

**Stand development patterns as a consequence of the
decline in *Austrocedrus chilensis* forests**

by

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ABSTRACT

The forests of *Austrocedrus chilensis* (D. Don) Pic. Sern. et Bizarri in Argentina suffer decline and mortality throughout their natural distribution known as '*mal del ciprés*'. While several aspects of this spatially unpredictable process of overstory tree mortality have been the focus of detailed studies, little attention has been committed to research on tree growth and stand dynamics in symptomatic forests or to examine stand development patterns and predict future stand structure.

The aim of this thesis is to gain a better understanding of stand dynamics in *A. chilensis* forests experiencing tree mortality from '*mal del ciprés*'. In order to achieve this goal, this thesis addressed three objectives: 1) to assess and study the temporal development of the radial growth decline at the tree and stand levels, 2) to evaluate the incidence of cambial mortality in living trees, and 3) to examine mortality patterns and their consequences for establishment of trees in the understory and growth of the surviving overstory trees.

Tree death in symptomatic *A. chilensis* forests is preceded by a decline in radial growth. The occurrence of the decline is independent of the position of the trees in the canopy and unpredictable in time. A high proportion of sampled living trees, including healthy and symptomatic trees growing in subcanopy and canopy positions, exhibited partial cambial mortality of up to 39 years. Following the decline in radial growth, partial death of the cambium, and loss of crown vigour, the mortality of *A. chilensis* trees was unpredictable and variable in time among stands. While mortality of overstory trees has led to the successful establishment of trees in the understory in all stands, the response of the residual overstory trees was variable.

This thesis represents the first study to intensively explore the dynamics of *A. chilensis* forests affected by '*mal del ciprés*'. Furthermore, this study is the first to examine

the occurrence of radial growth decline and cambial mortality and discriminate the incidence among trees differentiated by tree health and the relative position in the canopy.

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DEDICATION

*A mis padres (to my parents),
Maria Rosa y Eduardo.*

CO-AUTHORSHIP STATEMENT

The tables below indicate percentages of coauthors' contributions at each stage of research for each chapter.

Chapter 2 - Radial growth decline in *Austrocedrus chilensis* forests

	Mariano Amoroso	Bruce Larson	Lori Daniels	Peter Marshall	Total
Problem identification & research design	85	5	5	5	100
Performing the research	90	5	5	0	100
Data analyses	70	10	15	5	100
Manuscript preparation	70	10	15	5	100

Chapter 3 - Cambial mortality in declining *Austrocedrus chilensis* forests: implications for stand dynamics studies

	Mariano Amoroso	Bruce Larson	Lori Daniels	Peter Marshall	Total
Problem identification & research design	85	5	10	0	100
Performing the research	95	0	5	0	100
Data analyses	75	5	15	5	100
Manuscript preparation	75	5	15	5	100

Chapter 4 - Stand development patterns as a consequence of the mortality in *Austrocedrus chilensis* forests

	Mariano Amoroso	Bruce Larson	Lori Daniels	Peter Marshall	Total
Problem identification & research design	80	10	5	5	100
Performing the research	85	5	5	5	100
Data analyses	85	10	5	0	100
Manuscript preparation	75	10	10	5	100

1 INTRODUCTORY CHAPTER

1.1 Introduction

Austrocedrus chilensis (D.Don) Pic. Sern. et Bizarri, locally known as cordilleran cypress, is native to Patagonia, Argentina and one of the most important tree species in the region. *A. chilensis* forests represent the most extensive forest type in the northern part of the temperate subantarctic forests of Patagonia (Dimitri 1972).

Significant mortality of this species was reported during the last half of the 20th century throughout its range of distribution. Locally known as '*mal del ciprés*' (cypress sickness), this spatially erratic mortality process has been attributed to a forest decline (Baccalá et al. 1998; Filip and Rosso 1999; La Manna and Rajchenberg 2004). Over the years, the expansion of '*mal del ciprés*' has resulted in a qualitative and quantitative reduction of the *A. chilensis* forest area.

The description of the symptoms of '*mal del ciprés*', sites where it occurs, and possible causes have been the subject of extensive study; yet, the causes are still under investigation (El Mujtar and Andenmatten 2007). Although structural changes at the stand level as a consequence of '*mal del ciprés*' have been described, little is known regarding its effects on the stand dynamics of *A. chilensis* forests or how this disturbance may affect future patterns of forest development.

1.2 Literature review

1.2.1 *Austrocedrus chilensis* forests

Austrocedrus chilensis is an endemic species of the temperate subantarctic forests of Patagonia, Argentina (also referred as the Andean Patagonian forests) and is the conifer with the greatest geographical range in the country (Dimitri 1972). Its natural distribution

covers two elongated areas that parallel both sides of the Andes mountain range. On the Argentinean side, *A. chilensis* forests are distributed discontinuously at latitudes between 37° 08'S and 43° 43'S occupying a narrow strip (60-80 km wide) in the Andean foothills (Bran et al. 2002). Forests develop at sites widely ranging in moisture, receiving as little as 600 mm of total annual precipitation in the eastern limit of its distribution, and as much as 2000 mm in the western limit (Dezzotti and Sancholuz 1991). *A. chilensis* forests have very important environmental and landscape roles for the Patagonian Andean area as they surround most of the urban and rural communities and provide watershed protection, areas for recreation, and magnificent scenery. These forests are also economically important since they produce high quality wood for buildings and furniture, making *A. chilensis* one of the most important commercial tree species in the region.

Structurally, *A. chilensis* forests have been classified into three types: marginal, dense, and mixed (Dezzotti and Sancholuz 1991). The structural diversity of these forests is a consequence of the steep east-to-west gradient in precipitation in the rain shadow of the Andes (Veblen and Lorenz 1987). Marginal forests occur in the drier areas (total annual precipitation = 600 to 900 mm), typically on rocky outcrops and surrounded by Patagonian steppe, as monospecific patches of low-density, scattered trees. The mixed type occurs in wetter zones (1600 to 2000 mm) as denser forests mixed with the more mesic *Nothofagus* species, principally *Nothofagus dombeyi* (coihue). The proportion of *A. chilensis* in these mixed forests is inversely related to site moisture. It is in these mixed forests that the distribution of *A. chilensis* reaches its highest altitudinal limit (1000-1100 m a.s.l.). Dense forests, on the other hand, are primarily monospecific and occur between the two extremes along the precipitation gradient (900 to 1600 mm). The density and productivity of the dense forests vary considerably depending on the slope and exposure of the sites where they grow. Although this three-type classification has been widely accepted and used, recent genetic studies have described a fourth type composed of marginal populations located

along the eastern extremes of the precipitation gradient at sites that are usually drier than those of the marginal forests (Pastorino and Gallo 2002). This type is represented by small isolated groups of dispersed individuals, often with a multi-stemmed growth form, that are located at sites that acted as refugia during the Last Glacial Maximum (Pastorino et al. 2004).

Nearly all *A. chilensis* forests in northern Patagonia originated after natural or human-set fires (Veblen and Lorenz 1987, 1988; Kitzberger and Veblen 1999; Veblen et al. 1999). While on mesic sites *A. chilensis* regenerates together with *Nothofagus dombeyi* developing stratified even-aged stands (Veblen and Lorenz 1987; Veblen et al. 1992), on moderately mesic sites *A. chilensis* develops into pure even-aged post-fire populations (Veblen and Lorenz 1987, 1988). On more xeric sites towards the steppe, establishment occurs more slowly than in the west resulting in broadly even-aged and uneven-aged open woodlands (Veblen and Lorenz 1988). In dense *A. chilensis* forests the regeneration mode (sensu Grubb 1977) has been described as a fine-scale gap-phase mode and the regeneration niche corresponds to moderate-to-high light environments with understory plant cover and structure that vary depending on the season (Veblen et al. 1995; Gobbi and Schlichter 1998). Some authors have cited moisture and/or shade as important factors determining the successful establishment and survival of seedlings, as well as climatic conditions at the beginning of the growing season (Kitzberger et al. 2000). The presence of shrubs has also been recognized as beneficial in the successful establishment and regeneration of *A. chilensis* (Loguercio 1997; Loguercio et al. 1998; Gobbi and Schlichter 1998; Kitzberger et al. 2000). This facilitative nurse effect is very important during early stages of seedling establishment and growth; however, it may become a disadvantage once the individuals reach the sapling stage due to competition (Kitzberger et al. 2000; Letourneau et al. 2004). Less is known about later stages of development of these forests

and mechanisms and processes that perpetuate same species or lead to successional changes.

Historically, the principal disturbance types affecting the southern area of the Andes mountain range are landslides, earthquakes, glacial activity, fire, blowdown, grazing by introduced herbivores and logging (Veblen et al. 1992; Veblen et al. 1995). In northern Patagonia, fire, grazing, and logging have been identified as the most important disturbances as one moves eastwards where pure *A. chilensis* forests prevail (Veblen et al. 1992; Kitzberger et al. 1997). However, due to its current status, '*mal del ciprés*' should be considered as another important natural disturbance in the area where *A. chilensis* forests grow.

Management in *A. chilensis* forests is relatively recent and has a short history compared to forests in other parts of the world. The first resource management activities in these forests occurred at the end of the 19th century with the arrival of the first European settlers. Early timber management of the *Austrocedrus* forests usually involved high grading or selective harvesting of the largest and most economically valuable trees and salvage cutting of declining or dead trees without further intervention. Presently, harvesting and silvicultural practices in these forests requires a management plan. Even though silvicultural studies have been conducted in *Austrocedrus* forests (Costantino 1949; Schmaltz and Gonda 1991; Bava and Gonda 1993; Goya et al. 1995; Loguercio 1997), well-designed silvicultural systems and long-term forest management plans are still lacking. For example, current logging in many areas is limited to "salvage cuttings" of individual trees in stands that have recently burned or present signs of '*mal del ciprés*'. As well, the *Austrocedrus* forests have been commonly used since early times for grazing cattle in silvopastoral systems. While in some situations this activity is combined with some degree of cutting and

planning, in most cases the cattle is just allowed to freely graze in the forest representing a problem for the successful establishment of new trees in the understory.

Until recently the primary threats to the conservation of *A. chilensis* forests included conversion to plantations of exotic tree species, human-set fires, cattle grazing, and illegal logging particularly in the forests in proximity to expanding urban and rural areas (Bran et al. 2002). Combined, these changes have resulted in a quantitative reduction in the total area of the *A. chilensis* forest and have led to increased fragmentation in some areas. Given its recent spread and impacts on the forests, forest decline known as '*mal del ciprés*' has become a dominant agent of disturbance and a significant threat in *A. chilensis* forests (Hranilovic 1988).

1.2.2 The decline of *Austrocedrus chilensis* forests: '*mal del ciprés*'

1.2.2.1 Occurrence and causes

'*Mal del ciprés*' occurs throughout the natural distribution of *A. chilensis*. It was first reported about 60 years ago and since then its expansion and importance has increased (Varsavsky et al. 1975; Hranilovich 1988). Although '*mal del ciprés*' has been the focus of increasing research, especially over the last 15 years, its causes are still under discussion (El Mujtar and Andenmatten 2007). Several hypotheses regarding its origin have been proposed (Filip and Rosso 1999). These hypotheses include biotic factors such as introduced pathogenic fungus and basidiomycete fungi and abiotic factors such as climatic variability. As symptoms originate in the root system as root and stem rots, screening of soil pathogens (Rajchenberg et al. 1998) and fungi responsible for wood decay (Barroetaveña and Rajchenberg 1996) has been conducted; however, researchers concluded that these agents are secondary contributors to tree decline and death. Recent studies has shown that a new species of *Phytophthora* (*P. austrocedrae* Gresl. & E. M. Hansen) present in necrotic

lesions in the inner bark of roots, root collar, and stems of symptomatic trees is associated with and the primary cause of tree death (Greslebin and Hansen 2007; Greslebin et al. 2007). At the same time, abiotic factors contribute to the occurrence and development of the decline as triggering and predisposing factors. At the regional scale, sites at moderate altitudes with high precipitation (Baccalá et al. 1998) as well as those with poorly drained soils (La Manna and Rajchenberg 2004; La Manna et al. 2008a) are prone to develop the decline. Calí (1996) documented long-term radial decline in trees and related the onset of decline to warm-dry periods. Since large areas of *A. chilensis* forests have been affected for several decades, individual trees decline slowly, and mortality results from a complex interaction of biotic and abiotic factors (Manion 1991; Manion and Lachance 1992), '*mal del ciprés*' is classified as a type of forest decline (Baccalá et al. 1998; Filip and Rosso 1999; La Manna and Rajchenberg 2004).

1.2.2.2 Symptoms of '*mal del ciprés*' in trees

At the tree level, the symptoms are manifested below and above ground (Rajchenberg and Cwielong 1993; Rajchenberg et al. 1998; Filip and Rosso 1999). It is believed that symptoms originate in the root system and precede the loss of vigour and defoliation of the crown (Havrylenko et al. 1989; Hennon and Rajchenberg 2000). Below ground symptoms include root system decay that may affect the entire system or only some of the main roots. The decay can extend through the root collar into the base of the stem, developing brown rot in the sapwood and sometimes causing the tree to fall. The first visible symptom in the crown is chlorotic foliage, which progresses to partial or total withering and defoliation.

Radial growth decline and partial cambial mortality are additional symptoms associated with '*mal del ciprés*' (Rajchenberg and Cwielong 1993; Calí 1996). Studying two symptomatic stands in northern Patagonia, Calí (1996) quantified differences in radial

growth rates of symptomatic and dead trees relative to asymptomatic trees and inferred that radial growth decline can develop many years before crown symptoms are evident. As well, Calí (1996) showed that parts of the cambium of trees stopped forming rings as much as 75 years before its death, providing evidence of partial cambial mortality within individual trees. Similarly, Rajchenberg and Cwielong (1993) reported differences of up to 5 years among ring counts along different radii of individual trees. Although some trees persist by maintaining a small proportion of active cambium (Calí 1996), the final result of '*mal del ciprés*' is tree death.

1.2.2.3 *Distribution of symptoms within stands*

Within stands, '*mal del ciprés*' usually appears either as dispersed declining and dead trees or as aggregations of dead trees forming patches of varying sizes (Rosso et al. 1994; La Manna and Rajchenberg 2004). Research on the spatial distribution of the symptoms of the decline, including asymptomatic, symptomatic and dead trees, have shown several spatial and temporal patterns. Recent research recognized a disaggregated pattern of distribution of declining and dead trees in affected stands (La Manna and Rajchenberg 2004; La Manna et al. 2008a). Alternately, mortality apparently starts in multiple trees at various points in the stand and spreads developing patches or clumps of symptomatic and dead trees that are spatially segregated from the healthy individuals (Havrylenko et al. 1989; Rosso et al. 1994). Calí (1996) used tree-rings to partially reconstruct the decline spread for two plots in northwestern Patagonia. The plot maps resulting from that study described the decline progression at the stand level. Rosso et al. (1994) analyzed the spatial distribution of living, declining and dead trees within stands to infer spread; however, that study did not reconstruct or follow the development of symptoms over time. While these studies have provided important information on processes, aspects such as mortality and expansion rates

of the decline remain unknown. Research on the temporal and spatial development of the decline symptoms is needed.

1.2.2.4 *Effects at the stand level*

Tree mortality due to '*mal del ciprés*' causes significant changes in forest structure at the stand level. For example, several studies have shown that trees of all ages and size classes are prone to develop symptoms and die (Hranilovich 1988; Havrylenko et al. 1989; Rajchenberg and Ciewlong 1993; Loguercio et al. 1998). The death of canopy trees results in gaps that presumably expand into larger openings creating multiple stand edges. Such overstory disturbances have led in many forests ecosystems to changes in the total incident light levels reaching different points of a stand (Canham et al. 1990; Denslow and Spies 1990). The variation in the light regime within the disturbed area or tree-fall gap usually results in changes in the understory (Oliver and Larson 1996). Although such disturbances might provide opportunities for tree regeneration and for the forests to become uneven-aged, the establishment of new individuals in symptomatic forests and the microsite conditions under which recruitment might be favoured vary greatly among forests (Loguercio et al. 1998; La Manna et al. 2008b). Interactions with understory vegetation may also be important. After fire, the presence of shrubs in the understory facilitates the establishment of the *A. chilensis* regeneration (Loguercio et al. 1998; Gobbi and Schlichter 1998; Kitzberger et al. 2000), but whether the presence of shrubs in the understory as a consequence of gaps in symptomatic forests facilitates the establishment and growth of *A. chilensis* regeneration is unclear. In general, stand dynamics, development patterns, and future structure of symptomatic forests remains unknown.

1.2.2.5 Knowledge gaps

As '*mal del ciprés*' is still in progress in many areas (Rosso et al. 1994; Baccalá et al. 1998), there is an urgent need to understand the ecology and development of the decline in *A. chilensis* forests across its natural range of distribution. The fact that the cause/s of the decline have remained unknown has impeded actions to control or manage decline of these forests and basic knowledge must still be developed. Priority gaps in knowledge include tree level symptoms such the decline in radial growth of individual trees and the presence of cambial mortality, and forest dynamics and stand development patterns following mortality due to '*mal del ciprés*'.

The occurrence and incidence of a radial growth decline prior to death have received little attention and require more detailed studies. While Calí (1996) suggested that the radial growth decline could appear a long time before external symptoms are apparent, healthy trees were not included in his analyses. Consequently, several questions regarding the nature of the radial decline were left opened for further research. As radial growth decline seems to be a symptom associated with '*mal del ciprés*', its nature and implications on the dynamics of these forests are of great importance and has not been studied in detail yet.

Previous research and field observations have reported the presence of an asymmetrical radial growth in symptomatic living and dead trees present in declining *A. chilensis* forests (Rajchenberg and Cwielong 1993; Calí 1996). Despite these outcomes, no studies have tested the incidence of asymmetrical growth and partially missing rings in healthy trees due to cambial mortality. Additionally, the presence of cambial mortality could represent potential sources of error when determining tree ages and year of death on *A. chilensis* trees. This needs to be evaluated as it can have significant implications for stand dynamics studies based on retrospective analyses using tree rings.

Tree mortality as a consequence of '*mal del ciprés*' introduces structural changes at the stand level resulting in standing and fallen dead trees. The death of canopy trees produces gaps that presumably expand into larger openings creating multiple stand edges and conditions for the establishment of new trees. Although this suggests that these forests will become uneven-aged, previous studies have shown great variation in the establishment of new individuals in forests under these conditions (Loguercio et al. 1998; La Manna et al. 2008b). Furthermore, little effort has been dedicated to studying mortality patterns, stand dynamics, and predict the patterns of changes in stand structure over time in symptomatic forests (i.e. stand development) and future stand composition.

The structural changes at the stand level and changes in the recruitment of new individuals through time as a result of decline will probably introduce different dynamics to *A. chilensis* forests. This could, ultimately, lead to different stand development patterns compared to healthy forests. I predict mortality in *A. chilensis* forests will develop slowly over time. While trees can experience sudden death, most mortality events in these forests will occur following long periods of vigour loss and slow crown defoliation. Furthermore, tree death will be preceded by a decline in radial growth. As symptoms of '*mal del ciprés*' originate in the root system evidenced by the presence of partial root decay, the use of water by the affected trees will be restricted. While these trees will still have healthy crowns, the restricted use of water will reduce photosynthetic activity leading to a decline in radial growth. The competitive ability of the trees (i.e. canopy position) would also influence the radial growth, and might also result in the incomplete formation of rings at the base of the trees. Reduced photosynthesis will eventually lead to partial or total crown withering and defoliation. The restricted use of water and reduced growth of the affected trees will lead to an increase in the amount of below ground growing space (i.e. water and nutrients). Above ground growing space, primarily light, will not increase until crown defoliation develops.

As mortality builds up at each stand and more growing space becomes available, I expect that in the absence of other disturbances *A. chilensis* will establish slowly in the understory as successful establishment of this species occurs in moderate-to-high light environments resulting from fine-scale gaps. The rate of success and timing will be constrained by the ability of the remaining overstory trees to expand and fill the gaps created. The ability of the trees to respond will be influenced by the degree of the restriction in the use of water, the amount of defoliation, the seasonal growing conditions imposed by the climate, and the presence of other species and trees in the understory. The extent at which overstory trees will fill the gaps is, however, limited. As the number and size of the gaps increases from the death of more trees, overstory trees will not be able to expand quickly and therefore growing space will remain available. This will likely lead to more establishment in the understory. The different patterns of overstory growth releases and establishment in the understory will determine the stand development patterns. I do not predict a single stand development pattern; rather, patterns will emerge at each stand as a result of the incidence of the radial growth decline, the mortality patterns, and the seasonal variation in growing space on the processes of overstory tree growth and understory recruitment.

1.3 Research objectives

The aim of this study is to gain understanding about the forest stand dynamics in *A. chilensis* forests in Patagonia experiencing tree mortality from '*mal del ciprés*'. In order to achieve this objective, this thesis focuses on the following specific objectives:

- I. To assess and study the temporal development of the radial growth decline in *A. chilensis* forests affected by '*mal del ciprés*'.

- II. To evaluate the incidence of cambial mortality by the health condition and canopy position of the trees in declining *A. chilensis* forests.
- III. To study the mortality process in declining *A. chilensis* forests and the consequences on the recruitment of new individuals and the growth of the remaining trees.

1.3.1 Methodological approach

The study of forest stand dynamics is the key to understanding not only the effect of past disturbances on forest stands but also to evaluating how the availability of growing space (i.e. the sum of all growth resources) changes over time (Oliver and Larson 1996). Tree-ring analysis provides a means of obtaining such historical information. The analysis of tree cores was used to reconstruct stand establishment and structure over time, and to study past diameter growth patterns.

In order to examine forest stand development and tree growth, I conducted stand reconstruction studies (Stephens 1955). These field procedures have been successfully used to reconstruct stand structure over time and study forest dynamics (e.g. Henry and Swan 1974; Oliver and Stephens 1977; Larson 1986). The evaluation of the structural changes and tree growth through time will help to understand the processes arising as a result of the decline and understand stand dynamics. Ultimately my objective is to reconstruct past growth patterns to assess changes in the amount of occupied growing space, tree vigour and competition. Understanding stand development patterns in conjunction with the temporal reconstruction of the radial growth of the trees helped to understand the conditions and processes that have lead to the onset of the mortality, but more importantly, how the decline in radial growth may have influenced the mortality patterns and future development of the stands.

The research was conducted at the Reserva Forestal Loma del Medio – INTA (National Institute of Agricultural Technology) and the Area Natural Protegida Rio Azul – Lago Escondido in the vicinities of El Bolsón, province of Rio Negro (Argentina). Forests in the area have been described and classified as compact pure *A. chilensis* forests (Dezzotti and Sancholuz 1991; Seibert 1982), and are characterized by post-fire *A. chilensis*-dominated stands with variable presence of smaller size tree species such as *Lomatia hirsuta* (Lam.) Diels and *Maitenus boaria* Mol. These species form also part of the understory along with *Aristotelia maqui* L'Herit and *Schinus patagonicus*. At the landscape, forests in the sampling area appear as a mosaic composed of pure *A. chilensis* and mixed *A. chilensis* - *Nothofagus dombeyi* stands due to the changing topography. In these last stands, usually limited to sites with cooler east to southeast aspects, *N. dombeyi* could represent an important component of the overstory. Within this area, twelve *A. chilensis* - dominated stands with common symptoms of 'mal del ciprés' were chosen for sampling (Table 1-1). Most sites were about 450 m a.s.l. ranging from 367 to 523 m. Slopes were gentle with a maximum of 25 degrees, and the dominant aspect was east. Stands were dominated by *A. chilensis* in the overstory but there were a few stands with an important presence of other tree species such as *N. dombeyi* and *L. hirsuta* in the overstory too. In most stands these and other species were either minor components and/or limited to the lower diameter classes. The proportion of dead trees and trees with crown symptoms ranged from 40 to 73 % of the *A. chilensis* trees in the stands. Since the purpose of the study was to investigate the dynamics of the stands as a consequence of the overstory mortality caused by 'mal del ciprés', stands were selected with no evidence of recent grazing or past logging.

1.3.2 Thesis structure

In order to address the above specific objectives, this thesis successively addresses them in the following order:

Chapter 2 explores the use of dendrochronological techniques in combination with stand and tree level information to assess and study the temporal development of the radial growth decline in *Austrocedrus chilensis* forests affected by 'mal del ciprés'. With this purpose, I tested the hypotheses that i) healthy trees do not exhibit a decline in radial growth; ii) symptomatic living and dead trees exhibit a decline in radial growth relative to healthy trees growing in the same stand; iii) internal symptoms (i.e. radial decline) precede external symptoms (i.e. crown vigour lost); and iv) radial growth decline is independent of the canopy position of the trees.

Chapter 3 determines the incidence of cambial mortality in declining *Austrocedrus chilensis* forests and the effects it can have on interpretations of tree demography and stand reconstructions. Furthermore, I explored whether the presence of cambial mortality was independent of the health condition of the crown and canopy position of the trees in these forests.

Chapter 4 describes the stand development patterns in declining *Austrocedrus chilensis* forests. I conducted stand reconstruction studies to examine the changes in stand structure over time as a consequence of the overstory mortality and the implications of these structural changes on the establishment and growth of the residual overstory. This information helped, ultimately, to describe the stand dynamics and predict stand development patterns in declining *Austrocedrus chilensis* forests.

The Concluding chapter summarizes the major findings of this thesis, and discusses the management applications of the research findings and future research.

1.4 Figures

Table 1-1 Site and stand characteristics of the twelve sampling *Austrocedus chilensis* stands.

Stand	Elevation (m)	Slope (degrees)	Aspect	Total Density	Proportion of <i>A. chilensis</i>	Proportion of symptoms ¹
CE1	471	0	E	790	0.84	0.47
CE2	523	0-10	E-SE	1150	0.56	0.64
PP1	452	15-20	SE-E	1790	0.79	0.55
PP2	430	20	E	1750	0.83	0.73
PP4	450	20	E	890	0.89	0.52
K1	367	15	SE	1050	0.81	0.58
EU1	420	25	SE	1490	0.68	0.68
EU2	398	20	E	1260	0.75	0.72
RQ1	475	0-5	E	1410	0.62	0.63
RQ2	486	0-5	E	1400	0.61	0.55
CR1	453	5	NE-E	1590	0.69	0.52
CR2	456	15-25	NE-E	1950	0.54	0.40

¹ Symptoms include *A. chilensis* trees that were dead and or presented crown symptoms at the time of sampling.

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2 Radial growth decline in *Austrocedrus chilensis* forests¹

2.1 Introduction

Patterns of mortality in forest ecosystems around the world are well recognized and have been the subject of detailed study. Tree death can result as direct consequence of discrete events or disturbances (White 1979; Sousa 1984; White and Pickett 1985; Oliver and Larson 1996), response to environmental stresses (Jane and Green 1983; Bentancourt et al. 1993; Condit et al. 1995; Villalba and Veblen 1998; Williamson et al. 2000; Suarez et al. 2004), direct competition from other trees (Alaback 1982; Oliver et al. 1985; Peet and Christensen 1987; Waring 1987; Kobe et al. 1995; Lutz and Halpern 2006), or more complex interactions such as forest declines (Mueller-Dombois et al. 1983; Schütt and Cowling 1985; Hennon et al. 1990; Hess et al. 2002; Minorsky 2003). While tree mortality may occur in a relatively short period of time in some of these situations, in some other cases it can take longer periods of time as a consequence of multiple interactions (Waring 1987). Although several models have been developed to explain the death of trees and forests where the mortality process involves environmental stresses and the action of different biotic agents among other factors (Houston 1981; Mueller-Dombois 1983; Manion 1991), it has only recently been accepted that overall patterns of tree death normally involve complex processes which we are just beginning understand (Franklin et al. 1987).

Austrocedrus chilensis (D. Don) Pic. Sern. et Bizarri forests experience mortality throughout their natural distribution in Argentina. This spatially erratic process of overstory mortality, locally known as '*mal del ciprés*', was first documented about 60 years ago (Varsavsky et al. 1975; Hranilovic 1988). This mortality cannot be explained by a single

¹ A version of this chapter will be submitted for publication. Amoroso, M. M., Daniels, L. D., and Larson, B. C. Radial growth decline in *Austrocedrus chilensis* forests in Northern Patagonia.

agent. Rather, it is caused by a complex interaction of biotic and abiotic factors, which has led to the conclusion that '*mal del ciprés*' is a type of forest decline (sensu Manion 1991; Manion and Lachance 1992). This opinion has been shared by many (e.g. Calí 1996; Baccalá et al. 1998; Filip and Rosso 1999; La Manna and Rajchenberg 2004), but the cause of this disturbance is still under discussion (El Mujtar and Andenmatten 2007). A new species of *Phytophthora* (*P. austrocedrae* Gresl. & E. M. Hansen) present in necrotic lesions in the inner bark of roots, root collar and stems of symptomatic trees has been recently associated with the mortality of trees, and it is now believed to be the primary cause of tree death (Greslebin et al. 2007). Nonetheless, the role of secondary or contributing factors, such as climate variation, is unknown.

At the landscape level, mortality appears as randomly dispersed trees within stands, as well as aggregations of varying sizes (Rosso et al. 1989; Rosso et al. 1994; La Manna and Rajchenberg 2004). The occurrence of '*mal del ciprés*' has been closely related to sites at moderate altitudes with high precipitation (Baccalá et al., 1998) and those with poorly drained soils (La Manna and Rajchenberg 2004; La Manna et al. 2008).

Symptoms at the tree level are manifested below and above ground (Havrylenko et al. 1989; Rajchenberg and Ciewlong 1993; Rajchenberg et al. 1998; Filip and Rosso 1999; Greslebin et al. 2007). It is believed that symptoms originate in the root system first as the death of the root tissues precede crown symptoms (Havrylenko et al. 1989; Hennon and Rajchenberg 2000). Belowground symptoms include root decay that may affect the entire system or only some of the main roots. The decay can extend through the root collar to the base of the stem developing brown rot in the sapwood and causing, in some cases, the tree to fall (Havrylenko et al. 1989; Barroetaveña and Rajchenberg 1996; Greslebin et al. 2007). The most common visible symptom is chlorotic foliage, which is followed by withering and defoliation of part or the entire crown. Radial growth decline appears to be another symptom associated with the death of the trees and it has been hypothesized that it can begin long

before external symptoms are evident (Calí 1996). The decline in radial growth seems to be associated with asymmetrical radial growth and cambial mortality (Rajchenberg and Cwielong 1993; Calí 1996). Even though some trees are able to survive for a time by maintaining a small proportion of active cambium, this is followed by death resulting in standing and fallen dead trees (Havrylenko *et al.* 1989; Rajchenberg and Cwielong 1993; Phillip and Rosso 1999).

Working at two locations in northern Patagonia, Calí (1996) reported the presence of radial growth decline in symptomatic forests. While that study identified quantitative and qualitative differences of symptomatic and dead trees relative to a reference mean chronology of asymptomatic trees, healthy trees were not included in the analyses. Additionally, several questions regarding the nature of the radial decline were left for further research. While crown, stem and root symptoms have been widely studied and recently reviewed (El Mujtar and Andenmatten 2007), radial growth decline has not been studied in detail.

Tree rings have been successfully used to study the response of trees to disturbances (Lorimer and Frelich 1989; Cherubini *et al.* 1996; Nowacki and Abrams 1997) or environmental stresses (Pedersen 1998; Villalba and Veblen 1998; Suarez *et al.* 2004), as well as being good indicators of the history of tree growth prior to death (Cherubini *et al.* 2002; Marcais and Breda 2006). Likewise, several approaches have been proposed to study forest decline using dendrochronology (Hornbeck *et al.* 1986; Innes and Cook 1989; McClenahan 1995; LeBlanc 1996; Beier *et al.* 2008; Voelker *et al.* 2008). The objective of this study is to use dendrochronological techniques in combination with stand and tree level information to study the temporal development of the radial growth decline in *Austrocedrus chilensis* forests with symptoms of 'mal del ciprés'. Consequently, I tested the hypotheses that i) healthy trees do not exhibit a decline in radial growth; ii) symptomatic living and dead trees exhibit a decline in radial growth relative to healthy trees growing in the same stand; iii)

internal symptoms (i.e. radial decline) precede external symptoms (i.e. crown vigour lost); and iv) radial growth decline is independent of the canopy position of the trees.

2.2 Materials and methods

2.2.1 Study site and sampling

The study took place at the Reserva Forestal Loma del Medio – INTA (National Institute of Agricultural Technology) and the Area Natural Protegida Rio Azul – Lago Escondido in the vicinity of the city of El Bolsón, Rio Negro, Argentina (41°46' S 71°33' W). The area has a mean annual precipitation of 904 mm and a mean annual temperature of 9.3 °C (Servicio Meteorologico Nacional 1969, 1985, 1986). Soils at the study areas are deep, with a presence of volcanic ash, and have been classified as Andisoils (Lanciotti and Cremona 1999). Within these areas, I looked for stands meeting three conditions: (a) *A. chilensis* -dominated stands, (b) forests exhibiting symptoms of '*mal del ciprés*', and (c) no signs of logging or grazing. Since symptoms can be diverse, I concentrated on the visible criteria at the tree level: chlorotic foliage and defoliation in the crown of living trees and abundant dead trees. I chose twelve sites for sampling.

A 0.1-hectare plot was established at each site. Plots were square (31.6 x 31.6 m.) or rectangular (40 x 25 m.) depending on the local topography. All individual trees with a diameter at breast height (DBH) larger than 5.0 cm in the plots were tagged. Species, DBH, crown height class (dominant, codominant, intermediate and suppressed), and 'health condition' (0 to 5) were recorded. In order to assess 'health condition', I modified the classification proposed by Rajchenberg and Cwielong (1993). These authors classified trees into six health classes on a progressive scale (0 to 5) based on foliage condition, increasing percentage of defoliation, and bark characteristics, which are combined into three health

groups: (a) living healthy trees (classes 0 and 1), (b) living symptomatic trees (classes 2 and 3), and (c) dead trees (classes 4 and 5). At least one tree core was taken from all individuals to study past radial growth. Cores were taken perpendicular to the slope and at a height of approximately 30 cm above the ground. Transverse cross-sections were taken from 50 individuals where a good quality core could not be extracted because the bark and wood were decayed.

2.2.2 Dendrochronological methods

Tree cores were mounted and cross-sections glued to wooden boards. All samples were sanded following standard dendrochronological methods (Stokes and Smiley 1968). Samples were visually cross-dated and ring-width series were measured on a Velmex bench to the nearest 0.01 mm. All ring-width series were cross-dated using an existing master chronology (R. Villalba: Pampa del Toro; International Tree-Ring Data Bank, NOAA) and statistically verified using the program COFECHA (Holmes 1986; Grissino-Mayer 2001). Ring-width series that did not cross-date statistically and/or had low correlation coefficient values were visually checked to ensure proper cross-dating. Mortality dates on dead trees were determined by the calendar year of the outer-ring of the crossdated ring-width series.

Separate standard ring-width chronologies were built for healthy trees and for symptomatic and dead trees at each site. Ring-width series were standardized using the program ARS41_win (Cook and Krusic 2006). To preserve the long-term growth trends and to use them to detect the effects of '*mal del ciprés*' on growth, I standardized using a horizontal line by dividing each ring width by the mean ring width of the series (Veblen et al. 1991). For each standard chronology, I calculated upper and lower 95% confidence intervals to assess the presence of radial growth decline at the tree and stand levels.

I noted low radial growth rates in many trees that had been classified in the field as 'healthy' according to the condition of the crown. Therefore, I used an iterative, multi-step procedure to assess the presence of radial growth decline in these trees. To detect radial growth decline in trees with healthy crowns, the standardized ring-width series of each 'healthy' tree was plotted against the appropriate site-level standard chronology and its confidence intervals. If the ring-width series departed below the lower confidence interval limit for ≥ 10 years and did not recover, then the tree was classified as having radial growth decline. All trees exhibiting radial growth decline were removed from the 'healthy' tree chronologies. New standard chronologies and 95% confidence intervals for the healthy trees were derived for each site. Within each stand, the final healthy standard chronology was plotted against the chronology for symptomatic and dead trees to compare ring-width indexes over time. Differences between chronologies were considered significant for those years where the 95% confidence intervals did not overlap. The next step was to determine the presence of radial growth decline and/or estimate the year of the decline onset in symptomatic and dead trees as well as asymptomatic trees that showed radial growth decline and were removed from the 'healthy' chronology. This was done by visually comparing individual standardized series with the final 'healthy' standard chronology for each site using the following criteria. A series was considered as 'declining' when it departed below the lower confidence interval limit for ≥ 10 years and was not included in the 95% confidence interval of the data at the end of the chronology. For each declining series, the onset of the radial growth decline was visually determined as the year at which the series crossed the lower 95% confidence interval.

2.2.3 Analyses

Descriptive statistics for all standard ring-width chronologies were obtained using the program ARS41_win (Cook and Krusic 2006). To compare the healthy versus symptomatic chronologies within each site, descriptive statistics were calculated for the common interval of each pair of chronologies. These statistics included inter-series correlation, the signal-to-noise ratio, autocorrelation value, and the expressed population signal.

I determined the proportion of declining and non-declining trees in each stand in each of the three health groups: living healthy trees, living symptomatic trees, and dead trees. Mean and median proportions and the 50th and 95th percentiles were calculated and plotted on a box-plot graph. All declining trees in each stand were stratified by the health classes assigned in the field to examine the development of the external (i.e. crown vigour and defoliation) and internal (i.e. radial growth decline) symptoms. I used the year of the onset of the radial growth decline to calculate the means and standard deviations of decline onset year for each health class. Differences among health classes were tested using the NPAR1WAY procedure in SAS (2007). This procedure performs nonparametric tests for differences across a one-way classification and computes a one-way ANOVA test under the null hypothesis of no difference among classes. Differences between health classes were tested using the Mann-Whitney-Wilcoxon test for pair-wise multiple comparisons.

The dates of the decline onset were used to calculate the cumulative proportion of trees declining by decade in each stand and to determine the length of the radial decline (i.e. the number of years since the decline onset). The length of the radial growth decline at the tree level was calculated for both living and dead trees. For the living trees, it was calculated as the number of years between the dates of the decline onset and the year of sampling (2005). Decline length of dead trees was determined as the difference between the calendar year of the onset and the date of the outer-most ring. Mean and standard

deviations and the 50th and 95th percentiles of decline length were calculated and plotted on a box-plot graph.

I evaluated the proportion of declining and non-declining trees by height crown class (dominant, codominant, intermediate and suppressed) for all living trees. Dead trees were omitted from the analysis since it would be inaccurate to use a crown class assigned after death without knowing the position of the trees at the time of death. Additionally, since the number of trees in the different height crown classes varied among the sampled stands, the proportion of declining trees by crown height classes was weighted by the total number of trees in each crown class for each stand. Means, standard deviations and coefficients of variation among stands were calculated for each crown class.

2.3 Results

2.3.1 Mean ring-width chronologies

Chronology lengths of 78 to 128 years reflected the relatively young ages of the *Austrocedrus chilensis* stands that originated after extensive burning in the area in the 1890's to 1920's (Veblen et al. 1999). In general, the chronologies of symptomatic trees were more sensitive and longer than those for healthy trees; long chronologies are partially explained by the inclusion of dead trees in these chronologies that were slightly older than the living trees (Table 2-1). Mean sensitivity (MS) values were similar to those reported by Villalba and Veblen (1997). Inter-series correlation (ISC) values were high, denoting the strength of the common signal within the chronologies (Fritts 1976). In general, they were greater for the symptomatic chronologies compared to the healthy ones meaning symptomatic and dead trees are more sensitive to climate since they are stressed. The signal-to-noise ratio (SNR), another measure of the chronology quality (Fritts 1976), varied

among all chronologies and was greater for the symptomatic chronologies compared with the healthy ones. SNR values at five sites (K1, EU1, EU2, RQ1 and RQ2) were low, which could represent a potential problem for climate reconstruction studies; however, they represent an acceptable value for the ecological purpose of this study. Autocorrelation values (ACORR) ranged from 0.422 to 0.948 but most values were within normal values (0.6 to 0.8). In summary, the analysis of the four attributes revealed that symptomatic chronologies presented stronger statistics and were more sensitive to climate than the healthy chronologies in general.

The comparison of the healthy and symptomatic standard chronologies showed variable trends among the 12 *A. chilensis* stands (Figure 2-1). All symptomatic chronologies diverged from the healthy chronologies during recent decades, meaning the ring-width indices were consistently lower than the healthy chronologies. At six stands (CR1, CR2, PP1, PP4, K1 and RQ2) the two chronologies significantly diverged and remained significantly different over the study period. Conversely, chronologies for five of the stands (PP2, CE2, RQ1, EU2 and EU1) diverged significantly for periods of 1 to 25 years, but converged afterward and were not statistically different at the end of the study period. Lastly, one stand (CE1) showed no significant difference between the chronologies.

In those six stands where the chronologies significantly diverged and remained significantly different until the end of the study period, the years of departure between the chronologies were similar. Time of divergence for five of the six stands was between 1978 and 1982. For the other stands, the periods of significant departure between chronologies varied in time and the number of years. For example, stand PP2 exhibited an extended period of divergence from 1968 to 1993 while the other stands had short periods of less than five years (CE2: 1984-1989 and 1990-1991, RQ1: 1983-1988, EU2: 1994-1997, EU1: 1979-1983).

2.3.2 Radial decline patterns and length

Of the 1082 trees sampled, 657 (60 %) presented a decline in radial growth relative to the standard chronology representing healthy trees. The presence of radial growth decline was strongly related to the health condition of the trees (Figure 2-2). On average 29% (range 22-40%) of trees per site were classified as healthy in the field, but exhibited a decline in radial growth. As expected, evidence of a radial growth decline in symptomatic and dead trees was higher, averaging 70 and 85 percent per site, respectively. Conversely, an average of 30 and 15% of symptomatic and dead trees, respectively, showed no evidence of decline. The percentage of symptomatic trees among stands exhibiting decline was highly variable ranging from 6 to 95%. For dead trees, the range was only 73 to 100%.

Two common patterns were found among all the trees (living declining and dead) exhibiting a decline in radial growth related to the rate at which they declined (Figure 2-3). One pattern showed an abrupt decline followed by fairly constant minimal growth over time (Figure 2-3 A); the other, a slow decline over time (Figure 2-3 B). These patterns of decline was sometimes truncated in dead trees and showed signs of recovery. Some dead trees, exhibited a different patterns that showed an abrupt decline trend followed by a short period of slow growth prior to death (Figure 2-3 C). There were also trees that died suddenly without a reduction in radial growth compared to the healthy trees. Another interesting pattern found in some ring-width series was periods of growth recovery in the declining series (Figure 2-3 D). While in some cases it only represented a sudden growth increase over short periods of time before death or in-between the declining trend, it could also represent a recovery after an extended period of growth decline. The percentage of all declining trees exhibiting recovery periods was 11% on average, ranging from 0% (RQ2) to 24% (CE2).

The onset of the decline exhibited great variability among stands, starting as early as the 1910's for stand RQ1 and as late as the 1950's for stands CR1 and CR2 (Table 2-2). By 1949, 41% of the trees in stand RQ1 exhibited a decline in radial growth, but $\leq 20\%$ of trees exhibited evidence of decline in other stands, except stands CR1 and CR2 in which no trees exhibited radial growth decline. By 1959, radial growth decline was present in all stands. By 1979, 50% of all declining trees in all stands had exhibited radial decline and in two stands (RQ1, PP4) declining trees were $\geq 90\%$. Overall, two general patterns were evident in the cumulative rates of decline among the declining trees within stands. Some stands showed a gradual increase in the proportion of trees exhibiting decline in which about 40-50 years elapsed from the onset of decline in the first tree until 50% of all declining trees exhibited decline (PP1, EU1, CE2, RQ1, RQ2). Alternately, a group of stands showed an abrupt increase from 0 to $>50\%$ of declining trees concentrated between 1950's and 1960's (CR1, CR2, EU2, K1, PP2, PP4).

The length of the radial growth decline was variable among stands and between dead and living trees (Figure 2-4). It averaged 28 years for all trees and averaged 34 and 21 years for living and dead trees, respectively. Within stands, length of decline overlapped between individual living and dead trees, however the longest decline in all stands was in living trees. The maximum decline length was >50 years in nine stands, with a maximum of 80 years for stand RQ1.

2.3.3 Radial decline onset by health condition

The average decline onset for all stands varied significantly among the six health classes ($F = 4.32$, $p = 0.0043$, Table 2-3). On average, dead trees in classes 4 and 5 started declining in 1961, about 10 years before the symptomatic and healthy living trees. The

mean year of decline onset did not differ significantly among classes 1, 2 and 3, representing the healthy and symptomatic trees.

Within stands, there were two contrasting patterns in decline onset (Table 2-3). In six stands (CE2, PP2, PP4, EU2, CR1 and CR2) the trees that are now dead started to decline before the symptomatic trees and the healthy trees began to decline last. For these stands, the average time for transitioning from healthy to dead was 15 years; however, the pattern was significant only in stands PP2 and EU2. In five stands (PP1, K1, EU1, RQ1 and RQ2), trees classified as dead at the time of sampling did not start to decline before the symptomatic trees or healthy trees did not begin to decline last. In other words, the decline onset did not follow the development of the external symptoms. For example, in stands PP1, EU1 and RQ2 symptomatic trees (class 3) averaged a more recent decline date than healthy trees (class 1). Alternatively, stand RQ1 showed a similar average decline onset for the dead (class 5) and healthy trees (class 1), and the symptomatic trees (class 2) declined 10 years later. In stand K1 dead trees (class 4) averaged a more recent decline onset date compared to symptomatic trees (classes 2 and 3). Lastly, in stand CE1 no more than 6 years separated all health classes ($p = 0.9675$).

2.3.4 Decline by crown class

Radial decline appeared to be independent of the canopy position as declining trees were present in all crown height classes at all the stands (Figure 2-5). Mean percentages of declining trees by height crown class in all stands did not differ among crown classes resulting in 25, 26, 25 and 23% for dominant, codominant, intermediate and suppressed trees respectively. In general, the variation within each class was similar for intermediate and suppressed trees (coefficient of variation of 26.8 and 25.9%, respectively) while dominant trees had the highest variation (coefficient of variation of 37.4%) and codominant

trees had the lowest (coefficient of variation of 16.8%) variation. For example, stands CE1 and EU2 had a small percentage of declining trees in the dominant class and a much greater percentage of declining trees in the suppressed class. In contrast, stands PP1, K1 and CR2 had a higher proportion of declining trees in the dominant crown class compared to the suppressed class. Variability was greater when trees were grouped according to their growth potential within the canopy (dominant and codominant vs. intermediate and suppressed). For example, in stands CE1, EU2 and RQ1 at least 60% of the declining trees in the suppressed and intermediate classes and in stands PP1, K1 and CR2 more than 65% of declining trees were in the dominant and codominant classes.

2.4 Discussion

2.4.1 Radial growth decline in *Austrocedrus chilensis* forests

The present study confirms the presence of radial growth decline in *Austrocedrus chilensis* forests experiencing overstory mortality referred as '*mal del ciprés*' as suggested by (Calí 1996). Working at two symptomatic *A. chilensis* stands in northern Patagonia Calí (1996) reported the presence of radial growth decline in symptomatic and dead trees after comparing their growth trends to a reference chronology of healthy trees. The study presented here expanded these comparisons to 12 stands and assessed the presence of radial growth decline not only in dead and symptomatic trees but also in healthy individuals. Furthermore, this study is the first to discriminate the incidence of the radial decline by the health condition and the relative position of the trees in the canopy. I found evidence of radial growth decline in all health classes, including symptomatic, dead, and healthy or asymptomatic trees. On average, 70 and 80% of all symptomatic and dead trees, respectively, exhibited a decline in radial growth. In addition, 22 to 40% of the trees in each

stand that were classified in the field as having healthy crowns exhibited a decline in radial growth. Previous studies on '*mal del ciprés*' have reported the presence of external symptoms (i.e. loss of crown vigour and defoliation) in all size classes (Hranilovich 1988; Havrylenko et al. 1989; Rajchenberg and Cwielong 1993; Loguercio et al. 1998). This study found the presence of radial growth decline was independent of the canopy or crown height class of the trees. Although reduced growth rates can be expected in trees undergoing suppression (Bormann 1965) I found the radial growth decline was present in all canopy classes.

While the presence of a decline in radial growth was a common characteristic of most symptomatic trees, there seemed to be more than a single pattern of decline. I distinguished two contrasting patterns of radial growth among declining trees. Some trees experienced an abrupt decline followed by minimal growth over time, while others exhibited a slow, steady decline in radial growth over time. Both patterns were present in trees independent of their health class. However, some dead trees stopped growing and died shortly after an abrupt decline. This suggests that some trees undergo long periods of decline before dying, while other trees die sooner after decline. Similar differences in growth prior to death for *A. chilensis* were reported by Villalba and Veblen (1998) working at the eastern distribution of the species. These dissimilar patterns in decline preceding death reiterate the complexity of tree response to '*mal de ciprés*' and might help to better understand the possible causes behind this process. For example, the different rates of growth decline could be due to different intensities of the disturbance or agent triggering the onset of decline, genetic variability among individuals, or a combination of both causes.

Decline onset and decline length were variable among trees and stands. The year in which the first trees in each stand started declining ranged from as early as the 1900's and as late as the 1950's. These findings provide new information in relation to the historical development of '*mal del ciprés*'. Although the presence of this disturbance, identified by

external symptoms, was first reported in 1948 (Varsavsky et al. 1975) and in 1953 (Hranilovich 1988), this retrospective analysis shows that radial growth rates of trees in the study area started declining as early as 1900. While I believe this approach provides a reliable way to better understand decline in these forests, it might be difficult to accurately estimate the exact time of the decline onset (McClenahan 1995). While the first appearance of radial growth decline varied among stands, by the end of the 1950's radial growth decline was present in all stands and it increased considerably in subsequent decades. Like the decline onset, decline length exhibited great variation. While the maximum decline documented was 80 years, the maximum length of decline remains uncertain since many trees are living and still undergoing the process. The observed variation in the decline length and its apparent unpredictable nature among trees make mortality patterns among stands extremely difficult to predict since trees can die after periods of decline that vary from years to decades as stated above.

2.4.2 Development of internal and external symptoms

I found strong evidence that decline in radial growth preceded the development of the external symptoms such as the loss of crown vigour and subsequent defoliation. In 29% of trees with healthy, asymptomatic crowns, I detected significant radial growth decline. At the stand level, '*mal del ciprés*' was first identified by external symptoms and reported in 1948 (Varsavsky et al. 1975) and in 1953 (Hranilovich 1988). However, the retrospective analyses that I used showed that radial growth rates of trees in the study area started declining as early as 1900. The year in which the first trees in each stand started declining ranged from as early as the 1900's and as late as the 1950's. These findings provide new information in relation to the historical development of '*mal del ciprés*'.

In six of the sampled stands, the expression of external symptoms used to define different health classes of declining trees followed a logical progression through time. Based on the mean date of the decline onset, the dead trees (classes 4 and 5) started declining before living symptomatic trees (classes 2 and 3), and living healthy trees (classes 0 and 1) started to decline last or did not exhibit radial growth decline. For the rest of the stands, the onset of the decline did not follow a linear progression of the external symptoms through time. The lack of a chronological sequence in these stands is explained by the variability in the proportion of symptomatic trees exhibiting radial decline among all the sampled stands found in this study and suggested in previous research (Calí 1996). Therefore, as evidenced by the high proportion of symptomatic and dead trees exhibiting the decline signal and its presence in healthy, asymptomatic trees, I conclude the decline in radial growth was a common symptom of the trees in the studied stands and preceded the manifestation of symptoms in the crown.

This finding suggests that the initial reduction in radial growth at the tree level is not a direct consequence of reduced photosynthesis due to a loss of vigour and defoliation of the crown, but is caused by other mechanisms. Radial growth reductions are a consequence of a decrease in the amount of photosynthates allocated to secondary growth (Kozlowski et al., 1991). Cambial or secondary growth represents a lower priority in the allocation of photosynthates compared to primary growth and production of new foliage (Oliver and Larson 1996). This means a reduction in radial growth is expected before a decline in crown growth and vigour when photosynthates are limited, as has been documented in other species (Wallis and Reynolds 1965; Thies 1983). Therefore, the observed radial growth decline in *A. chilensis* that precedes crown symptoms is not due to a reduction in the photosynthetic area but must be a consequence of another mechanism that reduces photosynthesis. The simplest explanation for the reduced photosynthesis is reduced water uptake as a consequence of temporary or permanent damage to the root system. Damage

can be caused by both biotic and abiotic factors. As reported in previous studies, it is believed that '*mal de ciprés*' is caused by pathogens that infect the root system and symptoms of the disease start below ground as the root tissues are damaged and die before the disease spreads to the stem and causes crown symptoms (Havrylenko et al. 1989; Hennon and Rajchenberg 2000; Greslebin et al. 2007). Pathogen damage to the root system would decrease the ability of the trees to take water from the soil, reducing the photosynthetic activity and negatively affecting growth (Wallis and Reynolds 1965).

Alternately, reduced growth and partial root damage could also be as a consequence of climatic events as suggested by Calí (1996). Repeated droughts (Kitzberger et al. 1995; Villalba and Veblen 1998) and extended periods of unfavourable growth conditions for *Austrocedrus chilensis* were common during the 20th century in northern Patagonia (Villalba and Veblen 1997). Periods of below-average tree growth (Villalba and Veblen 1997) and mortality (Villalba and Veblen 1998) were reported after 1950, when episodes and rates of decline increased in our study area. Calí (1996) found that the onset of the decline was associated to warm-dry periods at one of his study sites and suggested this could have contributed to the death of the trees. Due to the complex pattern of *Austrocedrus* tree-growth response to climatic variation (Villalba and Veblen 1997), it is probable that the occurrence of the decline could be highly influenced by climatic conditions. Yet, the role of climate on the occurrence and development of the decline is still unclear and requires further investigation.

2.4.3 Implications for stand dynamics

Understanding mortality patterns is essential to predict future forest dynamics and development of stands (Oliver and Larson 1996). Knowledge of the temporal pattern of mortality at the stand level can help in forecasting changes in forest vegetation even if the

causal mechanisms of mortality are not fully understood. Furthermore, understanding the processes involved in tree death help to predict the amount of growing space becoming available (sensu Oliver and Larson 1996) and whether it is more likely to be filled by the remaining individuals in the stand or by establishment of new trees. While assessing growing space availability might be relatively simple if the trees die rapidly as a consequence of discrete and rapid events such as fires or windstorms, it is more challenging when tree deaths occur over longer periods of time as a consequence of multiple interacting factors (Waring 1987), such as the mortality process in *A. chilensis* forests.

The majority of the dead and dying trees experienced a decline in radial growth that varied in length and severity that was difficult to predict in time and among tree classes. The length of the decline varied from a couple of years to several decades and, regardless of decline length, patterns in radial growth ranged from abrupt decreases in radial growth to steady prolonged growth reductions. The decline in radial growth was not related to the competitive position of the trees in the canopy, suggesting that any tree in a stand is susceptible. The combination of these different decline patterns will influence the timing of release of growing space by the declining trees. For example, growing space would become available relatively quickly in the case of sudden declines, but it likely takes more time for the growing space to become available when decline is gradual and prolonged. Concurrently, the amount of available growing space will be determined by the relative canopy position of dead trees and, to some extent, by the pattern and degree of the radial decline.

In addition to the amount and the time it takes for the growing space to become available, from a stand dynamics point of view, it is also important to forecast which trees will use and benefit from the unoccupied growing space. This is determined by the ability of the remaining trees to respond and capture immediate or sudden increments in the amount of available growing space, and use it to grow by expanding their crowns and roots (Oliver

and Larson 1996). If not captured by the overstory trees, growing space becomes available to understory plants. As the decline in radial growth can precede the loss in crown vigour and defoliation, a reduction in the competitive ability of the trees and the amount of growing space used is expected. While this might just represent only a decrease in the use of growth factors such as water, low to intermediate decline in radial growth will likely be used by neighbouring trees if they have the ability to do it and are not under stress or also undergoing radial growth decline. If not taken, growing space may otherwise remain underused. More immediate and larger amounts of growing space could potentially be used by remaining overstory trees or for the establishment of new individuals in the understory. In the case of *A. chilensis*, this could lead to the recruitment of new individuals since this species has the ability to establish successfully in small openings or even under slight openings in the canopy as defined by its fine-scale gap-phase regeneration mode (Veblen et al. 1995; Gobbi and Schlichter 1998). The overall outcome will certainly be influenced also by the time and the amount of trees that start declining and dying at the stand level. In those stands where trees decline relatively at the same time or during short periods of time, understory development and recruitment might be promoted. On the other hand, if the trees decline at a longer temporal scale or the trees are more dispersed, the available growing space can be captured by remaining established overstory trees and perhaps lead to some degree of understory development.

2.5 Conclusion

The present study confirmed the presence of radial growth decline in *Austrocedrus chilensis* forests experiencing overstory mortality in Northern Patagonia. Furthermore, this study is the first to discriminate the incidence of the radial decline among trees differentiated by health condition and relative position in the canopy. Evidence of radial growth decline

was found in trees of all health classes, including healthy, symptomatic, and dead trees in all sampled stands. The use of tree ring records in combination with stand and tree level information allowed us to study the onset, extent and development of the radial growth decline in *A. chilensis* forests. Our results clearly indicate the usefulness of dendrochronological analyses to study temporal attributes of forest decline in northern Patagonia.

There is still some degree of uncertainty and disagreement related to the cause of tree mortality in these forests. A new species of *Phytophthora* present in symptomatic trees has been associated with the mortality but a potential link of the time of the decline onset to climatic variation also exists. As most trees can undergo long periods of growth decline before death, it might be appropriate to continue referring the mortality process in *Austrocedrus* forests as a forest decline. Future research on the subject needs to focus on the variability among radial decline onset and mortality and different possible causes of the radial growth decline including environmental stresses such as climate variation and their interactions with pathogens. As well, spatial analysis of the temporal development of the external and internal symptoms at the stand level would provide a spatiotemporal sequence that will help with the understanding of the mortality process in these forests.

2.6 Figures

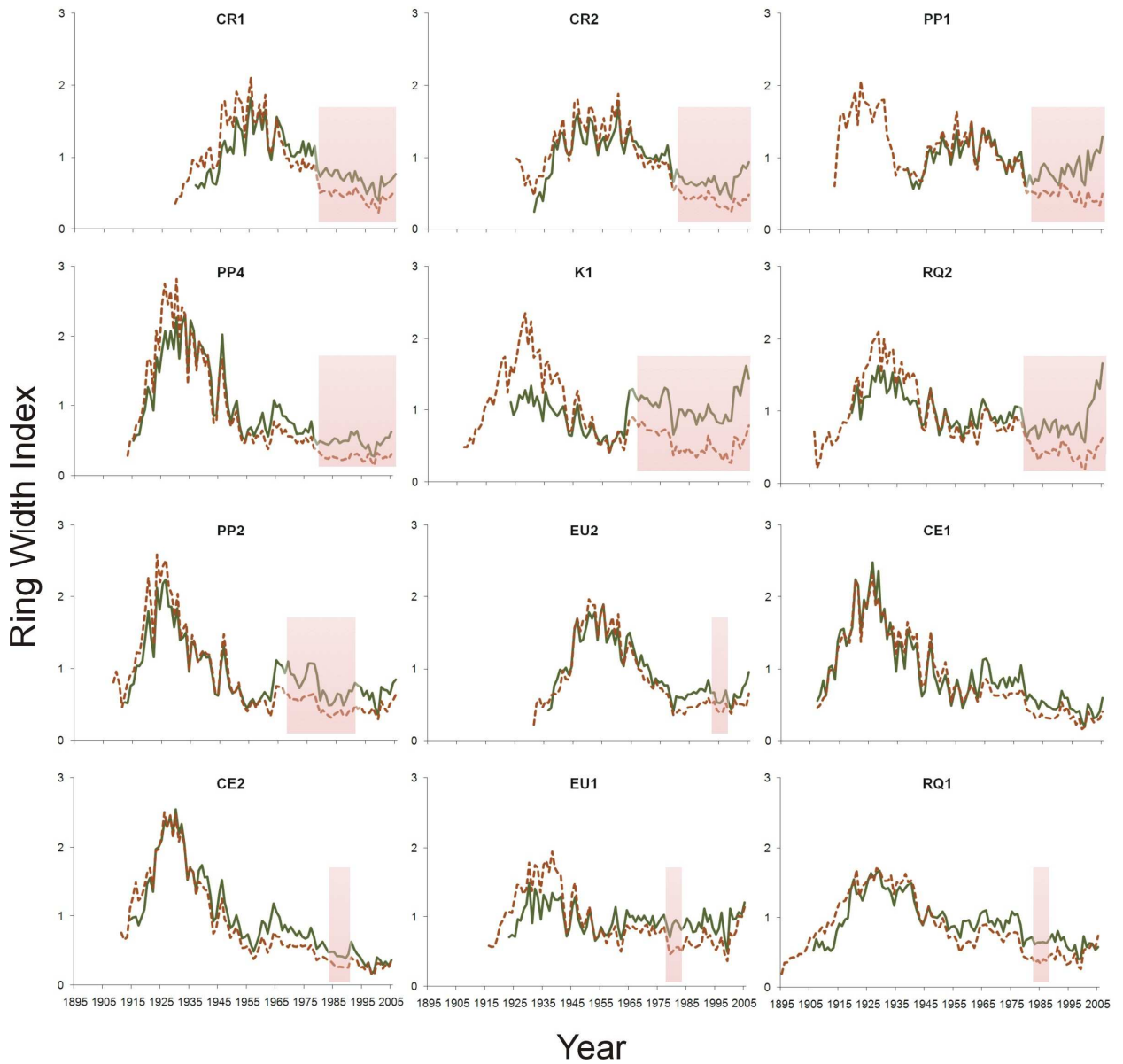


Figure 2-1 Mean ring-width chronologies for the healthy (solid) and symptomatic (dashed) trees for twelve *A. chilensis* stands. Shaded boxes indicate years statistically different as measured by the 95% confidence intervals.

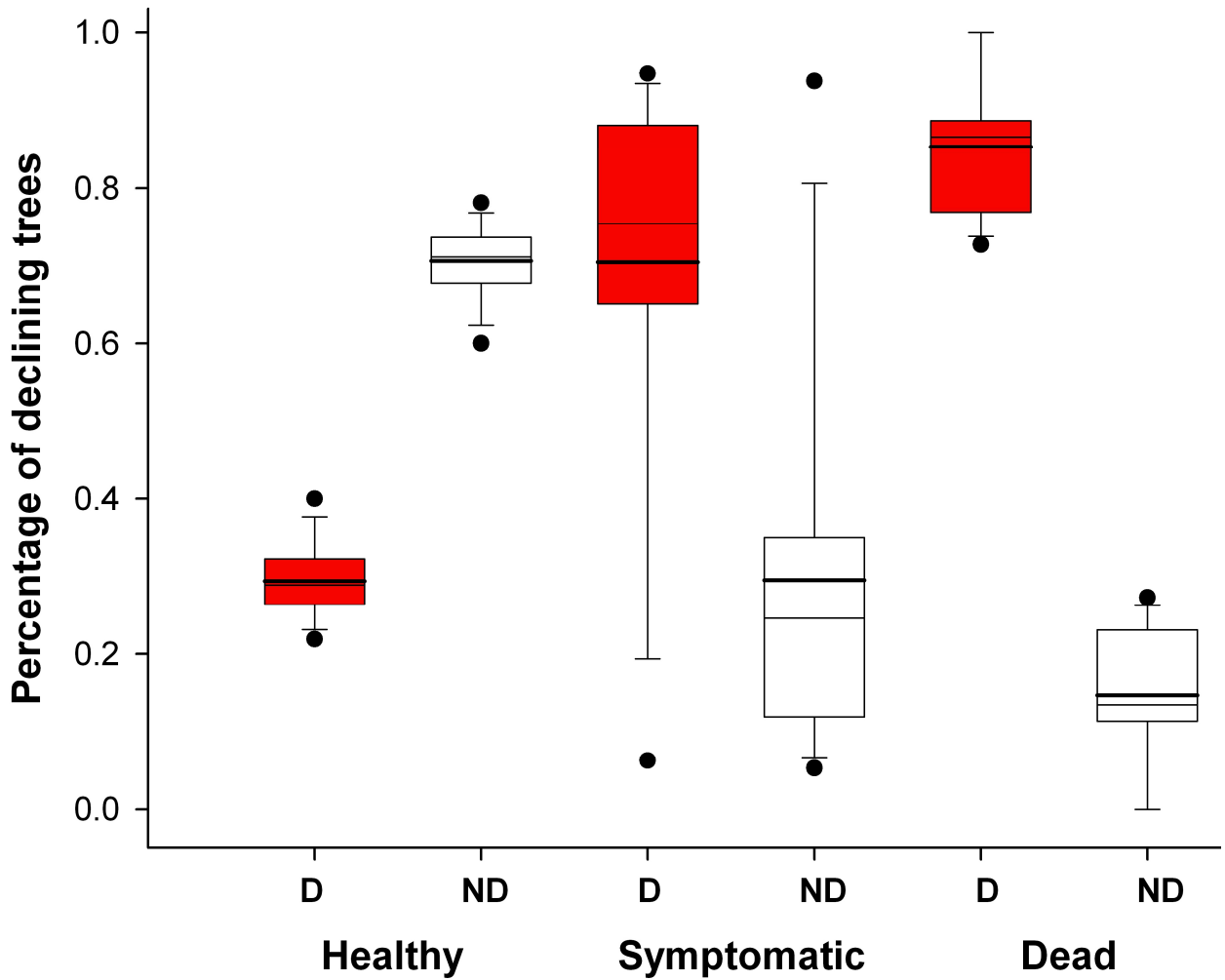


Figure 2-2 Proportion of declining (D, dark) and non-declining (ND, white) trees by health condition for twelve *A. chilensis* stands. In each box plot, the thick horizontal line is the mean; the thin horizontal line is the median; box limits are the 25th and 75th percentiles; bars are the 10th and 90th percentiles; dots represent the range of observations.

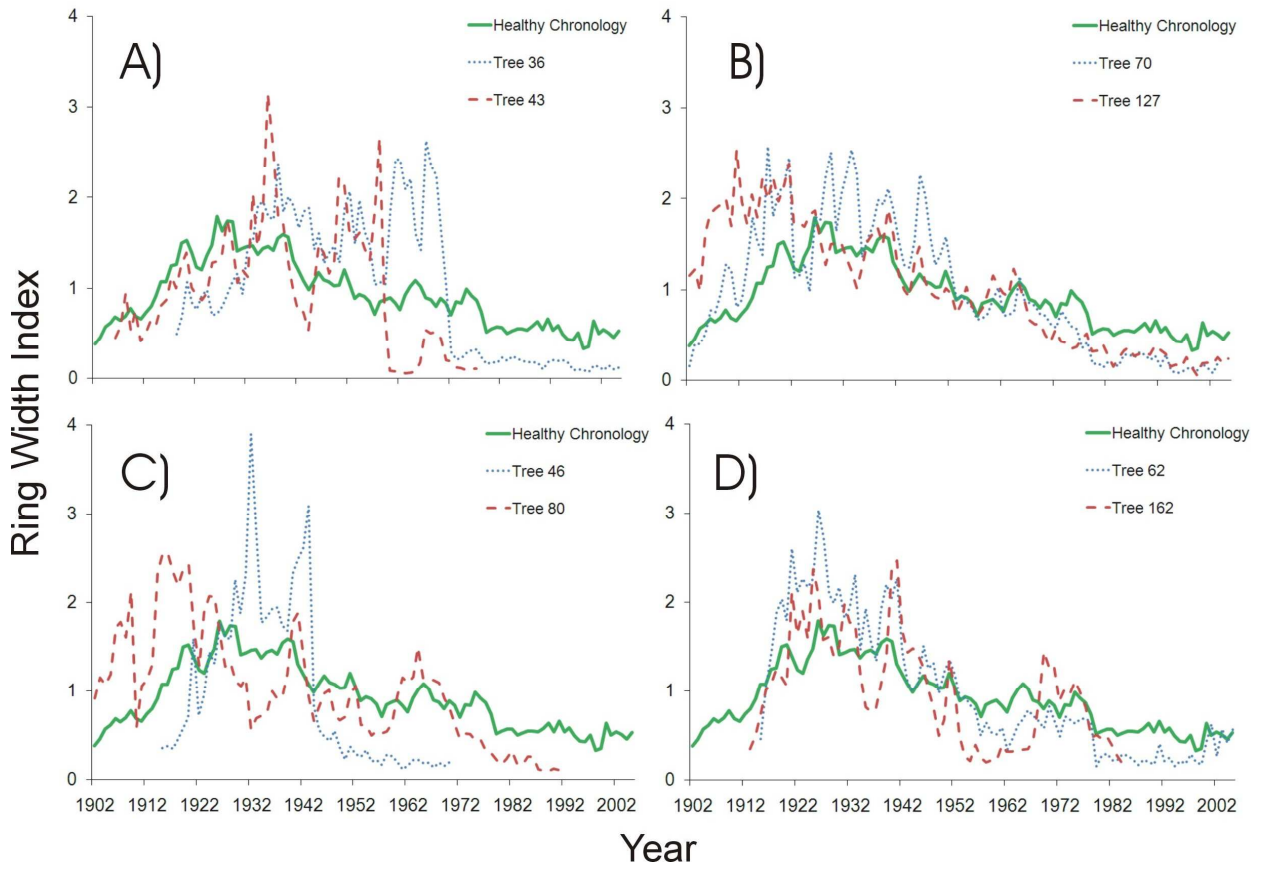


Figure 2-3 Ring-width series for trees at stand RQ1 showing abrupt (A) and slow (B) radial growth decline patterns, radial growth trends in dead trees (C), and recovery growth trends (D) compared to the reference mean ring-width chronology.

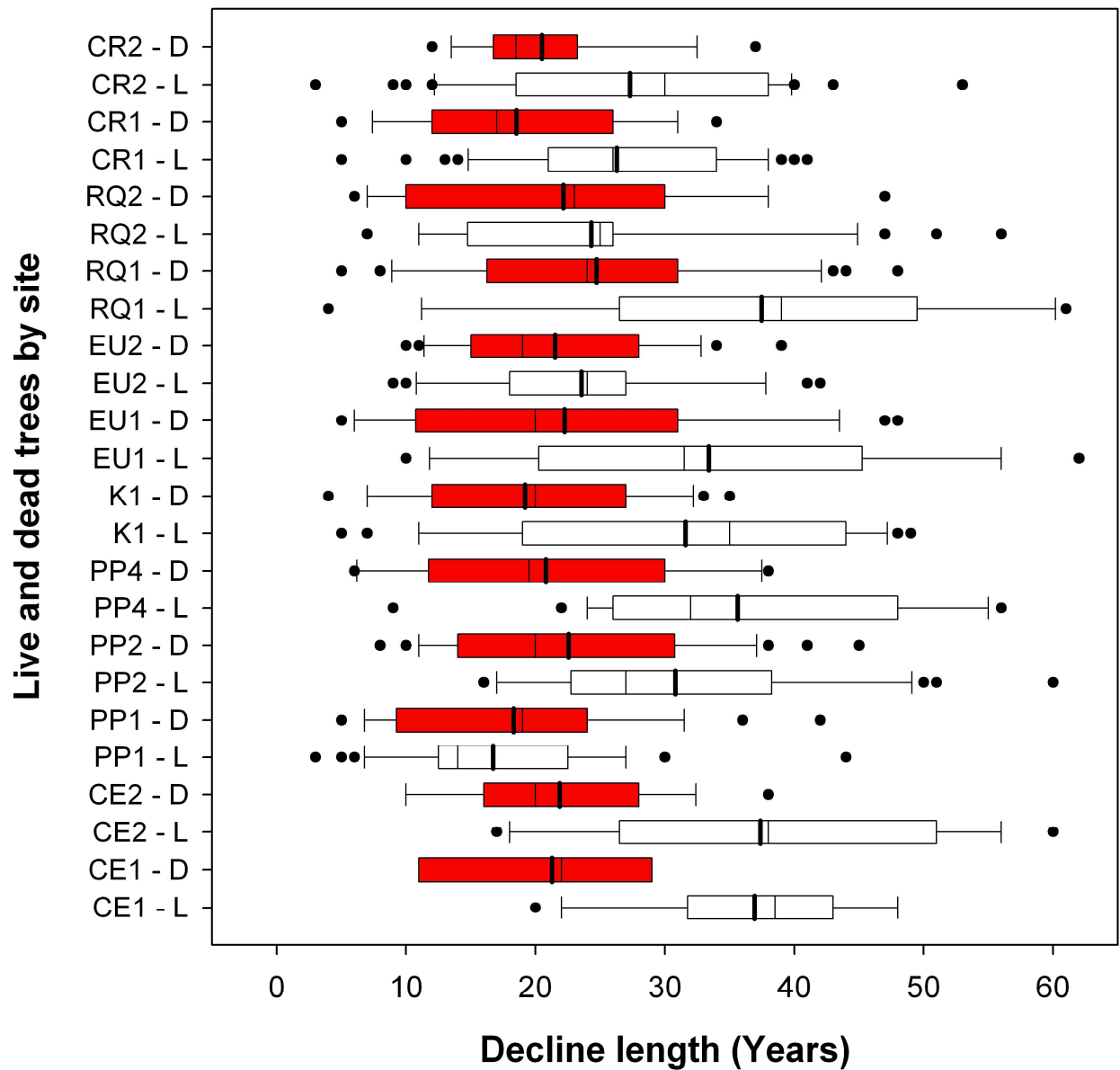


Figure 2-4 Number of years of radial decline for living (white) and dead (dark) trees at all sampled sites. In each box plot, the thick vertical line is the mean; the thin vertical line is the median; box limits are the 25th and 75th percentiles; bars are the 10th and 90th percentiles; dots represent the range of observations.

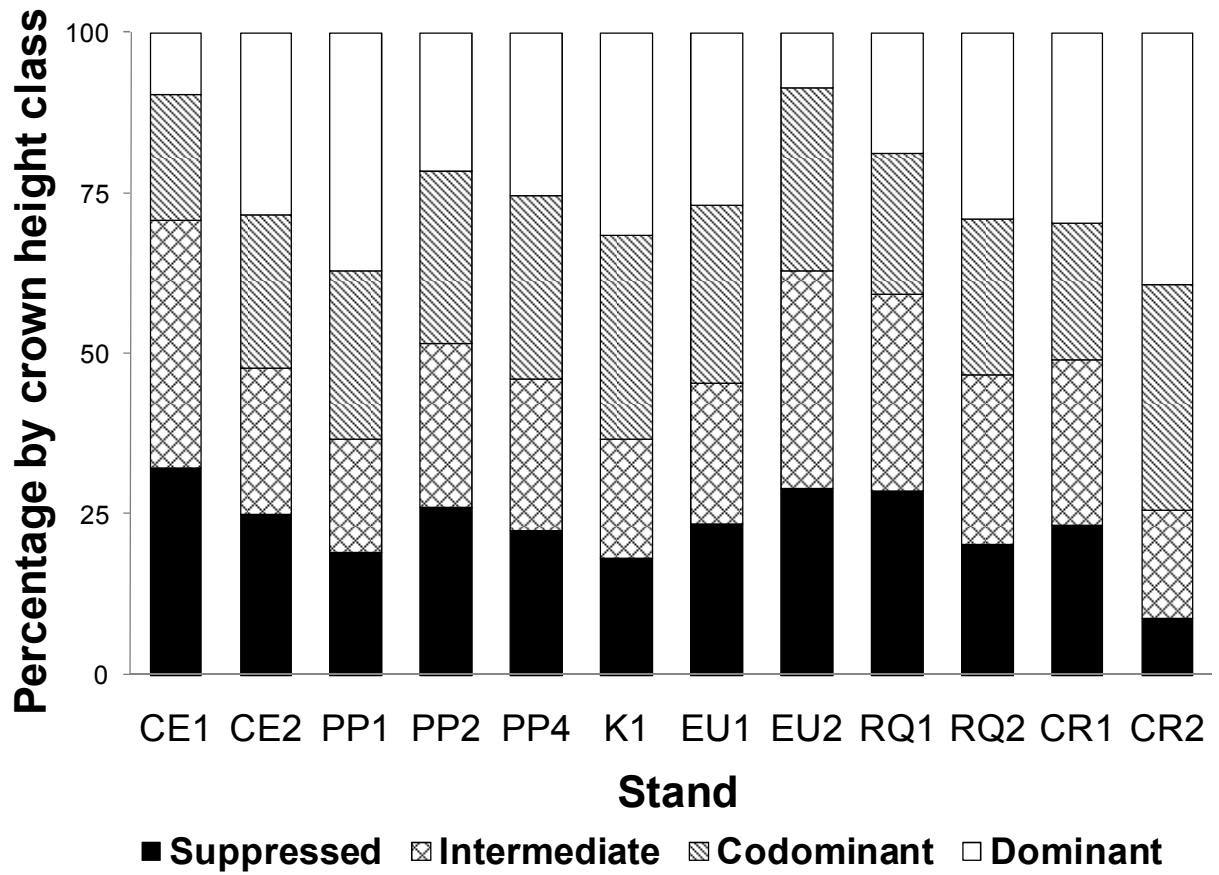


Figure 2-5 Proportion of declining trees by crown height classes for twelve *A. chilensis* stands weighted by the total number of trees in each crown class at each stand.

2.7 Tables

Table 2-1 Descriptive statistics for twenty four mean ring-width chronologies built from healthy (H) and symptomatic (S) trees from twelve *A. chilensis* stands.

Stand		N	Period	MS ¹	ISC ²	SNR ³	ACORR ⁴
CE1	H	25	1903-2005	0.214	0.439	17.977	0.715 (2)
	S	33	1905-2005	0.171	0.496	25.618	0.901 (1)
CE2	H	16	1908-2005	0.164	0.410	10.408	0.948 (1)
	S	54	1900-2005	0.188	0.398	27.744	0.820 (2)
PP1	H	42	1929-2005	0.175	0.322	18.083	0.642 (1)
	S	72	1877-2005	0.208	0.384	24.976	0.628 (3)
PP2	H	28	1895-2005	0.194	0.315	11.512	0.860 (1)
	S	109	1881-2005	0.177	0.529	64.039	0.712 (3)
PP4	H	28	1913-2005	0.172	0.505	22.486	0.682 (3)
	S	48	1905-2005	0.221	0.632	56.577	0.605 (2)
K1	H	26	1914-2005	0.151	0.162	4.252	0.759 (1)
	S	51	1905-2005	0.163	0.506	32.790	0.776 (2)
EU1	H	23	1917-2005	0.177	0.227	5.567	0.422 (1)
	S	64	1896-2005	0.161	0.322	19.460	0.882 (1)
EU2	H	17	1930-2005	0.176	0.301	6.037	0.669 (3)
	S	65	1912-2005	0.177	0.374	26.935	0.913 (1)
RQ1	H	16	1985-2005	0.119	0.171	3.103	0.899 (1)
	S	60	1876-2005	0.164	0.183	10.726	0.939 (1)
RQ2	H	21	1908-2005	0.169	0.148	2.949	0.751 (1)
	S	19	1889-2005	0.234	0.391	24.993	0.734 (2)
CR1	H	34	1932-2005	0.164	0.378	18.836	0.590 (4)
	S	58	1922-2005	0.201	0.526	38.845	0.876 (1)
CR2	H	34	1927-2005	0.172	0.268	10.614	0.873 (1)
	S	57	1914-2005	0.157	0.442	32.537	0.870 (1)

¹ Mean sensitivity; ² Inter-series correlation; ³ Signal-to-Noise Ratio; ⁴ Autocorrelation value (numbers in parenthesis indicate the autocorrelation order chosen using the Akaike criterion).

Table 2-2 Cumulative proportion of declining trees by decade for twelve *A. chilensis* stands.

Stand	n	1910- 1919	1920- 1929	1930- 1939	1940- 1949	1950- 1959	1960- 1969	1970- 1979	1980- 1989	1990- 1999	2000- 2005
CE1	26	0	0	0	0.08	0.31	0.69	0.85	0.96	0.96	1.00
CE2	44	0	0	0.02	0.20	0.45	0.66	0.89	0.98	1.00	1.00
PP1	76	0	0	0.01	0.13	0.21	0.26	0.53	0.74	0.97	1.00
PP2	96	0	0.02	0.04	0.17	0.36	0.73	0.86	0.98	1.00	1.00
PP4	39	0	0	0.03	0.21	0.51	0.74	0.90	1.00	1.00	1.00
K1	49	0	0	0.02	0.10	0.29	0.63	0.84	0.94	0.98	1.00
EU1	53	0	0	0.02	0.15	0.36	0.60	0.87	0.96	1.00	1.00
EU2	52	0	0	0	0.02	0.06	0.42	0.73	0.98	1.00	1.00
RQ1	51	0.06	0.06	0.14	0.41	0.61	0.84	0.94	0.98	1.00	1.00
RQ2	54	0	0.02	0.07	0.19	0.31	0.48	0.74	0.89	1.00	1.00
CR1	62	0	0	0	0	0.05	0.42	0.79	0.90	0.98	1.00
CR2	56	0	0	0	0	0.13	0.45	0.73	0.91	1.00	1.00

Table 2-3 Mean year of the decline onset by health classes for all trees at twelve A. chilensis stands. Numbers in parenthesis indicate standard deviations. Classes 5 and 4 represent dead trees, 3 and 2 living symptomatic trees, and 1 and 0 living healthy trees.

Stand	Health Classes					
	5	4	3	2	1	0
CE1	1966.6 (14.1)	1961.7 (14.6)	-	1967.9 (17.5)	1964.4 (7.3)	-
CE2	1960.7 (15.9)	1952.5 (0.7)	1962.6 (15.4)	1963.1 (10.0)	1969.7 (16.4)	-
PP1	1967.7 (15.9)	1964.2 (19.0)	1992 (10.0)	1982.4 (10.9)	1986.7 (10.1)	-
PP2	1956.2 (11.2)	1958 (22.6)	1967.8 (14.9)	1970.3 (9.9)	1971 (11.5)	-
PP4	1952.9 (10.3)	1958.3 (11.0)	1964.6 (14.5)	1963.7 (12.8)	1961.6 (12.6)	-
K1	1960.6 (14.0)	1970.8 (10.4)	1961.8 (21.0)	1967.6 (12.4)	1976.4 (8.4)	-
EU1	1960.9 (17.1)	-	1984.7 (0)	1966.7 (6.4)	1964.8 (9.1)	-
EU2	1967.7 (7.5)	1958.5 (19.1)	1979.6 (4.2)	1977.9 (9.7)	1978.7 (6.6)	-
RQ1	1952.8 (14.0)	1949.9 (19.3)	1944.5 (0.7)	1965.6 (15.7)	1953 (23.7)	-
RQ2	1954.5 (15.0)	-	1977.3 (5.6)	1981.5 (11.7)	1970.4 (16.8)	1975.8 (4.4)
CR1	1967 (10.7)	1970.5 (4.9)	1973.3 (7.3)	1974.7 (8.4)	1976.9 (11.1)	-
CR2	1964.3 (12.8)	1970.2 (10.7)	1973.2 (9.1)	1975.7 (9.2)	1971.9 (13.8)	-
Mean	1961	1961.4	1971	1971.4	1970.5	-

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3 Cambial mortality in declining *Austrocedrus chilensis* forests: implications for stand dynamics studies²

3.1 Introduction

Reconstruction of tree establishment and forest disturbances require accurate estimates of tree age and mortality dates. Age-class distributions have been used to describe tree establishment and invasion patterns at both the landscape and stand levels (e.g. Villalba and Veblen 1997; Daniels and Veblen 2004; Lafon 2004; Boyden et al. 2005). Tree death dates provide information regarding mortality patterns and can be used to elucidate growth responses among neighbouring residual trees (Veblen et al. 1991; Thompson et al. 2007), patterns in recruitment (Brown and Wu 2005; Suarez and Kitzberger 2008), and decay rates of snags and logs (Daniels et al. 1997; DeLong et al. 2005, 2008; Jones and Daniels 2008). Ideally, inferences about time since disturbance and cohort establishment can be made from static age-class histograms and complemented with additional evidence about the nature of the disturbance (Lorimer 1985; Veblen 1992; Johnson et al. 1994). However, when no other information is available we rely solely on precisely crossdated tree rings to provide the most accurate estimates of tree ages and mortality dates.

Austrocedrus chilensis (D.Don) Pic. Sern. et Bizarri, locally known as cordilleran cypress, is an endemic conifer of Argentina and Chile. In Argentina, it is distributed discontinuously between 37° 08'S and 43° 43'S occupying a narrow strip along the foothills of the Andes mountains (Bran et al., 2002). In the latter half of the 20th century, significant mortality of this species was detected throughout its range. Locally known as '*mal del ciprés*'

² A version of this chapter has been submitted for publication. Amoroso, M. M., and Daniels, L. D. Cambial mortality in declining *Austrocedrus chilensis* forests: implications for stand dynamics studies.

(cypress sickness), this form of tree death represents an important disturbance (Havrylenko et al. 1989) and has been attributed to a forest decline syndrome in several studies (Baccalá et al. 1998; Filip and Rosso 1999; La Manna and Rajchenberg 2004). Previous studies have shown that trees from all size classes are prone to develop crown symptoms and die (Hranilovich 1988; Havrylenko et al. 1989; Rajchenberg and Cwielong 1993; Loguercio et al. 1998). However, whether loss of crown health and vigour affects the growth rates, survivorship and mortality of trees in different canopy positions remains unknown. While the process of death of individual trees and the causes of '*mal del ciprés*' have been the focus of increasing research over the years (El Mujtar and Andenmatten 2007; La Manna et al. 2008), detailed studies of stand dynamics to test for the effects of tree death on development patterns in *A. chilensis* forests have yet to be completed.

Field observations and previous studies in declining *A. chilensis* forests have reported asymmetrical radial growth of symptomatic trees (Rajchenberg and Cwielong 1993; Calí 1996). Rajchenberg and Cwielong (1993) cut cross-sectional disks from trees that exhibited symptoms of '*mal del ciprés*' and counted rings along several radii of each disk. While they reported differences of 5 years among radii of individual trees, Calí (1996) reported that part of the circumference of a tree could remain without forming rings for 75 years before its death. Despite these outcomes, no studies have tested the incidence of asymmetrical growth and partially missing rings in healthy trees. Furthermore, these outcomes identify significant potential sources of error when determining tree ages and year of death and have significant implications for stand dynamics studies based on retrospective analyses using tree rings.

I studied the incidence of cambial mortality in declining *A. chilensis* forests and the effects it can have on interpretations of tree demography and stand reconstructions. I addressed two research questions: What is the incidence of cambial mortality in declining *A. chilensis* forests? Is the presence of cambial mortality independent from the health condition

of the crown and canopy position of the trees in these forests? I hypothesize that progressive foliage loss associated with '*mal del ciprés*' negatively affects photosynthesis and carbon allocation, ultimately affecting the complete production of cambium and ring formation at the base of trees. High-quality ring-width data from healthy and symptomatic trees provided us with a large dataset that enabled us to test the following hypotheses (stated as predictions):

- (a) Healthy trees produce annual rings that form around the full circumference of a tree and do not exhibit cambial mortality. Symptomatic trees do not produce complete annual rings; rings are incomplete around the circumference of the tree, providing evidence of cambial mortality.
- (b) Canopy trees in dominant and codominant height classes are less likely to exhibit cambial mortality than subcanopy trees in intermediate and suppressed height classes.
- (c) Combining a and b, I predict that the incidence of cambial mortality will be least in healthy canopy trees, greater in healthy subcanopy trees and symptomatic canopy trees, and greatest in symptomatic subcanopy trees.

I also used dendrochronology to estimate the year of onset of cambial mortality in individual trees and evaluate the resulting potential errors in estimates of tree ages.

3.2 Materials and methods

3.2.1 Study site and sampling

I sampled 12 stands near El Bolsón, Rio Negro, Argentina (lat. 41°46' S, long. 71°33' W) dominated by *A. chilensis* with symptoms of '*mal del ciprés*'. The most common symptoms include trees with chlorotic foliage and/or partial defoliation, as well as abundant

standing or fallen dead trees (Havrylenko et al. 1989; Rachenberg and Cwielong 1993; Fillip and Rosso 1999). In each stand a 0.1-hectare plot was established. In each plot, all living and dead trees with a diameter at breast height (DBH) larger than 5.0 cm were assessed for species, health condition and canopy position. Health condition was assessed using an adaptation of Rajchenberg and Cwielong's (1993) classification based on foliage condition, percentage of defoliation and bark characteristics. These authors defined six classes that I combined into three groups: (a) living, healthy or asymptomatic trees (classes 0 and 1), (b) living trees with symptoms including chlorotic foliage and partial defoliation (classes 2 and 3), and (c) recently dead and older dead trees in advanced decay (classes 4 and 5). Trees were assigned to one of two canopy positions after Smith et al. (1997): (a) canopy trees were in the dominant and codominant height classes and (b) subcanopy trees were in the intermediate and suppressed height classes.

Increment cores were taken from each tree, perpendicular to the slope and at a height of approximately 30 cm above the ground. More than one core was taken from 13 trees to ensure all the cores included sound sapwood and bark to guarantee that the outermost ring represented the ring formed most recently. Transverse cross-sections were taken from 45 trees from which I could not extract good quality cores due to wood decay and/or the absence of bark.

3.2.2 *Dendrochronological methods*

Cores were mounted and cross-sections were glued to wooden boards and sanded following standard dendrochronological methods (Stokes and Smiley 1968). Only cores that included the bark were used in subsequent analyses. For each of the cross-sections, I selected two radii to be measured using criteria to ensure comparability with the increment cores. Therefore, the two radii were a) perpendicular to the slope to avoid compression wood and b) included sound sapwood and bark. If these conditions could not be met, the

samples were excluded from subsequent analyses. Cores and radii were visually crossdated and ring-width series were measured on a Velmex bench to the nearest 0.01 mm. Ring-width series were statistically crossdated using the program COFECHA (Grissino-Mayer 2001) and an existing master chronology (R. Villalba: Pampa del Toro; International Tree-Ring Data Bank, NOAA) to determine the calendar year of the outer-most ring for each sample.

3.2.3 Analyses

I combined the data from the 12 plots and detected cambial mortality in living trees using the outer-ring dates from the crossdated ring-width series. For living trees, I expected the outer-ring date to be 2005, the year of sampling; outer-ring dates prior to 2005 provided evidence of cambial mortality. The onset of cambial mortality was defined as a calendar year of the outer-ring. I also quantified the time during which the cambial mortality lasts in living trees. I referred to this as cambial mortality duration and it was calculated as the difference between 2005 and the calendar year of the outer-ring.

I stratified all trees into four classes according to the health condition of the crown and canopy position, as assessed in the field. Classes were as follows: healthy canopy trees (H-C), healthy subcanopy trees (H-S), symptomatic canopy trees (S-C) and symptomatic subcanopy trees (S-S). For each class and all trees combined, I plotted absolute and cumulative frequency distributions of cambial mortality duration. For the subset of trees with evidence of cambial mortality, I examined the influence of the health condition and canopy position on the incidence of cambial mortality using a contingency table and Pearson's chi-square goodness of fit test (InfoStat 2002).

I compared ages derived from ring counts versus crossdating. The objective was to evaluate the accuracy of outer-ring dates on age estimates using pith dates at coring height. For the 83 (10.2 %) cores that did not intercept the pith I estimated the number of missed

rings (Duncan 1989), but I did not correct for the number of years for a tree to grow to coring height. For cores missing the pith the same correction was applied to the inner-ring date derived by counting or crossdating. For ring counts, I assumed the outer ring of live trees was 2005, the year of sampling. Age was calculated as the number of rings from the outer ring to the inner ring, inclusive, plus the correction for the number of rings to the pith. Problems with ring counts result in the presence of cambial mortality since the pith date will underestimate the age by the number of missed rings since the onset of the cambial mortality. Therefore for the latter method, the outer- and inner-ring dates were determined by crossdating and age was the outer-ring date minus the inner-ring date plus the correction for the number of rings to the pith plus one. I compared 1- and 15-year age class distributions using age estimates derived from ring counts and crossdating.

3.3 Results

3.3.1 Incidence of cambial mortality

Of the 1356 trees sampled in the 12 plots, 811 and 545 samples corresponded to living and dead trees, respectively. Of the 811 living trees, 53 % were classified in the field as healthy and 47 % were classified as symptomatic; 37 % occupied the upper part of the canopy while 63 % were in a subcanopy position (Table 3-1). Of the living trees, I found that 38 % (307) had an outer-most ring date prior to 2005, providing evidence of cambial mortality.

3.3.2 Influence of health condition and canopy position on incidence of cambial mortality

Of the trees with cambial mortality, 55.7, 25.7, 14.7 and 3.9 % corresponded to healthy subcanopy trees, symptomatic subcanopy trees, symptomatic canopy trees and healthy canopy trees, respectively (Table 3-1). Health condition and canopy position were significantly associated ($X^2 = 43.22$, $p < 0.0001$). Specifically, the likelihood for *A. chilensis* to present cambial mortality was determined primarily by tree position in the canopy. Independent of the crown vigour or amount of defoliation, subcanopy trees were more prone to cambial mortality than canopy trees. As well, the crowns of 171 subcanopy trees and 12 canopy trees appeared healthy although cambial mortality was present.

3.3.3 Onset and duration of cambial mortality

Outer-most ring dates for living trees ranged from 2005 to 1966; therefore, cambial mortality started as early as 1966. Cambial mortality duration ranged from 1 to 39 years with an average of 8.1 years (Figure 3-1). Duration of cambial mortality varied between subcanopy and canopy trees and, within canopy trees, it was influenced by health condition (Figure 3-1). Trees with cambial mortality duration ≤ 15 years were represented in all height classes, but the majority of the trees with cambial mortality of ≥ 20 years were subcanopy trees. Cambial mortality duration in healthy canopy trees was ≤ 6 years, but in symptomatic canopy trees the longest duration found was 22 years.

For all living trees, 62% did not present cambial mortality (y-intercept) and for those with cambial mortality the maximum duration was 39 years (x-value when line asymptotes at 1.0 in Figure 3-2). For 90% of these trees, cambial mortality duration was ≤ 11 years (Figure 3-2). The proportion of trees with cambial mortality and maximum duration were greatest for subcanopy trees and least for healthy canopy trees. About half of subcanopy trees had

cambial mortality and maximum duration exceeded 30 years. For symptomatic canopy trees, 25% had cambial mortality and the maximum duration was 22 years. Only 10% of healthy canopy trees had cambial mortality and the maximum duration was 6 years (Figure 3-2).

3.3.4 Potential errors when estimating tree age and impacts on age structure

The presence of cambial mortality represents a source of error when pith dates and ages are estimated using ring counts instead of crossdated ring-width series (Figure 3-3). In the age distribution with 1-year classes, only 62 % of age estimates based on ring counts were accurate; 38 % of ages were incorrect by up to 39 years due to cambial mortality. Based on the cumulative frequency of cambial mortality duration (Figure 3-2), 93 % of age estimates were in the correct 15-year age class. Although the 15-year classes of ring counts were more accurate, the representation of the age structure was less precise. The histograms depicting 1-year age classes had a bimodal distribution and the histograms based on 15-year age classes were unimodal.

3.4 Discussion

3.4.1 Cambial mortality, canopy position and health condition

While partial cambial mortality has been reported for other forest types (e.g. Larson et al. 1993, Daniels et al. 1997, Cherubini et al. 2002), this is the first study to systematically assess its incidence in *Austrocedrus chilensis* forests. Our results confirm long-term cambial mortality in declining *A. chilensis* trees as suggested in previous studies (Rajchenberg and Cwielong 1993; Cali 1996). A high proportion of the trees sampled exhibited cambial mortality including both healthy and symptomatic living trees growing in both subcanopy and

canopy positions. I found cambial mortality duration of up to 39 years in trees that were living at the time of sampling, with the onset of the cambial mortality as early as 1966. It is important to note that these criteria provide minimum estimates of duration of cambial mortality and maximum estimates of the year of onset respectively, as our increment cores did not necessarily intercept the point of origin of the cambial dieback. More accurate estimates would require destructive sampling to assess the entire circumference of each tree. Moreover, the duration of cambial mortality is a minimum estimate since the trees were alive at the time of sampling.

While Rajchenberg and Cwielong (1993) and Calí (1996) studied only symptomatic and dead trees, our results represent both symptomatic and healthy individuals. I found that about 60 % of the trees exhibiting cambial mortality corresponded to living trees that were classified as 'healthy' in the field. Initial observations and previous studies suggested the importance of this phenomenon in trees exhibiting symptoms of '*mal del cipres*'. However, our study shows the presence of cambial mortality in trees in declining forests independently of their apparent health condition assessed by their crown vigour. In contrast to our original hypothesis, both healthy and symptomatic trees are likely to produce incomplete rings around the circumference of the tree.

In agreement with previous studies (Bormann 1965; Lorimer et al. 1999; Cherubini et al. 2002; Parent et al. 2002), the presence of cambial mortality was found in a greater proportion (65 %) in suppressed trees, and cambial mortality of more than 20 years was found primarily in suppressed trees. Even though I hypothesised the incidence of cambium death or incomplete rings was likely to be found more on symptomatic trees, subcanopy trees classified as healthy (55.7 %) were in a greater proportion compared to subcanopy trees classified as symptomatic (25.7 %). Independently of the health condition, trees in suppressed conditions can stop producing complete rings at the base of the trunk because reduced crowns do not produce enough photosynthates to fulfil the requirements of the entire

tree (Bormann 1965; Marchand 1984). This process would be accentuated in symptomatic trees as a consequence of crown withering and defoliation. The photosynthates reduction product of crown vigour lost and defoliation could explain the presence of partial growth rings in symptomatic canopy trees.

Even though the study was carried out in symptomatic forests, I hypothesize that the phenomenon described here may also occur in *A. chilensis* forests where symptoms are not evident. Due to the high proportion of cambial mortality found in apparently healthy subcanopy trees one could hypothesize its presence might be related to the competitive disadvantage of trees in the lower canopy compared to those in the upper canopy. This hypothesis requires further research.

3.4.2 Implications for stand dynamics studies

The occurrence of cambial mortality in *A. chilensis* trees represents a source of error when pith dates and age estimates are obtained using ring counts instead of crossdated ring-width series. At an annual resolution only 62 % of age estimates were correct; the remaining 38 % of the ages were incorrect up to 39 years. These results have several implications in population studies limiting the usefulness of the data and the extent of the analyses. If one were studying the patterns of establishment of individuals over time and its relation to climatic variables, even when the counted distribution provides detailed information about the pattern, almost 40 % of the establishment dates will be incorrect reducing the possibility of sound analyses. Furthermore, the use of age estimates based on ring counts instead of crossdated ring-width series can lead to different temporal patterns in recruitment (Parent et al. 2002). The only approach to avoid such misinterpretations is by improving the accuracy of the age estimates using crossdating techniques rather than the simple ring count. In symptomatic *A. chilensis* forests, it is indispensable to have accurate

age estimates to make sound population dynamics interpretations at an annual resolution. If a less detailed demographic study is required, broader age classes using estimates based on ring count would provide greater agreement regarding the overall period of establishment. Results from the cumulative frequency of the cambial mortality duration indicated that 93 % of age estimates were correct using a 15-year age class. While this approach provides greater accuracy, the representation of the age structure will be less precise than an annual resolution. For example, the histogram based on 15-year age classes had a unimodal distribution, the histogram based on 1-year age classes had a bimodal distribution. These differences could lead to different hypotheses regarding development patterns. The cumulative frequencies presented here can be used to select an appropriate class-size to build age distributions in *A. chilensis* symptomatic forests when using tree ring count. If one would decide to be 90 % confident (x -value when line crosses 0.9) about the age structure, cumulative frequencies by health-canopy classes would provide with the error for the age estimate according to that level of confidence.

Additionally, the results presented in this study raise uncertainty about the potential error of determining the year of tree death. Results from the outer-ring dates show there could be variability of dates for the outer-most ring at different points on the tree circumference in both healthy and symptomatic living trees. The fact the outer-most ring at a given point of the circumference may or may not represent the actual date when the tree dies could affect the determination of the true year of death and, consequently, the identification of mortality patterns. From a stand dynamics point of view, it is important to determine whether the mortality dates obtained correspond to the time at when trees became physiologically dead and, therefore, stopped occupying growing space. The fact that resources are no longer used by the dead trees will allow other trees increase their growth rates and possibly allow new individuals to establish (Oliver and Larson 1996). Outer-most ring date errors due to the cambial mortality reported here would result in

inaccurate mortality dates if no cross-dating techniques are used, and thus, lead to wrong interpretations if compared to establishment dates or growth release patterns on residual trees. Furthermore, incorrect mortality dates determined by simply counting rings will result in erroneous interpretations while studying the relationship of mortality events with known disturbance regimes or the effects of environmental factors such as climatic variability on tree mortality. While the error on establishment dates and ages can be avoided by cross-dating the ring-width series, the correction of the error for the year of death due to cambial mortality is more complex. Crossdating will provide a precise date for the outer ring; however, this date might not be an accurate estimate of the year of death because of the cambial mortality phenomenon.

3.5 Conclusion

The results of this study confirm the existence of long-term cambial mortality in *A. chilensis* forests experiencing symptoms and mortality from what is locally known as ‘*mal del ciprés*’ and reiterate the importance of cross-dating techniques when determining tree ages and mortality dates. While onset dates for the cambial mortality are presented, the maximum duration is still uncertain since the trees were alive. The information presented here provides an estimate of error for tree ages and an example of the error in determining class-size for age distributions if only ring counting is used without crossdating. Additionally, the presence of cambial mortality raises uncertainty about the precision of determining the year of death.

Alternately, to improve the accuracy of death dates determined by crossdating, we recommend taking multiple increment cores or a full cross-section to increase the probability of determining the actual year of tree death. Cores or radii for analysis should preferentially include radii perpendicular to the slope as well as the radius oriented downslope to reduce the probability of missing rings. Cores should always include bark and sapwood. If partial

crown death or a reduction in crown vigour is evident, avoid areas on the bole directly underneath dead or chlorotic branches. Cores or disks may be sampled from higher on the stem to reduce the influence of cambial mortality and increase the chance of including all annual rings; however, these samples will be less suitable for estimating tree age. If establishment dates are needed to reconstruct disturbance history based on simple ring count only, the precision can be increased by excluding suppressed trees since they are of limited value (Lorimer et al. 1999), as well as they require extra effort while visually cross-dating due to of low ring width variability. While working with suppressed trees, stem analyses on the entire stem might be the best aging method to avoid missing rings even when cross-dating is used (Parent et al. 2002).

3.6 Figures

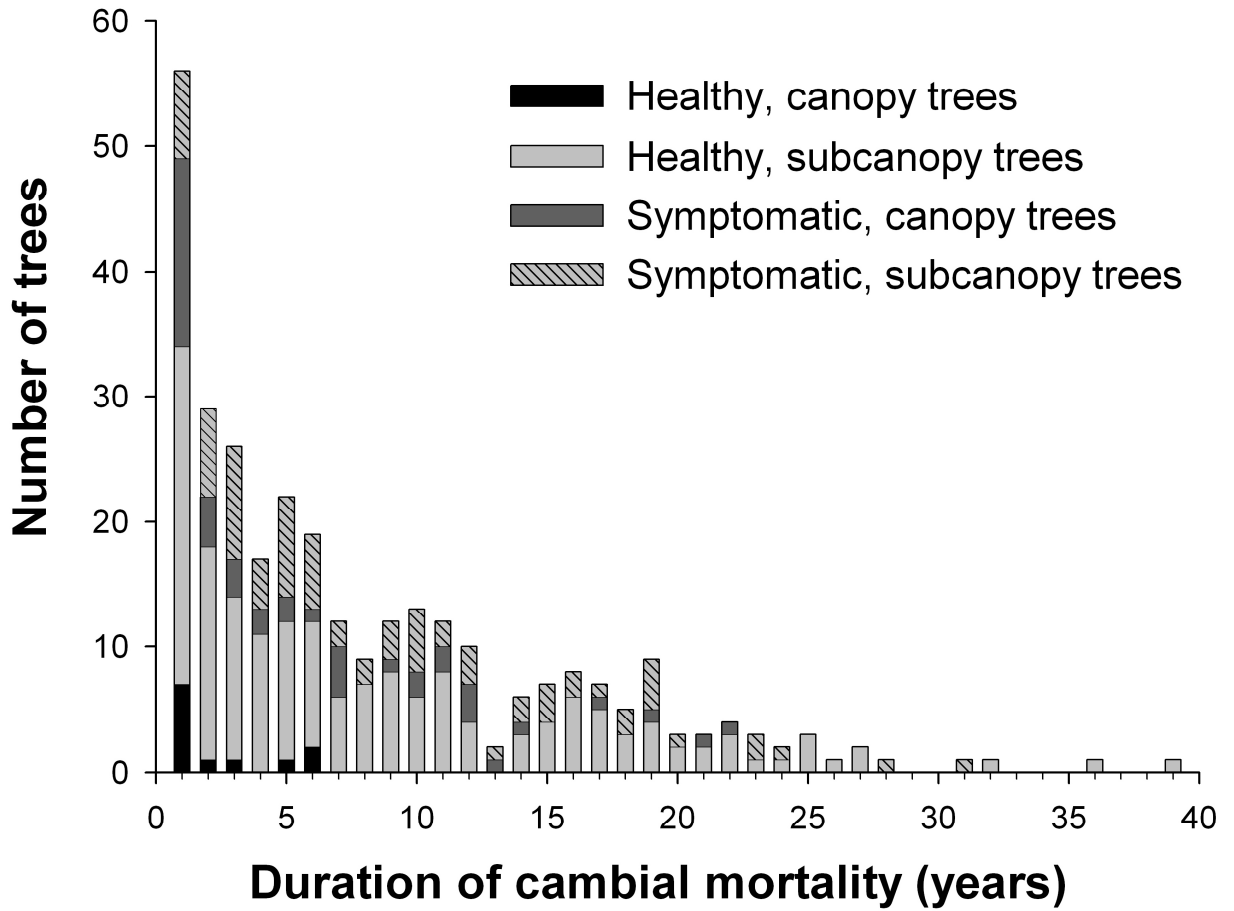


Figure 3-1 Cambial mortality duration by health - canopy classes.

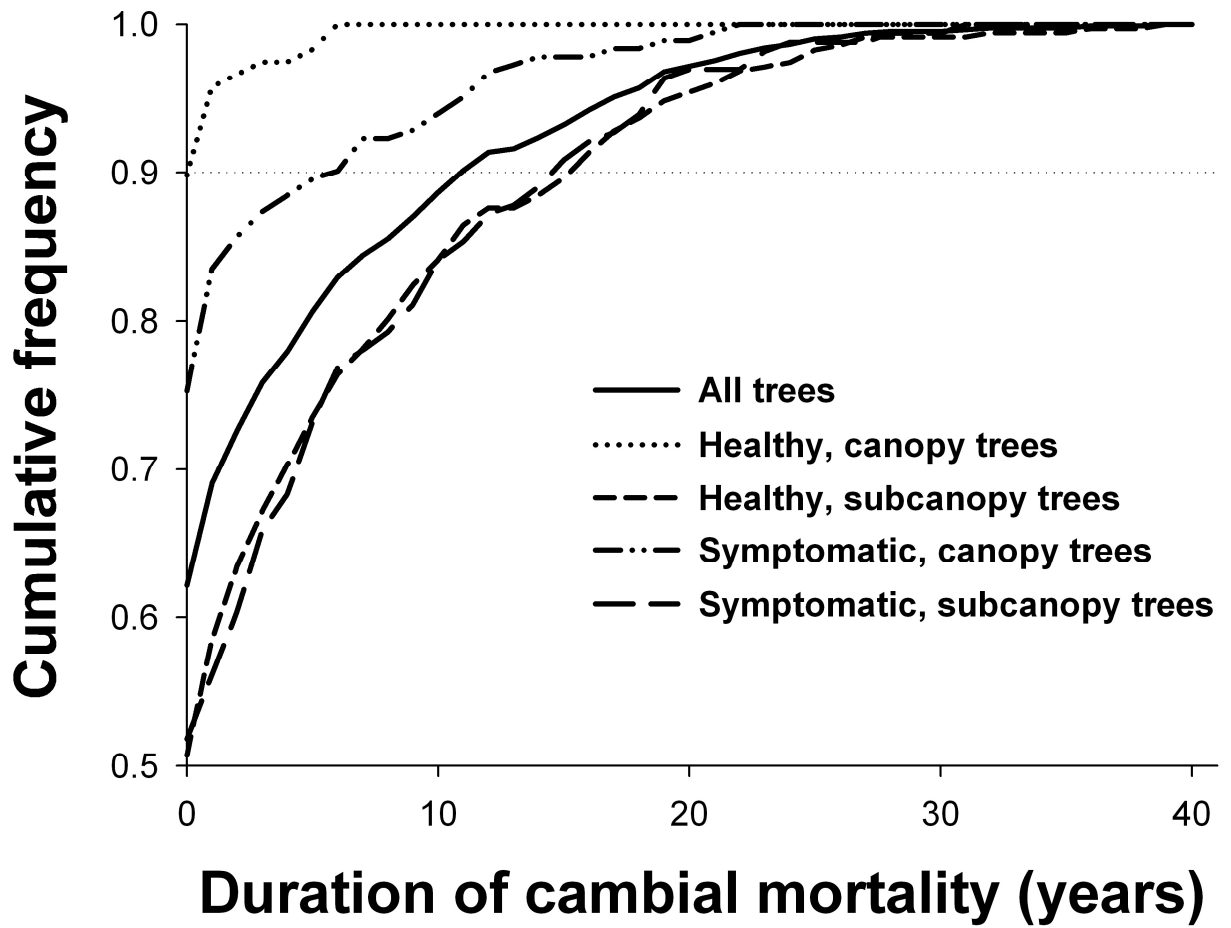


Figure 3-2 Cumulative frequencies of the cambial mortality duration by health-canopy classes.

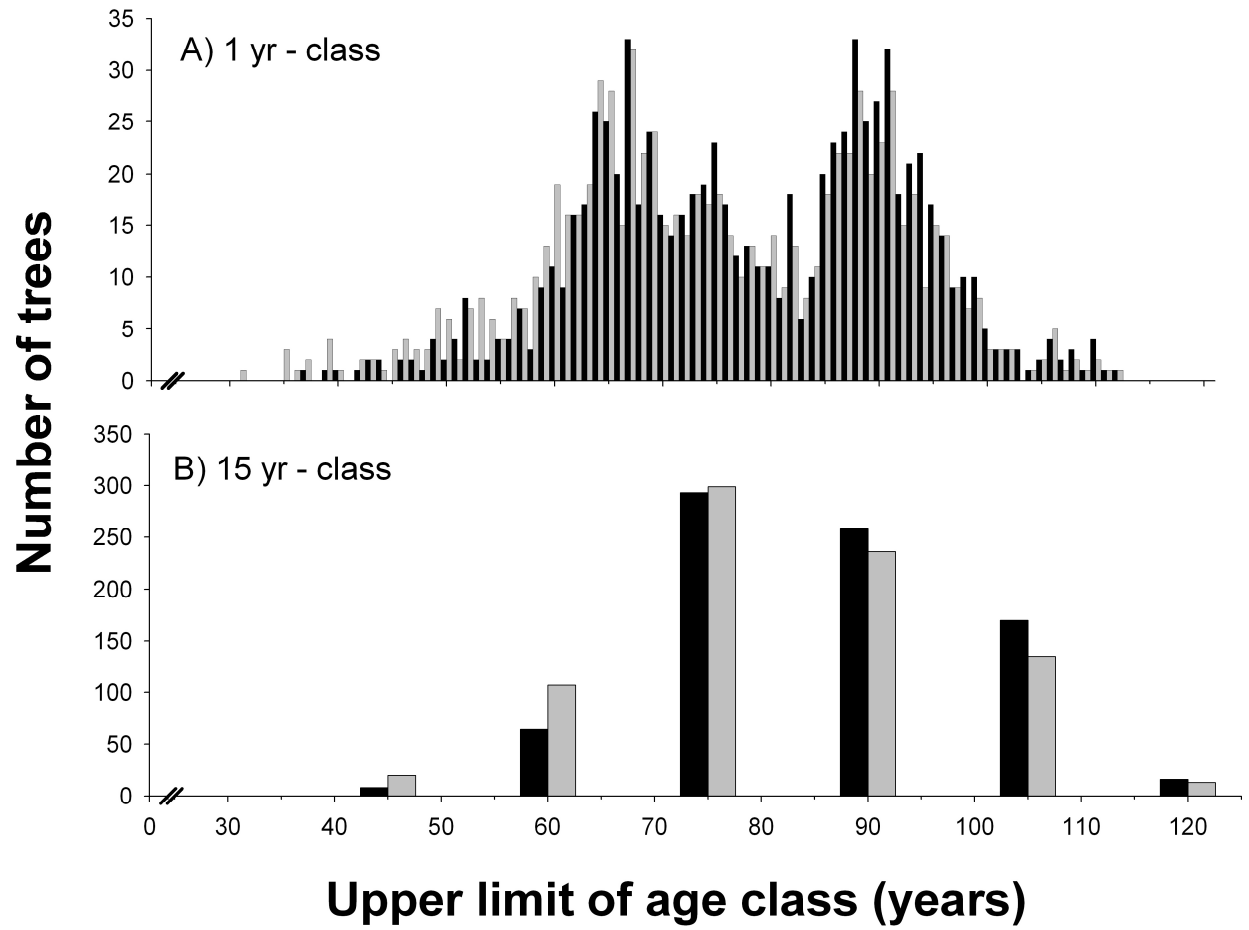


Figure 3-3 Age histograms of cross-dated (black) and counted (gray) ring-width series for two age classes: 1-year and 15-year.

3.7 Tables

Table 3-1 Distribution of 811 living *Austrocedus chilensis* trees stratified by health condition of the crown, canopy position of the trees, and presence of cambial dieback determined using dendrochronological analyses.

Health condition	Canopy position	Cambial dieback		
		No evidence	Present	Total
Healthy	Canopy	106	12	118
	Subcanopy	176	171	347
Symptomatic	Canopy	137	45	182
	Subcanopy	85	79	164
Total		504	307	811

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4 Stand development patterns as a consequence of the mortality in

Austrocedrus chilensis forests³

4.1 Introduction

Austrocedrus chilensis (D. Don) Pic. Sern. et Bizarri is an endemic conifer species of the temperate subantarctic forests of Patagonia, South America. Its natural distribution covers two elongated areas that parallel the Andes on both sides of this mountain range. On the Argentinean side, *A. chilensis* forests are distributed discontinuously at latitudes between 37° 08'S and 43° 43'S occupying a narrow strip (60-80 km wide) in the Andean foothills (Bran et al. 2002). The steep east-to-west gradient in precipitation in the rain shadow of the Andes drives dramatic changes in vegetation patterns (Veblen and Lorenz 1987). Forests develop at sites widely ranging in moisture, receiving as little as 600 mm in the eastern limit of its distribution, and as much as 2000 mm in the western limit (Dezzotti and Sancholuz 1991).

Structurally, *A. chilensis* forests have been classified into three types: marginal, dense, and mixed forests (Dezzotti and Sancholuz 1991). Marginal forests occur in the drier areas (total annual precipitation = 600 to 900 mm) as monospecific patches of low-density, scattered trees, typically on rocky outcrops and surrounded by Patagonian steppe. The mixed type occurs in wetter zones (1600 to 2000 mm) in denser stands mixed with the more mesic *Nothofagus* species, principally *Nothofagus dombeyi*. The proportion of *A. chilensis* in these mixed forests is inversely related to the site moisture. It is in these mixed forests that the distribution of *A. chilensis* reaches its highest altitudinal limit (1000-1100 m a.s.l.). Dense

³ A version of this chapter will be submitted for publication. Amoroso, M. M., and Larson, B. C. Stand development patterns as a consequence of the mortality in *Austrocedrus chilensis* forests in Northern Patagonia.

A. chilensis forests are primarily monospecific and occur between the two extremes along the precipitation gradient (900 to 1600 mm). Although this three-type classification has been widely accepted and used, recent genetic studies have described a fourth type composed of marginal populations located along the eastern extremes of the precipitation gradient at sites that are usually drier than those of the marginal forests (Pastorino and Gallo 2002). This type is represented by small isolated groups of dispersed individuals, often with a multi-stemmed growth form, that are located at sites that acted as small refugia during the Last Glacial Maximum (Pastorino et al. 2004).

The principal natural disturbance agents affecting *A. chilensis* forests are fire, wind, and earthquakes (Veblen et al. 1992; Veblen et al. 1995). Due to their proximity to populated areas, these forests are also exposed to great anthropogenic pressure. Grazing, logging and human-set fires are the most important anthropogenic disturbances as one moves eastwards where pure cypress forests prevail (Veblen et al. 1992; Kitzberger et al. 1997). Another disturbance that is poorly understood from a stand dynamics point of view is the mortality process locally known as '*mal del ciprés*' (cypress sickness). This disturbance was first detected more than five decades ago (Varsavsky et al. 1975; Hranilovich 1988) and currently affects forests throughout the range *A. chilensis* in Argentina. Due to its current impacts and their ecological and economical implications, this disturbance might represent the most important disturbance in many areas where *Austrocedrus* forests grow.

Unlike other disturbances, '*mal del ciprés*' is not explained by a single agent. Rather, tree deaths occur gradually and result from a complex interaction of abiotic and biotic factors (Manion 1991; Manion and Lachance 1992), which has led to the classification of '*mal del ciprés*' as a type of forest decline (Baccalá et al. 1998; Filip and Rosso 1999; La Manna and Rajchenberg 2004). Sites at moderate altitudes with high precipitation (Baccalá et al., 1998) as well as those with poorly drained soils (La Manna and Rajchenberg 2004, 2008a) are considered predisposed to the decline. The onset of the decline has been related to climatic

events such as warm-dry periods (Calí 1996). A recent study associated a new species of *Phytophthora* (*P. austrocedrae* Gresl. & E. M. Hansen) with the mortality of trees, and it is believed to be the primary cause of tree death (Greslebin et al. 2007); yet, the causes of the 'mal del ciprés' are still under investigation (El Mujtar and Andenmatten 2007).

The most common visible symptoms of 'mal del ciprés' include trees with chlorotic foliage, crowns with partial withering that progresses to total defoliation, as well as standing or fallen dead trees (Havrylenko et al. 1989; Rajchenberg and Cwielong 1993; Fillip and Rosso 1999). Mortality appears as aggregations of dead trees forming patches of varying sizes or as dispersed declining and dead trees within stands (Rosso et al. 1994; La Manna and Rajchenberg 2004) and affects all tree size classes (Hranilovich 1988; Havrylenko et al. 1989; Rajchenberg and Cwielong 1993; Loguercio et al. 1998).

The presence of this disturbance suggests that these forests may become uneven-age, but previous studies have shown that the establishment of new individuals in forests under these conditions is highly variable (Loguercio et al. 1998; La Manna et al. 2008b). Successful establishment of *A. chilensis* in healthy stands occur in small openings in the canopy and this species is described as having a fine-scale gap-phase regeneration mode (Veblen et al. 1995; Gobbi and Schlichter 1998). Even though canopy mortality in symptomatic *A. chilensis* forests appears unpredictable and variable (Loguercio 1997; Loguercio et al. 1998; Calí 1996), I hypothesize that, in the absence of other disturbances (i.e. grazing or logging), tree deaths will provide opportunity for successful recruitment of *A. chilensis* in the understory of symptomatic forests. Furthermore, I hypothesize the changes in stand structure and the recruitment of new individuals through time as a consequence of the decline and mortality of overstory trees will lead to different stand development patterns in *A. chilensis* forests.

While several aspects of 'mal del ciprés' have been the focus of detailed studies, little effort has been dedicated to study the stand dynamics in symptomatic forests and

predict stand development patterns and future stand structure. The aim of this research is to gain more understanding about the forest stand dynamics in *A. chilensis* forests in Patagonia as a consequence of 'mal del ciprés'. Specifically, I want to examine the changes in stand structure over time and the implications these structural changes have on regeneration process and stand dynamics. Ultimately I would like to predict potential stand development patterns in declining *A. chilensis* forests.

4.2 Materials and methods

4.2.1 Study site and sampling

This study was conducted at two locations in the vicinity of the city of El Bolsón, Rio Negro, Argentina (41°46' S 71°33' W): the Reserva Forestal Loma del Medio – INTA (National Institute of Agricultural Technology) and the Area Natural Protegida Rio Azul – Lago Escondido. The area has a mean annual precipitation of approximately 904 mm and a mean annual temperature of 9.3 °C (Servicio Meteorologico Nacional 1969, 1985, 1986). It is characterized by post-fire *A. chilensis*-dominated forests with variable presence of smaller size tree species such as *Lomatia hirsuta* (Lam.) Diels and *Maitenus boaria* Mol. These two species could also form part of the understory along with *Aristotelia maqui* L'Herit and *Schinus patagonicus*. While these forests have been described and classified as compact pure *A. chilensis* forests (Dezzotti and Sancholuz 1991; Seibert 1982) the landscape in the sampling area is actually a mosaic composed of pure *A. chilensis* and mixed *A. chilensis* - *Nothofagus dombeyi* stands due to the changing topography. Soils at both study areas are deep, containing volcanic ash, and have been classified as Andisols (Lanciotti and Cremona 1999).

Within these two areas I chose 12 *A. chilensis* - dominated stands with common symptoms of 'mal del ciprés' for sampling (Table 4-1). Since the purpose of the study was to investigate the dynamics of the stands as a consequence of the overstory mortality, stands were selected with no evidence of recent grazing or past logging. At each stand a 1000 m² plot was established. Plots were square (31.6 x 31.6 m.) or rectangular (40 x 25 m.) depending on the local topography. In each plot, all living and dead trees with a diameter at breast height (DBH) larger than 5.0 cm were tagged. The following information was recorded for each tree: species, DBH, crown height class, and 'health condition'. Crown height class (dominant, codominant, intermediate or suppressed) was assigned after Smith et al. (1997). The health condition of all *A. chilensis* trees was assessed using an adaptation of the classification proposed by Rajchenberg and Cwielong (1993). These authors classified trees into six health classes on a progressive scale (0 to 5) based on foliage condition, increasing percentage of defoliation, and bark characteristics, which are combined into three health groups: (a) living healthy trees (classes 0 and 1), (b) living symptomatic trees (classes 2 and 3), and (c) dead trees (classes 4 and 5). All living and dead *A. chilensis* and other major tree species were cored for age determination. Cores were taken perpendicular to the slope and as low as possible on the stem (approximately 30 cm above ground); the coring height was recorded for later total age estimation. More than one core was taken from some trees to ensure that the cores included sound sapwood and bark to guarantee that the outermost ring was present. Transverse cross-sections were taken from 50 individuals where a good quality core could not be extracted because the bark and wood were decayed. Within each plot I established nine circular 30 m² regeneration subplots (3.09 m. in diameter) at an equidistance of 10 m. In each subplot, all seedlings and saplings larger than 50 cm in height and with a DBH smaller than 5 cm were destructively sampled for age determination.

4.2.2 Dendrochronological methods

Cores were mounted and cross-sections were glued to wooden boards and sanded following standard dendrochronological methods (Stokes and Smiley 1968). From each cross-section I selected two radii to be measured. To ensure comparability with the increment cores I used the following criteria: the two radii were a) perpendicular to the slope to avoid compression wood and b) included sound sapwood and bark. Cores and radii were visually cross-dated and ring-width series were measured on a Velmex bench to the nearest 0.01 mm. All ring-width series were statistically cross-dated using an existing master chronology (R. Villalba: Pampa del Toro; International Tree-Ring Data Bank, NOAA) and the program COFECHA (Holmes 1986; Grissino-Mayer 2001). Ring-width series that did not cross-date statistically and/or presented low correlation coefficient values were visually cross-dated.

All seedlings and saplings were cut at the root collar to obtain cross-sections for age determination. For a subsample of 40 seedlings per species and stand I obtained extra cross-sections at 25 and 50 cm of height for age correction due to coring height of the overstory trees. All samples were sanded following the same dendrochronological methods described above, and tree rings were counted using a microscope to determine number of years from bark to pith.

4.2.3 Analyses

Age at the coring height of the samples was calculated as the difference between the year of sampling (2005) and the year of the inner-most ring plus one more year; the year of each inner ring was determined by crossdating. For the 335 cores (26 %) that did not intercept the pith I estimated the number of missed rings (Duncan 1989). Additionally, I

corrected for the number of years for each tree to grow to the coring height. For this correction, I counted the rings of seedlings at 0, 25 and 50 cm of height and calculated the number of years required for each seedling to grow to 25 and 50 cm tall. Seedlings were stratified by stand and species and I estimated height growth rates and classified seedlings as fast- or slow-growing based on height growth rates that were above or below the mean, respectively. I then calculated two linear growth curves, one from 0-25 cm and another from 25-50 cm, and applied the corrections for the coring height to each overstory tree based on the species and growth rates (fast- vs. slow-growth). For overstory trees, growth rates were calculated as diameter at coring height divided by the number of years at coring height and assessed relative to the mean. Total age estimates were calculated as:

Total Age = Age at coring height + Number of missed rings to pith + Number of years to coring height

The resulting ages from trees and regeneration were combined in 5-year age classes for each site to build histograms and examine stand establishment and tree recruitment over time. Overstory DBH measurements were classified in 5 cm diameter classes to build diameter histograms.

Tree information in relation to the health class and height crown class was combined for all sampled stands into a contingency table to examine tree health in relation to the position in the canopy.

Mortality dates were determined as the calendar year of the outer ring of the crossdated ring-width series from snags and logs and were used to estimate mortality rates. Mortality rates (MR) were calculated as:

$$MR = [(N_t/N_o)/t]*100$$

where N_t is the number of dead trees in each plot in the interval t , N_0 is the total number of trees in the plot, and t represents the interval of time (years). Mortality rates were calculated annually and averaged in 10-year periods starting in 1945, the earliest onset of the mortality among all stands.

Using the crossdated ring-width series I reconstructed standing living, dead, and total basal area (BA) per hectare over time for each of the twelve stands. From this, I calculated yearly overstory mortality as the ratio of the dead BA (both standing snags and fallen logs) over the total BA.

$$\text{BA mortality} = (\text{BA}_{\text{Dead}} / \text{BA}_{\text{Total}}) * 100$$

Mortality rates estimated from BA were calculated annually and averaged in 10-year periods starting in 1945.

To study the individual growth response of *A. chilensis* and *N. dombeyi* trees to overstory mortality, the percent-growth change was calculated according to the technique of Nowacki and Abrams (1997). Percent-growth change (GC) for a year is equal to $(M_2 - M_1) / M_1$, where M_1 equals the average growth over the prior 10 years and M_2 equals the average growth over the subsequent 10 years. Positive GC represents releases, and negative GC represents suppression. A 10-year span for radial-growth averaging (i.e. a running mean) was selected since it tends to average out short-term growth responses related to climate, while capturing growth changes associated with canopy disturbance (Leak 1987; Nowacki and Abrams 1997). Release events were identified for each tree based on the ring-width measurements. The criteria used to classify the degree of release were: major releases for > 100% GC; moderate releases for 50-100% GC, and minor releases for 50-25 % GC.

Another criterion while identifying release events resulting from canopy disturbances is the

number of years during which a release event is sustained. Releases of different degrees (major, moderate and minor) extended from 1 year up to a decade among trees. Even though the running mean method tends to eliminate growth changes not associated with canopy disturbances, releases sustained for a few years may still occur from short-term climatic trends (Rubino and McCarthy 2004). Visual inspection of the ring-width series confirmed that releases sustained up to 3 years could be the result of the variability in tree growth and not related to canopy disturbances (Figure 4-1). In many cases these short-term releases corresponded to years following very narrow rings (e.g. 1962, Figure 4-1 C and D). Therefore, the minimum period for which an increase in GC must be sustained to be considered a release event in this study was 4 years (Figure 4-1 A and B). The years in which growth releases were initiated were recorded. Analyses were performed using the ARSTAN (Cook 1985) and JOLTS (Holmes 1999) programs simultaneously. Using the stand dynamics options in the ARSTAN program, I calculated release events in ring-width series based on changes in percent-growth by calculating a running mean of 10 years and following the percent-growth change criteria defined above. The JOLTS program was used to calculate net releases and suppressions in radial growth. This program calculates the occurrence, coincidence and duration of growth releases and suppressions based on user-defined criteria. I used a running mean of 10 years and factors of 1.25, 1.5, and 2, representing the change from pre- to post-event growth rates that correspond to >25 %, 50-100 %, and >100 % GC, respectively. Histograms for each stand were built indicating the number and magnitude of the releases. Information about the releases was combined with tree level information to create a contingency table to examine the distribution of the different releases among crown classes.

4.3 Results

4.3.1 Stand composition and health assessment

Although all stands were dominated by *A. chilensis* in the overstory, there were some stands with an important presence of other tree species (Figure 4-2 A). Both *Nothofagus dombeyi* (ND) and *Lomatia hirsuta* (LM) were present in the overstory of some stands. Nevertheless, with the exception of the stands where *N. dombeyi* was > 15 % of the relative density (CE2, EU1, RQ1, RQ2), no other species were competing with *A. chilensis* in the upper part of the canopy. *L. hirsuta*, *Aristotelia maqui* (AM) and *Schinus patagonicus* (SP) were either minor components (< 15%) and/or limited to the lower diameter classes in all stands, with the exception of stands CR1 and CR2 where *L. hirsuta* accounted for > 30% of small and medium size trees.

The health assessment of the *A. chilensis* trees in the field indicated that combined symptomatic and dead trees accounted for 40 to 73 % of the trees in the stands (Figure 4-2 B). Overall, 25.7 % of the *A. chilensis* trees presented crown symptoms, 33.7 % were dead, and 40.5 % appeared healthy. There was variability in the proportion of trees in each health group (i.e. symptomatic, dead and healthy trees) among stands (Figure 4-2 B) and among canopy positions (Table 4-2). On average, a similar proportion of trees exhibited crown symptoms in each canopy position class. In contrast, the proportion of dead trees was inversely proportional to the position of the trees in the canopy; almost 60 % of the dead trees were suppressed. Similar results were found for healthy trees that did not exhibit symptoms; on average, more than half of the healthy trees were in a suppressed position, accounting for almost a quarter of all the sampled trees.

4.3.2 Overstory age and diameter classes

Tree establishment began as early as the 1870's for 8 stands and as late as the early 1900's for 4 stands (EU1, EU2, CR1, CR2, Figure 4-3). Apart from a small proportion of trees that established later in the second half of the 20th century, most of the overstory tree establishment occurred before 1950. Most overstory trees that established after 1950 were *N. dombeyi*. The establishment period of the current overstory trees varied from 30 to 70 years among stands. For example, stands such as CE1, CE2, and EU1 established in a period of 30 to 35 years. Other stands, such as K1 and RQ1, had a longer period of recruitment that lasted up to 7 decades. Although the beginning and end of the establishment period was clearly defined in some stands, tree establishment was discontinuous in other stands. For example, in stands CE2 or RQ1 new individuals established after an abrupt decline and lack of establishment for about a decade. While late establishment could slightly change the shape of the histograms, all histograms followed unimodal distributions. However, there were differences in the temporal pattern of establishment among stands. While some of the stands exhibited a slightly left-skewed distribution (PP1, PP2, PP4), others such as K1 or RQ1 were right-skewed.

Diameter histograms of the overstory trees exhibited two different distributions (Figure 4-4), even though the overstory trees were well represented across all the DBH classes (5 to 55 cm) in all stands. The inverse J-shaped distribution in which there was a larger number of trees in the smaller DBH classes with smaller number as the class increased, occurred in most stands. However, in stands CE1, CE2 and PP4, there were equal numbers of trees in the smaller and intermediate diameter classes. While *A. chilensis* individuals were present in all diameter classes, the distribution of *N. dombeyi* among classes was related to its proportion in the stand. In those stands where *N. dombeyi* accounted for > 15 % of the relative density (CE2, EU1, RQ1 and RQ2), the trees were well

represented throughout all DBH classes. Where this species was a minor component (density < 15 %), trees were present only in the smaller DBH classes.

4.3.3 Mortality patterns

Reconstruction of the mortality events showed tree mortality as early as the 1940s with most deaths occurring after 1970 (Figure 4-5). While most stands had experienced some degree of mortality before 1960, two stands (CR1 and EU2) had no evidence of mortality until the 1970s. Mortality events appeared irregularly dispersed through time in most stands but there were some stands in which most trees died in a period of 30 to 40 years (CE1, CE2, CR1, CR2). There was no common pattern of mortality; rather, it was random and different among stands.

Overall mean annual mortality for all stands was 0.57 % ranging from 0.26 (CR1) to 1.01 % (RQ1) (Table 4-3). Annual mortality rates based on stems per ha ranged from 0.07 to 1.67 % among stands and varied considerably at all stands for the six 10-year periods studied. On average, the periods of 1976-1985 and 1986-1995 had the greatest mortality rates. However, annual mortality rates were different when calculated using basal area (BA) instead of number of dead trees. On average, annual BA mortality rates were almost 50 % higher than rates calculated using stems per ha (0.81 vs. 0.57) and ranged from 0.02 to 2.88 %. Annual BA mortality rates were highest, on average, for the periods of 1986-1995 and 1996-2005. Therefore, the number of dead trees was higher between 1976 and 1995 but tree deaths had a greater effect on BA between 1985 and 2005. Mortality values based on BA depict the combination of the number and size of the dead trees in relation to the rest of the stand.

The reconstruction of living, dead, and total basal area allowed assessment of the cumulative mortality over time and the relative abundance of dead versus living trees in each stand through time (Figure 4-6). Mortality has accounted on average for 13 % of the

total basal area, ranging from as little as 2 % in some stands (CR1) to more than 20 % in others (K1, PP1). This analysis also showed differences in the temporal patterns of mortality. In some stands dead trees accumulated relatively slowly over time (PP4, EU1, CR2); in others (CE1, CE2, K1, RQ1, RQ2) it increased abruptly over the last 40 years.

Age estimates of the overstory and understory trees were combined to depict overall tree establishment at each stand (Figure 4-7). Since only individuals taller than 50 cm were included in the analysis, establishment during the most recent years is underestimated. Overall tree establishment exhibited different distributions from those of the overstory trees alone (Figures 2), clearly denoting recent recruitment in all stands. While the establishment of the overstory trees exhibited histograms with unimodal distributions, the inclusion of the understory trees resulted in histograms with bimodal distributions. There is clear evidence in all stands that after periods of no or low recruitment to the overstory following the establishment of the initial cohort, new individuals have been successfully establishing over the last 50 to 60 years. This general pattern is clearly distinctive in some stands where there was no or low recruitment over short periods of time after establishment of the initial cohort (CE1, CE2, PP4, EU1, RQ1, RQ2). In other stands, the differences between cohorts are less accentuated (PP1, K1, EU2).

Interestingly, there seemed to be no clear pattern in relation to the time of establishment of new individuals in the understory and the occurrence of mortality events in the overstory. Most of the sampled stands started to exhibit an increase in the recruitment of individuals after the onset of the mortality. However, several of the stands showed establishment in the understory before the onset or the majority of the mortality (CE2, PP4, K1, EU2, CR1). This might even be the case for two more stands (PP1, CR2, Figure 4-5) if a few isolated dead trees at the onset of the mortality were not be considered.

There are both absolute and relative differences in the number of individuals that established after the overstory trees established. Compared to the number of trees that

established in early stages of stand development (i.e., stand initiation) (Figure 4-2), the recruitment in the following six decades varied from low (PP1, PP2, PP4, EU2) to high (CE1, CE2, K1, EU1, RQ2). As well, recruitment of *N. dombeyi* has increased in some stands. The number and proportion of *N. dombeyi* recruited in the second half of the 20th century compared to *A. chilensis* increased in the late 1970's and early 1980's in stands CE2, EU1, EU2, RQ1 and RQ2. For some of these stands *N. dombeyi* represented most of the tree establishment over the last 20 to 25 years.

4.3.4 Overstory growth release

The radial growth responses of overstory trees since the onset of the mortality varied among stands, exhibiting different numbers of releases and percent-growth changes among trees (Figure 4-8). In some stands (PP1, PP2, K1, EU1, EU2, RQ2, CR2), trees exhibited releases during and immediately after deaths of single or multiple trees suggesting some synchrony between processes. Within this group of stands the number of releases associated with mortality was relatively constant through time in some stands (PP1, EU1, EU2, RQ2, CR2), whereas in other stands the number of releases was higher in earlier decades at the onset of the mortality (PP2, K1). In contrast, other stands exhibited a different pattern in which the degree of synchrony was less and trees exhibited no or a low number of releases during periods of tree mortality (CE1, CE2, PP4, RQ1, CR1).

The percent-growth change (GC) of trees that released following overstory tree mortality also varied in number and through time (Figure 4-8). In general, minor (25-50 GC) and moderate (50-100 GC) releases occurred evenly between mortality onset and the present. Major releases (> 100 GC), more commonly occurred after the 1950s and 1960s when most trees began to die in the stands. Minor releases (> 25 GC) accounted for almost half of the total number of all releases at all stands (48 %), followed by moderate releases

(36 %) and major releases (16 %). All types of releases occurred in all stands but minor and moderate releases were more constant compared to major releases. While in some stands the number of major releases was minimal (PP4, EU2, RQ1, CR1, CR2), in others it represented a high proportion of the total number of releases (CE1, PP2, K1).

Tree growth releases in response to the changing environment created by the mortality of overstory trees were inversely proportional to the position of the tree in the canopy. On average, 44, 26, 19 and 11 % of trees that released were in the suppressed, intermediate, codominant and dominant height classes, respectively (Table 4-4). The highest proportion of major and moderate releases was in suppressed trees; none of the dominant and codominant trees exhibited a major release.

4.4 Discussion

4.4.1 Mortality onset and pattern

Mortality in *Austrocedrus chilensis* forests affected by 'mal del ciprés' appears to be unpredictable and variable in time. While the onset of the mortality in this study area dated from as early as 1940-1950, as reported for other areas in Patagonia (Varsavsky et al. 1975; Hranilovich 1988; Calí 1996), most mortality events occurred after 1970. It is interesting that even among stands in close proximity, the onset of the mortality varied by as much as 25 years. After the onset, mortality was unpredictable, resulting in different patterns and variable rates among stands. Mortality rates also varied depending on whether they were calculated using trees per hectare or basal area. Expressed as the number of trees that have died since the 1940's, annual mortality rates differed considerably among stands, ranging from 0.07 to 1.67 %. Most stands experienced less mortality in the last 10 years than in the previous 10 or 20 years. On average, the periods between 1976-1985 and 1986-

1995 recorded the highest mortality rates. Estimates of annual mortality rates based on basal area showed different temporal patterns. Mortality rates ranged from 0.02 to 2.88 %. In some stands where mortality rate estimates based on trees per hectare had diminished in the last 10 years, mortality estimates based on BA were equivalent or even higher. Average mortality rates based on BA depicted that the periods of 1986-1995 and 1996-2005 resulted in the highest rates. These estimates differ from those calculated using density as basal area mortality estimates depict the combination of the number and size of the dead trees in relation to the rest of the stand. This shows then that trees that died in the later decades were greater in size relative to the rest of trees and presumably corresponded to trees in upper canopy positions.

As reported in previous studies, mortality affected all tree size classes (Hranilovich 1988; Havrylenko et al. 1989; Rajchenberg and Cwielong 1993; Loguercio et al. 1998). As well, this study found that the occurrence of mortality was inversely related to the position of the trees in the canopy as approximately 60 % of the dead trees were in the suppressed height class. In contrast, trees classified in the field as symptomatic occurred in similar proportions among height crown classes. Since I expect that trees with chlorotic foliage and partial defoliation will eventually die, I expected the proportion of trees in both symptomatic and dead classes to be comparable. One possible reason for the high mortality of suppressed trees compared to the other crown classes is that dead trees in suppressed positions at the time of sampling could have died at different times and stages of stand development. At the time of death, some trees may have occupied an intermediate, co-dominant or dominant position in the canopy relative to the other trees; however, the surviving trees have subsequently grown. Alternately, the high proportion of dead suppressed trees could be the result of trees dying as a consequence of density-dependent mortality as many trees die during the 'stem exclusion stage' (sensu Oliver and Larson

1996) from direct competition from other trees (Oliver et al. 1985; Peet and Christensen 1987; Lutz and Halpern 2006).

Although the mortality dates represent a precise measure of the outer ring derived from crossdated ring-width series, they provide only best estimates of the actual year of death of the trees. Inaccuracies result due to the potential occurrence of partial cambial mortality (Chapter 3) and the fact that only one tree core was sampled from most trees. Examination of the outer-ring dates of both healthy and symptomatic living trees indicated variation at different points around the circumference of individual trees (Chapter 3). Overall, for 38% of living trees outer-ring dates differed by up to 39 years from the year of sampling, although the difference was <10 years for 26% of the trees. Therefore, the mortality dates presented in this study provide the best estimates of the year in which the tree died, but may not represent the actual year of death. Moreover, the probability and degree of error varied among trees in different health and canopy height classes, with the greatest error in subcanopy symptomatic trees and the least error in canopy trees. Although these inaccuracies influenced the determination of the true year of mortality events and may have influence interpretations of temporal patterns, they had the greatest impact on interpretations at the annual time scale and decreased for interpretations at the decadal time scale.

While previous studies have examined mortality in symptomatic forests (Calí 1996; Loguercio et al. 1998), this study is the first to quantify long-term mortality rates in *A. chilensis* forests using high-quality ring-width data. In a previous study, Calí (1996) provided accurate estimates of mortality dates in two stands and partially reconstructed its spatial development; yet, mortality rates were not determined. Loguercio et al. (1998), estimated mortality rates up to 6.5% over a period of 8 years using volume records obtained from salvaging operations; but, it was not clear whether the initial cuts may have included trees that have died before the beginning of the salvage. The results from this study describe

long-term mortality patterns at a larger number of stands over several decades; however, the mortality patterns presented here are incomplete. Mortality occurs at early stages of development as a result of direct competition from other trees (Oliver et al. 1985; Peet and Christensen 1987; Lutz and Halpern 2006) and sometimes cannot be perceived at later stages. *A. chilensis* grows in a relatively dry climate and standing and fallen dead trees usually decay slowly and remain in good condition due to the high resin content of this species allowing successful crossdating (Villalba and Veblen 1998). However, trees that might have died at early stages would have had small diameters and either were not large enough to be included in this study or may have decayed and were not present at the time of sampling. Additionally, mortality estimates presented here represent those of the sampled stands only and do not provide average or potential estimates at the landscape level as the sampled area represents only part of this species range of distribution.

4.4.2 Mortality effects at the stand level

Canopy disturbances are important determinants of the structure and dynamics of forest ecosystems (Spies et al. 1990; Oliver and Larson 1996). The death of trees in the overstory is an important ecological process as resources used by those trees become available for others. Although the released growing space remains available for a variable period of time, it will eventually be used either by the residual overstory trees if they are able to expand their crowns and roots or for the establishment of new individuals in the understory (Oliver and Larson 1996). The death of overstory trees in *A. chilensis* stands resulted in the establishment of new individuals in the understory and a variable release response of trees in the overstory.

Overall, the bimodal distributions of tree establishment histograms clearly depicted significant recruitment in the understory after the establishment of the overstory. Following

the establishment of the overstory, and after variable periods with no or low recruitment in the understory, trees have been successfully establishing at all stands over the last 50 to 60 years. While in some stands there was a distinctive period with no or low recruitment in between overstory and understory tree establishment, in other stands different periods of establishment were less accentuated.

Relative to the number of individuals in the overstory, recruitment and establishment in the understory varied among stands. Understory establishment was low in some stands (PP1, PP2, PP4 and EU2) and high in others (CE1, CE2, EU1, RQ1 and RQ2). With the exception of stand EU1, the latter group of stands were on flat sites or those with much gentler slopes compared to those with low relative recruitment. As differences between sites can affect early colonization and development of *A. chilensis* stands (Veblen and Lorenz 1987), these same site characteristics may act as physical barriers for later recruitment.

Even when it is believed recruitment results from an increase in the amount of available growing space due to overstory mortality, the abundance and success of the establishment and the temporal pattern could be influenced by short-term climatic variability (Villalba and Veblen 1997). As well, the increasing recruitment of *N. dombeyi* in some stands was interesting. In stands CE2, EU1, EU2, RQ1 and RQ2, the number and proportion of *N. dombeyi* trees recruited during the second half of the 20th century increased compared to *A. chilensis* trees (Figures 4-3 and 4-7). In some stands *N. dombeyi* accounted for most of the establishment over the last two decades. This group of stands, as well as some stands with fewer *N. dombeyi*, were on sites with cooler east to southeast aspects.

The occurrence and magnitude of the releases in the overstory varied over time and relative to the position of the trees in the canopy. The majority of the overstory trees in all stands released after the onset of the mortality; however patterns varied among stands. In some stands trees released immediately after single or multiple mortality events suggesting some degree of synchrony between the two processes, while in other stands trees showed

no or low number of releases during mortality events. Whether or not some degree of synchrony occurred, more overstory releases took place in the years following the onset of the mortality in half of the sampled stands. After this, the number of releases decreased and was relatively constant. The occurrence of releases was also influenced by the position of the tree in the canopy. Only 30 % of the releases occurred in trees in the upper part of the canopy (dominant and codominant classes) while the remainder occurred in trees in subcanopy positions (suppressed and intermediate classes). Furthermore, almost all major releases and 75 % of the moderate releases occurred in subcanopy trees. While this response is frequently observed in temperate forests (e.g. Nowacki and Abrams 1997), it might also relate to the mortality patterns. Suppressed and intermediate trees would release following the death of a neighbouring tree that is in the same or greater height classes. Releases of dominant and codominant trees, on the other hand, would be expected only after the death of an overstory tree; the death of small understory trees does not liberate enough growing space for overstory trees to benefit. Of all dead trees, ≥ 80 % were in subcanopy positions explaining the low proportion of releases in dominant and codominant trees. Even if some of these dead trees had been in upper canopy at the time of their death, the small proportion of releases of dominant and codominant trees suggests either the dead trees were not in the proximity of the trees to initiate a release in its neighbours, or that the dead trees must have been smaller than their neighbours even at the time of death.

Tree health also influences the ability of a tree to release after growing space becomes available. While releases were observed in both healthy and symptomatic trees, the lack of release in some trees, delayed release in relation to mortality events (i.e. lack of synchrony between processes), and the low percent-growth change of the response in some trees, could be influenced by the lack of vigour and reduced growth rates of some trees due to '*mal del ciprés*' (Chapter 2). Strong evidence of radial growth decline was found in both healthy and symptomatic trees in all the sampled stands. Major releases represented

only 16 % of the total number of releases and in most cases took place at the onset of the mortality, not in the last few decades. Moderate (48 %) and minor releases (36 %) were more evenly distributed over the last five decades. It seems that as radial decline develops over time, it limits the magnitude of the releases.

The recruitment in the understory and the growth response of the residual overstory trees resulting from the overstory mortality showed patterns that differed among stands. However, when the responses are examined together, some general patterns emerged. As defined by the fine-scale regeneration mode of *A. chilensis* (Veblen et al. 1995; Gobbi and Schlichter 1998), no significant establishment in the understory occurred until there was a minimal degree of canopy disturbance resulting from the overstory mortality. After the onset of mortality, recruitment of new trees and releases in the overstory occurred in the next decades. There were some stands, such as CE1 and CR2, where a high level of understory establishment corresponded to low number of releases. Stands PP1 and RQ2 exhibited a constant number of releases through time after tree death resulting perhaps in moderate establishment in the understory in relation to the overstory density. There was a group of stands (PP2, EU1, and RQ1) where the establishment of new individuals did not occur until some degree of mortality was present in the overstory. This coincided with a high number of early releases in the overstory trees. The ability of the overstory trees to expand and occupy the available growing space may have limited the amount of establishment in the future decades.

In those stands where conditions were suitable for individuals to establish in the understory prior to the onset of mortality, fewer overstory trees released and the magnitudes of release were relatively low as trees began to die (CE2, PP4, EU2, and CR1). It seems that competition for belowground resources might limit the ability of overstory trees to expand at sites where the understory tree layer is well developed.

Aside from the evidence presented here, overstory responses and understory recruitment in the presence of mortality could be influenced by climate. Synergetic effects with climate need to be studied as the occurrence of periods of positive and negative growth conditions and establishment for *A. chilensis* in Northern Patagonia exist (Villalba and Veblen 1997, 1998).

4.4.3 Stand dynamics

A. chilensis stands in the area of El Bolsón established following stand-replacing fires. Vast areas of forests in northern Patagonia were deliberately burned with the arrival of the first Europeans between 1890 and 1920 to increase the area for pasture, resulting in the current forest structure (Willis 1914; Veblen and Lorenz 1987; Kitzberger and Veblen 1999; Veblen et al. 1999). Unimodal establishment distributions in these forests result from relatively shade intolerant species colonizing sites where growing space becomes suddenly available as a result of stand-replacing fires (Veblen and Lorenz 1987; Dezzotti 1996). On relatively mesic sites, *A. chilensis* establishes over a period of 50 to 60 years starting shortly after a fire, forming dense even-aged stands (Veblen and Lorenz 1987, 1988; Kitzberger 1994). Even when *A. chilensis* dominated the overstory at the time of sampling, there were other species of trees and shrubs that were present at the time of establishment and might have dominated the earlier stages of the stand initiation. Following stand-replacing fires in the area, xeric tree species such as *Lomatia hirsuta*, and *Schinus patagonicus* and other shrubs establish (Veblen and Lorenz 1987; R. Criado personal communication 2007). Some of the differences in the time of establishment among the stands in this study can be partially explained by differences between sites which may have delayed early colonization and influenced the future development (Veblen and Lorenz 1987).

As the initial trees colonized the site and all the growing space was occupied, conditions became unfavourable for further recruitment of new individuals (Veblen and Lorenz 1987; Dezzotti 1996) and stands entered the stem exclusion phase (Oliver and Larson 1996). Even though *A. chilensis* is considered relatively shade tolerant, considerable mortality is expected to occur during this stage due to the competition for resources among trees (Alaback 1982; Oliver et al. 1985; Peet and Christensen 1987; Waring 1987; Kobe et al. 1995; Lutz and Halpern 2006). Truncated and narrower diameter distributions, such as the ones presented here, usually result from the death of trees that were not able to compete during stem exclusion. Stand reconstructions based on living trees at later times may not be able to detect these mortality events (Oliver and Larson 1996). This early mortality would not only include *A. chilensis* but also other species that dominated the stand at earlier stages such as *L. hirsuta*, *A. maqui* and *S. patagonicus*.

Once the canopies close, the establishment of *A. chilensis* seedlings in the understory is prevented as shaded conditions are not appropriate for its establishment (Veblen and Lorenz 1987; Veblen et al. 1992). In some stands, the transition from stem exclusion to understory reinitiation may be accelerated by windthrow and the creation of gaps, favouring the establishment of regeneration in the understory (Veblen et al. 1992). Large gaps would favour the more shade intolerant *N. dombeyi* while smaller gaps would favour *A. chilensis* (Veblen et al. 1995; Dezzotti 1996; Gobbi and Schlichter 1998). If dense stands on mesic sites are not subjected to such disturbances, they continue growing. As the understory reinitiation stage is reached (i.e. maturity), stands enter a phase where the regeneration occurs in gaps of small size (Veblen et al. 2004). Since *A. chilensis* requires light conditions associated with gaps to establish successfully beneath the canopy and the gaps occur irregularly in space and time, successful regeneration is also sporadic (Veblen et al. 1995; Gobbi and Schlichter 1998). As was the case for previous studies, I found no

evidence of successful establishment occurring in most stands during the stem exclusion stage.

Alternately, stands that establish on sites with poor soil water drainage (La Manna and Rajchenberg 2004, 2008a) or at moderate elevations with greater precipitation (Baccalá et al. 1998) undergo periodic tree mortality even during the stem exclusion stage. While in some stands the death of trees during the stem exclusion stage could potentially allow some establishment in the understory as a consequence of small gaps, it seems recruitment is not successful until more growing space becomes available due to the death of trees in the upper part of the canopy.

As mortality occurs over time, more growing space becomes available allowing for both recruitment and releases in the overstory. The ability of residual trees to respond and the magnitude of the response will be influenced by tree canopy position, tree health, and the contribution of the understory to moisture competition. Trees in subcanopy positions seem more responsive to the changing environment relative to dominant and codominant trees. However, declining trees have limited capacity to use the unoccupied growing space (Chapter 2). Therefore in stands with large numbers of declining trees, there is a greater chance that more regeneration will successfully establish in the understory, along with shrubs and herbaceous vegetation. While the effect of shrubs and herbaceous vegetation on *A. chilensis* recruitment and establishment has been recognized to be beneficial following stand-replacing fires (Loguercio 1997; Loguercio et al. 1998; Gobbi and Schlichter 1998; Kitzberger et al. 2000), the role of competition with understory and overstory trees for limiting resources (i.e. water) over the long term and in partially disturbed canopy stands is unknown.

Even when *A. chilensis* dominates the overstory and the majority of the recruitment in most stands, there are situations where the local topography and aspect lead to the recruitment and establishment of *N. dombeyi* in the understory. Recruitment of this species

had been reported in mixed *A. chilensis*–dominated forests (Dezzotti 1996) and mixed *N. dombeyi*-*A. chilensis* old-growth stands (Veblen 1989); however, little was known about its establishment in stands affected by ‘*mal del ciprés*’ until now. Where the recruitment of *N. dombeyi* is favoured, changes are already underway in the overstory composition as indicated by its presence in larger diameter classes and the upper part of the canopy. The shift in canopy composition results in new stand development patterns. Although seed source and aspect might play an important role in tree establishment of *N. dombeyi*, larger openings as a result of increasing levels of mortality of *A. chilensis* may result in more establishment of *N. dombeyi*, which is relatively shade-intolerant (Veblen et al. 1981; Veblen 1989). Once established, *N. dombeyi* will most likely outcompete *A. chilensis* due to its relatively higher growth rates (Veblen and Lorenz 1987; Dezzotti 1996). This represents a gradual but important shift in the species composition leading to the development of mixed species stands on mesic sites. This type of change is less likely in other *A. chilensis* forest types, such as the marginal forests or drier dense forests, where the lack of seed source and the lower moisture regimes may limit the establishment of *N. dombeyi*.

Since mortality predictions are particularly difficult given the unpredictable nature of ‘*mal del ciprés*’, it is difficult to predict the amount of future growing space within a stand. However, as overstory trees continue to die and surviving overstory trees are also declining in growth, it seems unlikely overstory trees will be able to occupy newly released growing space. Therefore, more recruitment of understory trees to the overstory and establishment of new regeneration is predicted in the absence of additional disturbances that could affect growth rates and seedling success. Additionally, as the overstory density decreases, trees could become more susceptible to damage by wind producing larger gaps. As a result of the combined effects of ‘*mal del ciprés*’, natural disturbances, and stand development, the single-cohort stands that initiated with a narrow range of ages after fire have become uneven aged with a wide range of tree ages and sizes 100 years after initial establishment.

4.5 Conclusion

This study is the first to quantify and describe long-term mortality patterns and rates using high-quality tree-ring data in *A. chilensis* forests affected by 'mal del ciprés'. After the onset of mortality within stands, tree death was irregular resulting in different patterns and variable rates among stands. The death of overstory trees in *A. chilensis* stands resulted in the establishment of new individuals in the understory and the release of trees in the overstory. Residual overstory trees exhibited growth releases that varied in time, number and percent-growth change among trees and stands. The success of the establishment in the understory in the last five decades varied among stands. The end result has been stands that initiated as single-cohort with a narrow range of ages and have become uneven-aged with a wide range of ages in approximately 100 years. It is expected that in the absence of other stand replacing disturbances more recruitment to the understory will occur due to 'mal del ciprés' or by fine-scale disturbances such as windthrow.

Results of this study provide a better understanding of the stand development patterns and the structural changes in *A. chilensis* forests affected by decline due to 'mal del ciprés'. This better understanding should form the baseline for learning more about the nature of the forest decline and help in the design and implementation of management strategies that could result in the amelioration of its consequences.

4.6 Figures

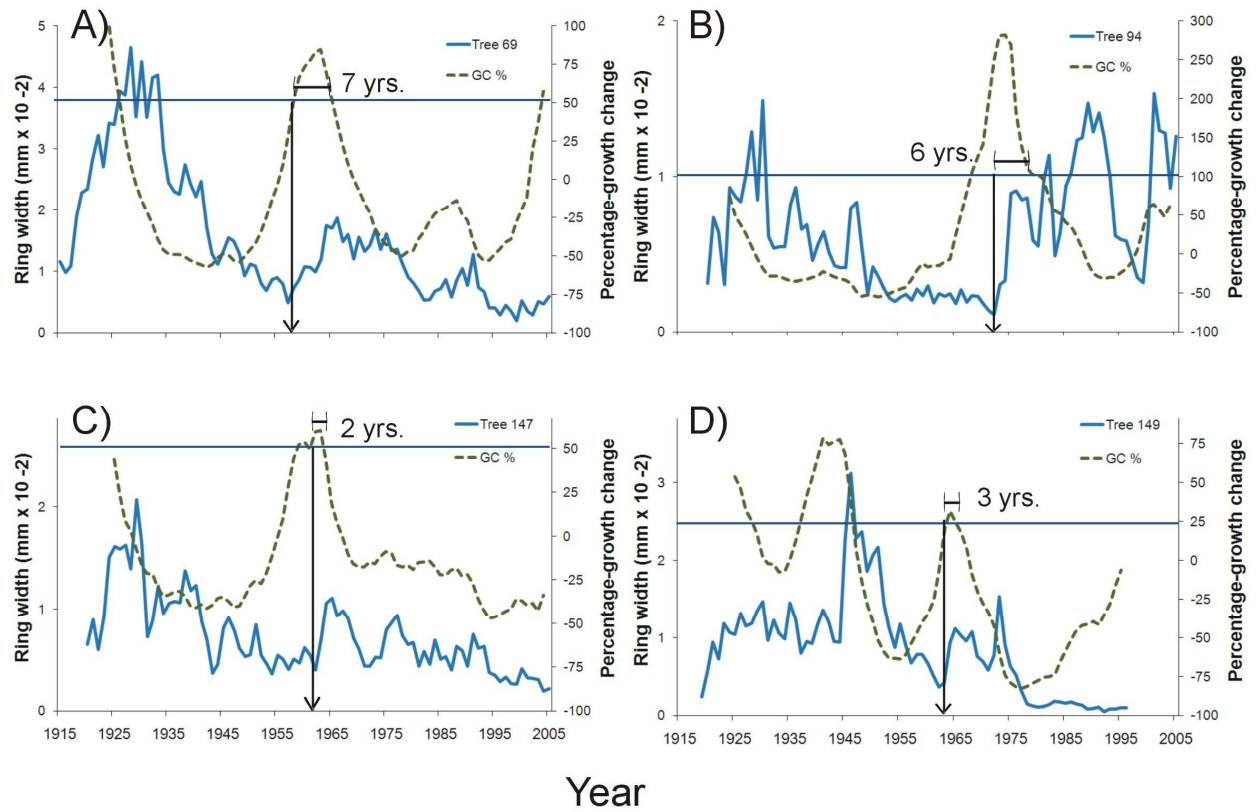


Figure 4-1 Ring-width and percentage-growth change (GC) for *Austrocedus chilensis* trees showing: moderate (50-100% GC) and major (>100% GC) canopy release events sustained for 7 and 6 years respectively (A and B), and short-term changes less than 4 years (C and D).

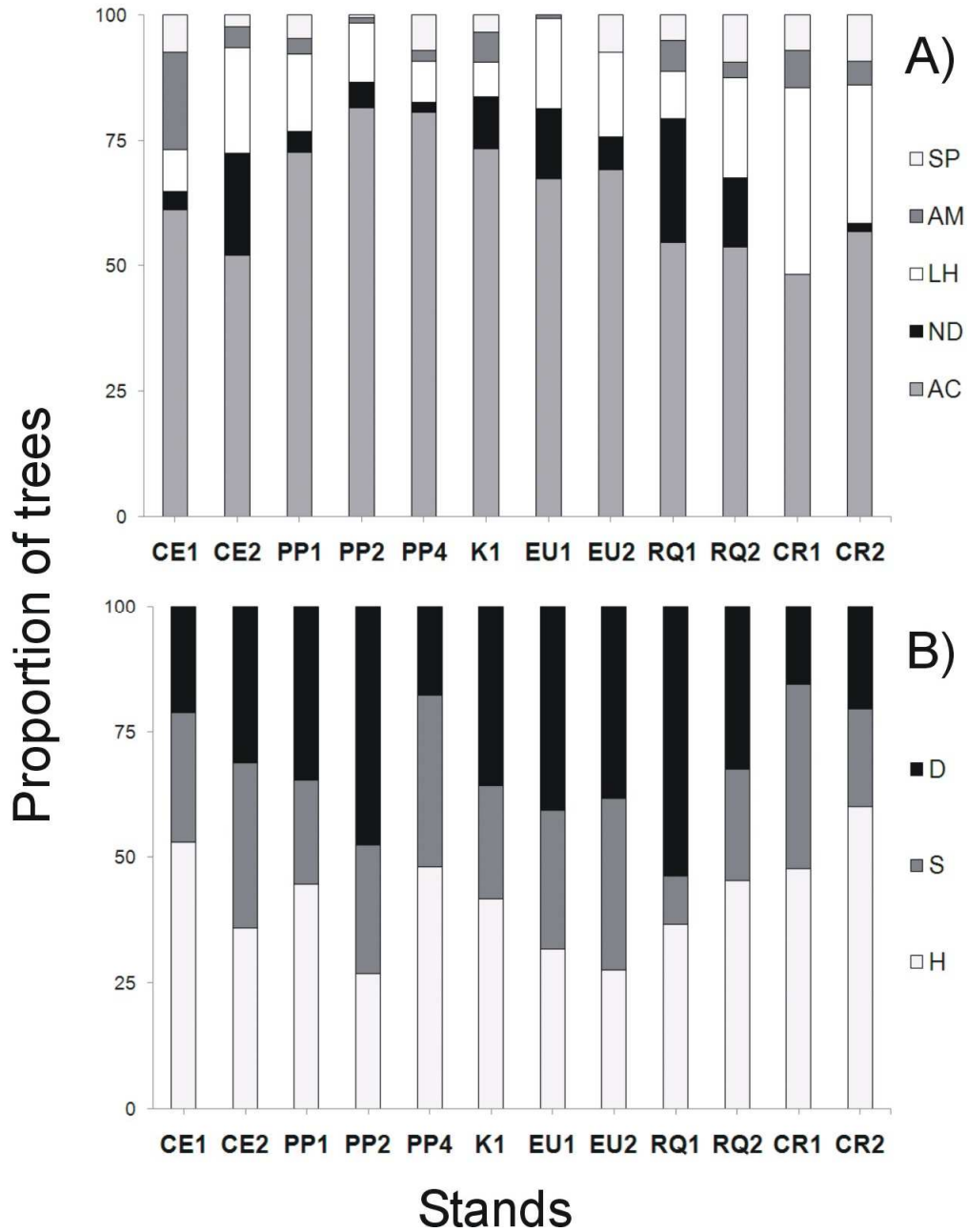


Figure 4-2 Overstory composition (A) and health assessment (B) for twelve *Austrocedrus chilensis* stands in the area of El Bolsón. Species codes are AC = *Austrocedrus chilensis*, ND = *Nothofagus dombeyi*, LH = *Lomatia hirsuta*, AM = *Aristotelia maqui*, and SP = *Schinus patagonicus*. Health groups are H = healthy, S = symptomatic, and D = dead.

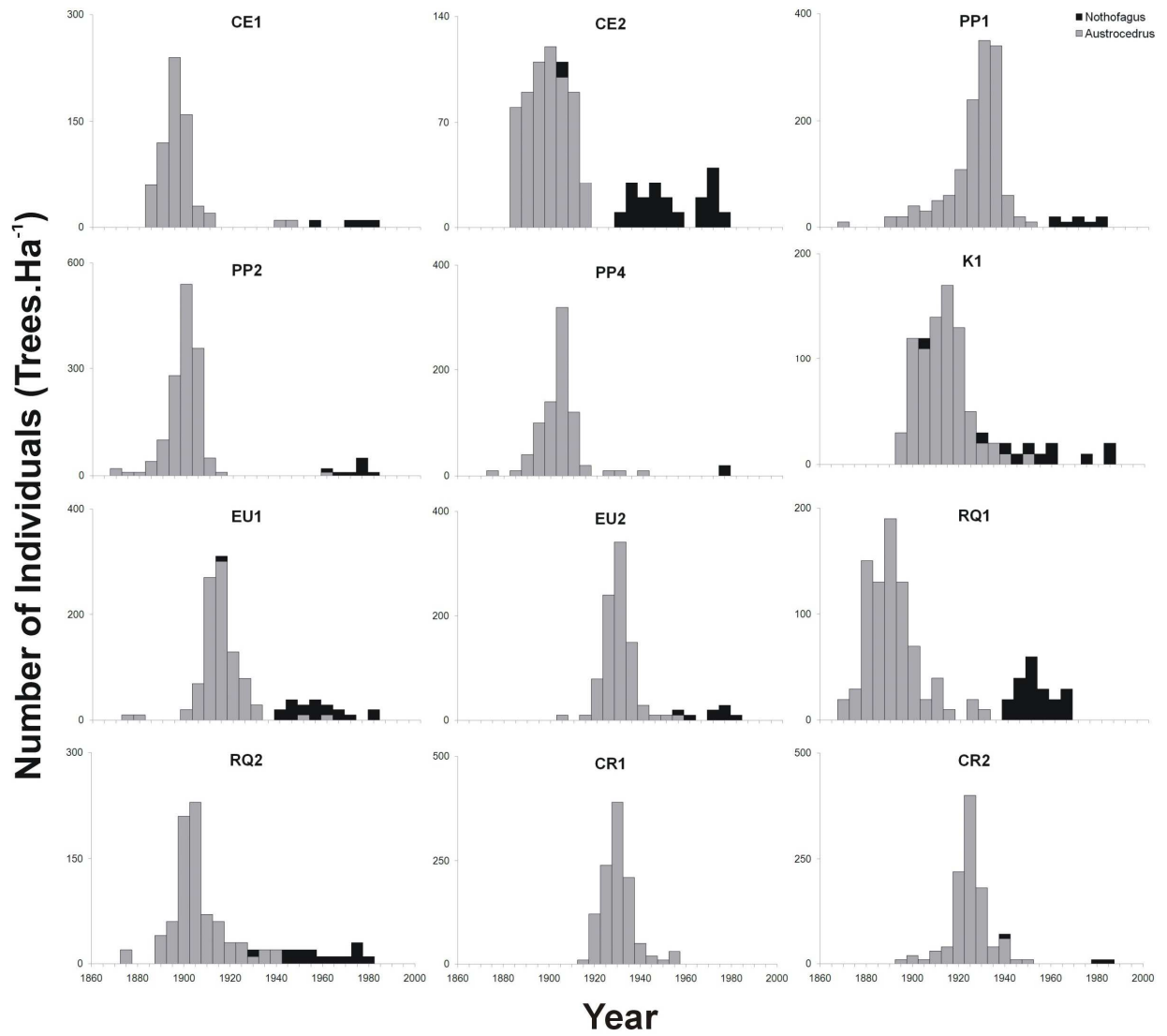


Figure 4-3 Establishment dates of the overstory trees (> 5 cm DBH) by species in 5-year age classes for twelve *Austrocedrus*-dominated stands.

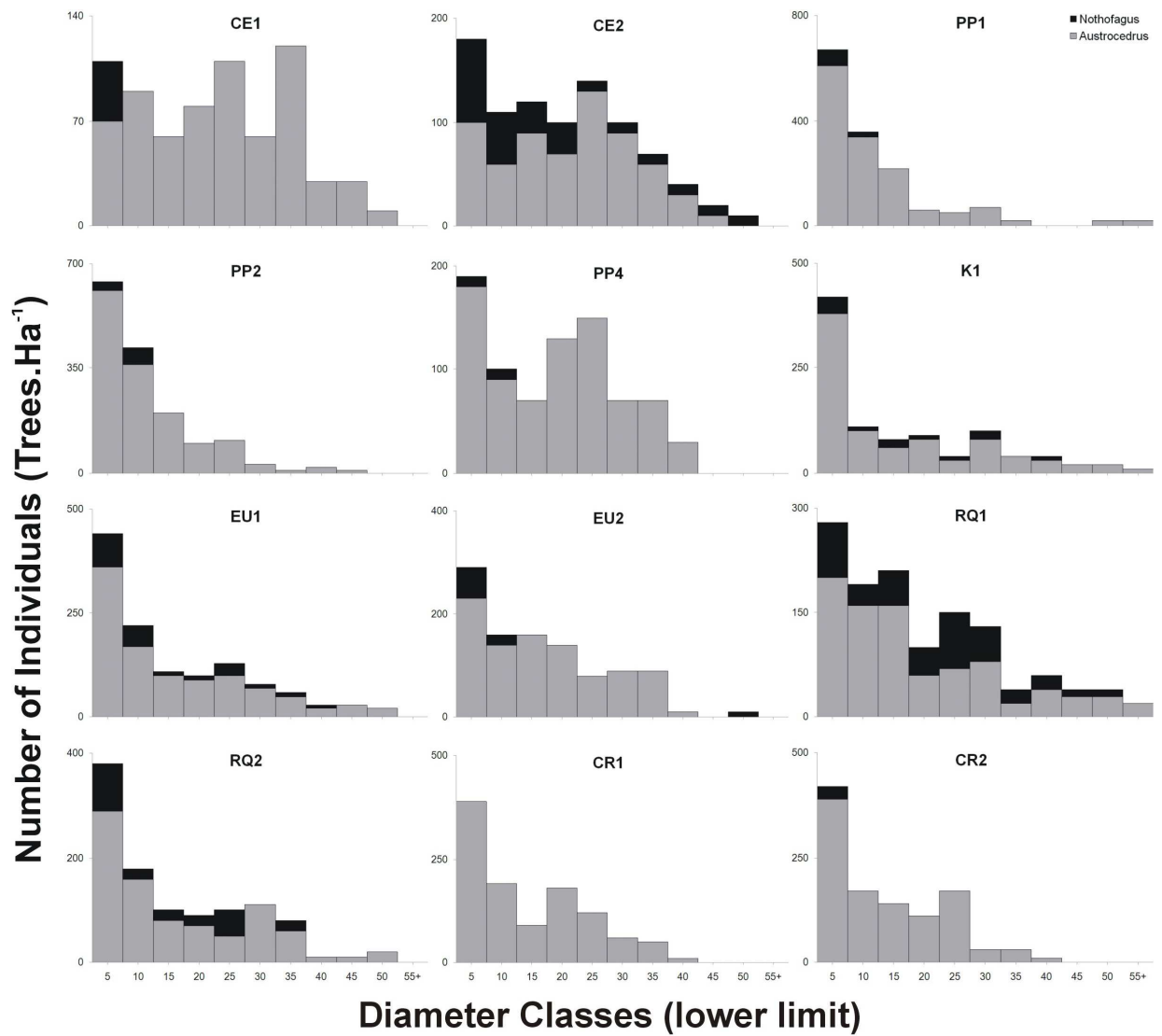


Figure 4-4 Diameter distribution of the overstory trees (> 5 cm DBH) by species in 5-cm classes for twelve *Austrocedrus*-dominated stands.

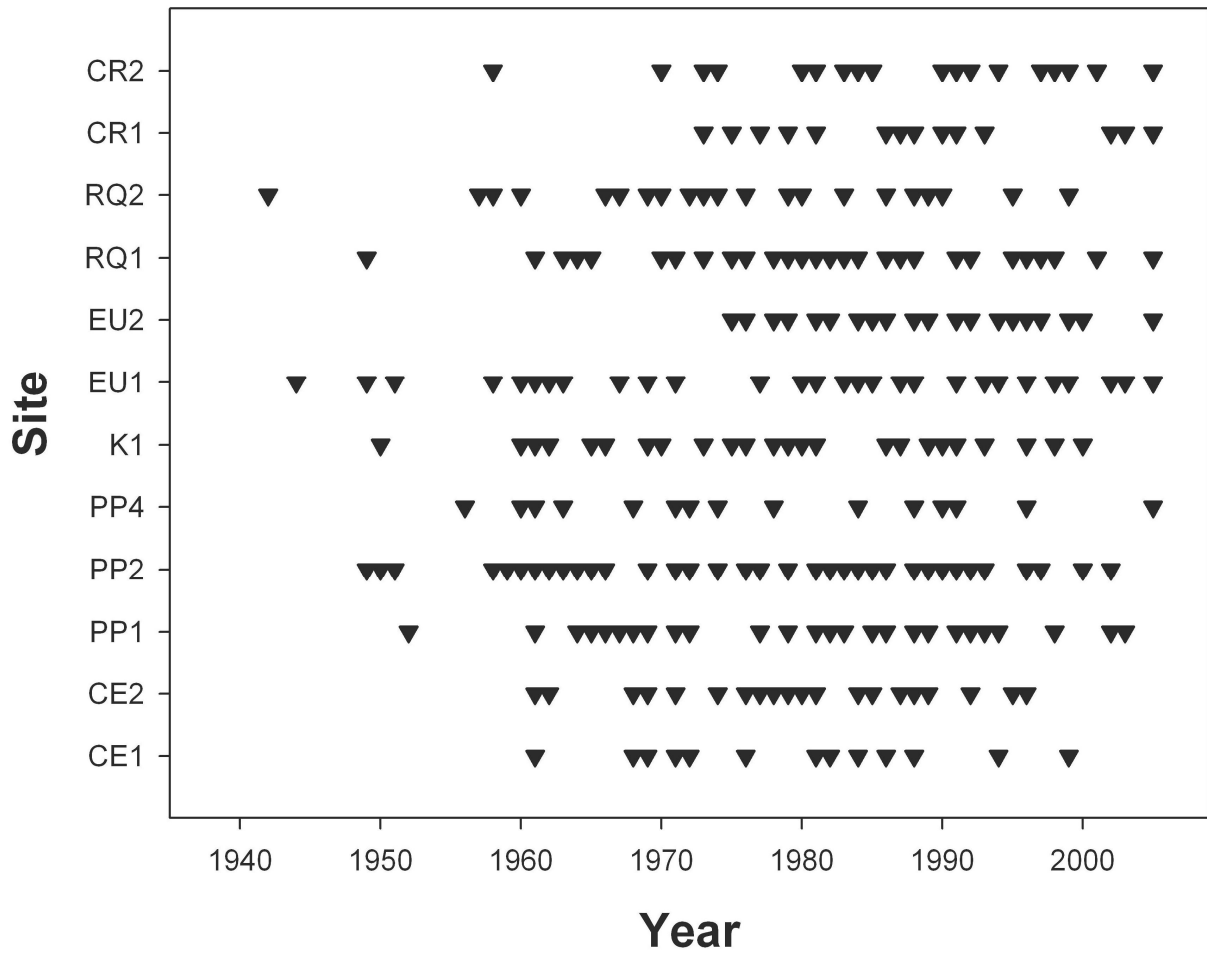


Figure 4-5 Mortality events at twelve *Austrocedrus*-dominated stands determined by the outer-ring date.

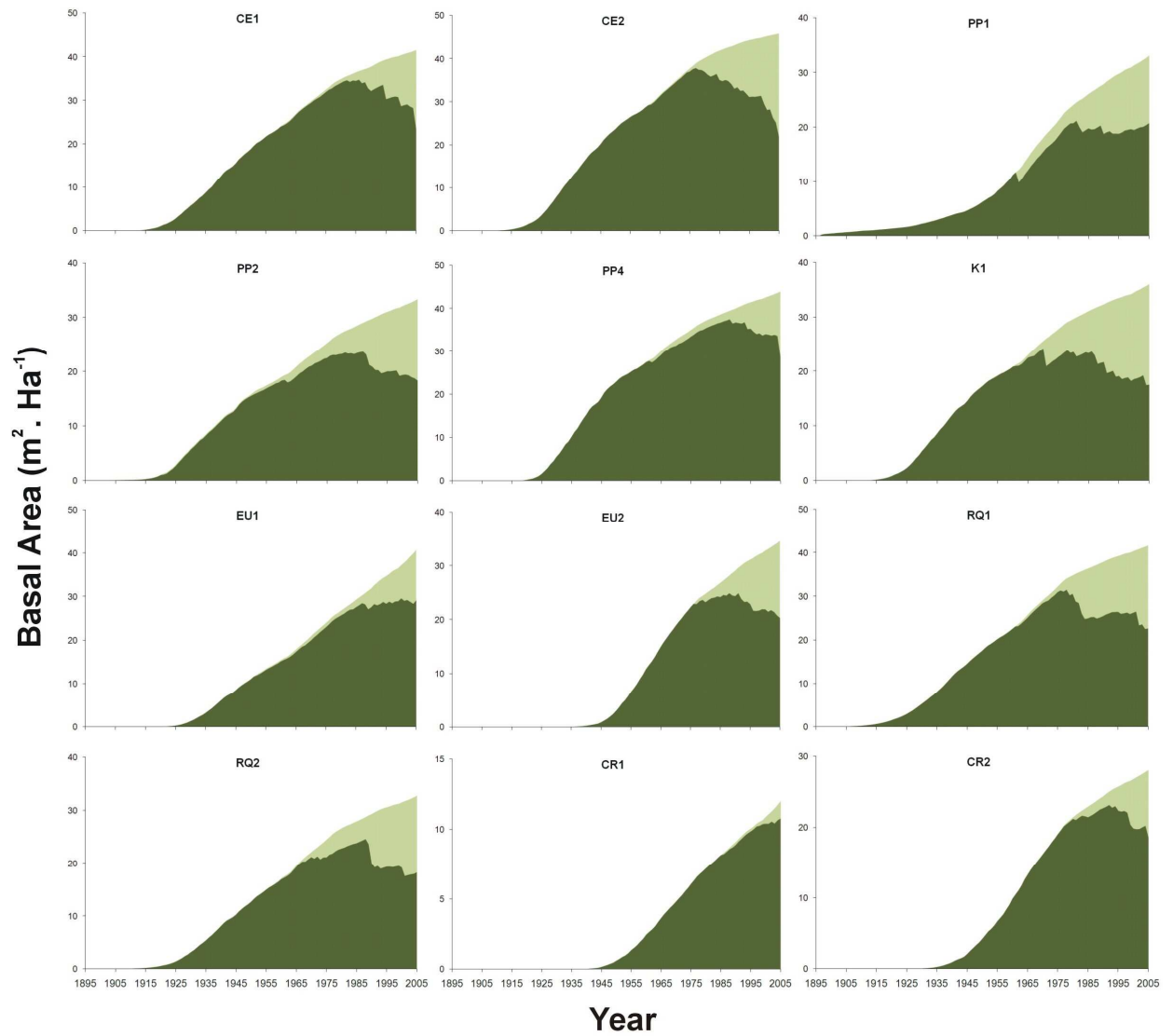


Figure 4-6 Total basal area reconstruction over time for twelve *Austrocedrus*-dominated stands. Dark green corresponds to living basal area and light green to dead standing and fallen basal area.

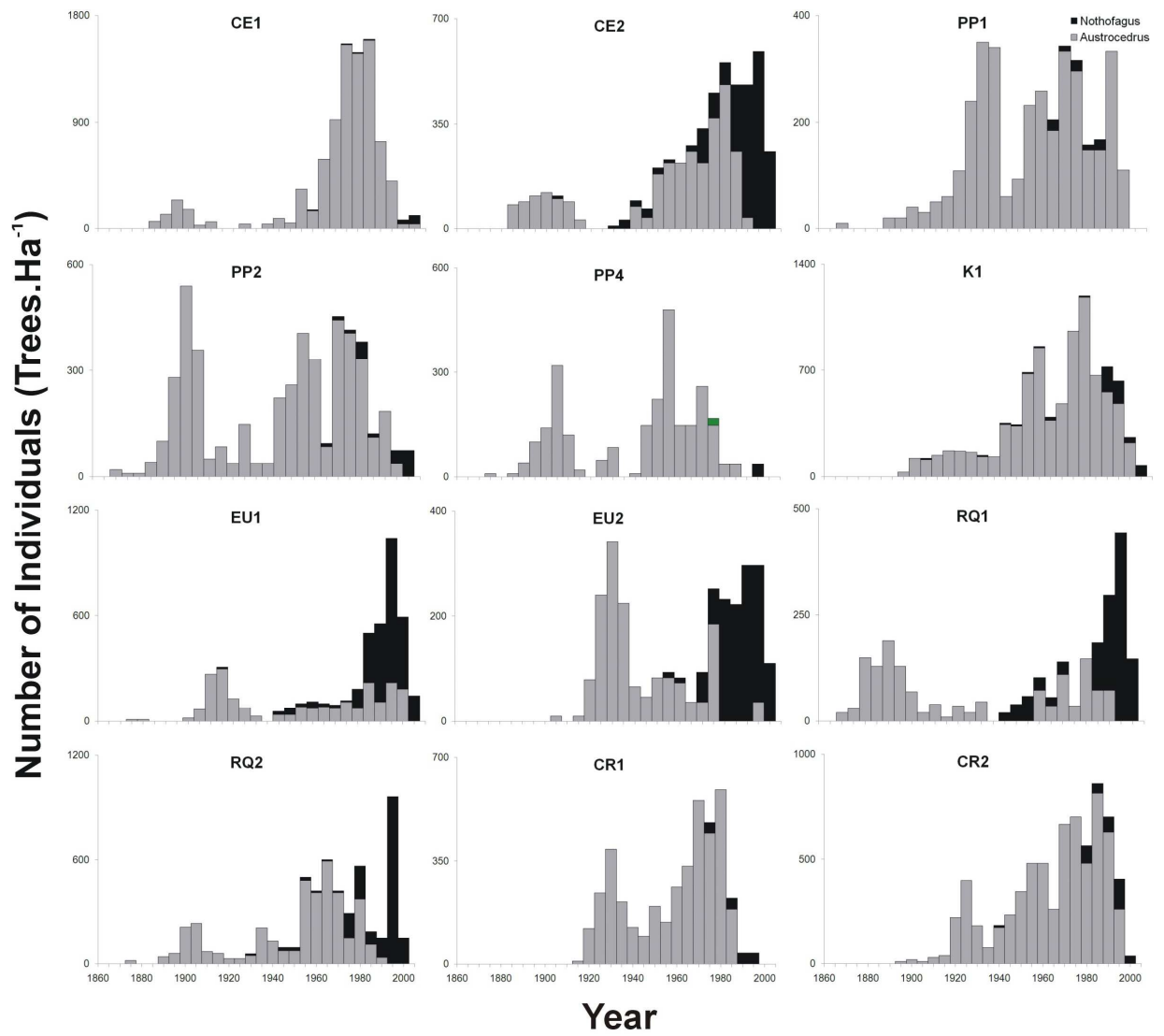


Figure 4-7 Establishment dates of the overstory and understory trees by species in 5-year age classes for twelve *Austrocedrus*-dominated stands.

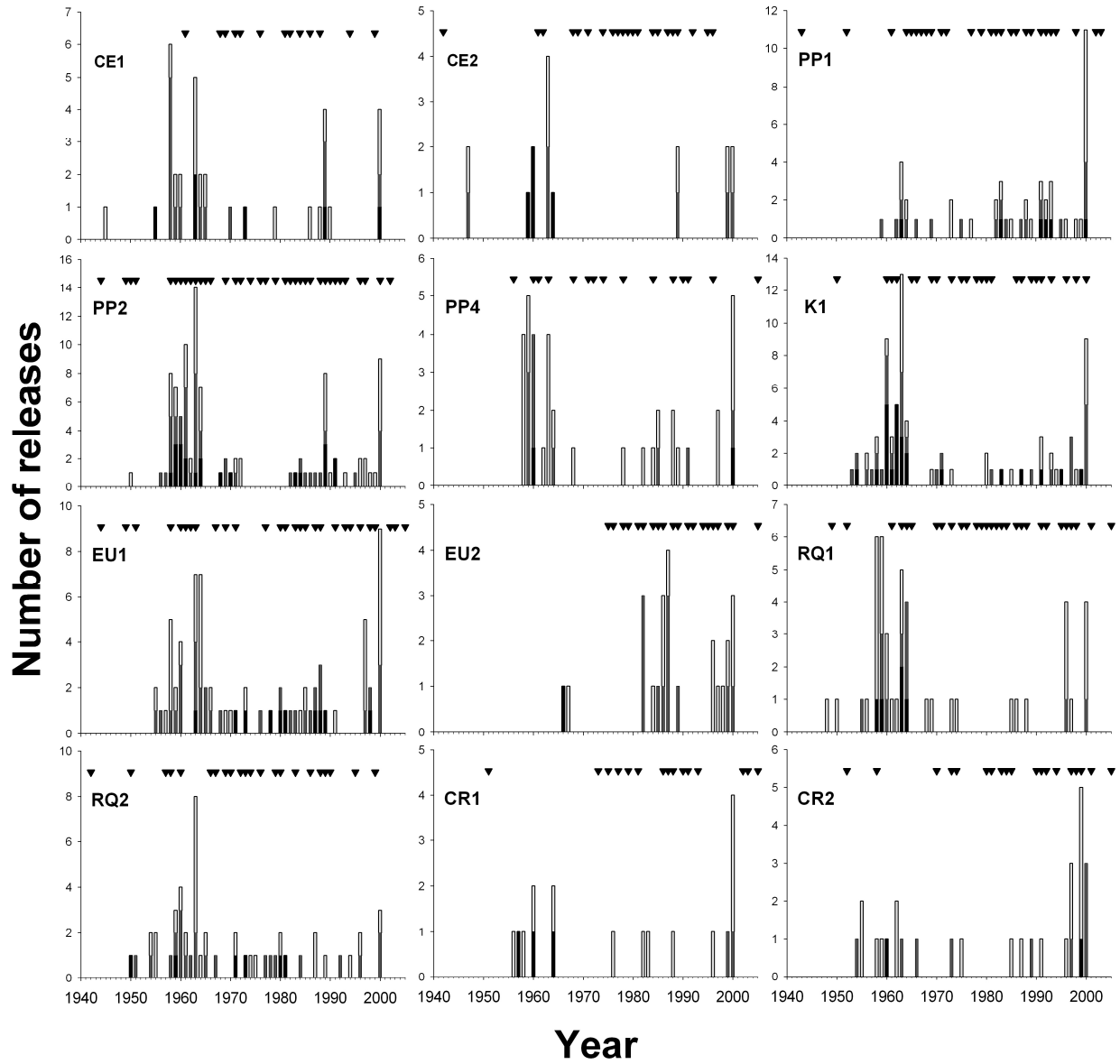


Figure 4-8 Overstory mortality events (solid triangles) and individual growth response (releases) of overstory trees (vertical bars) by percent-growth change (GC). Black bars represent high releases (> 100% GC), dark grey bars medium releases (50-100% GC), and light grey bars low releases (50-25 % GC).

4.7 Tables

Table 4-1 Characteristics of sampling *Austrocedrus chilensis* stands in the area of El Bolsón.

Stand	Plot ^a	Elevation (m)	Slope (degrees)	Azimuth	Aspect	Density (TPH)
CE1	R	471	0	90	E	790
CE2	S	523	0-10	100	E-SE	1150
PP1	S	452	15-20	120	SE-E	1790
PP2	S	430	20	90	E	1750
PP4	S	450	20	85	E	890
K1	S	367	15	130	SE	1050
EU1	R	420	25	130	SE	1490
EU2	R	398	20	90	E	1260
RQ1	S	475	0-5	90	E	1410
RQ2	S	486	0-5	90	E	1400
CR1	R	453	5	70	NE-E	1590
CR2	S	456	15-25	55	NE-E	1950

^a Plots were square (S) or rectangular (R) depending on the local topography.

Table 4-2 Percentage distribution of all *Austrocedrus chilensis* trees stratified by health condition of the crown and height crown class.

Health Class	Height Crown Class				Total
	D	C	I	S	
Healthy	3.6	5.2	8.3	23.5	40.5
Symptomatic	4.2	8.7	6.8	6.0	25.7
Dead	1.1	3.9	9.2	19.4	33.7
Total	8.9	17.8	24.3	49.0	100

Table 4-3 Annual mortality rates since mortality onset at all sampled *Austrocedrus chilensis* stands based on density (trees per hectare) and basal area per hectare.

	Density						Mean
	1945-1955	1955-1965	1966-1975	1976-1985	1986-1995	1996-2005	
CE1	0	0.15	0.63	0.50	0.52	0.36	0.36
CE2	0	0.79	0.34	1.29	0.83	0.22	0.58
PP1	0.07	0.29	0.45	1.38	1.01	0.30	0.58
PP2	0.21	1.18	0.57	1.24	1.31	0.44	0.82
PP4	0	0.64	0.27	0.28	0.43	0.30	0.32
K1	0.12	0.36	0.63	0.95	1.22	0.50	0.63
EU1	0.20	0.52	0.44	0.34	1.61	0.85	0.66
EU2	0	0	0.11	1.25	1.70	0.90	0.66
RQ1	0.11	0.47	0.88	1.56	1.67	1.37	1.01
RQ2	0	0.36	1.56	0.58	0.62	0.16	0.55
CR1	0	0	0.18	0.37	0.69	0.31	0.26
CR2	0	0.10	0.29	0.71	0.32	0.79	0.37
Mean	0.06	0.40	0.53	0.87	0.99	0.54	0.57

	Basal area						Mean
	1945-1955	1955-1965	1966-1975	1976-1985	1986-1995	1996-2005	
CE1	0	0.09	0.11	0.39	1.85	2.18	0.77
CE2	0	0.09	0.13	1.50	1.46	2.36	0.92
PP1	0.02	1.97	0.27	1.36	1.67	0.44	0.95
PP2	0.21	0.64	0.40	0.83	2.00	1.25	0.89
PP4	0	0.33	0.21	0.09	1.04	2.12	0.63
K1	0.03	0.22	1.80	0.86	2.06	1.18	1.03
EU1	0.19	0.18	0.20	0.28	1.43	1.36	0.60
EU2	0	0	0.02	1.07	1.89	1.84	1.20
RQ1	0.02	0.25	0.21	2.88	0.36	1.53	0.88
RQ2	0	0.12	1.33	0.30	2.42	1.03	0.87
CR1	0	0	0.01	0.09	0.22	0.91	0.38
CR2	0	0.01	0.03	0.64	0.75	2.26	0.62
Mean	0.05	0.39	0.43	0.85	1.43	1.54	0.81

Table 4-4 Distribution of growth releases by percent-growth change (GC) and height crown class.

Release Type	Height Crown Class				Total
	D	C	I	S	
100 GC	0.4	1.7	4.8	9.5	16.4
50 GC	3.7	7.3	8.7	15.1	34.7
25 GC	7.1	10.2	12.4	19.1	48.8
Total	11.2	19.3	25.9	43.6	100

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5 CONCLUDING CHAPTER

5.1 Conclusions

First detected more than five decades ago, and presently found across the range of distribution of *A. chilensis* in Argentina, the tree mortality process known as '*mal del ciprés*' is still in progress in many areas (Varsavsky et al. 1975; Hranilovich 1988). Due to its current status and the ecological and economical implications, '*mal del ciprés*' represents the most important disturbance in some of the areas where *A. chilensis* forests grow. Therefore, there is an urgent need to better understand the ecology of this disturbance. While several aspects of '*mal del ciprés*' have been the focus of detailed studies, little effort has been dedicated to studying the stand dynamics of symptomatic forests and examining stand development patterns in order to predict future stand structure. Understanding of the stand development patterns in forests affected by this disturbance provides a baseline for designing management strategies that could help ameliorate its consequences. Limited understanding of the natural dynamics of these forests and the fact that the specific cause(s) of the mortality remain(s) unknown has impeded successful actions to control it and develop adequate management guidelines.

My aim in this thesis was to increase understanding about the forest stand dynamics in *A. chilensis* forests in Patagonia as a consequence of the tree mortality process '*mal del ciprés*'. In order to achieve this goal, I focused on three objectives. The first of these objectives was to assess the temporal development of radial growth decline at both the stand and tree level in 12 stands, with reference to the health condition and canopy position of the trees. The second objective was to evaluate the incidence of cambial mortality on all living trees in these stands, again with reference to the tree health and canopy position of the trees. The last objective was to examine the tree mortality process in these stands and

the consequences this had on the establishment of trees in the understory and the growth of the residual overstory trees.

In order to achieve these objectives, I conducted stand reconstructions using dendrochronological methods, techniques that are widely used to examine tree growth and forest stand development. These field procedures allowed me to reconstruct stand structure over time, examine tree growth to assess the presence radial growth decline, investigate how the decline in radial growth may have influenced mortality patterns and future development of the stands, and examine overall forest stand dynamics.

Tree mortality in *A. chilensis* forests is an erratic process that is preceded by a decline in radial growth (Chapter 2). As predicted, the decline in radial growth precedes the development of symptoms in the crown as evidenced by significant below-average growth rates prior to death in the majority of dead trees and during recent decades in most symptomatic trees and a third of the healthy trees. Therefore, the decline in radial growth relates to less photosynthetic activity which precedes loss of crown vigour and defoliation by many years. The occurrence of the decline was independent of the position of the trees in the canopy and was unpredictable in time. The time of the onset and the length of the radial decline varied greatly among trees and stands. Decline onset dates ranged from the early 1900's to the 1950's and trees could undergo a decline in radial growth that varied from years to decades (up to 80 years). Furthermore, two contrasting patterns of radial growth were distinguished among healthy and symptomatic trees. Some trees experienced an abrupt decline followed by minimal growth over time, while others exhibited a slow, steady decline in radial growth over time.

As trees reduced their growth rates and vigour, many of them experienced the partial death of the cambium around the circumference of the stem (Chapter 3). A high proportion of the living trees sampled in this study exhibited partial cambial mortality, including both healthy and symptomatic trees growing in subcanopy and canopy positions. *A. chilensis*

trees in symptomatic forests can experience cambial mortality over long periods of up to 39 years and its incidence and duration was greater in suppressed trees. The presence of this phenomenon is a potential source of error and raises uncertainty when determining the year of tree death by crossdating. As the outer-most ring at different points on the tree circumference can present different dates, the outer-most ring of dead trees at a given point of the circumference may or may not represent the actual date when the tree died. This could affect the determination of the true year of death and the identification of mortality patterns.

Following the decline in radial growth, partial death of the cambium, and loss of crown vigour, the mortality of *A. chilensis* trees was unpredictable and variable in time among stands (Chapter 4). Mortality dated from as early as the 1940's and has continued to present, with most mortality occurring after 1970. After its onset, the mortality events occurred irregularly resulting in different patterns and variable rates among stands. The occurrence of radial growth decline and cambial mortality might have affected tree death, also impacting on the dynamics of these forests. As predicted, mortality of overstory trees led to the successful establishment of trees in the understory in all stands. The response of the residual overstory trees was, on the other hand, variable. In the decades that followed the onset of the mortality in each stand, trees established successfully in the understory. Relative to the density of the overstory, understory establishment was low in some stands and high in others. Site characteristics may have some influence on this, as well as in the composition of the understory denoted by the high recruitment of *N. dombeyi*. While overstory trees in almost all stands released after the onset of the mortality, the pattern was not distinctive, and varied in time, number and magnitude (percent-growth change) among trees. In some stands, releases occurred after single or multiple mortality events suggesting some degree of synchrony between processes, while in others this was not the case. More than two-thirds of the releases occurred in trees in subcanopy positions (suppressed and

intermediate height classes) accounting for almost all major releases and 75 % of the moderate releases. This variation in the response of the residual overstory trees is also influenced by the fact that most symptomatic and many healthy trees are simultaneously undergoing a decline in radial growth (Chapter 2). Even when the patterns of recruitment in the understory and the overstory response varied greatly among stands, when examined together, some general patterns emerged.

Overstory trees responded to the release of growing space resulting from the death of trees unless total photosynthesis was restricted by factors affecting the photosynthesis process (root decay and crown defoliation) or restricted seasonal growing conditions. The response, as expected, was variable among stands. In some stands, early crown expansion and growth release limited the establishment of new individuals in the understory. Increasing mortality and limited ability of the remaining trees to expand into more and larger gaps allowed more recruitment in the understory over time. On other stands, the limited capacity of the remaining trees to expand following the death of some trees allowed the establishment of trees in the understory. The poor response of the trees, as evidenced by the low number and magnitude of the growth releases, might have been affected by the high incidence of radial growth decline. In addition to this, the presence of new trees in the understory could have increased the competition for belowground resources limiting the growth of the overstory trees more. In the stands where some trees established prior to the mortality onset, competition might have increased even more. Where none of the previous general patterns occurred, the growth response of the overstory was constant and the establishment of new trees in the understory was variable.

This thesis represents the first study to intensively explore the dynamics of *A. chilensis* forests affected by '*mal del ciprés*'. Furthermore, it is the first to examine the occurrence of radial growth decline and cambial mortality and discriminate their rates of

incidence among trees differentiated by crown health condition and relative position in the canopy. Understanding the effects of '*mal del ciprés*' through time was possible using dendrochronological techniques in combination with detailed stand and tree level information. Careful selection of sites allowed for the reconstruction and study of the dynamics in these forests in the absence of other disturbances such as grazing and logging that can confound interpretations regarding regeneration. Specifically, where logging had occurred in the past, complete reconstruction of mortality patterns would have been impeded.

This study was restricted to the central distribution of this species, more specifically, to the area surrounding El Bolsón, Argentina. While it can be argued that this area represents a great proportion of the dense forests where '*mal del ciprés*' occur, there are also other areas where its incidence is of great importance and significant research on the topic has been carried out. Therefore, even when no other studies have addressed the overall dynamics of this disturbance in *A. chilensis* forests, the results presented here represent only the sampled region.

5.2 Management implications

Efforts have been made at the stand level to stop the spread of symptoms and tree mortality due to '*mal del ciprés*'. Past and present management in declining *A. chilensis* forests has been limited to the harvesting of the dead and symptomatic trees in most situations. These sanitation and salvage cuttings are intended to anticipate or prevent damage, as well as salvage wood to limit economic losses. While this represents an initial attempt to reduce the advance of the mortality, no new management practices have been implemented. Furthermore, although the understanding of the mortality process in these forests has improved, no silvicultural systems have been designed to fit these specific

circumstances or developed to incorporate our new knowledge regarding this disturbance (Smith et al. 1997). Although major emphasis is placed on establishing tree regeneration in declining forests, little is known about the regeneration process and stand dynamics in symptomatic forests and how this information can be utilized in management.

Based on my results, I recommend that tree density should be thinned as crown symptoms develop since radial growth rates in symptomatic trees are most likely already decreasing. From a stand productivity and economic management point of view, declining trees do not represent a net benefit. Although growing slowly, these declining trees still compete for limiting resources that could be used more efficiently by other trees. Since trees compete intensively with neighbouring trees, growth resources used by declining trees would likely be gained by neighbour trees after the thinning. As well, removal of declining trees by thinning would create conditions for establishment of new trees in the understory.

Little to no establishment of trees occurred during the stem exclusion stage of stand development with closed canopy conditions, but as mortality progressed and overstory cover decreased, variable recruitment in the understory was observed. The removal of symptomatic trees before death could promote earlier and increased regeneration compared to waiting until trees die before removing them. I anticipate that on cool, southern aspects after removing overstory trees and reducing canopy cover, the establishment of *N. dombeyi* could be promoted. Due to higher growth rates of *N. dombeyi* compared to *A. chilensis*, this management intervention could result in a shift in the canopy dominant species and suppression of the *A. chilensis* regeneration. If mortality due to 'mal del ciprés' continues and eventually affects the new *A. chilensis* saplings, *N. dombeyi* might be a suitable replacement.

The extent, magnitude and timing of the thinning interventions should be also carefully considered since the resistance of some trees to windthrow damage decreases as overstory density is reduced. This is exacerbated by the fact that the root system of many

trees will decay over time as '*mal del ciprés*' spreads through the stand. Since the objective of the thinning is to promote the establishment of new trees and to create uneven-aged stands, major emphasis needs to be put on protecting existing seedlings and saplings at the harvest interventions. Studies should be conducted to explore other management actions, such as site preparation or competition control; these could complement the thinning operation to enhance recruitment and survival in the understory.

Since site characteristics can influence shifts in the composition and structure of future stands, they should be included as criteria used when deciding on optimum interventions in *A. chilensis* forests. Sites with warm, north aspects and moderate to steep slopes will most likely present the most difficult situations for the recruitment and establishment of new *A. chilensis* trees. These sites might best be avoided for active management.

5.3 Future research

Radial growth decline and mortality patterns in *A. chilensis* forests are described in this thesis; however, the factors leading to the development of both processes were not the object of study. According to previous studies in northern Patagonia, extended periods of unfavourable climatic conditions that resulted in below-average growth, and periods of high rates of mortality of *A. chilensis* trees were common during the 20th century (Villalba and Veblen 1997, 1998). As briefly discussed in this thesis, these periods coincide with many decline onset dates and most of the mortality events. Calí (1996) found that warm-to-dry periods could have triggered the decline onset and contributed to the death of the trees at one of his study sites. This evidence and the complexity of the climatic influences on *A. chilensis* radial growth (Villalba and Veblen 1997) suggest that the occurrence of the decline

could be highly influenced by climatic conditions. The complex and synergetic effects of climatic variability with the forest decline process in these forests require further evaluation.

Previous studies in symptomatic forests have described the spatial distribution and partially reconstructed the temporal development of the decline at the stand level (Havrylenko et al. 1989; Rosso et al. 1994; Cali 1996). However, no research has reconstructed and analyzed the development of the decline at spatial and temporal scales that simultaneously provided a spatial-temporal sequence. While this thesis has added to the existing knowledge by precisely reconstructing radial growth decline and tree mortality, the inclusion of spatial analyses at the stand level would provide information on expansion rates of the decline and tree deaths within stands. This information is crucial to understanding more about the ecology of '*mal del ciprés*' and would complement the study of the stand dynamics presented in this thesis.

Lastly, as the patterns of tree growth, stand development, and overall stand dynamics represent only those of the sampled area, expanding this type of analysis to other areas where '*mal del ciprés*' occurs is recommended. The retrospective approach presented in this thesis has successfully provided new information about the dynamics of these forests. This needs to be explored elsewhere to gain full understanding of regional effects and implications of this disturbance on the long-term persistence of *A. chilensis*, an endemic species of high ecological and economic importance in the temperate subantarctic forests of Argentina.

5.4 References

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