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Early post-fire succession in a *Nothofagus glauca* forest in the Coastal Cordillera of south-central Chile

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Abstract. The temperate deciduous species *Nothofagus glauca* (Phil.) Krasser exhibits characteristics commonly found in fire-adapted vegetation, yet the role of fire in the evolutionary history of the vegetation in south-central Chile has not been well investigated. We examined the effects of a wildfire on early succession in a *Nothofagus glauca* forest in the Coastal Cordillera of south-central Chile by comparing data from a burned forest to the vegetation in an adjacent, unburned stand.

Results from this study suggest that species present on the site at the time of disturbance and species subsequently dispersed onto the site play an important role in early post-fire succession in this ecosystem. In both the first and second growing seasons following fire, 77% of the species found in the burned plots were also present in the unburned forest. Invasive species, particularly exotic invaders, were also important in early post-fire succession. All of the species found in the unburned forest were native to Chile, and 69% represented endemic taxa. In contrast, 28 species were present on the burned plots that were absent from the unburned forest and many of these invasive species (43%) were exotic taxa. *Pinus radiata* D. Don was particularly successful in invading these disturbed forests.

The importance of persistent native species indicates that the majority of the plants associated with this forest type exhibit adaptations to survive fire. However, the presence and success of exotic invaders, particularly *Pinus radiata*, is disturbing in light of the unique and highly fragmented vegetation endemic to the area. Future research is warranted to investigate the effects that exotic invasive species may have in the post-fire development of the native forest remnants.

Additional keywords: exotic species; invader species; non-persistent species; persistent species; Pinus radiata.

Introduction

Fire is an important process in the dynamics of many terrestrial ecosystems and those plants that have evolved in the presence of fire as a natural disturbance exhibit adaptations for survival (Bond and van Wilgen 1996). While whole plant communities exist in some places that depend on regular fires to maintain their dominance on a site, other types of vegetation have evolved without fire or with very infrequent fires. Human manipulation of natural fire regimes, through the increased frequency of fire or through fire suppression in naturally fire-prone areas, can have lasting consequences on the vegetation of a given area.

The temperate deciduous hardwood *Nothofagus glauca* which dominates in the Coastal Cordillera of south-central Chile exhibits a thick, scaly bark (Santelices 1997) and is a

prolific sprouter after clearcuts (Donoso 1993). Both of these characteristics are common in fire-adapted species, but do not by themselves indicate adaptations to fire. There exists no documentation of the frequency of fire in the coastal mountain range of central Chile prior to European settlement. Although the region is characterized by a mediterranean climate with warm, dry summers, the low incidence of lightning and the lack of historically documented fires would seem to indicate an ecosystem that did not evolve with frequent fires (Donoso 1981). It is, therefore, possible that these seemingly fire-adapted characteristics of *Nothofagus glauca* are the result of an evolutionary history that did not include frequent fires. It is also possible that the evolutionary history of the region included frequent fires, allowing plants to evolve and adapt to their presence, only to have fire eliminated as a natural disturbance at a later period under a different climatic regime. Villa (1995) studied the paleoenvironment of the Coastal Cordillera of central Chile during the Holocene and concluded that the region was dominated by a hot and dry period \approx 5000 years ago, and that cooler and moister conditions began \approx 4000 years BP. Unfortunately, no paleoecological studies documenting the history of the frequency of fire have been conducted in the region to date.

The role of fire as a natural disturbance has been studied in other vegetation types in Chile. The Araucaria araucana-Nothofagus antarctica forests of the southern Andes are adapted to fire, with the ignition source in these forests being volcanic activity and lightning (Burns 1993). In addition, Veblen et al. (1995) documented the importance of fire in the evolutionary history of the southern forests of Chile. Carbon particles in sediments studied in southern Chile chronicle the occurrence of fire in the southern Andes beginning ≈10 000 years ago (Heusser 1987; Heusser et al. 1988). The sclerophyllous vegetation, or matorral, of the central depression in Chile's mediterranean region has been shown to be very similar vegetatively and structurally to those communities found in the California chaparral region and other mediterranean regions worldwide (Kummerow 1973; Specht 1988). All of these ecosystems are adapted to the presence of fire as a natural disturbance (Naveh 1975; Archibold 1995). Fire in the mediterranean regions of Chile may be associated more with the presence of humans, beginning ≈11 000 years ago, than with natural causes (Mooney 1977). However, Fuentes and Espinoza (1986) argue that fire, ignited by volcanic activity, was present as a selective force before human occupation of the region. They used carbon sediments dating back 45000 years ago (Heusser 1983) and the high incidence of volcanic activity during that period as evidence to argue for the presence and selective pressure of fire. Moreover, the vegetation in the Chilean matorral has been shown to contain fire-adapted regeneration strategies, such as fire-induced germination, presence of lignotubers and rapid sprouting capacity (Altieri and Rodríguez 1974; Araya and Avilés 1981; Montenegro et al. 1983).

Study area

The native vegetation in the Coastal Mountains of central Chile, or the 'Maulino Forest', consists of temperate deciduous forests dominated by *Nothofagus glauca* at higher elevations (100–900 m), with other species of *Nothofagus* and hydrophytes in moister ravines and sclerophyllous vegetation at lower elevations (Donoso 1993). Due to the geographic isolation of the country, the vascular flora of Chile contains one of the highest percentages of endemic species of any locale in the world. Of the 5739 species found in continental Chile, 46% are endemic to the country (Marticorena 1990) and many endemics are limited in

distribution to the central region. Approximately 80% of the country's population live in central Chile, between 31° 11' S and 35° 51' S latitude (Fuentes 1990). As a result, most of the species listed as endangered, threatened or rare by the Chilean government are limited in distribution to this area (Benoit 1989). Central Chile was recently listed as one of the 25 biodiversity hotspots for conservation on the planet, making studies of native vegetation and their management not only important, but urgent as well (Myers *et al.* 2000).

Chilean vegetation has been subjected to a long history of anthropogenic influence beginning primarily with the Spanish Colonization in 1540, including agricultural endeavors, urbanization, forest resource extraction and human-ignited fires (Armesto et al. 1994). The Spanish colonizers first used fire as a weapon against the indigenous people, and later to clear cropland and rangeland (Cartwright 1968). Within the past 50 years, the plight of the native forests in the Coastal Cordillera of Chile has been exacerbated by the widespread replacement of native vegetation with fast-growing exotic plantation species such as Pinus radiata D. Don and Eucalyptus globulus Labill. (Lara and Veblen 1993), and an increased frequency of forest fires (CONAF 1998). The VII Region, in south-central Chile, covers a land area of approximately 3.4 million ha and today has approximately 1.27 million ha of land in exotic tree plantations and agricultural areas (37.2%), and only 1.37 million ha of native vegetation left (40.2%) (Universidad Austral de Chile et al. 1998). The native vegetation remaining in this region is found in increasingly isolated remnants, interspersed in a matrix of forest plantations and agricultural crops.

Pinus radiata is particularly susceptible to wide-spread fire due to the often extensive plantations that the species occupies, its high flammability, the dry summer months of the mediterranean-type climate and the uninterrupted fuel loads characteristic of these sites (Lara and Veblen 1993). It is not uncommon for fires that start in plantations to spread into the adjacent native vegetation. During the 1997-1998 summer season, there were 5329 wildfires documented in Chile that burned 2966 ha of plantations and 84731 ha of native vegetation. While the number of wildfires has remained virtually constant over the past 6 years, the area of burned plantations has been drastically reduced from ≈10831 ha in 1992–1993 to less than 3000 in 1997–1998 (CONAF 1998). In contrast, the area of native vegetation affected by fire has increased from 35560 ha to almost 85000 ha in the same time period (CONAF 1998).

Nothofagus glauca, a species endemic to the Coastal Cordillera and Andean foothills of Central Chile, is no exception to this history of degradation. Urzúa (1975) calculated the natural distribution of the species to be approximately 900000 ha, with the vast majority of the forests limited to the south-central portion of the country. A more recent study of the actual distribution of the species

estimated *Nothofagus glauca* to be present on 45000 ha in the Andean foothills of south-central Chile (Rodríguez *et al.* 1991), yielding a very conservative estimate of 90000 ha remaining in the country, or $\approx 10\%$ of the original extent of these forests. In 1973, *Nothofagus glauca* was placed on a list of species in danger of extinction (Muñoz 1973), and is presently listed by the Chilean government as vulnerable to extinction (Benoit 1989). Other endemic arboreal species listed as endangered are limited in distribution to the 'Maulino Forests' of the Coastal Cordillera, such as *Nothofagus alessandrii* Esp., *Nothofagus leonii* Esp., *Gomortega keule* (Mol.) Baillon, and *Pitavia punctata* Mol. (San Martín and Donoso 1995).

The Nothofagus glauca forests that remain are second growth forests (Donoso 1981), found in increasingly isolated fragments among plantations of *Pinus radiata*, in ravines and areas of steep slope where plantation forestry becomes impracticable. While the wood of *Nothofagus glauca* was originally used in the construction of boats (Pimstein 1974) and for furniture (Hoffman 1991), it is used today primarily for firewood and the production of charcoal. In addition to the drastic reduction of habitat and continued extraction of the wood, the *Nothofagus glauca* stands remaining are subject to frequent fire. These fires normally start as human-caused wildfires or site preparation fires in the *Pinus radiata* plantations and often burn into the adjacent native vegetation.

Of special concern is the possibility for the invasion of these disturbed sites by exotic species prevalent in the plantation matrix that dominates the landscape today. The serotinous cones characteristic of *Pinus radiata* provide a ready seed source following fire. The well-dispersed seeds of *Pinus radiata* should allow it to rapidly invade disturbed areas where seedling competition has been reduced or eliminated, especially on those sites with an exposed mineral seed bed such as occurs after an intense fire. Increasingly, *Pinus radiata* trees can be seen intermingled with the native flora, possibly as a result of disturbance in these areas. While *Pinus radiata* has not invaded large areas in Chile at present, this is more than likely due to the fact that most plantations were not established until after 1970 (Richardson and Higgins 1998).

This paper investigates the effects of a wildfire on early succession in a *Nothofagus glauca* (Phil.) Krasser forest in the Coastal Cordillera of south-central Chile. It describes the early successional response of the vegetation to a wildfire that occurred in February of 1997 (mid-summer) by comparing data from the burned forest to the vegetation in an adjacent, unburned stand. Specifically, the study examines the following questions for this endangered ecosystem:

(1) What plant species are important components of early post-fire succession?

(2) What life history characteristics allow these species to persist or invade after a fire? and

(3) How important are exotic species in the re-colonization of burned forests?

Materials and methods

The study was conducted in the school forest 'Costa Azul', property of the Universidad Católica del Maule, located in the Coastal Cordillera of Chile (35° 37' S and 72° 45' W) (Fig. 1). The school forest is typical of the present day landscape in the Coastal Cordillera, with 195 ha in exotic plantations, principally Pinus radiata, and 85 ha of native forests, principally Nothofagus glauca forests located along stream courses and on steep slopes. The mediterranean-type climate is characterized by a conspicuous summer drought of at least 2 months duration and a mild winter rainy season (Amigo and Ramírez 1998). The dry summer months typical of the mediterranean region are attenuated in the Coastal Cordillera by high relative humidity and humid, cool winds from the Humboldt current of the Pacific Ocean (San Martín and Donoso 1995; Litton and Santelices 1996). Annual precipitation is 943 mm, all falling as rain, and the average annual relative humidity is 73%. The average annual temperature is 13.8°C, with a mean maximum of 24.4°C in the hottest month (January) and a mean minimum of 6.0°C during the coldest month (July) (Ulriksen et al. 1979; Specht 1988). Soils of the region are relatively well developed and characterized by dioritic composition and deep weathering (Wright 1959-1960; Weischet 1970).

On 19 February 1997, a fire of human origin started in a recently harvested pine plantation. The fire spread onto the school forest resulting in an intense surface/crown fire. A total of 19 ha of forest burned, including 6 ha of native vegetation. In the *Nothofagus glauca* forest the fires burned 100% of the fine fuels in the standing vegetation, the vast majority of the understory biomass, and the entire litter layer down to the mineral soil. No vegetative regrowth was observed until the following spring (November 1997).

In April of 1997, five permanent plots (5×5 m) were established in each of six separate 5×25 m belt transects, three in the burned forest and three in an adjacent unburned *Nothofagus glauca* forest. The three belt transects in each site were located in homogeneous areas within 50 m of each other. Vegetation measurements were taken in April 1997, November 1997, April 1998 and December 1998, yielding data from three different growing seasons for the unburned plots and two different growing seasons for the burned plots. November 1997 and April 1998 measurements were averaged to give data for the 1997–1998 growing season. During each measurement period, all 5×5 m plots were estimated for all vascular plants using cover class values. A modification of the Braun-Blanquet cover classes and Tüxen-Ellenberg midpoints (van der Maarel 1979) were used for the field measurements and the subsequent analysis of the abundance data. Cover class values



Fig. 1. Map of south-central Chile depicting the study area (*) in the Coastal Cordillera.

Stand characteristics are snown only for the dominant overstory species <i>Nothojagus glauca</i>							
	Slope (%)	Aspect (°)	Elevation (m)	Age (yr)	Height (m)	dbh (cm)	Density (trees ha ⁻¹)
Burned 1	61	217	175	58.7 (3.7)	10.5 (0.5)	20.7 (1.0)	2100
Burned 2	45	204	180	59.3 (1.8)	10.2 (0.5)	17.3 (1.0)	1900
Burned 3	71	182	170	60.0 (1.2)	9.0 (0.5)	15.5 (0.6)	1700
Unburned 1	70	210	190	59.7 (2.9)	7.4 (0.7)	17.6 (2.4)	1200
Unburned 2	50	185	200	62.3 (3.1)	8.5 (0.7)	17.0 (1.5)	2100
Unburned 3	52	204	185	63.3 (2.6)	9.7 (0.9)	18.0 (2.5)	2000

 Table 1. Environmental and stand characteristics (mean ± 1 SE) for plots in the burned and unburned study areas

 Stand characteristics are shown only for the dominant overstory species Nothofacus glauca

(used in Tables 2–4) are as follows: + = < 1%; 1 = 1-5%; 2 = 5-25%; fee 3 = 25-50%; 4 = 50-75%; and 5 = 75-100%. The mid-point values used for each class were 0.5%, 2.5%, 15.0%, 37.5%, 62.5%, and 87.5%, the unburned area were averaged across all plots and taken as an estimate of the pre-fire vegetation in the burned area, and the absolute frequency was determined based on all plots in all three years. In addition, the abundance estimates for the species in the 15 plots from the burned area

determined for each species for each growing season. A floristic list was compiled for all vascular plants encountered in the study, and the geographic origin and growth form were determined for each species (Appendix 1) (Muñoz 1959; Rodríguez *et al.* 1983; Marticorena 1990; Hoffman 1991). A voucher specimen was collected for each vascular plant species and placed in the herbarium of the Escuela de Ciencias Forestales, Universidad Católica del Maule in Talca, Chile. The scientific names follow Marticorena and Quezada (1985) for native species and Matthei (1995) for exotic species.

were averaged over each growing season, and absolute frequency was

For the purposes of this paper, plant species that occupy an area after a disturbance (i.e. fire) can be classified into two categories: persistent species and invaders. In addition, those species that disappear after a disturbance, at least initially, can be classified into a third category of non-persistent species. In this study, persistent species are defined as those that occur in unburned forests and can also be found in burned forests in the first growing season following a disturbance. These species survive disturbance through their capacity to sprout or by on-site seed storage and dispersal. The persistent species category can be further divided into increasers and decreasers, where increasers are those species that increase in cover/frequency following a disturbance and decreasers are those that decrease. Invaders are those species that occur in the first growing season following a disturbance, but are not present in the unburned forest. Invaders occupy a site following disturbance either through germination of dormant seeds or by seed dispersal from adjacent areas.

Ideally, the most reliable approach to studies of secondary plant succession is to compare changes in a given site over time, including site observations from before the disturbance. A second approach is to compare post-disturbance sites with nearby, undisturbed areas. Since data were not collected on the burned forest prior to the fire, comparisons between the unburned and burned areas are contingent upon the assumption that the unburned forest is an accurate indication of the pre-fire conditions in the burned area. The burned and unburned areas used in this study are geographically proximate, as well as similar in environmental and stand characteristics (Table 1), and thus they should represent a legitimate comparison.

The experimental design consists of a pseudoreplicated study in that there is no replication of the primary treatment, fire. For this reason, statistical analyses, and the use of standard error bars, have not been incorporated (Hurlbert 1984). Despite this shortcoming, the authors feel that the results contain useful information for scientists and managers, especially in light of the paucity of information available on the subject matter for this region.

Results

The unburned *Nothofagus glauca* forest exhibited distinct overstory, mid-canopy, understory and herbaceous layers. The dominant overstory species was *Nothofagus glauca*, although other species (e.g. *Persea lingue* (R. et P.) Nees ex Kopp and *Nothofagus obliqua* (Mirb.) Oerst.) occasionally penetrated into the overstory canopy. Numerous broadleaf evergreen trees and lianas dominated the middle canopy, and the understory was composed of evergreen and deciduous shrubs. The herbaceous layer was somewhat sparse, more than likely the result of increased competition for light, nutrients, and water in the closed forest.

Burned plots were characterized by the absence of a litter layer, a large amount of standing dead biomass, and a relatively open canopy that allowed greater solar radiation and a more diverse understory. *Nothofagus glauca* sprouted principally from the crown (from unaffected pre-fire buds or dormant buds insulated by the bark), and also by means of basal sprouts on a few individuals that experienced more intense scorching during the fire. A species of bamboo (*Chusquea quila* Kunth) that sprouted vigorously following the fire dominated the understory, along with other on-site sprouters and species dispersed onto the site from adjacent areas. *Pinus radiata* seedlings germinated readily on the mineral seedbed that occurred after the fire and were prevalent throughout the burned area.

Geographic origin and conservation status

Of the 35 vascular plant species found in the unburned forest, all were native and 24 were endemic to Chile (Fig. 2). No exotic species were found in the unburned plots. The total number of species in the burned plots was 48 in the first growing season after the fire and 51 in the second, compared to 35 in the unburned plots (Fig. 2). The increased species richness on burned plots was due principally to invasion by exotic species. Ten exotics were present after one growing season, representing 21% of the flora found in the burned

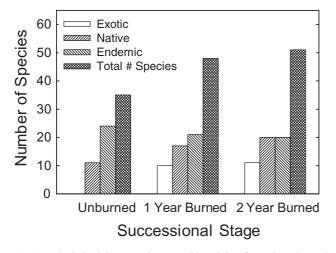


Fig. 2. Floristic richness and geographic origin of taxa in unburned and burned (1 and 2 years post-fire) plots.

plots. The number of endemic species stayed roughly the same over the two growing seasons in the burned plots (21 in the first year and 20 in the second), and the number of non-endemic native species increased (17 in the first year and 20 in the second) (Fig. 2).

Only two species listed as rare by the Chilean government, *Citronella mucronata* (R. et P.) D. Don and *Scutellaria valdiviana* (Clos) Epling, and one listed as vulnerable to extinction, *Nothofagus glauca*, were present in the study area (Benoit 1989). Both *Scutellaria valdiviana* and *Nothofagus glauca* were present on 100% of the burned plots by the end of the second growing season (Table 2). *Citronella mucronata* was present in the unburned forest with very low cover and frequency values (Table 3); it is not known if its absence in the burned plots is a direct result of fire or merely the fact that it was not present on the site prior to the disturbance.

 Table 2. Cover class and frequency values for persistent species (i.e. species present in the unburned and burned plots)

 Percentage cover for the cover class values is given under Materials and methods

Persistent species by growth form	Cover Class			Frequency (%)		
	Unburned	Burned Year 1	Burned Year 2	Unburned	Burned Year 1	Burned Year 2
Perennial herbs						
Adiantum chilense Kaulf.	1	+	1	100	50	73
Blechnum hastatum Kaulf.	1	+	+	73	7	20
Francoa appendiculata Cav.	+		+	13		7
Libertia sessiliflora (Poepp.) Skottsb.	1	+	+	60	13	20
Nassella chilensis (Trin.) Desv.	+	1	2	40	93	93
Scutellaria valdiviana (Clos) Epling	1	1	1	100	93	100
Senecio yegua (Colla) Cabr.	+	+		7	10	
Lianas						
Dioscorea humifusa Poepp.	+	+	+	20	20	7
Herreria stellata R. et P.	+	1	1	27	30	47
Lapageria rosea R. et P.	1	+	+	93	27	27
Evergreen shrubs						
Aristotelia chilensis (Mol.) Stuntz	+	1	1	27	77	100
Chusquea quila Kunth	2	2	2	80	93	93
Pernettya insana (Mol.) Gunckel	1	1	1	100	93	93
Podanthus mitiqui Lindl.	+	+	+	27	40	40
Ugni molinae Turcz.	2	1	1	100	93	93
Deciduous shrubs						
Adesmia elegans Clos	+	1	1	13	93	93
Ribes sp.	+	+	+	40	40	47
Viola portalesia Gay	1	1	1	100	93	93
Broadleaf evergreen trees						
Aextoxicon punctatum R. et P.	2	+	+	73	3	7
Azara integrifolia R. et P.	1	1	1	47	47	53
Cryptocarya alba (Mol.) Looser	+	+	+	20	20	33
Escallonia pulverulenta (R. et P.) Pers.	1	+	+	80	10	27
Gevuina avellana Mol.	2	+	+	73	27	27
Lithrea caustica (Mol.) H. et A.	1	+	1	53	13	33
Lomatia hirsuta (Lam.) Diels ex Mabr.	1	+	+	87	17	20
Luma apiculata (DC.) Burret	1	+	+	53	3	7
Broadleaf deciduous trees						
Nothofagus glauca (Phil.) Krasser	4	2	2	100	100	100
Nothofagus obliqua (Mirb) Oerst.	+	+	+	7	13	13

Non-persistent species by growth form	Cover class	Frequency (%)
Evergreen shrubs		
Myrceugenia obtusa (DC.) Berg	+	7
Senecio acrisione (Hook. et Arn.) B. Nord.	1	53
Deciduous shrubs		
Calceolaria biflora Lam.	+	13
Eupatorium glechonophyllum Less.	+	7
Broadleaf evergreen trees		
Citronella mucronata (R. et P.) D. Don	+	7
Lomatia dentata (R. et P.) R. Br.	1	2
Persea lingue (R. et P.) Nees ex Kopp	1	27

Table 3.	Cover class and frequency values for non-persistent species (i.e. species
	present in the unburned plots but absent in burned plots)
Percent	tage cover for the cover class values is given under Materials and methods

Persistent species

Persistent species were important in early succession on the burned plots (Table 2). In both the first and second growing season following fire, 77% of the species initially found in the unburned forest were also found in the burned plots. Certain understory species (e.g. *Chusquea quila, Scutellaria valdiviana, Pernettya insana* (Mol.) Gunckel and *Viola portalesia* Gay) exhibited cover values comparable to the unburned forest in the first growing season after the fire. All of these species are woody and sprouted vigorously from underground rhizomes and rootstocks following the disturbance.

Of the 28 vascular plant species that persisted in the burned plots, four increased in percentage cover and frequency after fire (Table 2). Nassella chilensis (Trin.) Desv. is a graminoid endemic to Chile, but common in the understory of Nothofagus glauca stands. Both the coverage and the frequency of Nassella chilensis increased substantially following fire, more than likely as a result of decreased competition for sunlight and soil resources. The remaining increasers were Herreria stellata R. et P., a woody vine, which increased slightly in coverage and more significantly in frequency; Aristotelia chilensis (Mol.) Stuntz, a facultative deciduous shrub; and Adesmia elegans Clos, a deciduous shrub. Both shrub species increased dramatically in frequency in the burned plots. Aristotelia chilensis has been reported previously to be an important pioneer species following disturbance (Donoso 1978; Rodríguez et al. 1983), and by the second growing season after fire it was present on 100% of the plots in the burned area.

Ten of the 28 persistent species were classified as decreasers (Table 2). Of these 10 taxa, *Blechnum hastatum* Kaulf., a fern, and *Libertia sessiliflora* (Poepp.) Skottsb., a bulbous perennial, were herbaceous species. The decrease in importance of these two species was unexpected in that they both have underground storage organs that should allow for post-disturbance sprouting. The remaining eight decreasers

were woody taxa. *Lapageria rosea* R. et P., a woody vine, decreased in both cover and frequency following the fire. *Ugni molinae* Turcz. is an important component of the understory vegetation in these forests and, while it did decrease in coverage from 15% to 2.5%, it was still present on 93% of the burned plots. Likewise, *Nothofagus glauca* was present on 100% of the burned plots due to its high sprouting capacity, but was reduced significantly in coverage. The remaining five decreasers (*Aextoxicon punctatum* R. et P., *Escallonia pulverulenta* (R. et P.) Pers., *Gevuina avellana* Mol., *Lomatia hirsuta* (Lam.) Diels ex Mabr., and *Luma apiculata* (DC.) Burret) were all broadleaf evergreen trees from the mid-canopy strata. All of these five trees decreased considerably in both cover and frequency in the burned plots.

Non-persistent species

Seven of the 35 species found in the unburned forest were not found in the burned plots after 2 years and all were woody taxa (Table 3). Due to the low cover and frequency of six of these species in the unburned forest (*Myrceugenia obtusa* (DC.) Berg, *Calceolaria biflora* Lam., *Eupatorium glechonophyllum* Less., *Citronella mucronata*, *Lomatia dentata* (R. et P.) R. Br. and *Persea lingue*), it is quite possible that they were not present on the burned plots prior to the fire. However, it is also possible that some or all of these species were present on the burned plots prior to the fire, and simply did not respond well to this disturbance. *Senecio acrisione* (Hook. et Arn.) B. Nord. was the only species abundantly present in the unburned forest that was not found in the burned plots.

Invaders

Twenty-eight species were present on the burned plots that were absent from the unburned forest (Table 4). Of these plants, 11 were perennial herbs and 9 were annual herbs. Importantly, 12 of the invader species represent exotic taxa (Appendix 1). *Pinus radiata* was found on 87% of the burned

Invader species by growth form	Cover class		Freque	Frequency (%)	
	Year 1	Year 2	Year 1	Year	
Perennial herbs					
Cirsium vulgare (Savi) Ten.	1	1	80	67	
Conyza bonariensis (L.) Cronq.		+		40	
Dichondra sericea Sw.	+	1	63	80	
Gnaphalium viravira Mol.		+		40	
Modiola caroliniana (L.) G. Don	+	+	7	7	
Myosotis scorpioides L.	+	+	37	37	
Oxalis corniculata L.	+	+	27	13	
Relbunium hypocarpium (L.) Hemsl.	1	1	73	73	
Solanum nigrum L.	+	+	23	13	
Stachys sp.	+	1	47	40	
Tropaeolum ciliatum R. et P.	+		17		
Annual herbs					
Calandrinia compressa Schrad. ex DC.	1	+	93	7	
Polygonum convolvulus L.	+	+	20	33	
Senecio vulgaris L.	1	2	70	73	
Sonchus oleraceus L.	+	+	20	7	
Tagetes sp.	+	+	20	47	
Trifolium angustifolium L.	+	+	13	13	
Vicia vicina Clos.	+		13		
Lactuca serriola L.		+		20	
Leontodon taraxacoides (Vill.) Mérat		+		7	
Lianas					
Mutisia spinosa R. et P.	+	+	13	13	
Evergreen shrubs					
Polygala gnidioides Willd.		+		7	
Deciduous shrubs					
Baccharis concava (R. et P.) Pers.		+		7	
Calceolaria glandulosa Poepp. ex Benth.		+		13	
Colletia spinosa Lam.	+	+	17	20	
Sphacele chamaedryoides (Balbis) Briq.	+	+	20	27	
Needleleaf evergreen trees					
Pinus radiata D. Don	1	1	87	87	

 Table 4.
 Cover class and frequency values for invaders (i.e. species not present in the unburned plots but present in the burned plots)

Percentage cover for the cover class values is given under Materials and methods

plots after only 1 growing season (Table 4). While it did not represent substantial cover at the end of the study, the seedlings appeared healthy and vigorous, and are likely to increase in cover and importance with time. Other exotic species with a high absolute frequency were *Cirsium vulgare* (Savi) Ten. and *Senecio vulgaris* L. Important native pioneer species included *Conyza bonariensis* (L.) Cronq., *Dichondra sericea* Sw., *Gnaphalium viravira* Mol., *Relbunium hypocarpium* (L.) Hemsl., *Stachys* sp., and *Tagetes* sp.

Discussion

Trends in early post-fire succession

Data from this study suggest that species present on the site at the time of disturbance and species subsequently dispersed onto the site play an important role in early post-fire succession in a *Nothofagus glauca* forest. Of species that disperse onto the site from surrounding areas, exotic invaders are significant components of early succession. These exotic invaders (e.g. *Pinus radiata*) may become important in later succession, adding a new dimension to the development of these forests (Agee 1998; Scholes and Nowicki 1998). Based upon this study, there is little indication that a single fire will negatively affect those species of conservation concern that are present in the study area. However, for long-term management decisions the unknown effects of a potentially shortened fire return interval should be taken into consideration.

Most of the *Nothofagus glauca* forests that remain today are found as fragments on steep terrain in a matrix of exotic pine and eucalypt plantations. An intense disturbance such as fire poses threats not only to the native biota of these forests, but also to the soil resource. If a late growing season fire occurs, such as is common in this region, the winter rainy period poses a threat in terms of soil erosion and site degradation (e.g. Diaz-Fierros *et al.* 1990). However, the rapid re-colonization of these sites following fire by persistent species should play an important role in minimizing soil degradation. Soil erosion on burned sites in our study area was minimal (Litton and Santelices, unpublished data), even though the litter layer was consumed down to the mineral soil during the fire and vegetation regrowth did not occur until the spring following the rainy season. Soil structure and mineral and nutrient concentrations should be restored within a relatively short period of time as litter, predominantly woody immediately following the fire, contains more fine litter as vegetation re-colonizes the area.

Growth form and life history characteristics

The vast majority of species present in the unburned forest were persistent following fire, and the adaptations that they have for surviving fire vary. Whether or not these adaptations are a result of an evolutionary history that included fire is still unknown, but our data indicate an ecosystem well adapted to disturbance by fire. Nothofagus glauca sprouted vigorously from the crown and also exhibited basal sprouting in a few individuals. Aerial sprouts could be the result of unaffected pre-fire buds but, due to the magnitude and severity of the canopy fire that occurred, they more likely represent dormant buds (i.e. epicormic buds) that were protected by the characteristic thick bark of the species. All of the other tree species that re-established on the burned site did so by means of basal sprouting. It is unknown if the rapid canopy closure that is occurring as a result of the sprouting of Nothofagus glauca will affect the survival and development of these other species into the mid-canopy strata characteristic of mature stands.

The understory shrub species were completely consumed in the fire, but sprouted vigorously from below-ground rhizomes and rootstocks. These species should play an important role in soil stabilization immediately following disturbance. The persistent herbaceous species survived fire from underground reserves as well, while the invasive perennials and annuals were likely dispersed onto the site from the surrounding matrix of unburned plantation forests. Moreover, it is possible for these species to occur as a result of seed bank storage. Both the persistent and invasive perennials and invasive annuals seem to have benefited from the increased solar radiation and decreased competition for water and soil resources.

Exotic species

The abundance of invasive exotic species in the burned plots should be of concern for managers. Most are annual herbs that disperse into the disturbed native forests from outside seed sources, and they outnumber native pioneer species dispersed onto the site in absolute number of species and in their cover and frequency. Their presence in Chile is associated with agricultural activities in the Central Valley and the more recent spread of plantation forestry in the coastal mountains (Matthei 1995). Many are found dispersed along roads and in disturbed areas (i.e. in exotic plantations and agricultural areas), presenting a ready source of seeds for the subsequent invasion of disturbed areas of native forest.

Of particular concern is the abundance of the coniferous tree seedlings of Pinus radiata in the burned plots. While exceptions do exist (e.g. Tasmania, volcanic soils in the Southern Andes), most conifers in the Southern Hemisphere are relatively unimportant in natural areas in terms of numbers and abundance (Enright and Hill 1995). Likewise, native conifers in this forest community are absent or play very minor roles (San Martín and Donoso 1995). However, many introduced pines are spreading rapidly and replacing native species in niches where there was naturally very little competition (Richardson and Higgins 1998). The fast growing plantations of Pinus radiata reach reproductive maturity rapidly and yield a seed source that germinates readily on the exposed mineral seed beds that occur as a result of fire. Besides competing with native species for resources, these trees, once established, may create a forest floor that changes soil structure and mineral and nutrient content (Scholes and Nowicki 1998), as well as stand fire susceptibility (Lara and Veblen 1993; Agee 1998).

The lack of documentation of pine invasion in Chile is surprising in light of the biology of the species and the ease with which it became established in the burned plots in this study. Pinus radiata is already an established invasive species in South Africa, Australia and New Zealand, all countries where it was originally planted as an ornamental and later for wood production (Richardson and Higgins 1998). Richardson and Bond (1991) have shown that the range limits of pines are controlled, to a large extent, by the interactions of their seedlings with the environment and the vegetation present in a given area. There is a constant rain of seeds onto a site that, if mature, is resistant to their establishment. When changes in site characteristics occur, such as those following a fire, the seedlings are able to establish and expand the range of the species. The seedlings present on the burned plots in this study have successfully survived two growing seasons and are unlikely to be negatively affected by the long, dry summers characteristic of the region. Moreover, the rapid canopy closure that is occurring as a result of canopy sprouting of Nothofagus glauca is unlikely to affect Pinus radiata seedlings, as they are capable of surviving in the understory of forests in direct competition for light (Walker 1984). Even if fire returns to the site before the pines are reproductively mature, there will be an almost constant source of seed from the adjacent plantations for re-establishment to occur.

This study investigated the early successional response of the vegetation in a *Nothofagus glauca* stand to a wildfire in the coastal mountain range of south-central Chile. Continued sampling of the permanent plots that were installed will allow for future analysis of the development of these forests following fire. While this study represents one locale in the distribution of *Nothofagus glauca*, it provides valuable information on the response of the vegetation to fire. The post-fire success of the majority of the native plant species seems to indicate an ecosystem well adapted to fire. However, the invasion of the disturbed forest by exotic species may well change the post-fire dynamics of the system.

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Appendix 1. Species list, origin, and growth form of all vascular plants encountered in the study area

Species	Family	Origin	Growth form
Adesmia elegans Clos	Fabaceae	Endemic	Deciduous shrub
Adiantum chilense Kaulf.	Adiantaceae	Native	Perennial herb (rhizomatous)
Aextoxicon punctatum R. et P.	Aextoxicaceae	Native	Broadleaf evergreen tree
Aristotelia chilensis (Mol.) Stuntz	Elaeocarpaceae	Native	Evergreen shrub
Azara integrifolia R. et P.	Flacourtiaceae	Endemic	Broadleaf evergreen tree
Baccharis concava (R. et P.) Pers.	Asteraceae	Endemic	Deciduous shrub
Blechnum hastatum Kaulf.	Blechnaceae	Native	Perennial herb (rhizomatous
Calandrinia compressa Schrad. ex DC.	Portulacaceae	Native	Annual herb
Calceolaria biflora Lam.	Scrophulariaceae	Native	Deciduous shrub
Calceolaria glandulosa Poepp. ex Benth.	Scrophulariaceae	Native	Deciduous shrub
Chusquea quila Kunth	Poaceae	Native	Evergreen shrub
Cirsium vulgare (Savi) Ten.	Asteraceae	Exotic	Perennial herb
Citronella mucronata (R. et P.) D. Don	Icacinaceae	Endemic	Broadleaf evergreen tree
Colletia spinosa Lam.	Rhamnaceae	Native	Deciduous shrub
Conyza bonariensis (L.) Cronq.	Asteraceae	Native	Perennial herb
Cryptocarya alba (Mol.) Looser	Lauraceae	Endemic	Broadleaf evergreen tree
Dichondra sericea Sw.	Convolvulaceae	Native	Perennial herb
Dioscorea humifusa Poepp.	Dioscoreaceae	Endemic	Perennial vine
Escallonia pulverulenta (R. et P.) Pers.	Saxifragaceae	Endemic	Broadleaf evergreen tree
Eupatorium glechonophyllum Less.	Asteraceae	Endemic	Deciduous shrub
Francoa appendiculata Cav.	Saxifragaceae	Endemic	Perennial herb
Gevuina avellana Mol.	Proteaceae	Native	Broadleaf evergreen tree
Gnaphalium viravira Mol.	Asteraceae	Native	Perennial herb
Herreria stellata R. et P.	Liliaceae	Endemic	Woody vine
Lactuca serriola L.	Asteraceae	Exotic	Annual herb
Lapageria rosea R. et P.	Philesiaceae	Endemic	Woody vine
Leontodon taraxacoides (Vill.) Mérat	Asteraceae	Exotic	Annual herb
Libertia sessiliflora (Poepp.) Skottsb.	Iridaceae	Endemic	Perennial herb (bulbous)
Lithrea caustica (Mol.) H. et A.	Anacardiaceae	Endemic	Broadleaf evergreen tree
Lomatia dentata (R. et P.) R. Br.	Proteaceae	Endemic	Broadleaf evergreen tree

Appendix 1.	(Continued)
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Species	Family	Origin	Growth form
Lomatia hirsuta (Lam.) Diels ex Macbr.	Proteaceae	Native	Broadleaf evergreen tree
Luma apiculata (DC.) Burret	Myrtaceae	Native	Broadleaf evergreen tree
Modiola caroliniana (L.) G. Don	Malvaceae	Exotic	Perennial herb
Mutisia spinosa R. et P.	Asteraceae	Endemic	Woody vine
Myosotis scorpioides L.	Boraginaceae	Exotic	Perennial herb (rhizomatous)
Myrceugenia obtusa (DC.) Berg	Myrtaceae	Endemic	Evergreen shrub
Nassella chilensis (Trin.) Desv.	Poaceae	Endemic	Perennial herb
Nothofagus glauca (Phil.) Krasser	Fagaceae	Endemic	Broadleaf deciduous tree
Nothofagus obliqua (Mirb.) Oerst.	Fagaceae	Native	Broadleaf deciduous tree
Oxalis corniculata L.	Oxalidaceae	Exotic	Perennial herb
Pernettya insana (Mol.) Gunckel	Ericaceae	Endemic	Evergreen shrub
Persea lingue (R. et P.) Nees ex Kopp	Lauraceae	Endemic	Broadleaf evergreen tree
Pinus radiata D. Don	Pinaceae	Exotic	Needleleaf evergreen tree
Podanthus mitiqui Lindl.	Asteraceae	Endemic	Evergreen shrub
Polygala gnidioides Willd.	Polygalaceae	Native	Evergreen shrub
Polygonum convolvulus L.	Polygonaceae	Exotic	Annual herb
Relbunium hypocarpium (L.) Hemsl.	Rubiaceae	Native	Perennial herb
Ribes sp.	Saxifragaceae	Native	Deciduous shrub
Scutellaria valdiviana (Clos) Epling	Lamiaceae	Endemic	Perennial herb
Senecio acrisione (Hook. et Arn.) Nord.	Asteraceae	Endemic	Evergreen shrub
Senecio vulgaris L.	Asteraceae	Exotic	Annual herb
Senecio yegua (Colla) Cabr.	Asteraceae	Endemic	Perennial herb
Solanum nigrum L.	Solanaceae	Exotic	Perennial herb
Sonchus oleraceus L.	Asteraceae	Exotic	Annual herb
Sphacele chamaedryoides (Balbis) Briq.	Lamiaceae	Endemic	Deciduous shrub
Stachys sp.	Lamiaceae	Native	Perennial herb
Tagetes sp.	Asteraceae	Native	Annual herb
Trifolium angustifolium L.	Fabaceae	Exotic	Annual herb
Tropaeolum ciliatum R. et P.	Tropaeolaceae	Endemic	Perennial herb (rhizomatous)
Ugni molinae Turcz.	Myrtaceae	Endemic	Evergreen shrub
Vicia vicina Clos	Fabaceae	Endemic	Annual herb
Viola portalesia Gay	Violaceae	Endemic	Deciduous shrub