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Temporal patterns of radial growth in declining *Austrocedrus chilensis* forests in Northern Patagonia: The use of tree-rings as an indicator of forest decline

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ABSTRACT

Using dendrochronology, combined with tree- and stand-level information, we reconstructed the temporal dynamics of '*mal del ciprés*', a widespread decline of *Austrocedrus chilensis* forests in Argentina. We developed 12 new site-specific ring-width chronologies representing the growth of trees with no external (crown) or internal (radial growth) symptoms of decline. By comparing the ring-width series of individual trees with these reference chronologies, we detected reduced radial growth, likely due to '*mal del ciprés*', in 301 symptomatic and dead overstory trees out of 1082 sampled trees. Radial growth decline also occurred in 67 living trees with asymptomatic crowns providing evidence that radial growth decline can be an early indicator of '*mal del ciprés*'. The length of the radial growth decline averaged 27 years for all trees and was 29 and 22 years for living symptomatic and dead overstory trees, respectively; the maximum decline length was 80 years. At the site level, the onset of radial growth decline ranged from the early 1920s to the 1960s, preceding dates reported in historical records. By 1979, $\geqslant$75% of trees per site exhibited radial growth decline. We conclude that decline in radial growth precedes crown symptoms in at least some *A. chilensis* trees in forests with '*mal del ciprés*'. Reduced radial growth prior to external crown symptoms implies that water uptake had been reduced, possibly because of root damage from *Phyophthora* or drought or their interactions. It also suggests salvage harvests that aim to eradicate trees with crown symptoms and facilitate growth of residual trees may not be the most effective management response to '*mal del ciprés*'.

1. Introduction

Patterns of tree mortality in forest ecosystems around the world have been the subject of detailed study. Tree death, nevertheless, normally involves complex processes that are difficult to understand and reconstruct (Franklin et al., 1987). For example, tree death can occur as a result of allogenic processes such as disturbances (White and Pickett, 1985) or environmental stresses such as drought (Condit et al., 1995; Villalba and Veblen, 1998; Williamson et al., 2000), or autogenic processes such as direct competition from neighboring trees (Alaback, 1982; Kobe et al., 1995; Lutz and Halpern, 2006). In most cases, tree death results from complex interactions of multiple factors and can result in broad-scale forest decline (Mueller-Dombois et al., 1983; Hennon et al., 1990; Minorsky, 2003). Several conceptual models have been developed to explain tree death and forest decline in which mortality involves environmental stresses interacting with different biotic agents in forests of various ages and stages of development (Houston, 1981; Mueller-Dombois, 1983; Manion, 1991).

While tree death can be abrupt, occurring in a relatively short period of time, it can also be gradual (Waring, 1987). Several studies have reported significant radial growth reductions prior to tree death (Pedersen, 1998; Villalba and Veblen, 1998; Bigler et al., 2004, 2007; Drobyshev et al., 2007). This often occurs as a consequence of an environmental stress such as drought. Nevertheless, reductions in radial growth are also expected in trees dying due to inter-tree competition as resources become limiting for growth, particularly during biomass accumulation and self-thinning stages of stand development (Kozlowski et al., 1991; Oliver and Larson, 1996; Franklin et al., 2002; Cherubini et al., 2002). While growth reductions and mortality resulting from disturbance, environmental stress, or competition are now better understood, retrospectively differentiating cause of growth decline and death is extremely difficult as it could result from complex interactions (Pedersen, 1998; Cherubini et al., 2002; Hartmann and Messier, 2008).

Austrocedrus chilensis (D. Don) Pic. Sern. *et* Bizarri forests experience stand-level mortality of overstory trees throughout their natural range of distribution in Argentina. This temporally

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unpredictable process of tree mortality (Amoroso and Larson, 2010a), locally known as '*mal del ciprés*' (cypress sickness), was first documented about 60 years ago (Varsavsky et al., 1975; Hranilovic, 1988). Mortality in these forests appears to be the result of complex interactions between biotic and abiotic factors, which has lead to the conclusion that '*mal del ciprés*' is a type of forest decline (sensu Manion, 1991; Baccalá et al., 1998; Filip and Rosso, 1999; La Manna and Rajchenberg, 2004; Amoroso and Larson, 2010a). A new species of *Phytophthora* present in necrotic lesions of symptomatic trees has been associated with the mortality of the trees and suggested to be the primary cause of tree death (Greslebin et al., 2007; Greslebin and Hansen, 2009, 2010). Alternatively, it is believed cavitation could be the cause of death in trees and that *Phytophthora* acts as a secondary agent (El Mujtar, 2009). Other research has suggested that mortality could be influenced by climate variation (Amoroso and Larson, 2010a; Mundo et al., 2010) and inter-tree competition and suppression during early stages of stand development following stand-replacing fires (Amoroso and Larson, 2010a).

Trees in declining *A. chilensis* forests present diverse symptoms before dying. Tree-level symptoms are manifested below and above ground (Havrylenko et al., 1989; Filip and Rosso, 1999; Greslebin et al., 2007). Below-ground symptoms include root decay that may affect the entire system, and that can extend through the root collar to the base of the stem (Havrylenko et al., 1989; Greslebin et al., 2007; Greslebin and Hansen, 2010). The most common visible above-ground symptoms are chlorotic foliage, followed by crown withering and defoliation that ultimately lead to standing and fallen dead trees (Havrylenko et al., 1989; Rajchenberg and Cwielong, 1993; Filip and Rosso, 1999). It is believed that symptoms originate in the root system and death of the root tissues precedes crown symptoms (Havrylenko et al., 1989). Preliminary evidence indicates decline in radial growth could be another symptom associated with '*mal del ciprés*' (Mundo et al., 2010).

Tree-ring analyses have been used successfully to study the response of trees to disturbance (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997) and environmental stress (Villalba and Veblen, 1998; Suarez et al., 2004), to evaluate tree growth prior to death (Cherubini et al., 2002; Dobbertin, 2005; Marçais and Breda, 2006), and to investigate causes of forest decline (McClenahen, 1995; LeBlanc, 1996; Beier et al., 2008). In this study we hypothesized that radial growth decline is a symptom that can be used as an early indicator of '*mal del ciprés*'. In previous studies, the development of '*mal del ciprés*' has been described based on observation of external symptoms, the manifestation of the crown symptoms and death of the overstory trees. If radial growth decline is an internal symptom of '*mal del ciprés*', then tree-ring analyses have the potential as a more precise indicator of the onset of decline. Therefore, our first objective was to determine if trees exhibit a decline in radial growth prior to death and whether the onset of the radial growth decline precedes the loss of vigor and defoliation of the crown, the primary external symptoms of '*mal del ciprés*' in living trees. Our second objective was to reconstruct the temporal dynamics of '*mal del ciprés*' in *A. chilensis* forests using radial growth of individual overstory trees. Using high-quality ring-width data from a large sample of trees in declining forests, in combination with tree- and stand-level information, we compared the radial growth of dead trees, symptomatic living trees, and asymptomatic trees growing within stands and quantify variation in the onset and duration of the radial growth decline among stands.

2. Materials and methods

2.1. Study site and sampling

The study took place near 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. Soils at the study areas are Andisols, and have a deep profile with presence of volcanic ash. Forests in the area are characterized by post-fire *A. chilensis*-dominated stands with variable presence of other species such as *Nothofagus dombeyi* and smaller size tree species such as *Lomatia hirsuta* (*Lam.*) Diels and *Maytenus boaria* Mol. For this study, we 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 of '*mal del ciprés*' can be diverse, we focused on visible criteria at the tree level: chlorotic foliage and defoliation in the crown of living trees and abundant dead trees. We randomly selected twelve sites for sampling from a population of declining stands meeting the above conditions (Table 1).

A 0.1-hectare permanent sample plot was established at each site. Plots were square (31.63 × 31.63 m) or rectangular (40.0 × 25.0 m) depending on local topography. All trees with a diameter at breast height (DBH) larger than 5.0 cm in the plots were tagged. We recorded species, DBH, crown height class (dominant, codominant, intermediate and suppressed), and 'health condition' based on foliage condition, increasing percentage of defoliation, and bark characteristics (Rajchenberg and Cwielong, 1993). Health condition classes were: living asymptomatic trees, living symptomatic trees, and dead trees. Increment cores were taken from all tagged trees to study past radial growth. Cores were extracted perpendicular to the slope and c.30 cm above the ground. Multiple cores were taken to ensure the sample intercepted or was close to the pith and included sound sapwood and bark so that the outer ring was the last ring formed on living and dead trees (Amoroso and Daniels, 2010). Transverse cross-sections (c.30 cm above the ground) were taken from 50 individuals from which we could not extract good quality cores due to wood decay or the absence of bark. Of the 1082 cores collected from *A. chilensis* trees, 335 cores (26%) did not intercept the pith and we estimated the number of missed rings using geometry (Duncan, 1989); the applied corrections were all <10 years, minimizing missed information on the initial growth rates of the trees.

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). For the cross-sections, we selected and measured two radii that were (a) perpendicular to the slope to avoid compression wood and (b) included sound sapwood and bark to ensure comparability with the increment cores. 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, ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/measurements/southamerica/arge080.rwl) and statistically verified using the program COFECHA (Grissino-Mayer, 2001). Mortality dates of dead trees were defined as the calendar year of the outer-ring of the crossdated ring-width series.

To detect the effects of '*mal del ciprés*' on radial growth, we needed to (1) characterize growth rates of trees in absence of external and internal symptoms, (2) ensure trees with and without symptoms responded similarly to climate, and (3) compare the radial growth of trees with no symptoms with the growth rates of trees exhibiting symptoms of decline. Site-specific standard ring-width chronologies were built for trees that were classified in the field as asymptomatic based on their crown characteristics. Ring-width series were standardized using the program ARS41_win (Cook and Krusic, 2006). Since our objective was to detect the effects of '*mal del ciprés*' on radial growth, we standardized

Table 1
Stand characteristics and health assessment for the 12 *Austrocedrus chilensis* study sites sampled near El Bolsón, Argentina. Species codes are AC = *Austrocedrus chilensis* and OT = other species including *Nothofagus dombeyi*, *Lomatia hirsuta*, *Aristotelia chilensis* and *Schinus patagonicus*. Crown health classes are H = healthy, asymptomatic trees, S = symptomatic trees, and D = dead trees.

Site	Elevation (m.a.s.l.)	Slope angle (°)	Slope aspect (°)	Density (n ha^{-1})	Relative composition (%)		Crown health class (%)		
					AC	OT	H	S	D
CE1	471	0	90	790	61	39	53	26	21
CE2	523	0–10	100	1150	52	48	36	33	31
PP1	452	15–20	120	1790	73	27	45	20	35
PP2	430	20	90	1750	81	19	27	26	48
PP4	450	20	85	890	81	19	48	34	18
K1	367	15	130	1050	73	27	42	22	36
EU1	420	25	130	1490	67	33	32	28	40
EU2	398	20	90	1260	69	31	28	34	38
RQ1	475	0–5	90	1410	55	45	36	10	54
RQ2	486	0–5	90	1400	54	46	45	22	33
CR1	453	5	70	1590	49	51	48	36	16
CR2	456	15–25	55	1950	57	43	60	19	21

using a horizontal line by dividing each ring width by the mean ring width of the series. This method has been used to detect past disturbance events as it preserves the long-term growth trends of individual trees and scale their absolute growth rates allowing direct comparison of the relative growth rates of trees of different sizes (Veblen et al., 1991; Kitzberger et al., 2000; Mundo et al., 2010). For each site, we calculated upper and lower 95% confidence intervals for the standard chronology.

We visually assessed the standardized ring-width series of individual trees and noted low radial growth rates near the bark of many trees that had been classified in the field as ‘healthy’ according to crown condition. Therefore, we used an iterative, multi-step procedure to assess the presence of radial growth decline in these trees by plotting the standardized ring-with series of each ‘healthy’ tree against its corresponding site-level standard chronology and its confidence intervals. If the ring-width series departed below the lower confidence interval limit for $\geqslant 10$ 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. For each site, the subset of trees with asymptomatic crowns that did not exhibit radial growth decline was combined to derive new standard and residual chronologies (hereafter “final healthy” chronologies) that represented only the growth pattern of the trees without external and internal symptoms of decline. Similarly, all trees with symptomatic crowns, dead trees, and the trees with asymptomatic crowns but radial growth decline (e.g. those excluded from the final healthy chronology) were combined to form the “final declining” standard and residual chronologies. Standardization was done using the program ARS41_win (Cook and Krusic, 2006) as described above. Descriptive statistics, including the inter-series correlation, signal-to-noise ratio, autocorrelation value, and expressed population signal, were calculated and compared for the common interval of the final healthy and declining standard chronologies for each site.

To ensure that trees with and without radial growth decline responded to the climate similarly, we plotted the common interval of the final healthy and declining residual chronologies from each site and compared them using correlation analyses for their common intervals. Each site-level pair of residual chronologies exhibited similar trends over time (data not shown), with significant correlation coefficients of 0.70–0.94, indicating similar responses to climate variation so that differences in growth of individual trees were due to a non-climatic factors.

2.3. Radial growth decline

At the tree-level, individual standardized ring-width series were compared with the corresponding site-level final healthy standard chronology and its 95% confidence intervals to detect the presence of radial growth decline and estimate the year of onset of the decline. All dead trees, trees with symptomatic crowns, and the trees with healthy crowns that had been removed from the preliminary healthy chronologies were assessed. A series was considered to be ‘declining’ when it departed below the lower 95% confidence interval limit of the healthy chronology for $\geqslant 10$ years and did not recover. Ring-width series from dead trees exhibiting a radial growth reduction for $\geqslant 5$ years prior to death were also considered ‘declining’. We observed a ‘recovery’ in some trees, in which radial growth increased and surpassed the lower 95% confidence interval of the healthy chronology for $\geqslant 2$ years but then departed again below the lower 95% confidence interval limit. For each declining series, the onset of the radial growth decline was determined as the year in which the series crossed the lower 95% confidence interval and did not recover.

We used percentile of diameter at onset of decline, a measure of relative tree size that could be reconstructed from tree rings, to differentiate probable causes of low growth rates in individual trees. This approach assumed large overstory trees were strong competitors in which declining radial growth was mostly likely due to ‘*mal del ciprés*’, while small understory trees were weak competitors so that radial growth decline could be due to inter-tree competition or ‘*mal del ciprés*’. To establish a criterion for differentiating understory from overstory trees, we assessed the diameters and height classes of the living trees at the time of sampling. For each tree, we calculated its percentile of diameter by ranking its diameter relative to all other living trees in the stand. When data from all stands were combined, 90% of the trees classified in the field as dominant and codominant had diameters equal to or above the 50th percentile. Next, we reconstructed the diameter of individual trees at the onset of the radial growth decline using the crossdated ring-width series of all living and dead trees from each site. The reconstructed diameter of each tree at the onset of decline was compared to the reconstructed diameters of all trees growing in the same stand in that year. If the calculated percentile of diameter at decline onset was $\geqslant 50$, the tree was classified as an overstory tree at decline onset. If it was <50, the tree was classified as an understory tree at decline onset.

We combined the data from all sites and determined the number of trees exhibiting radial growth decline stratified by reconstructed canopy position at onset of decline and crown health condition observed in the field.

2.4. Site-level analyses

The length of the radial growth decline was calculated for individual symptomatic and dead trees. For the living trees, it was calculated as the number of years between the onset of decline and the year of sampling (2005). Decline length of dead trees was the difference between the calendar years of decline onset and the outer-most ring. At the site level, we calculated the mean, standard deviation and maximum decline length for symptomatic and dead trees. We compared the year of the onset of radial growth decline among symptomatic and dead trees using the NPAR1WAY procedure in SAS (2007). The NPAR1WAY procedure is a nonparametric test for differences across a one-way classification that computes an empirical distribution function statistic, which tests whether the distribution of a variable is the same across different groups. Differences were tested using the Mann–Whitney–Wilcoxon test.

In the final analysis, we reconstructed the temporal development of radial growth decline using only the overstory trees (i.e. reconstructed canopy position at onset of decline), as these trees were most likely to be declining due to '*mal del ciprés*' and the outcomes could be compared to dates reported in documentary records. The dates of radial growth decline onset for individuals were used to calculate the cumulative proportion of declining trees per decade per site and to estimate the length and magnitude of the radial growth decline (i.e. the number of years since the decline onset) at the site level.

3. Results

3.1. Mean ring-width chronologies

Chronology lengths of 73–128 years (Table 2) reflected the young age of the *A. chilensis* stands that originated after extensive burning in the area in the 1890–1920s (Veblen et al., 1995). In general, the chronologies of symptomatic and dead trees were longer than for asymptomatic trees; the difference in length is partially explained by the presence of dead trees that established slightly earlier than the living trees. Mean sensitivity (MS) values were similar to those reported by Villalba and Veblen (1997). Inter-series correlation (ISC) values were high in most cases denoting the strength of the common signal within the chronologies. The signal-to-noise ratio (SNR) showed high values in general except for two sites and five healthy chronologies. While these low SNR values would limit their use for climate reconstructions, the chronologies remain valuable for our assessment of radial growth decline. Autocorrelation values (ACORR) ranged from 0.42 to 0.95 but most values were comparable to other studies (Villalba and Veblen, 1997). Overall, the ISC and SNR values were greater for the symptomatic chronologies than the healthy ones meaning symptomatic and dead trees are more sensitive to climate since they are stressed and more sensitive to environmental variation.

3.2. Radial growth decline in individual trees

Of the 1082 *A. chilensis* trees sampled, 632 (58%) trees presented a decline in radial growth relative to the final standard chronology representing the growth of asymptomatic trees at each site. Two common patterns in the rate of decline of radial growth were found (Fig. 1). One pattern included an abrupt (1–3 years) decline followed by relatively constant narrow rings over time (Fig. 1A); the second pattern included a gradual and constant decline in radial growth over time (Fig. 1B). Overall, 176 (22%) and 456 (78%) trees showed an abrupt and a gradual decline in radial growth, respectively.

Of the 632 trees with radial growth decline, 368 (58%) and 264 (42%) trees were classified as overstory and understory trees, respectively, at the onset of radial growth decline based on reconstructed diameters. Of the declining trees, 127 (20%) were classified as having asymptomatic crowns in the field, 235 (37%)

Table 2
Descriptive statistics for standard ring-width chronologies for *Austrocedrus chilensis* built from trees with healthy, asymptomatic crowns (*H*) versus symptomatic and dead (*S*) trees at 12 sites.

Site	Crown class	*N*	Length	MS[a]	ISC[b]	SNR[c]	ACORR[d]
CE1	*H*	25	102	0.214	0.439	17.977	0.715 (2)
	S	12	101	0.152	0.455	6.102	0.589 (1)
CE2	*H*	16	97	0.164	0.410	10.408	0.948 (1)
	S	18	105	0.141	0.534	12.359	0.705 (2)
PP1	*H*	42	76	0.175	0.322	18.083	0.642 (1)
	S	35	128	0.210	0.476	7.431	0.487 (3)
PP2	*H*	28	110	0.194	0.315	11.512	0.860 (1)
	S	42	101	0.163	0.510	14.116	0.647 (1)
PP4	*H*	28	92	0.172	0.505	22.486	0.682 (3)
	S	23	93	0.135	0.659	27.024	0.609 (2)
K1	*H*	26	91	0.151	0.162	4.252	0.759 (1)
	S	27	100	0.158	0.547	25.324	0.784 (1)
EU1	*H*	23	88	0.177	0.227	5.567	0.422 (1)
	S	24	95	0.148	0.419	5.154	0.793 (1)
EU2	*H*	17	75	0.176	0.301	6.037	0.669 (3)
	S	28	93	0.222	0.477	10.104	0.858 (1)
RQ1	*H*	16	120	0.119	0.171	3.103	0.899 (1)
	S	21	129	0.161	0.303	3.250	0.806 (1)
RQ2	*H*	21	97	0.169	0.148	2.949	0.751 (1)
	S	27	116	0.218	0.438	6.281	0.758 (2)
CR1	*H*	34	73	0.164	0.378	18.836	0.590 (4)
	S	19	76	0.172	0.293	3.312	0.639 (1)
CR2	*H*	34	78	0.172	0.268	10.614	0.873 (1)
	S	34	85	0.201	0.566	12.886	0.755 (1)

[a] Mean sensitivity.

[b] Inter-series correlation.

[c] Signal-to-noise ratio.

[d] Autocorrelation value (numbers in parenthesis indicate the autocorrelation order chosen using the Akaike criterion).

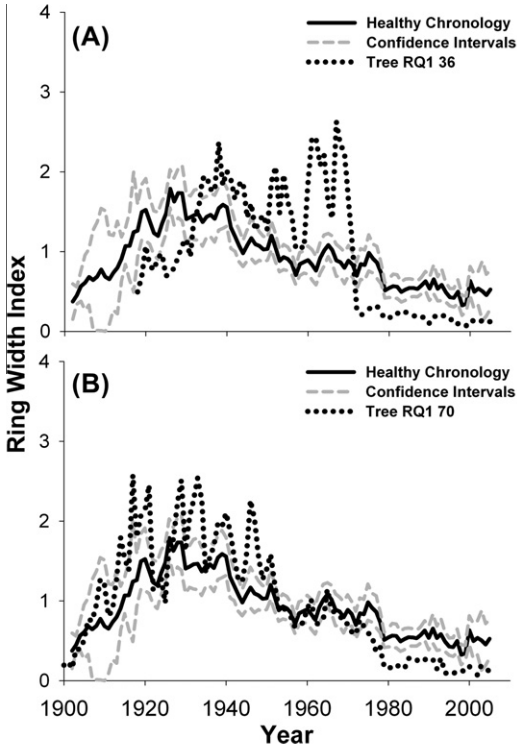

Fig. 1. Selected ring-width series (dotted black) for *Austrocedrus chilensis* trees showing abrupt (A) and gradual (B) radial growth decline patterns relative to the 'final healthy' standardized ring-width chronology (solid black) and its 95% confidence intervals (solid gray). Site-level healthy chronologies were derived from trees with asymptomatic crowns and no evidence of radial growth decline. They provided a reference for assessing individual trees to determine presence and year of onset of radial growth decline.

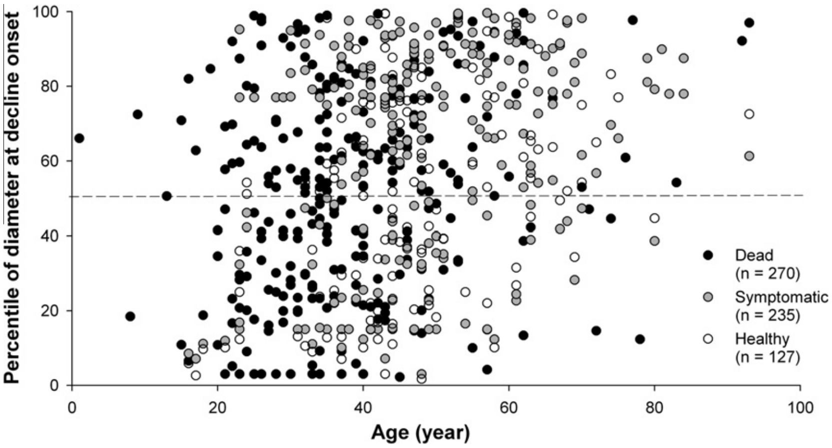

Fig. 2. Relative size (percentile of diameter at decline onset) and age for 632 *Austrocedrus chilensis* trees with radial growth decline. Black, gray and white symbols represent dead trees, trees with symptomatic crowns, and trees with asymptomatic crowns, respectively. Trees with diameters ⩾50th percentile at onset of radial growth decline (horizontal dashed line) was classified as overstory trees, most likely declining due to '*mal del ciprés*'. Trees below the line were classified as understory trees, declining due to competition and/or '*mal del ciprés*'.

presented crown symptoms, and 270 (43%) were dead at the time of sampling (Fig. 2, Table 3). The relative size (percentile of diameter) of trees at onset of decline was independent of their age (Fig. 2). Similarly, neither tree relative size nor age at onset of decline differed between overstory and understory trees or among trees with asymptomatic and symptomatic crowns versus dead trees (Fig. 2).

Of the 368 overstory trees with radial growth decline, 301 presented crown symptoms or were dead (Table 3). Another 67 trees exhibited radial growth decline and were classified as overstory trees at the onset of decline but had asymptomatic crowns at the time of sampling.

3.3. Site-level development of radial growth decline

Overall, the average year of radial growth decline onset for the overstory trees varied significantly between dead and symptomatic trees ($F = 4.11$, $p = 0.007$; Fig. 2). On average, trees that were dead at the time of sampling started declining in 1960, about 10 years before the onset of decline in living symptomatic trees.

The length of the radial growth decline varied between dead and symptomatic overstory trees and among sites (Table 4). It averaged 27 years for all trees and was 29 and 22 years for all living symptomatic and dead trees, respectively. The mean and maximum decline lengths were longer in living than dead trees at all sites, except EU2 and RQ1 where the maximum decline length corresponded to dead trees. The maximum decline length was 80 years and was ⩾50 years at six sites.

Table 3
Austrocedrus chilensis trees with radial growth decline stratified by crown health condition and canopy position at the onset of decline for 12 stands with '*mal del ciprés*'. Canopy position was classified using the percentile of tree diameter at onset of decline which was reconstructed using tree rings. Trees in the lower/upper 50th percentile were classified as understory/overstory trees. Values in parenthesis indicate percentages of understory and overstory trees in each crown health class.

Crown health condition	Canopy position		
	Understory	Overstory	All
Asymptomatic	60 (23)	67 (18)	127
Symptomatic	76 (29)	159 (43)	235
Dead	128 (48)	142 (39)	270
All trees	264	368	632

The onset of radial growth decline in overstory trees exhibited great variability among sites, starting as early as the 1920s (PP2 and RQ2) and as late as the 1960s (CR1, Table 5). By 1960, radial growth decline was present in overstory trees at all sites. By 1979, ⩾75% of declining overstory trees at all sites had exhibited radial growth decline. Within sites, temporal patterns of radial growth decline were variable (Table 5). At five sites (PP1, PP2, EU1, RQ1 and RQ2), 30–50 years elapsed from the onset of decline in the first tree until ⩾50% of all declining trees exhibited decline, with a relatively steady increase in the proportion of declining trees over time. Alternately, at four sites (CE1, CE2, PP4 and K1) the proportion of declining trees abruptly increased to ⩾50%, concentrated mostly in the 1950s and 1960s. Lastly, at sites CR1 and CR2 the proportion of declining trees increased abruptly in the 1970s and 1980s.

4. Discussion

4.1. Radial growth decline in A. chilensis forests

In this study we assessed the incidence, nature and development of radial growth decline in *A. chilensis* forests experiencing widespread tree mortality referred as '*mal del ciprés*'. We found evidence of radial growth decline in 301 trees (28% of all trees) that were classified as overstory trees at the onset of decline and had crown symptoms or were dead when sampled. Combined, these

Table 4
Lengths of radial decline in years for living *Austrocedrus chilensis* trees with symptomatic crowns and dead trees for each site.

Site	Symptomatic trees			Dead trees		
	n	Mean ± S.D.	Maximum	*n*	Mean ± S.D.	Maximum
CE1	4	38 ± 7	48	2	17 ± 18	29
CE2	11	41 ± 14	60	5	26 ± 11	38
PP1	15	20 ± 10	44	22	18 ± 10	42
PP2	20	32 ± 9	50	27	23 ± 11	45
PP4	11	39 ± 12	56	5	28 ± 9	38
K1	18	37 ± 14	49	16	20 ± 9	35
EU1	13	35 ± 16	62	14	21 ± 14	48
EU2	9	22 ± 7	30	13	20 ± 9	34
RQ1	10	42 ± 16	61	13	30 ± 20	80
RQ2	14	23 ± 12	56	16	21 ± 13	47
CR1	11	26 ± 6	34	0	0 ± 0	0
CR2	23	27 ± 9	40	9	22 ± 7	37

Table 5
Cumulative proportion by decade of overstory *Austrocedrus chilensis* trees with radial growth decline likely due to '*mal del cipré's*' for the 12 sites. Gray shading indicates the decade in which 50% or more of the declining trees at each site exhibited a decline in radial growth.

Site	*n*	1910–1919	1920–1929	1930–1939	1940–1949	1950–1959	1960–1969	1970–1979	1980–1989	1990–1999	2000–2005
CE1	6	0.00	0.00	0.00	0.00	0.50	0.67	0.83	1.00	1.00	1.00
CE2	16	0.00	0.00	0.00	0.13	0.63	0.75	0.94	1.00	1.00	1.00
PP1	37	0.00	0.00	0.03	0.27	0.38	0.43	0.76	0.86	0.97	1.00
PP2	47	0.00	0.04	0.06	0.17	0.36	0.66	0.85	0.98	1.00	1.00
PP4	16	0.00	0.00	0.06	0.25	0.56	0.75	0.94	1.00	1.00	1.00
K1	34	0.00	0.00	0.03	0.15	0.41	0.82	0.85	0.91	0.97	1.00
EU1	27	0.00	0.00	0.04	0.15	0.37	0.52	0.85	0.93	1.00	1.00
EU2	22	0.00	0.00	0.00	0.00	0.00	0.41	0.77	0.95	1.00	1.00
RQ1	23	0.00	0.00	0.05	0.33	0.52	0.76	0.86	0.90	1.00	1.00
RQ2	30	0.00	0.03	0.07	0.23	0.33	0.53	0.70	0.87	1.00	1.00
CR1	11	0.00	0.00	0.00	0.00	0.00	0.36	0.91	0.91	1.00	1.00
CR2	32	0.00	0.00	0.00	0.00	0.03	0.38	0.75	0.91	1.00	1.00

internal and external symptoms provide strong evidence of radial growth decline in overstory trees due to '*mal del cip*rés'. Reductions in radial growth prior to death of *A. chilensis* trees due to environmental stress also has been observed along the eastern margin of the species range (Villalba and Veblen, 1998). Similarly, significant differences in radial growth patterns between trees with and without crown symptoms have been reported in mesic *A. chilensis* forests with '*mal del ciprés*' (Calí, 1996; Mundo et al., 2010). However, the latter studies reported on a limited number of trees and sites or focussed on living symptomatic trees only. In this study, we assessed radial growth decline on a large number of trees with asymptomatic and symptomatic crowns, as well as dead trees, at 12 sites. Furthermore, we discriminated the incidence of the radial growth decline among trees of different crown health conditions and canopy positions at onset of decline, to reconstruct the temporal dynamics of radial growth decline at the tree and site levels.

A long period of decline in radial growth that significantly exceeded the narrowing of ring widths with size that is typical of healthy trees was a common characteristic of overstory symptomatic and dead trees in *A. chilensis* stands with '*mal del ciprés*'. Nevertheless, the type of radial growth decline within overstory trees was variable. Most trees experienced a gradual, steady decline in radial growth, while the rest exhibited an abrupt decline followed by persistent low growth rates over time. Similarly, radial growth decline onset and length were variable among trees and sites. The year in which the first trees at each site started declining ranged from the 1920s to the 1960s. While the initial manifestation and development of radial growth decline varied among sites, by 1960s radial growth decline was present at all sites. These findings, based on tree-ring analyses, provide new information that compliments historical documentation of the development of '*mal del ciprés*'. Historically identified in the field using external symptoms including crown condition and tree death, the presence of '*mal del ciprés*' was first reported in 1948 (Varsavsky et al., 1975) and 1953 (Hranilovic, 1988). Subsequent studies have reported mortality as early as the 1940s for different areas in Patagonia (Relva et al., 2009; Amoroso and Larson, 2010a). However, our retrospective analyses showed that radial growth rates of some trees showed abnormal patterns of decline as early as the 1920s. Other studies have successfully used dendrochronological techniques to study tree growth prior to death (Cherubini et al., 2002; Dobbertin, 2005; Marçais and Breda, 2006) and found evidence of prolonged reductions in radial growth prior to tree death (Pedersen, 1998; Bigler et al., 2007; Drobyshev et al., 2007). We propose that tree-ring analyses can be useful for detecting '*mal del ciprés*' before crown symptoms have developed and could serve as an early indicator of decline, even in forests of apparently healthy trees.

In related research, we hypothesized that the progressive foliage loss associated with '*mal del ciprés*' reduced the photosynthetic capacity of trees, negatively affecting cambial activity and the formation of complete rings around the stem near the base of trees (Amoroso and Daniels, 2010). In contrast, in this study we found that a decline in radial growth can precede the development of the crown symptoms such as loss of vigor and defoliation. Specifically, 67 trees exhibited a decline in radial growth and were classified as overstory trees at the onset of decline, but had asymptomatic crowns at the time of sampling. As living symptomatic and dead trees can undergo long periods of radial growth decline but the transition from asymptomatic to symptomatic crowns and from symptomatic to dead trees occurs over short intervals of 1–3 years (Havrylenko et al., 1989; Rosso et al., 1994; El Mujtar et al., 2011), we infer that the decline in radial growth can precede the manifestation of symptoms in the crown of at least some *A. chilensis* trees. This inference assumes that the observed trees with radial growth decline will develop crown symptoms over time, which can be verified or refuted by monitoring our sample sites through time. Similar reductions in radial growth before a decline in crown vigor have been documented in *Pseudotsuga menziesii* (Mirb.) Franco and *Acer saccharum* Marsh, when photosynthates were limited (Wallis and Reynolds, 1965; Thies, 1983; Duchesne et al., 2003). Radial (secondary) growth represents a lower priority in the allocation of photosynthates compared to the production of new foliage and height (primary) growth (Oliver and Larson, 1996). If the photosynthetic activity of a tree is reduced, the amount of photosynthates allocated to secondary growth will decrease, leading to radial growth reductions (Kozlowski et al., 1991). We hypothesize the decline in radial growth in *A. chilensis* trees with '*mal del ciprés*' results from reduced photosynthetic activity which may precede loss of crown vigor and defoliation by many years.

Without a decrease in the photosynthetic area of a tree, water availability is the other factor that can affect photosynthesis. For trees with asymptomatic crowns, restricted uptake of water would reduce photosynthetic activity leading to a decline in radial growth and, eventually, to partial or total crown withering and defoliation as secondary growth is a lower priority for photosynthates (Kozlowski et al., 1991; Oliver and Larson, 1996). Temporary or permanent damage to the root system can be caused by biotic and abiotic factors. For the *A. chilensis* forests that we studied, we propose two non-mutually exclusive hypotheses to explain root damage that would restrict water uptake and photosynthesis. First, a new species of *Phytophthora* has been associated with symptomatic *A. chilensis* trees and proposed as the primary cause of tree death and forest decline due to '*mal del ciprés*' (Greslebin et al., 2007; Greslebin and Hansen, 2009, 2010). Pathogen damage to the root system would decrease the ability of the trees to take water from the soil, reducing photosynthetic activity and negatively affecting growth (Wallis and Reynolds, 1965; Joseph et al., 1998; Mallett and

Volney, 1999). Alternately, reduced growth or root damage could be a consequence of climatic events. Repeated droughts (Kitzberger et al., 1995; Villalba and Veblen, 1998) and extended periods of drought causing below-average tree growth for *A. chilensis* were common during the 20th century in northern Patagonia (Villalba and Veblen, 1997) and were concurrent with increased frequency of radial growth decline in our study area. Working in forests with symptoms of '*mal del ciprés*' at the same region, Mundo et al. (2010) found that the radial growth of living symptomatic trees was consistently lower than in asymptomatic trees following extreme drought events. Given the complexity of this species' radial-growth response to climatic variation (Villalba and Veblen, 1997), the occurrence of radial growth decline could be highly influenced by climatic conditions as hypothesized by Calí (1996) and Mundo et al. (2010). As well, it is possible that both root damage from *Phytophthora* and drought may occur over time and these two mechanisms may interact to drive '*mal del ciprés*'. Their relative effects on radial growth decline of individual trees and development of '*mal del ciprés*' at stand- and landscape-scales remains unclear and warrants further investigation. One approach is to assess the presence of necrotic lesions caused by *Phytophthora* in addition to crown symptoms and radial growth decline. Necrotic lesions form on the inner bark at the root collar of infected *A. chilensis* trees, but are often discontinuous around the stem (Greslebin et al., 2007; Greslebin and Hansen, 2009). Lesions are best detected by removing the outer bark around the circumference at the root collar; however, this method may affect the survival of assessed trees. Since we aimed to monitor tree survival and stand development at our sites through time, we did not assess necrotic lesions in this study.

4.2. Forest decline and stand dynamics

Although the causes of '*mal del cipres*' have been the subject of several detailed studied over the last years (e.g. La Manna and Rajchenberg, 2004; El Mujtar, 2009; Greslebin and Hansen, 2010), understanding the effects on and interactions with forest stand dynamics has just begun (Amoroso and Daniels, 2010; Amoroso and Larson, 2010a). Specifically, we lack of full understanding of the relationships between '*mal del ciprés*' and the processes associated with stand development. In related research we reported the challenges of differentiating among causes of tree mortality in declining stands because mortality due to '*mal del ciprés*' and due to other processes could occur simultaneously (Amoroso and Larson, 2010a). In our study area, *A. chilensis* mortality may result from a biotic agent such as *Phytophtora*, abiotic factors such as climatic variation, natural processes such as self-thinning due to competition during early stages of development of the forests, or the combination of several of these factors.

In this study, we have proposed that radial growth decline is an early indicator of '*mal del ciprés*' that can be combined with other evidence to differentiate among causes of death. We detected radial growth decline in 632 trees, of which 58% and 42% were classified as overstory and understory trees, respectively, based on their diameter at the onset of the decline relative to other trees at the same site. We applied a conservative approach and used only overstory trees exhibiting radial growth decline in our temporal reconstruction of '*mal del ciprés*', assuming that the onset of abnormally low radial growth in large trees was likely due to a cause other than inter-tree competition. Conversely, the understory trees were excluded from our temporal reconstructions. Since we were working in post-fire, even-aged stands that were 70–130 years old, we assumed understory trees were weak competitors and radial growth decline due to competition during the stem exclusion stage could not be differentiated from that due to '*mal del ciprés*'. At the same time, some understory trees had symptomatic crowns so the decrease in radial growth may have been due to '*mal del ciprés*' combined with competition effects. For dead understory trees, we could not retrospectively differentiate the cause of decline and death.

Our temporal reconstructions based on the onset of radial growth decline in overstory trees revealed patterns consistent with the documentary records of forest decline due to '*mal del ciprés*' (Varsavsky et al., 1975; Hranilovic, 1988; Relva et al., 2009) and the temporal patterns of tree mortality previously documented at the study sites (Amoroso and Larson, 2010a). They also exhibited great variability within and among sites. The onset of radial decline varied from steady increases in the number of declining trees to abrupt increases in the number of trees with radial growth decline over short periods of time in the 1950–60s and 1970–80s. This variability in temporal patterns supports the hypothesis that the decline and death of trees in forests with '*mal del ciprés*' are caused by a combination of factors, including allogenic and autogenic processes that act synergistically.

As our understanding of the nature of '*mal del ciprés*' forest decline increases, this knowledge should become the baseline to design and implement management strategies aimed to ameliorate its consequences. Traditionally, management has been reactive with sanitation or salvage harvests applied to *A. chilensis* forests to remove dead trees and trees with crown symptoms and facilitate the growth of the retained trees. Based on our results, these treatments are not always beneficial. We have shown that trees can undergo extended periods of radial growth decline before death and, in some trees, before the development of external crown symptoms. Therefore, some salvage harvests take place after radial growth decline is widespread and individual trees have been declining for long periods. Since some trees may be undergoing radial growth decline but have asymptomatic crowns, not all retained trees will respond positively to salvaging (Amoroso and Larson, 2010a). One solution is to use radial growth analyses, combined with assessment of crown symptoms, to monitor for and detect the onset of '*mal del ciprés*'. However, as an internal symptom, radial growth decline is difficult to detect and highly variable among individual trees at the site level and this may not be feasible except at local scales. An alternate, proactive management response is to identify the site conditions (soil type, precipitation, aspect) where '*mal del ciprés*' is likely to develop and establish monitoring sites. Management prescriptions that aim to create conditions for successful establishment of new trees in the understory (Amoroso and Larson 2010a, 2010b), will be more effective for long-term forest recovery than attempts to remove trees already showing evidence of decline.

5. Conclusion

The use of tree-ring records in combination with tree- and stand-level information allowed us to study the onset of radial growth decline relative to crown symptoms in individual trees and to reconstruct the temporal development of '*mal del ciprés*' in declining *A. chilensis* stands. This study was the first to discriminate the incidence of the radial decline among asymptomatic, symptomatic and dead trees and to use tree-ring evidence as an early indication of tree decline in *A. chilensis* forests.

Since most trees undergo long periods of radial growth decline before death and declining patterns vary greatly suggesting interactions or multiple causes, it is appropriate to continue referring to '*mal del ciprés*' as a type of forest decline. Our tree-ring evidence is consistent with two possible causes of decline. A new species of *Phytophthora* has been associated with tree mortality; yet it is unknown whether *Phytophthora* infects trees causing the radial decline or attacks trees already weakened and declining. There is, in addition, a potential link between the timing of the decline onset and climatic variation. These two causes might not be mutually exclusive. Rather, they could well be interrelated as in the case of many forest declines, which include complex and interacting processes leading to loss of tree vigor and mortality. Future research needs to focus on the variability in timing of radial decline onset and subsequent tree mortality and to differentiate possible causes including environmental stresses such as climate variation and its interactions with pathogens.

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