Does drought incite tree decline and death in *Austrocedrus chilensis* forests?

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Abstract

Questions: Is *mal del ciprés,* the widespread decline and death of *Austrocedrus chilensis* trees, caused by a single pathogen or multiple factors? Using a novel dendrochronological approach, we disentangled the influences of climatic variation on the radial growth decline and death of *A. chilensis* trees in declining forests. We distinguish possible causes of reduced radial growth and mortality from autogenic processes driven by stand development. We present a conceptual model of forest decline including multiple factors that predispose, incite and contributed to decreased radial growth and death of *A. chilensis*.

Location: *A. chilensis* forests on mesic sites in northern Patagonia, Argentina.

Methods: We used dendrochronology to determine the years of (1) onset of radial growth decline of 301 living and dead trees stratified by canopy position at decline onset, and (2) mortality of 339 trees stratified by radial growth patterns and canopy position at death. Events were years with low or high numbers of trees initiating decline or dying. We tested the hypothesis that onset of decline and mortality were concurrent with drought for individual trees, using contingency tables, and for events, using superposed epoch analysis.

Results: Climatic variability acts as an environmental stress inciting and contributing to stand-level forest decline. The onset of radial growth decline and mortality of individual trees were significantly associated with summer moisture deficits. High-magnitude onset-of-decline and mortality events were concurrent with adverse climatic conditions.

Conclusions: Climatic variation and drought incite and contribute to tree- and stand-level decline and mortality in *A. chilensis* forests. Deciphering the effects of stand development is critical as autogenic processes independently drive tree mortality and mediate the effects of climatic variability on *A. chilensis* forest decline. Based on our results, we present a conceptual model within the framework of a forest decline process, and conclude *A. chilensis* mortality is a forest decline process driven by complex interactions between allogenic abiotic and biotic factors and autogenic stand development processes. Site conditions, genetic variation and sex of trees are predisposing factors that likely interact with the pathogen *Phytophthora*.

Introduction

Given recently documented climatic change and forecast global warming in the 21st century, there is increasing concern about the effects on forest ecosystems (Dale et al. 2001; Adams et al. 2009; Allen 2009). Numerous studies have documented increased rates of tree mortality and forest decline in diverse forests around the globe, seemingly due to drought and extreme heat in recent decades (Williamson et al. 2000; Guarín & Taylor 2005; Allen et al. 2010; van Mantgem et al. 2009). There is growing evidence that other forest ecosystems could be at risk as well (Seager et al. 2007; Adams et al. 2009; Peng et al. 2011). The effects of gradual climate change are exacerbated by extreme events which are difficult to predict but are expected to become more common in the future (IPCC 2012). The evidence supporting these assertions is compelling; nevertheless, uncertainties remain about how forest

ecosystems are responding to increasing mean temperature and more frequent and intense extreme climatic events.

Mortality patterns in forests have been the subject of detailed study, particularly in forests with increasing rates of decline and mortality that have been related directly and indirectly to global warming (Allen et al. 2010). Yet, tree death commonly involves multiple processes that are difficult to understand and reconstruct. Death can result from allogenic processes, such as disturbances or environmental stress (White & Pickett 1985; Villalba & Veblen 1998; Williamson et al. 2000), and autogenic processes, such as both genetic and stand dynamics, i.e. direct competition from neighbouring trees (Alaback 1982; Kobe et al. 1995; Lutz & Halpern 2006). In addition, tree death can be caused by complex interactions of different factors (Mueller-Dombois et al. 1983; Hennon et al. 1990; Minorsky 2003). In the latter case, mortality can involve environmental stress factors interacting with different biotic agents in forests of various ages and stages of development, resulting in broad-scale forest decline (Houston 1981; Mueller-Dombois 1983; Manion 1991). Forest declines worldwide are indeed driven by many factors, which interact in complex ways and are often exacerbated by climate, making them difficult to disentangle (e.g. Pedersen 1998; Cherubini et al. 2002; Hartmann & Messier 2008; Camarero et al. 2011).

Austrocedrus chilensis (D.Don) Pic. Sern. *et* Bizarri forests experience stand-level decline and mortality of overstorey trees at mesic sites throughout their natural range of distribution in northern Patagonia. This type of forest decline, locally referred as '*mal del ciprés*' (cypress sickness), is characterized by tree mortality preceded by a decline in radial growth and canopy cover, but it is temporally unpredictable process (Amoroso & Larson 2010; Mundo et al. 2010; Amoroso et al. 2012). The cause(s) of *mal del ciprés* remain(s) unresolved as tree mortality in these forests appears to result from complex interactions among biotic and abiotic factors (Calí 1996; La Manna & Rajchenberg 2004; Greslebin et al. 2007; El Mujtar 2009; Greslebin & Hansen 2009, 2010; Amoroso & Larson 2010; Mundo et al. 2010; Amoroso et al. 2012). Furthermore, autogenic processes such as inter-tree competition at different stages of stand development occur simultaneously with *mal del ciprés*, making it challenging to differentiate among causes of tree decline and mortality (Amoroso & Larson 2010; Amoroso et al. 2012).

In related research, we hypothesized that restricted water uptake due to extreme droughts could reduce photosynthetic activity leading to a decline in radial growth and eventual tree death (Amoroso et al. 2012). Our hypothesis parallels findings by Mundo et al. (2010), who assessed the radial growth in 25 trees with decline

symptoms including low tree vigour indicated by chlorotic or defoliated crowns. They measured a persistent reduction in radial growth, the onset of which was influenced by climatic conditions during the previous growing season. Although these authors showed compelling results, living and dead trees in different canopy positions were not included to test for different responses among trees. We know of no stand-level studies that have investigated the influence of climatic variation on the radial growth decline of a large number of dead and living trees in declining *A. chilensis* forests, or have considered the influence of unfavourable climatic conditions on the year of death of declining and non-declining trees in these forests.

Tree-ring analyses have been used successfully to reconstruct growth and mortality patterns to study the response of trees to environmental stress (Villalba & Veblen 1998; Suarez et al. 2004), evaluate tree growth prior to death (Cherubini et al. 2002; Dobbertin 2005; Marçais & Breda 2006) and investigate causes of forest decline (McClenahen 1995; LeBlanc 1996; Beier et al. 2008). In this study, we examined the role of inter-annual climatic variation as an inciting factor contributing to the radial growth decline and death of trees in declining forests. To achieve this objective, we examined the effect of climatic variability (1) on the onset of radial growth decline on a large number of dead and living trees, to discriminate the incidence of the radial growth decline by the canopy position of the trees at the decline onset; and (2) on the time of death of the trees, to discriminate different radial growth patterns by canopy position at death. Our ultimate goals were to shed light on the role of climate in the decline and death of *A. chilensis* trees and to contextualize our results with previous research to distinguish between possible causes and interactions of allogenic (abiotic and biotic factors) and autogenic (stand development) processes in the development of the forest decline. For the latter goal, we present a conceptual model within the framework of a forest decline process (sensu Manion 1991; Manion & Lachance 1992) that can help elucidate the role of allogenic and autogenic processes driving *mal del ciprés*.

Methods

Study sites and sampling

This 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 near El Bolsón, Rio Negro, Argentina (41°46′ S, 71°33′ W). Mean annual temperature is 9.3°C and total annual precipitation is 904 mm. Soils are Andisols, with a deep profile and presence of volcanic ash. Forests in the area are characterized by post-fire *A. chilensis*-dominated

stands. Within the ca. 2500 ha study area, we identified *A. chilensis*-dominated stands exhibiting symptoms of *mal del ciprés*: >40% of dead trees and living trees with chlorotic foliage and defoliation of the crown. We excluded stands with signs of logging or grazing, and we randomly selected 12 sites for sampling (Table 1; Amoroso & Larson 2010; Amoroso et al. 2012).

One permanent sample plot was established at each site and sampled in 2006 to achieve multiple objectives (Amoroso & Larson 2010; Amoroso et al. 2012), including the climatic analyses presented in this study. Plots were 0.1-ha in size and shape varied with local topography (31.63 m × 31.63 m or 40.0 m × 25.0 m). In each plot, all living and dead overstorey trees with a DBH > 5.0 cm were tagged and sampled. For each tree, we recorded species, DBH, crown height class (dominant, co-dominant, intermediate and suppressed), and 'health condition' [living asymptomatic, living symptomatic (i.e. trees with chlorotic foliage and defoliation of the crown) and dead], based on Rajchenberg & Cwielong (1993) and Amoroso & Larson (2010). To assess radial growth, we extracted increment cores perpendicular to the slope at 30-cm height from all trees. Multiple cores were taken from each tree to ensure that at least one of the samples intercepted or was close to the pith and to include sound sapwood or bark so that the outer ring was the last ring formed on living and dead trees (Amoroso & Daniels 2010). Transverse cross-sections (ca. 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.

Dendrochronological methods

Tree cores and cross-sections were processed and visually cross-dated following standard dendrochronological methods (Stokes & Smiley 1968). For the cross-sections, we selected and measured two radii that were perpendicular to the slope, to avoid compression wood and included sound sapwood and bark to ensure comparability with the increment cores. All ring-width series were measured on a Velmex bench to the nearest 0.01 mm, cross-dated using an existing master chronology (R. Villalba: Pampa del Toro; International Tree-Ring Data Bank, NOAA, Boulder, CO, US, ftp://ftp.ncdc.noaa.gov/pub/data/paleo/treering/measurements/southamerica/arge080.rwl), and statistically verified using the program COFECHA (Holmes 1983; Grissino-Mayer 2001).

We estimated the date of onset of the radial growth decline due to *mal del ciprés* following the method developed by Amoroso et al. (2012). This method is an iterative, multi-step procedure developed to (1) characterize growth rates of trees in the absence of external and internal symptoms of decline, (2) ensure all trees respond similarly to climate, and (3) compare the radial growth of trees with no symptoms with the growth rates of trees exhibiting symptoms of decline (Amoroso et al. 2012). The onset of the radial growth decline in the trees was estimated by comparing individual standardized ring-width series with the corresponding site-level standard chronology of the healthy trees (asymptomatic, non-declining trees) and its 95% confidence interval (CI). The onset of the radial growth decline was determined as the year in which the series crossed the lower 95% CI and did not recover. All dead trees and living trees with symptomatic crowns were assessed. Ring-width series were standardized using the program ARS41_win (Cook & Krusic 2006). A horizontal line dividing each ring width by the mean ring width of the series was used in order to preserve the long-term growth trends of individual trees and to scale their absolute growth rates, allowing direct comparison of the relative growth rates of trees of different sizes (e.g. Veblen et al. 1991; Amoroso et al. 2013).

Table 1. Site and stand characteristics for 12 *Austrocedrus chilensis* stands in the area of El Bolsón, Argentina. Diameter represents mean value and SD in parenthesis. Trees with symptoms represent the proportion of dead trees and living trees with chlorotic foliage and defoliation of the crown in each stand.

Stand	Elevation (m a.s.l)	Slope (°)	Azimuth (°)	Density (n·ha^{-1})	Diameter (cm)	Trees with Symptoms (%)	Sampled Trees (n)
CE1	471	0	90	790	19.3 (13.5)	54	66
CE2	523	0–10	100	1150	19.2 (14.4)	64	64
PP1	452	15–20	120	1790	12.6 (10.1)	65	121
PP2	430	20	90	1750	13.0 (8.0)	73	119
PP4	450	20	85	890	18.5 (11.8)	52	79
K1	367	15	130	1050	15.8 (12.7)	58	80
EU1	420	25	130	1490	16.4 (11.4)	40	91
EU2	398	20	90	1260	16.7 (11.6)	72	94
RQ1	475	0–5	90	1410	19.1 (13.0)	64	87
RQ2	486	0–5	90	1400	15.8 (11.4)	55	86
CR1	453	5	70	1590	13.3 (10.4)	52	100
CR2	456	15–25	55	1950	12.8 (8.4)	40	95

To differentiate probable causes of low growth rates in individual trees, we reconstructed the diameter of each tree at the onset of decline using the cross-dated ring-width series to determine the percentile of diameter at onset of decline as a measure of relative tree size (Amoroso et al. 2012). Our previous research has shown that the canopy position of 90% of the trees assessed in the field corresponded to their percentile of diameter. The percentile is ≥50 for overstorey trees and <50 for understorey trees (Amoroso et al. 2012). Thus we assumed that overstorey trees (percentile ≥50 at decline onset) were successful competitors in which declining radial growth was mostly likely due to *mal del ciprés*, while understorey trees (percentile <50) were less successful competitors so that radial growth decline could be due to inter-tree competition or *mal del ciprés*.

Mortality dates of dead trees were estimated as the calendar year of the outer-most ring of the cross-dated ring-width series. For dead trees, the outer-most ring of the cross-dated ring-width series estimated the last growing season during which the trees were alive. The trees may have died at the end of the growing season after secondary growth was complete. Alternatively, they may have died in the subsequent winter or the growing season of the year following the formation of the outer-most ring (e.g. outer-ring +1; Cherubini et al. 2002; Jones & Daniels 2012; Bigler & Rigling 2013). Differentiating between the two growing seasons was not possible using our samples; therefore, we assumed of the outer-most ring represented the year of death, unless otherwise noted.

We separated the dead trees into three categories: (1) non-declining trees that did not exhibit suppressed radial growth before death, (2) declining overstorey trees exhibited radial growth decline prior to death where the percentile of diameter at onset of decline was ≥50, and (3) declining understorey trees exhibited a radial growth decline prior to death and the percentile of diameter at onset of decline was <50. We hypothesized that non-declining trees most likely died due to causes other than *mal del ciprés* (background mortality, climate or other allogenic causes), declining overstorey trees most likely died due to *mal del ciprés*, and declining understorey most likely died due to inter-tree competition and/or *mal del ciprés*.

Tree-ring and climate analyses

We determined the absolute frequencies of onset of radial growth decline in overstorey trees and mortality of all trees for the 12 sites combined. Relative frequency (%) of onset of decline was calculated for each year as the absolute frequency divided by the number of overstorey trees that were alive but did not exhibit decline (i.e. trees with the potential to exhibit decline). For mortality, we differentiated (1) non-declining trees, (2) declining overstorey trees and (3) declining understorey trees, and calculated relative frequencies (%) for each class by dividing the number of trees that died by the number of living trees in each year.

Regional precipitation and temperature records were created from the monthly climate data from three nearby climate stations (Table 2). Initially, the precipitation and temperature records were analysed separately. Within each station record, the data for each month were standardized by subtracting the monthly mean from each monthly value and dividing by the respective SD to generate monthly departures, positive or negative SD from a mean of 0.0 (i.e. *z*-scores). The monthly departure records for the three stations were averaged so that they were equally weighted in the resulting regional records. A monthly moisture index was computed for the period 1914 to 2005 as the regional monthly precipitation departure minus the temperature departure (Villalba & Veblen 1998; Daniels & Veblen 2000, Daniels & Veblen 2004). Using the monthly moisture indices we computed seasonal indices for spring and summer (i.e. average of the monthly values for all possible combinations of two to six consecutive months from Sept through Mar) and a growing season index (i.e. average of monthly values for the 7 mo from Sept through Mar, inclusive). In the final step, the monthly and seasonal moisture indices were standardized to generate positive or negative departures. Negative moisture index departures resulted from below-average precipitation and/or above-average temperature, and indicated drought.

The relative frequency distributions of the onset of decline and year of death dates were used to examine the influence of the climate on the decline and mortality of trees in *A. chilensis* forests with *mal del ciprés*. Analyses were conducted separately on each of the three mortality classes described above (non-declining, declining overstorey and declining understorey trees). Analyses were repeated using (1) all years in which more than one tree exhibited onset of decline or died (hereafter 'events'), (2) years in which no trees exhibited onset of decline or died (hereafter 'non-events') and (3) 'high-magnitude events', the subset of event years when many trees exhibited onset of decline or died. High-magnitude events were identified with a three-step process. We first determined whether the Poisson or negative binomial distribution function best described the relative frequencies of onset of decline and death. By comparing the density plots we selected the negative binomial distribution as the function with the best fit for each variable. Second, we estimated the values of the parameters of the distribution (μ) and obtained 95% CI using maximum-likelihood analyses using the function *fit.distr* of the MASS package in R software (R Foundation for Statistical Computing,

Table 2. Meteorological records used for comparing onset of radial growth decline and mortality dates with climatic variation.

Station	Latitude S	Longitude W	Elevation (m)	Record Period	Parameter	Source
Collun-co	39°58′	71°12′	875	1912–1998	P	HIDRONOR
				1912–1989	T	
Bariloche	41°09′	71°16′	825	1905–2009	P	SMN
				1914–2009	T	
Esquel	42°54′	71°20′	785	1951–2003	P	SMN
				1951–2009	T	

P, mean monthly precipitation; T, mean monthly temperatura; SMN, Servicio Meteorológico Nacional (Argentina); HIDRONOR, Hidroeléctrica Norpatagónica S.A.

Vienna, AT). Third, the upper limits of the CI were used as threshold values. Years in which the relative frequency of onset of decline or death exceeded the threshold were considered high-magnitude events.

We used two approaches to test the hypothesis that decline and mortality events were concurrent with years of drought. First, we tested if onset of decline and mortality events were associated with positive vs negative moisture indices using tests of proportions. For each study period, we stratified years into positive and negative departures. We compared the proportion of years with positive/negative departures against the proportions calculated for years and trees with onset of decline (87 yr from 1914–2000, after year 2000 it was not possible to ensure that low growth persisted >5 yr; Amoroso et al. 2012) and mortality (92 yr from 1914–2005). The stratification and comparative analyses of the proportions were conducted on all possible combinations of the moisture indices for the spring and summer months and the growing season. We repeated the analyses on mortality dates using the year following the outer-most ring (i.e. outer ring +1; 92 yr from 1915–2006) since we could not differentiate the exact growing season in which trees died.

Second, we used continuous climate data in superposed epoch analyses (SEA; Swetnam 1993; Grissino-Mayer 1995) to give a more nuanced understanding of the magnitude of climatic variation associated with decline and mortality and test for potential lag effects. SEA were performed using the EVENT program (v 6.02P, http://www.ltrr.arizona.edu/software.html) to quantify inter-annual relationships between onset of decline or mortality events and the moisture indices, and to contrast these with climatic conditions during non-event years. Separate analyses were conducted on the high-magnitude events, all events and non-events for the onset of decline and each of the three mortality classes. We superposed a 5-yr window of contemporaneous (event years) and lag (3 yr prior and 1 yr after events) departures from the monthly, seasonal and growing season moisture indices on each event. For this analysis we used only the mortality dates based on the outer-most ring, as the assessment of the year after the mortality events was equivalent to assessing the outer ring

+1 yr. Significance levels were determined from bootstrapped 95% CI estimated from 1000 Monte Carlo simulations performed using random sampling with replacement (Mooney & Duval 1993).

Results

Climatic influence on radial growth decline of symptomatic and dead trees

Of the 1082 *A. chilensis* trees sampled at the 12 sites, 301 trees (28%) presented a decline in radial growth relative to the final standard chronology at each site and were classified as overstorey trees at the onset of decline based on reconstructed diameters. Onset of radial growth decline occurred over a wide range of dates between 1917 and 2000. At least one tree exhibited onset of decline in 74 of 92 yr studied (80%); no onset was observed in only 18 yr. High-magnitude events in which 5–25% of the sampled trees exhibited onset of decline occurred 17 times (1943, 1949, 1953, 1956, 1957, 1961, 1962, 1963, 1967, 1973, 1974, 1978, 1979, 1980, 1982, 1984 and 1992; Fig. 1).

Of the monthly and seasonal (2- to 7-month combinations) moisture indices we tested (data not shown), only the December–February moisture index exhibited significant relationships with the year of the onset of radial growth decline. Onset of decline was associated with negative departures of the December–February moisture index (i.e. drought), but was significant at the tree level only (Table 3). Over the study period, 62% (54 of 87) of years had negative departures. Most years with onset of decline (67%, 46 of 69 yr) were concurrent with drought, but these proportions did not differ significantly ($P = 0.276$). In contrast, 75% (227 of 301) of trees began to decline during droughts, which significantly exceeded the proportion of drought years ($P = 0.007$). Onset of decline occurred in 85% (46 of 54) of years with negative departures, but occurrence was significantly lower in years with positive departures (70%, 23 of 33 yr; $P = 0.042$). The SEA corroborated these results: the December–February moisture indices exhibited negative departures (droughts) for the year of the onset of radial growth decline. The 17 high-magnitude onset-of-decline events were significantly
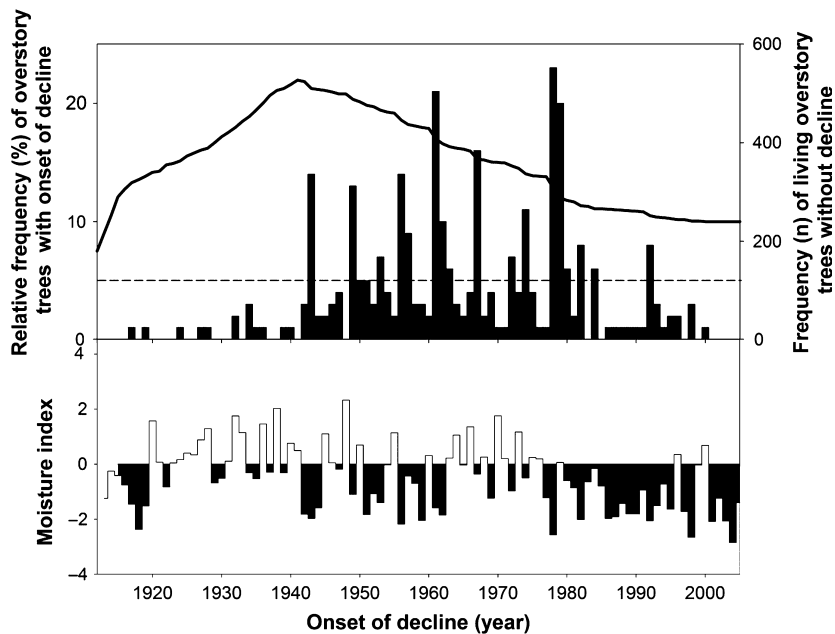
Fig. 1. Onset of decline of 301 overstory *A. chilensis* trees in comparison with the December-February moisture index from 1914 to 2005. In the top panel, relative frequency (bars) is the percentage of overstory trees exhibiting onset of decline in each year relative to the number of living overstory trees that did not exhibit decline but had the potential to exhibit decline (line). The horizontal dashed line indicates the threshold value above which relative frequencies indicate high-magnitude onset of decline events. In the bottom panel, negative departures (black bars) indicate low moisture indices or drought years resulting from low precipitation and/or warm temperature; positive departures (white bars) indicate high moisture indices resulting from abundant precipitation and/or cool temperature.

associated with December–February drought (Fig. 2a). The 74 yr in which more than one tree exhibited onset of decline (i.e. all events) were associated with negative moisture index departures (Fig. 2b), but the relationship was not significant. In contrast, the 18 yr with no onset of radial decline were associated with positive departures but the relationship was not significant (Fig. 2c).

Climatic influence on mortality events and mortality patterns

Out of the 1082 sampled trees, 339 (31%) were dead, of which 108 (32%), 153 (45%) and 78 (23%) were declining overstorey trees, declining understorey trees and non-declining trees, respectively. Tree death began as early as the 1940s, with most deaths occurring after 1970 (Fig. 3). While inter-annual mortality patterns varied, six mortality events based on outer-ring dates (1961, 1976, 1979, 1981, 1988 and 1991) were common for all mortality classes, independently of the differences in growth history (declining vs non-declining) and canopy position of the trees (overstorey vs understorey) at the time of death. While only two of these six mortality events were concurrent with high-magnitude onset-of-decline events, the years following mortality events (i.e. outer ring +1) were concurrent with four of the decline events.

The year of death exhibited significant relationships only with the December–February moisture index; other monthly and seasonal moisture indices were not significant (data not shown). Tree mortality estimated from the year of and year following the outer-ring dates was associated with negative departures of the December–February moisture index (Table 3). Most years of death (75% based on outer ring and 74% based on outer ring +1) were concurrent with drought, but the proportions did not differ significantly from the 64% (59 of 92) of drought years over the study period ($P = 0.074$ and 0.113, respectively). The deaths of 339 trees were more common during drought years (76% based on outer ring and 78% based on outer ring +1), which significantly exceeded the proportion of drought years ($P = 0.012$ and 0.003, respectively). Using SEA, we found only one significant association between mortality events and climatic conditions (Fig. 4). The high-magnitude mortality events for declining overstorey trees ($n = 16$) were significantly associated with negative departures of the December–February moisture index for the year following formation of the outer-most ring (i.e. outer ring +1; Fig. 4a). Although not significant, trees exhibiting decline were generally associated with negative moisture indices prior to death (Fig. 4a,b), while trees showing no decline before death (Fig. 4c) and years with no tree

Table 3. Proportion of years with positive or negative moisture index departures compared with relative measures of the occurrence of the onset of radial growth decline in overstorey trees and tree deaths. For each process (decline or mortality), the proportions of years with positive or negative departures over the study period were compared to the proportions of years and trees exhibiting change during positive or negative departures were tested against the proportions for all years for each study period (α = 0.05).

| Type of Process Categories for Comparison	N	December–February Moisture Index Departures		Test of Proportions (P-Values)
		Positive n (%)	Negative n (%)	
Onset of Radial Growth Decline in Overstorey Trees				
Years (1914–2000)	87	33 (38)	54 (62)	–
Years with Onset of Decline	69	23 (33)	46 (67)	0.276
Trees with Onset of Decline	301	74 (25)	227 (75)	0.007
Mortality Date (Year of the Outer-most Ring)				
Years (1914–2005)	92	33 (36)	59 (64)	–
Years of Death	57	14 (25)	43 (75)	0.074
Tree Deaths	339	82 (24)	257 (76)	0.012
Mortality Date (Year Following the Outer-most Ring)				
Years (1915–2006)	92	33 (36)	59 (64)	–
Years of Death	57	15 (26)	42 (74)	0.113
Tree Deaths	339	75 (22)	264 (78)	0.003
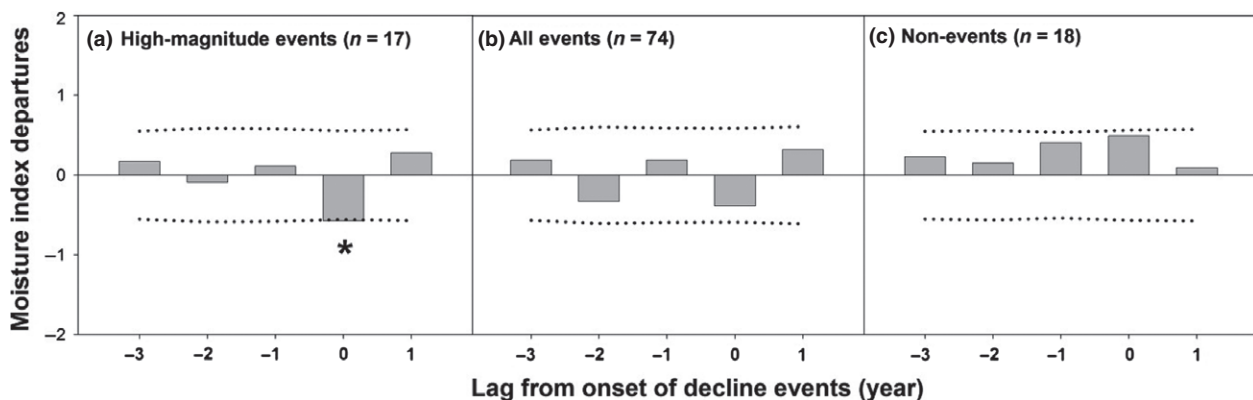
Fig. 2. Association between onset of decline events and the December-February moisture index from 1914 to 2005. Panels show (**a**) high-magnitude events, (**b**) all events and (**c**) years with no onset of decline (non-events). Dashed lines represent the 95% confidence limits based on 1000 Monte Carlo simulations. The asterix indicates a statistically significant departure (P < 0.05) from the mean.

deaths (Fig. 4d) were associated with positive moisture indices.

Discussion

Drought as a triggering factor of radial growth decline and mortality

Our results indicate a strong association between the onset of the radial growth decline in overstorey *A. chilensis* trees and the occurrence of droughts in late spring and summer (Dec–Feb in the southern hemisphere). The onset of radial growth decline of individual trees and high-magnitude events, years when a large proportion of trees exhibited onset of decline, were significantly associated with years of moisture deficits. Late spring and summer droughts triggered immediate radial growth decline in 197 overstorey trees, 65% of the 301 declining or dead overstorey trees. Furthermore, the 17 high-magnitude onset-of-decline events were concurrent with major (i.e. 1956, 1961, 1962 and 1978; Fig. 1) and moderate droughts (i.e. 1957, 1967 and 1984; Fig. 1). Our results corroborate and expand on those of Mundo et al. (2010), who found that the growth of 25 symptomatic living trees was consistently lower than paired asymptomatic trees following the occurrence of extreme drought events.

In previous research on *mal del ciprés* we hypothesized that restricted water uptake due to extreme climatic events (i.e. drought) would reduce photosynthetic activity lead-
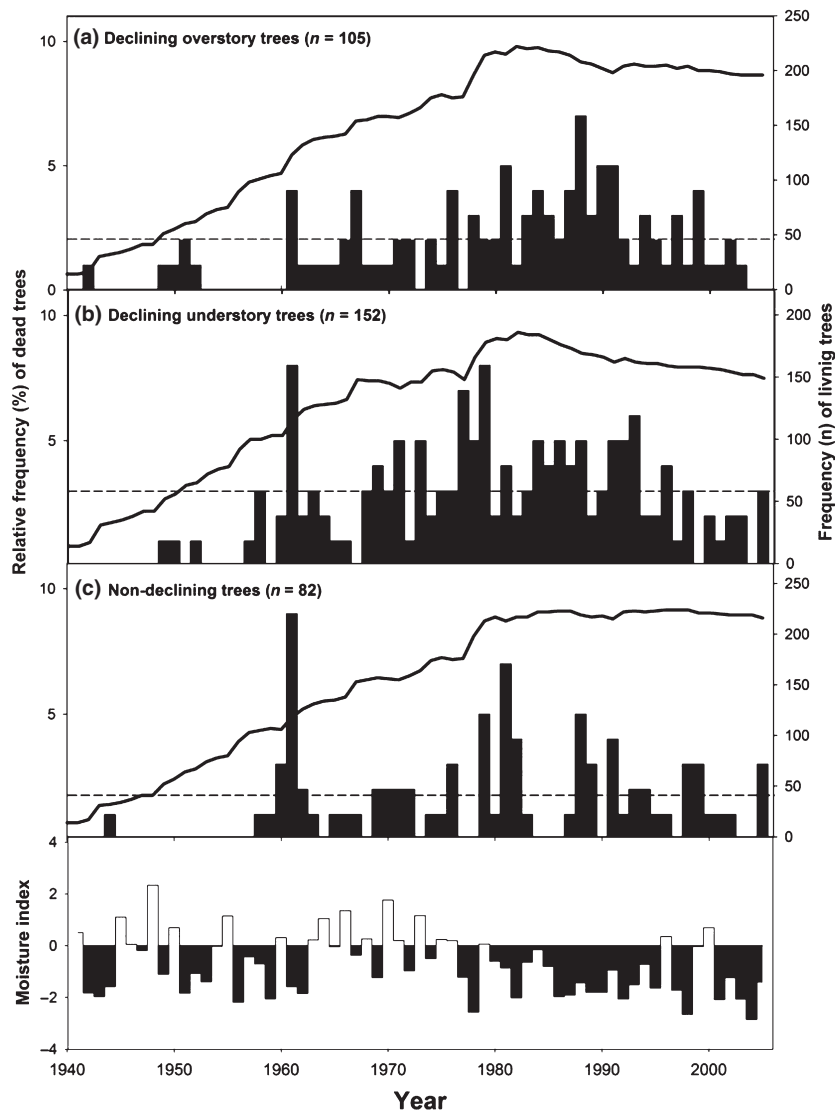
Fig. 3. Year of death (outer-ring dates) of 339 *A. chilensis* trees in comparison with the December-February moisture index from 1940 to 2005. Trees were stratified by mortality class: (**a**) declining overstory trees, (**b**) declining understory trees and (**c**) non-declining trees. In the top three panels, relative frequency (bars) is the percentage of trees that died in each year relative to the number of living trees (line). The horizontal dashed line indicates the threshold value above which relative frequencies indicate high-magnitude mortality events. In the bottom panel, negative departures (black bars) indicate low moisture indices or drought years resulting from low precipitation and/or warm temperature; positive departures (white bars) indicate high moisture indices resulting from abundant precipitation and/or cool temperature.

ing to a decline in radial growth and eventual tree death (Amoroso et al. 2012). Our findings are consistent with other studies showing that the growth of *A. chilensis* is strongly and positively correlated with spring and early summer precipitation (Villalba & Veblen 1997; Mundo et al. 2010). Similarly, several studies have shown that reduced radial growth rates in declining forests can be driven by severe drought, particularly in forests with a dry growing season climate (e.g. Suarez et al. 2004; Martín-Benito et al. 2008; Linares et al. 2010; Camarero et al. 2011; Gea-Izquierdo et al. 2014).

The significant association of mortality based on the cross-dated outer-ring dates and growing season drought indicate that some trees died in the same year in which their outer-most ring was formed. However, the stronger associations between the following year (i.e. outer ring +1) and onset-of-decline events and drought suggest a higher proportion of trees died in the growing season after the formation of their outer-most ring (Cherubini et al. 2002; Jones & Daniels 2012; Bigler & Rigling 2013). The lagged response we documented for the high-magnitude mortality events shows that declining overstorey trees commonly
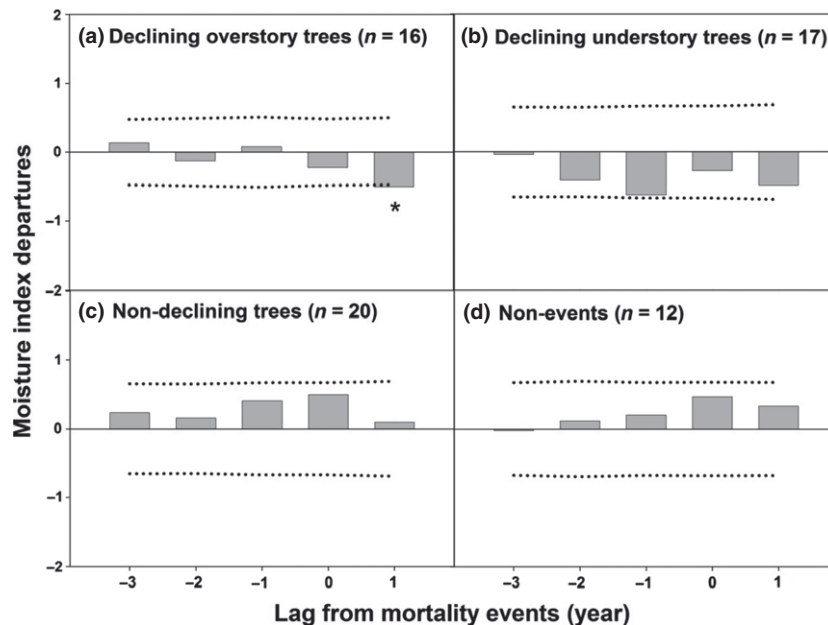
Fig. 4. Association between high-magnitude mortality events and the December–February moisture index from 1914 to 2005. Trees were stratified by mortality class (**a**) declining overstory trees, (**b**) declining understory trees and (**c**) non-declining trees, and contrasted with (**d**) years with no mortality (non-events). In (**a**, **b** and **c**), *n* is the number of high-magnitude mortality events per class; in (**d**), *n* is the number of years with no mortality in any of the three classes (determined in Figure 3). Dashed lines represent the 95% confidence limits mean based on 1000 Monte Carlo simulations. The asterix indicates a statistically significant departure ($P < 0.05$) from the mean.

formed their last ring 1 yr prior to significant droughts (lag of +1; Fig. 4a). This outcome gives the illusion that tree death preceded drought by 1 yr. Rather than a spurious result, it appears that many trees formed their last ring in the growing season before their death, then died during drought in the subsequent growing season before they produced an annual ring. For this subset of trees, our estimated timing of mortality based on the year of the outer-most ring was inaccurate by 1 yr. Accounting for this physiological and methodological artefact, we conclude the deaths of declining overstorey trees during high-magnitude mortality events were concurrent with significant droughts.

The significant association between tree mortality and summer moisture deficit is consistent with other research on the effects of climatic variability on tree deaths in northern Patagonia. Exceptionally dry springs and summers have been associated with episodes of widespread *A. chilensis* mortality at the regional level (Villalba & Veblen 1998). Furthermore, the periods of high mortality in our study coincide with dry and warm climatic conditions which have driven forest and tree-line dynamics across precipitation and elevation gradients in the region (Villalba & Veblen 1997; Daniels & Veblen 2004; Suarez & Kitzberger 2010). Nevertheless, we found only one significant relationship between mortality events and adverse climatic conditions even after stratifying trees by canopy position

and growth pattern of the trees at time of death. Only the mortality of declining overstorey trees was significantly associated with adverse late spring and summer climatic conditions.

The lower number of high-magnitude mortality events ($n = 6$) relative to onset-of-decline events ($n = 17$) may be partly explained by spatial and temporal aspects of our research. Previous research has shown intra-regional variation in the intensity of drought affects *A. chilensis* mortality patterns (Villalba & Veblen 1998). Thus, the weaker association between climate and tree mortality may relate to the mesic sites included in our study vs the strong drought-driven mortality of trees in drier ecotonal forests (Villalba & Veblen 1997, 1998). Mediation of drought effects on mesic sites is also consistent with our observation that only high-magnitude mortality events were significantly associated with drought.

Temporally, it is possible that the outer-ring dates that we determined by cross-dating accurately represented the last ring formed but not the year of tree death for each tree (Cherubini et al. 2002; Jones & Daniels 2012; Bigler & Rigling 2013). Some species exhibit prolonged lags with tree deaths occurring years to decades after acute drought stress (Pedersen 1998; Bigler et al. 2007; Suarez & Kitzberger 2010). A 1-yr discrepancy between the outer-most ring and probable year of death linked to drought was evident from climate-mortality analyses. A similar phenomenon

would explain the relatively weak association between all mortality events and drought that we observed (Fig. 4). Living trees in declining *A. chilensis* forests exhibit cambial mortality or death of part of the cambium, causing incomplete formation of rings around the circumference (Amoroso & Daniels 2010). As a result, outer-ring dates vary around the circumference of declining living and dead trees. Almost 40% of the living trees exhibit cambial mortality and in about 75% of the living symptomatic canopy trees in the studied symptomatic *A. chilensis* forests exhibited cambial mortality, denoted as an outer-ring date different from the expected date, which is most likely to occur in the last year (Amoroso & Daniels 2010). Although we made a concerted effort to sample the last ring formed by each living (i.e. multiple cores including sapwood and bark) and dead tree (i.e. cross-sectional disks to identify the most complete radius for analysis), our year of death dates may not have been accurate at an annual resolution. Errors were most likely for the subset of trees that died after low and moderate intensity droughts and when other factors contributed to mortality.

Austrocedrus chilensis forest decline as a result of multiple factors

The stand-level decline and mortality in *A. chilensis* forests has been extensively studied using a range of methodological and disciplinary approaches; nevertheless, authors differ with respect to the cause(s) of tree death and the decline of these forests. One pronounced discrepancy among interpretations is the number of causal factors responsible for the tree deaths, ranging from a single biotic agent to the combined effects of biotic and abiotic factors. For example, authors who assign a single causal factor to tree mortality refer to this process as a disease, explaining the name *mal del ciprés* (cypress sickness; e.g. Greslebin & Hansen 2010). Those who explain tree deaths as the result of more than one factor have framed it as a forest decline process. As our findings and previous research (El Mujtar 2009; Mundo et al. 2010; El Mujtar et al. 2011) highlight the role of climatic variability on the decline and death of trees in these forests, here we present a framework for interpreting mortality of *A. chilensis* as a forest decline process driven by multiple factors (sensu Manion 1991; Manion & Lachance 1992). Complex interactions between abiotic and biotic factors acting at different spatial and temporal scales predispose trees, and incite and contribute to the development of the symptoms leading to the subsequent death of trees over large areas.

Several factors have been identified that may simultaneously predispose trees to decline. Site condition is one of them. The occurrence of decline and mortality is not random among stands, but is directly related to particular site conditions within landscapes. Several studies have reported that stand-level decline of *A. chilensis* occurs on sites at low and moderate elevations with poor soil water drainage and those with higher precipitation (Havrylenko et al. 1989; Baccalá et al. 1998; Filip & Rosso 1999; La Manna & Rajchenberg 2004; La Manna et al. 2008, 2012). Within stands, genetic variation and the sex of trees (*A. chilensis* is a dioecious species) appear to be important as predisposing factors. An assessment of molecular markers has identified genetic differences between individuals with and without symptoms (El Mujtar 2009). Another study reported that female trees were more prone to develop symptoms of decline than male trees (El Mujtar et al. 2012). Inciting or triggering factors include both abiotic and biotic agents. Consistent with our findings, several studies have concluded that drought can initiate the decline process and determine the timing of the onset of decline in radial growth (El Mujtar 2009; Mundo et al. 2010; El Mujtar et al. 2011). Short duration droughts might weaken individuals, making them more susceptible to subsequent factors, including biotic agents. Several studies have shown the importance of *Phytophthora austrocedrae* as an agent of forest decline, causing necrotic lesions in the root system and conduction tissues at the base of the trunk of *A. chilensis* trees (Greslebin et al. 2007; Greslebin & Hansen 2009, 2010; Vélez et al. 2012). Drought-induced stress that reduces the growth capacity of trees could also make them more susceptible to *P. austrocedrae,* which would act as a secondary agent of decline by generating necrotic lesions and contributing to the eventual death of trees (El Mujtar 2009). Our study, while not conclusive, strongly suggests that climatic variability can trigger the death of stressed trees. Extreme droughts have contributed to widespread death of *A. chilensis* (Villalba & Veblen 1998) and can kill weakened trees exhibiting symptoms of decline.

Finally, it is important to recognize that radial growth decline and mortality of *A. chilensis* can result from causes other than those mentioned above. Although radial growth reductions preceding the death of trees are often a consequence of drought and other environmental stresses (Pedersen 1998; Villalba & Veblen 1998; Bigler et al. 2007), such growth reductions are also expected in trees dying due to inter-tree competition during the biomass accumulation and the self-thinning stages of stand development (Oliver & Larson 1996; Cherubini et al. 2002; Franklin et al. 2002). Similarly, mortality occurs as a result of direct competition from other trees at these stages of stand development (e.g. Kobe et al. 1995; Lutz & Halpern 2006). Many declining *A. chilensis* forests are even-aged forests that initiated after widespread fires that burned at the turn of the 19th century (Veblen et al. 1999). Thus in these forests, inter-tree competition at different stages of stand development would occur simultaneously with *mal*

del ciprés and would explain the radial growth decline and death of some trees (Amoroso & Larson 2010; Amoroso et al. 2012). Furthermore, it is possible that intense competition predisposed these trees to develop radial growth decline, exacerbated by short-term stress caused by drought (Linares et al. 2010). Yet, differentiating *mal del ciprés* from autogenic processes related to stand development makes determining the cause(s) of tree growth decline and mortality extremely difficult (Amoroso & Larson 2010; Amoroso et al. 2012) and requires further exploration.

Conclusion

Forest declines worldwide are driven by multiple factors and result from complex interactions (e.g. Pedersen 1998; Cherubini et al. 2002; Hartmann & Messier 2008; Camarero et al. 2011). In this study, we used a large data set to present a novel approach to disentangle the role of climatic variation on the radial growth decline and death of trees in declining *A. chilensis* forests. This study is the first to date onset of radial growth decline and mortality of individual trees, while simultaneously accounting for differences in growth history and canopy position of the trees. Our results provide strong evidence that climatic variability acts as an environmental stress inciting and contributing to stand-level forest decline. The onset of radial growth decline and mortality of individual trees were significantly associated with summer moisture deficits. High-magnitude onset-of-decline and mortality events (after accounting for methodological artefacts) were concurrent with adverse climatic conditions. These outcomes form the basis of a conceptual model of *A. chilensis* mortality as a forest decline process driven by complex interactions between abiotic and biotic factors that predispose (site conditions, genetic variation, sex of trees), incite (climatic variability, pathogen) and contribute (climatic variability, pathogen) to stand-level decline. This framework formalizes the alternate hypothesis to single causal agents of *A. chilensis* decline by emphasizing the role and importance of climatic variability as a driver of decline. Our novel research approach and framework can be applied elsewhere to better understand the impacts of climatic variability and its interactions with abiotic and biotic factors and to guide forest management adaptations to climate change.

Acknowledgements

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