 1991. Increased nutrient availability in topsoils under conifers in the South Island high country. *New Zealand Journal of Forestry Science* 21: 165-179.

<sup>17</sup>Gobbi, M. and T. Schlichter. 1998. Survival of *Austrocedrus chilensis* seedlings in relation to microsite conditions and forest thinning. *Forest Ecology and Management* 111: 137-146; Veblen, T.T., C. Donoso, T. Kitzberger, and A.J. Rebertus. 1996. Ecology of Southern Chilean and Argentinean *Nothofagus* forests. Chapter 10 in T.T. Veblen, R.S. Hill, and J. Reed, editors. *Ecology and Biogeography of Nothofagus forests*. Yale University Press, New Haven.

especially strong as a result of the Antarctic ozone hole – although little monitoring has taken place in northern Patagonia, increased ultraviolet radiation has been noted at Argentina's southern tip, likely as a result of the thinning gaseous shield.<sup>18</sup>

For plants, excessive radiation can damage leaves and break down healthy cells. Although plants require light for photosynthesis – to make the sugars that fuel their metabolism – when light levels are too high, leaves can't handle all the light energy bombarding them, and the photosynthetic machinery gets backed up. The excess light energy, instead of helping to generate energy, bounces around and wreaks havoc on cellular structures. This process, called photoinhibition, stresses plants, and for young seedlings like those in the clearcuts, it may be a significant factor leading to decline and death.

It's beginning to sound like a harsh world out there for these struggling seedlings. But abiotic – or non-biological – factors are not the only challenge. Northwestern Patagonia, in addition to having many introduced plants, also hosts a number of introduced animals. And perhaps first and foremost among these, from a young tree's point of view, are the deer.

Although Nahuel Huapi National Park supports populations of two native deer species, the pudu (*Pudu pudu*) and the huemul (*Hippocamelus bisulcus*), it is the exotic species that are most abundant. The native pudu, a miniature deer about the size of a medium dog, is threatened by hunting and predation by feral dogs.<sup>19</sup> The huemul is also struggling, partly due to poaching and partly as a result of contact with diseases of domestic livestock.<sup>20</sup> In addition, the natives may be in decline due to competition with

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<sup>18</sup>"Increased Ultraviolet in Argentina." 1993. *Science News* 144(1): 15.

<sup>19</sup>Veblen, T.T., T. Kitzberger, and E. Raffaele. 1997. Nahuel Huapi and Lanin National Parks: A Guide Prepared for a Field Conference on Fire and Global Change. Inter-American Institute for Global Change Field Conference: Fire and Global Change in Temperate Ecosystems of Western North and South America. Bariloche, Argentina, January 3-4, 1997.

<sup>20</sup>Ibid.

exotic species: elk (*Cervus elaphus*) and European deer (*Dama dama* and *Axis*). These three members of the deer family all emigrated from Europe in the early twentieth century, with the help of human colonists.<sup>21</sup> Just as people sought to landscape Patagonia with familiar trees, the idea of hunting familiar wildlife species also appealed to them. And like the exotic conifers, the introduced deer have met unprecedented success in their new home – perhaps because the predators they faced in their original environments, which included bears and wolves, are absent in Patagonia.

Deer have had significant impacts on vegetation in Nahuel Huapi National Park. Ecological studies by Thomas Veblen of University of Colorado, Monica Mermoz of the Argentine National Park Service and others have confirmed that regeneration of understory trees and shrubs has been suppressed by deer browsing.<sup>22</sup> Because deer prefer some species over others, browsing can favor growth of some plants while inhibiting the regeneration of others. This in turn can alter patterns of natural regeneration in Patagonian forests.

Might deer be affecting regeneration after exotic conifers plantations are removed? It is certainly possible. In one clearcut on Isla Victoria, I observed numerous scattered piles of deer pellets, as well as matted grasses where deer bed down. Walking out to our field site, we'd often catch glimpses of reddish brown bodies bounding away – so clearly deer frequent the area. In addition, many of the shrubs in the clearcut showed evidence of browsing. Based on my observations, however, it was difficult to determine whether deer browsing is affecting regeneration of coihue, cipres and radial – none of the three species were growing back!

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<sup>21</sup>Ibid.

<sup>22</sup>Veblen, T.T., M. Mermoz, C. Martin, and E. Ramilo. 1989. Effects of exotic deer on forest regeneration and composition in northern Patagonia. *Journal of Applied Ecology* 26: 711-724; Veblen, T.T., M. Mermoz, C. Martin and T. Kitzberger. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. *Conservation Biology* 6: 71-83.

In one particular clearcut, at "Puerto Madera" (Port Wood), ten species of shrubs and trees were growing back naturally. These species included both native and exotic shrubs, as well as ponderosa pine and Douglas fir. We inventoried a sample of the vegetation in the clearcut, and surprisingly turned up only one native tree! Seedlings of the three most common tree species were completely absent.

This ecological mystery piqued my curiosity, and in addition, I felt that understanding the factors preventing native tree regeneration would prove important to the Park Service's restoration programs. So I decided to conduct some experiments.

The goal of these ecological experiments was to examine various factors that might be inhibiting regeneration of coihue, cipres and radial. Based on my observations, I suspected that herbivory (browsing by deer) and harsh climatic conditions (sun, exposure to wind and desiccation) might be critical determinants of seedling survival. To examine these factors, we set up two experiments, both of which used different treatments to pinpoint the factors affecting seedling growth and survival.

In the first experiment, we used cages to prevent deer browsing, and shrubs to shelter seedlings from sun and wind. The effect of cages should be simple – to keep hungry deer mouths from reaching tree seedlings – whereas the effects of shrubs may be more complex. Other ecological studies have shown that shrubs sometimes benefit young seedlings by providing protection from harsh environmental conditions. In addition, the places where shrubs are growing may be rich in organic matter or have more favorable soil conditions than other sites. There are two potential reasons for this: first, shrubs may survive and grow in especially favorable sites; or second, shrubs may create more favorable sites as they grow, trapping organic material at their bases and supporting an active community of soil microorganisms.

In the "shrub/cage experiment," seedlings of coihue, cipres and radial were planted in one of four different situations: they were placed in the open without cages, in the open

inside cages, near shrubs without cages, or near shrubs and inside cages. By creating these combinations, we were able to look at the effects of shrubs and cages individually, as well as trying to understand if shrubs and cages together interacted to produce better or worse conditions for seedlings to grow.

The second experiment was simpler. In this study, we simply planted seedlings in the open, or under a cloth canopy that provided shade. The objective here was to look at one factor in isolation, and to answer the question, "Do seedlings fare better when they are partially shielded from the sun?"

So what did we find? As in many ecological experiments, the results were complex. In the first experiment, all three species fared better near shrubs than in the open, supporting the idea that shrubs provide some sheltering effect. But what is the source of that effect? This remains unclear. We thought the second experiment might shed some light (so to speak) on the mechanism by which shrubs seem to benefit young tree seedlings. Perhaps it is the shade provided by shrubs that help the young seedlings survive.

Surprisingly, however, seedlings of all three species were less healthy after eight weeks in the shade than their sun-exposed counterparts. So perhaps shade is not the key to shrubs' effects after all. Or, it is possible that the *amount* of shade a plant experiences may be crucial in determining the balance between too much and too little sun. With *too little* shade (or too much sun), a plant may be overwhelmed by the sheer intensity of light energy it receives, and accordingly, suffer damage – but with *too much* shade, a young plant may not receive sufficient light to survive and grow. Fortunately, we measured light levels in both experiments, and although these measurements cannot decisively tell us how plants are responding to changes in radiation, they can provide some indication of whether our prediction – that the amount of light is key – is plausible.

Those seedlings planted near shrubs received almost 70% of the ambient light – the amount of light available in the open. In contrast, under shade cloth canopies, only about 15% of the available light reached the young seedlings. These data suggest that perhaps seedlings in the second experiment received too much shade. To test this hypothesis, it would be useful to conduct similar experiments with multiple levels of shade. For example, an experiment where groups of seedlings were grown in 25%, 50%, 75% and full light would provide a fuller sense of how plants respond to changes in solar radiation.

In addition, as mentioned earlier, the effects of shrubs may not be limited to providing shade, so a whole series of new experiments would be required to tease apart the reasons why seedlings planted near shrubs tended to do better than those in the open. For the purposes of designing restoration treatments, however, it may be sufficient simply to know that shrubs help, regardless of the reason. But to conclude firmly that shrubs do help, we would need to conduct additional experiments, at different sites and in different years, to determine how broadly applicable our results truly are.

So what about the deer? They, too, play a role. However deer – like you and I – won't eat just *anything*; they have preferences. In our experiment, both coihue and cipres were quite popular, but radial was infrequently browsed. Of the plants without cages, deer nipped all of the cipres and coihue seedlings, but only 20% of the radial. This result squares with earlier work by Maria Relva and Thomas Veblen, whose research suggests that radial is not a particularly palatable plant.<sup>23</sup> So to regenerate, radial may not require protection from deer's dangerous jaws, though cipres and coihue probably will.

An effective restoration program for Patagonian trees will need to take such species-specific differences into account. Each of the native trees we studied occupies a somewhat unique ecological niche: coihue grows in mesic regions not far from the Andes

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<sup>23</sup>Relva, M., and T.T. Veblen. 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. *Forest Ecology and Management* 108: 27-40.

and their associated precipitation, whereas cipres and radial both tolerate drier conditions, extending further eastward into the rainshadow of the Andean cordillera. The different ranges of the three species suggest that they may each have unique requirements for water and perhaps respond differently to drought. In addition, the three species likely differ in their responses to various light levels, and their susceptibility to desiccation by wind.

These species-specific differences make restoration a difficult task, because a "one-size-fits-all" approach to replanting natives is likely to fail. Furthermore, restoration in former pine and Douglas fir plantations requires not only encouragement of native trees, but control of exotics. Thus far, Park Service personnel have been tackling the exotic colonists directly, with machetes. Ultimately, this may be the only way to prevent reinvasion. However gaining further knowledge about native species and what they need to survive, as well as an understanding of the *interactions* between native and exotic plants, may assist restorationists in designing more effective programs.

In Argentine Patagonia, control of exotic conifers and ensuing ecological restoration holds significant promise. The Park Service recognizes the problem and has begun to take action. Researchers from Argentina and abroad are growing interested in studying the ecology of conifer invasions, and how to control them. And a new foundation has sprung up, aimed specifically at restoring invaded and degraded sites. Fundacion Peninsula Rauli<sup>24</sup> promises something the Park Service desperately needs for restoration projects in northern Patagonia: money. However the foundation offers other resources as well. Eduardo Castro Cisneros, the foundation's director, runs his own greenhouse and cultivates hundreds of native plants each year. In addition, Castro Cisneros is establishing collaborative relationships with the Park Service, and with university researchers.

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<sup>24</sup>Fundacion Peninsula Rauli, Eduardo Castro Cisneros, Director, C.C. No. 216, San Martin de los Andes, Q 8370 ZAA, Neuquen, Argentina



Ecological restoration often crucially depends on partnerships among scientists, land managers and citizens. Restoration has been described as both an art and a science, requiring both head and heart. Ecological research can assist us in understanding how invaded ecosystems function, and how we might be able to maintain native biodiversity in northern Patagonia. However the solutions will be complex. They will require negotiation, experimentation and long-term commitment. My hope is that the young partnerships between scientists and restorationists will continue to grow and flourish, and that accordingly, native forests will flourish as well.

## **CHAPTER 5**

### **Summary And Conclusions**

This thesis has begun to lay a scientific foundation for ecological restoration of former exotic tree plantations in Argentine Patagonia. Restoration of these sites is particularly important, because clearcut plantations have the potential to be recolonized by non-native trees, whose offspring are likely to spread beyond plantation boundaries and invade native plant communities. Widespread evidence from elsewhere in the Southern Hemisphere shows that pines are capable of invading a diverse array of ecosystems, and that once invading trees are widespread, they may be extremely difficult to control.

In Argentine Patagonia, the opportunity to prevent biological invasion by exotic conifers still exists; however it is tempting to ignore invasive species at the early stages of invasion, because the problem may appear small and insignificant. Again, evidence from plant invasions around the world illustrates that what begin as small, isolated populations of exotic species can become large and widespread, although the accelerated spread may not occur for decades or even centuries after initial introduction.

The Administracion de Parques Nacionales of Argentina has wisely identified the potential threat posed by exotic conifer plantations, and removing these plantations from Nahuel Huapi National Park is the first step in preventing invasion. However, improved restoration techniques are needed to ensure that reinvasion does not occur, and limited information exists at present regarding the factors that limit native tree regeneration in clearcut sites.

Although additional study is needed, a number of key points emerge from the descriptive and experimental work in this thesis, which are outlined below.

## NATIVE TREE REGENERATION

- Clearcuts are a stressful environment for planted native tree seedlings. One year after planting, the condition of many seedlings was poor, and it is likely that many more trees will die over the course of the second year. Repeated plantings in different years and at different sites have largely failed, suggesting that restoration techniques must be adjusted to compensate for the harsh conditions native seedlings face.
- *N. dombeyi*, *A. chilensis* and *L. hirsuta* all fared better when planted near shrubs than when planted in open sites. This suggests that shrubs may facilitate young tree seedlings, although the mechanism of facilitation is not known. Additional work on the ecophysiology and autecology of native tree seedlings may help to identify the mechanisms that underlie improved survival near shrubs.
- The microclimatic data presented here can assist in generating hypotheses about how environmental conditions affect native tree seedlings. However, more specific data are needed to determine how environmental variables affect seedling growth and survival. Microclimatic measurements do not necessarily reflect the conditions that plants experience: for example, leaf temperature and air temperature may differ depending on wind, evaporative cooling and a variety of other factors. Ecophysiological approaches that examine leaf temperature, photosynthetic response, water and nutrient use may be illuminating, particularly in conjunction with microclimatic measurements.
- In sites where deer are abundant, herbivory may be an important factor limiting regeneration of native trees, particularly *A. chilensis* and *N. dombeyi*. *L. hirsuta* appears to be less palatable to deer, and restoration techniques may be better directed toward other limiting factors for this species.

## SOILS

- Soil nutrient levels in clearcut plantations vary from site to site, though for a few variables, a consistent pattern emerged. Although the differences were not significant in

every case, all clearcuts had lower total nitrogen than nearby native forest. This result could reflect higher nutrient leaching, more rapid mineralization, or the loss of nitrogen inputs from litterfall in clearcut areas (T. deLuca, pers. comm.).

- Soil nutrient levels were much more variable in native forests than in clearcuts. The source of this variation is unknown, however, the greater variability and generally higher mean nutrient levels for native forests suggests that more fertile microsites may be available in forests than in clearcuts. Additional work is needed to test this hypothesis, and to determine its significance - if any - for plant growth.

### **NATIVE-EXOTIC INTERACTIONS**

- In any invaded ecosystem, exotic and native plants interact, and these interactions play an important role in determining how invasion will affect community structure. In this study, we found that *Mutisia spinosa* interacts with regenerating *P. ponderosa* and *P. menziesii* in a clearcut plantation at Puerto Madera. For both *P. menziesii* and *P. ponderosa*, *M. spinosa* appears to slow the growth of young trees. However, both exotic conifer species grew very rapidly, regardless of colonization by *Mutisia*, suggesting that the native vine is unlikely to inhibit reinvasion.

### **FUTURE WORK: RESTORATION, MONITORING AND PUBLIC EDUCATION**

Because successional processes are complex, future research will be needed to refine our understanding of factors that limit native tree regeneration, and to design restoration practices that promote native species and prevent reinvasion by pines (*Pinus spp.*) and Douglas fir (*Pseudotsuga menziesii*).

Additional scientific research is needed in the following areas:

- Autecology of native and exotic plants in clearcut plantations

- The role of early stages of plant growth on succession: how do seed inputs affect successional processes? What conditions do native tree species need to germinate and survive early in development?
- Factors affecting native tree survival to maturity: What factors affect growth and survival after the seedling stage? Do native tree seedlings planted in the presence of shrubs eventually overtop the shrubs? Do shrubs compete with tree seedlings at any stage of development?
- Inter-site variation in successional processes: Why do different clearcut sites develop different plant communities? Can results from native tree regeneration experiments be generalized to other sites?

In addition, restoration work should be placed into the context of a larger plan for controlling exotic conifer invasion in Argentine Patagonia. Such a plan would consider the current distribution of exotic trees and their potential to invade surrounding vegetation, and would evaluate the social and economic incentives for establishing plantations of exotic trees. In addition, a comprehensive program would educate and involve the public in setting priorities for conservation. Ultimately, the decision to control exotic species is not scientific, but rather based in human values. Once a commitment to control of exotics and conservation of native plant communities is established, scientific research can help determine how to effectively reach these goals. In general, and particularly in democratic societies, conservation measures are unlikely to succeed without public support.

Although invasion by exotic conifers potentially poses a serious threat to native biodiversity in Patagonia, the current situation also provides an opportunity. Restoration programs that involve the public can benefit conservation in many ways. For example, volunteers can help plant native trees, accomplishing a task that would tax the limited personnel and resources of the Argentine national park service. In addition, such programs may not only benefit restoration in the immediate sense; they also may have

important long-term effects. Restoration, construed broadly, involves not only revitalizing the world "out-there" - it can also be a process of human renewal and reconnection with nature. Through restoration work, people who know little about plants become personally involved in conservation of native ecosystems. Such work may give native biodiversity a chance to survive, and give us an opportunity to appreciate it more deeply.

## APPENDIX

Summary Data for Clearcut Exotic Conifer Plantations  
Nahuel Huapi National Park, Patagonia, Argentina

Table 1. Site History for clearcuts on Isla Victoria and the Huemul Peninsula. Data on plantation species are based on personal observation (Puerto Madera), personal communication with Monica Mermoz, Administracion de Parques Nacionales Argentina (Pampa Pseudotsuga), and Chauchard et al. 1998 (Huemul Peninsula). The data for the Huemul are somewhat ambiguous about the presence of *Larix* at the various sites. All cutting and planting dates were obtained from Monica Mermoz, except for the 1998 plantings, which were part of the research described in this thesis.

Site	Plantation Species	Date Cut	Date - Species Planted
<i>Isla Victoria</i>			
Puerto Madera	<i>P. ponderosa</i> <i>P. menziesii</i>	1986-1994	1998 - <i>A. chilensis</i> , <i>N. dombeyi</i> , <i>L. hirsuta</i>
Pampa Pseudotsuga	<i>P. menziesii</i>	1997	1997 - <i>A. chilensis</i> , <i>N. dombeyi</i> , <i>L. hirsuta</i> 1998 - <i>A. chilensis</i> , <i>N. dombeyi</i> , <i>L. hirsuta</i>
<i>Huemul Peninsula</i>			
Rodal 1	<i>Pinus spp.</i> <i>P. menziesii</i>	1990-1991	1991 - <i>A. chilensis</i> , <i>N. dombeyi</i> 1992 - <i>N. dombeyi</i>
Rodal 4	<i>Larix sp. (?)</i> <i>Pinus spp.</i> <i>P. menziesii</i> <i>Larix sp. (?)</i>	1991	1991 - <i>A. chilensis</i> , <i>N. dombeyi</i> 1992 - <i>N. dombeyi</i>

Table 1 continued.

Site	Plantation Species	Date Cut	Date - Species Planted
<i>Huemul Peninsula</i>			
Rodal 6	<i>Pinus spp.</i>	1991	1991 - <i>A. chilensis</i> , <i>N. dombeyi</i>
	<i>P. menziesii</i>		1992 - <i>N. dombeyi</i>
Rodal 8	<i>Larix sp. (?)</i>	1991-1995	1992 - <i>N. dombeyi</i>



Table 2. Relative abundance (%) of woody species and woody material in clearcut sites. Data are from line transects taken at each site. For Puerto Madera, 1998 data are from 6 90-m line transects, 1999-A data are from 6 50-m line transects, and 1999- B data are from 6 45-m line transects. Huemul Peninsula data are all based on 6 45-m transects from each site.

Species	Puerto Madera			Huemul Peninsula			
	1998	1999-A	1999-B	Rodal 1	Rodal 4	Rodal 6	Rodal 8
<i>Mutisia spinosa</i>	64.9	39.4	32.8	20.3	2.6	---	9.3
<i>Diostea juncea</i>	1.0	27.0	8.6	0.4	0.8	---	0.9
<i>Rubus sp.</i>	2.0	9.6	---	---	---	---	---
Stump	5.0	7.2	7.9	3.7	16.5	8.8	21.0
<i>Pseudotsuga menziesii</i>	0.8	5.5	21.0	13.7	---	0.5	---
<i>Rosa eglanteria</i>	3.4	4.8	0.4	5.1	2.3	7.8	1.3
<i>Ribes magellanicum</i>	0.6	2.1	7.9	1.8	---	---	0.9
<i>Pinus ponderosa</i>	5.7	1.4	---	---	---	---	7.6
<i>Berberis buxifolia</i>	1.6	1.0	0.9	---	---	1.9	---
<i>Berberis darwinii</i>	10.8	0.9	3.0	0.8	---	---	---
<i>Buddleja globosa</i>	---	0.8	2.6	---	---	---	---
<i>Luma apiculata</i>	0.4	0.2	0.01	---	---	---	---
<i>Aristolelia maqui</i>	0.1	0.3	8.5	---	0.1	---	---
Woody debris	3.3	---	10.9	8.9	6.2	2.6	21.1
<i>Schinus patagonicus</i>	0.6	---	3.4	---	2.7	1.0	0.2
<i>Baccharis linearis</i>	---	---	---	12.7	62.0	73.5	23.5
<i>Pinus sp.</i>	---	---	---	9.9	---	---	---
<i>Cytisus scoparius</i>	---	---	---	8.5	---	---	---
<i>Pinus contorta</i>	---	---	---	3.1	---	---	10.3

Table 2 continued.

Species	Site						
	<i>Puerto Madera</i>			<i>Huemul Peninsula</i>			
	1998	1999-A	1999-B	Rodal 1	Rodal 4	Rodal 6	Rodal 8
<i>Pinus sylvestris</i>	---	---	---	1.3	---	---	---
<i>Acaena ovalifolia</i>	---	---	---	1.0	---	---	---
<i>Nothofagus dombeyi</i>	---	---	---	0.3	0.9	---	---
<i>Senecio filaginoides</i>	---	---	---	---	4.6	0.2	---
<i>Austrocedrus chilensis</i>	---	---	---	1.2	---	---	---
<i>Adesmia boronioides</i>	---	---	---	---	---	3.7	4.2

Table 3. Summary of community characteristics for clearcut sites on Isla Victoria and Peninsula Huemul. Diversity was calculated using Simpson's  $D$  ( $1/\sum P_i^2$ ); equitability is diversity/total richness. Percent cover represents the relative abundance of plant species in the clearcuts, with stumps and woody debris excluded.

Site	Richness			Equitability	Diversity	% Cover
	Native	Exotic	Total			
<i>Puerto Madera</i>						
1998	7	4	11	0.17	1.92	35
1999-A	8	4	12	0.29	3.53	43
1999-B	9	2	11	0.41	4.52	49
<i>Huemul Peninsula</i>						
Rodal 1	9	4	13	0.56	7.30	46
Rodal 4	7	1	8	0.19	1.53	18
Rodal 6	6	2	8	0.18	1.44	25
Rodal 8	6	3	9	0.46	4.12	9