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INFLUENCES OF LARGE-SCALE CLIMATIC VARIABILITY ON EPISODIC TREE MORTALITY IN NORTHERN PATAGONIA

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Abstract. In the context of potential global warming, it is critical that ecologists bridge the typically local spatial scale of ecology to the regional scale of climatology by linking ecosystem responses to variations in the large-scale synoptic controls of regional climates. In northern Patagonia, Argentina, we related regional-scale tree mortality events over the past ~100 years to annual and decadal-scale climatic variations associated with changes in the major synoptic climatic controls of the southeastern Pacific region, including the El Niño–Southern Oscillation (ENSO). In nine stands of *Austrocedrus chilensis,* a xeric conifer, we used dendrochronological techniques to date the outermost tree ring on dead-standing and fallen trees to estimate the dates of tree death for 336 trees. To evaluate climatic conditions during periods of high tree mortality, we used regional records of precipitation and temperature from six climate stations and also used a regional set of 24 tree ring chronologies from *Austrocedrus.*

Good preservation of the resinous wood of *Austrocedrus* allowed relatively precise dating of tree deaths over the past ~90 years. Episodes of massive tree mortality coincide with exceptionally dry springs and summers during the 1910s, 1942–1943, and the 1950s. Although there is a general regional synchroneity of tree death associated with drought, intra-regional variations in the intensity of droughts, as interpolated and mapped from the regional network of tree ring chronologies, are also reflected by north-to-south variations in tree mortality patterns.

Periods of drought and associated tree mortality during the 20th century in northern Patagonia are strongly associated with above average sea level atmospheric pressure off the coast of Chile at the same latitudes. Temperature and precipitation in northern Patagonia are highly influenced by the intensity and latitudinal position of the southeastern Pacific anticyclone, which, in turn, are greatly affected by ENSO. Tree mortality in northern Patagonia appears to be intensified by extreme events of the Southern Oscillation and is more strongly coincident with El Niño events along the coast of northern Peru. These results, in combination with previously established climatic influences on fire occurrence and tree seedling establishment, strongly link stand-level and regional-scale forest dynamic processes in northern Patagonia with variations in large-scale atmospheric conditions.

Key words: Austrocedrus chilensis; *climatic variability; dendrochronology; drought; El Niño–Southern Oscillation; forest dynamics; northern Patagonia; tree mortality.*

INTRODUCTION

Climate variability is a major influence on tree population dynamics both indirectly through effects on climatically related disturbances such as fire and insect outbreaks, and directly through influences on tree establishment and mortality. In the context of potential global warming, ecologists are challenged to bridge the traditionally local spatial scale of ecology to the regional scale of climatology by linking ecosystem responses to variations in the large-scale synoptic controls of regional climates. Recently, ecologists have documented the importance of hemispheric-scale climatic variations to regional and local fire regimes (e.g., Swetnam and Betancourt 1990, Johnson and Wowchuk 1993, Swetnam 1993). Most studies of the effects of climatic variation on tree demography have focused on the establishment and survival of tree seedlings as reflected in tree population age structures (e.g., Kullman 1989, Baker 1990, Little et al. 1994), but there is relatively little research that relates tree mortality to large-scale climatic mechanisms (but see Betancourt et al. 1993, Szeicz and MacDonald 1995). Periodic droughts lasting a year to more than a decade offer ecologists the opportunity to apply historical techniques to analyze the impacts of climatic variation on tree mortality patterns and improve our understanding of ecosystem responses to large-scale climatic variability.

Although information on tree death is critical for understanding stand dynamics and for managing ecosystems, tree mortality is one of the least understood processes in ecology (Franklin et al. 1987, Mueller-

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This work is dedicated to Julian Szeicz (1965–1998), Queens University, Kingston, Ontario, Canada.

Dombois 1987, 1993). Tree mortality occurs across a range of spatial and temporal scales from the death of a single tree to widespread mortality affecting thousands of trees more or less synchronously over areas of many square kilometers as in the case of many well known "forest declines" (Auclair 1993, Innes 1993, Mueller-Dombois 1993). Some causes of tree mortality such as wildfires and windthrow are obvious, but in most cases the causes of tree death are complex and multifaceted (Franklin et al. 1987, Mueller-Dombois 1987, 1993, Stewart 1989, Pedersen, 1998). An insect outbreak, for instance, may be the proximate cause of death, whereas preconditioning factors such as lack of nutrients may not be obvious. Although climate-induced environmental stress, such as floods, droughts, and extremes of temperatures have long been recognized to be important in the death of tree seedlings (Franklin et al. 1987, Stewart 1989), recognition of the importance of climatic factors in extensive episodes of decline and death of mature trees has been slower and less universal (Auclair 1993, Innes 1993, Hennon and Shaw 1994).

Episodes of mortality of adult trees have sometimes been attributed to droughts in a range of ecosystem types from xeric woodlands to temperate rain forests (Plummer 1904, Phillips 1909, Meinecke 1925, Balch 1927, Hursh and Haasis 1931, Jane and Green 1983, Betancourt et al. 1993). However, little or no information is available on the recurrence of drought-induced mortality episodes in the same stands. Similarly, possible relationships of drought-induced mortality episodes to large-scale synoptic climatic patterns have received scant attention by ecologists (but see Betancourt et al. 1993).

In northern Patagonia, Argentina, we used dendrochronological techniques to examine potential influences of climatic variability on the mortality of the xeric conifer *Austrocedrus chilensis* near the forest–steppe ecotone. We dated episodes of massive tree mortality over the past 100 years along an ~400 km north-to-south transect, and related them to climatic variation based on analyses of both the instrumental climatic record and tree ring chronologies. Finally, we related the occurrence of drought-induced mortality to variations in the large-scale climatic mechanisms, including El Niño–Southern Oscillation, that influence the regional climate of northern Patagonia.

STUDY AREA

Climate

Our study area includes the foothills of the Andes and the adjacent Patagonian plains at latitudes 39 to 43° S in Argentina (Fig. 1). The main determinants of the climate of midlatitude southern South America are the circum-Antarctic cyclonic belt to the south, the southeastern Pacific high-pressure cell to the northwest, and the north-south-trending mountain barrier of the Andes (Taljaard 1972, Miller 1976, Prohaska 1976, Pittock 1980*a*, *b*, Aceituno 1988). The Andean Cordillera is an effective barrier to the westerlies, so that mean annual precipitation varies from 4000 to 6000 mm on the Chilean side of the Andes to <200 mm ~100 km east of the crest of the Andes in Argentina (Almeyda and Saez 1958, Barros et al. *unpublished report* ["Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén." Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Cinco Saltos, Río Negro, Argentina]). Mean annual temperatures vary from 10°C on

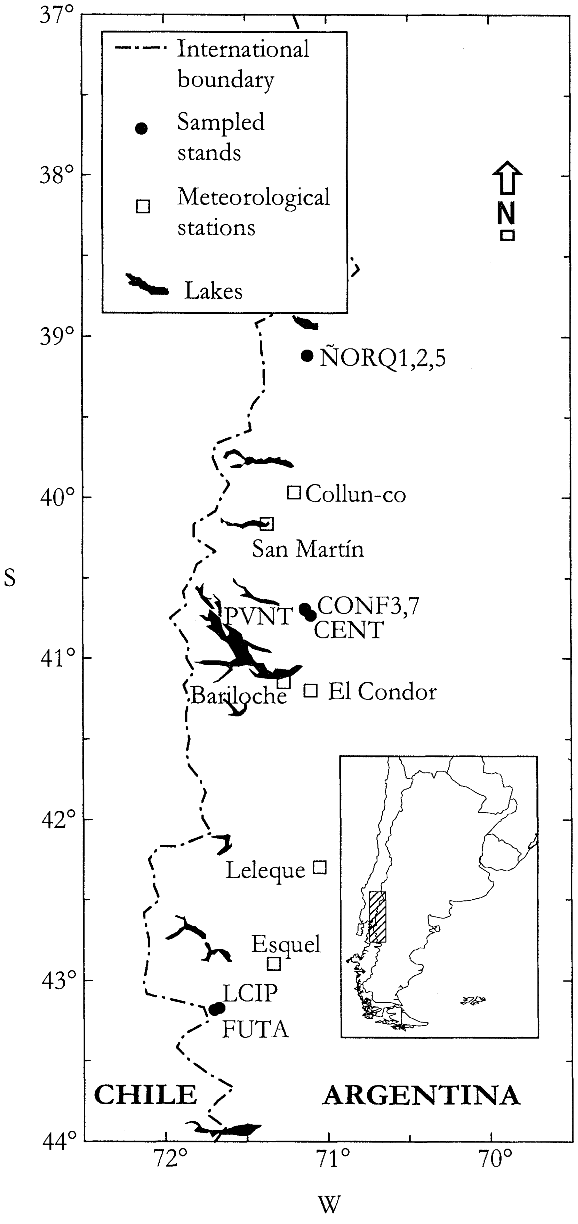

FIG. 1. Map of northern Patagonia east of the Andes, showing stands sampled for dating of tree death. Stand codes are given in Table 1.

TABLE 1. Site characteristics for tree mortality analysis.

Site	Plot code	Latitude (°S)	Longitude (°W)	Elevation (m)	Aspect	Slope (°)	Size (m)	No. of trees live	No. of trees dead
Ñorquinco 1	ÑORQ1	39°07′	71°07′	1135	NE	15–45	40 × 30	46	36
Ñorquinco 2	ÑORQ2	39°07′	71°07′	1160	NE	10–20	60 × 50	49	61
Ñorquinco 5	ÑORQ5	39°07′	71°07′	1100	NE	10–20	50 × 30	41	41
P. del Viento	PVNT	40°42′	71°09′	910	E	10–30	···		20
Confluencia 3	CONF3	40°42′	71°08′	870	E	20–45	60 × 30	77	48
Confluencia 7	CONF7	40°42′	71°08′	865	NE	25–40	90 × 30	47	62
El Centinela	CENT	40°44′	71°06′	805	E	10–30	···		20
Los Cipreses	LCIP	43°10′	71°41′	550	NE	15–35	···		30
R. Futaleufú	FUTA	43°11′	71°42′	470	NW	5–15	20 × 20	59	18

the west side of the Andes, to 6°C in the subalpine deciduous forest near treeline, and 8°C at the steppe–forest transition east of the Andes (Almeyda and Saez 1958, Gallopín 1978). Continentality is more marked on the Patagonian plains (Minetti 1989).

Seasonal and annual variations in precipitation are closely related to changes in the intensity and latitudinal positions of the southeastern Pacific high-pressure cell off the coast of Chile (30 to 45° S), which result in shifts in the westerly storm tracks. On average 40% of the precipitation occurs in winter (June–August; Miller 1976) which is when westerly storm tracks are at their northernmost position (Pittock 1980*a*). The strength of the subtropical high is closely related to the anomalous Pacific tropical convection associated with El Niño–Southern Oscillation (ENSO; Aceituno 1988, Karoly 1989). During El Niño events (negative phase of the Southern Oscillation), pressure is anomalously low over the eastern sector of the Pacific, particularly in the domain of the subtropical high (Aceituno 1988). Concurrent with El Niño events, winter precipitation is abundant, particularly in central Chile between 30° and 35° latitude (Aceituno 1988, Rutllant and Fuenzalida 1991), but also in northern Patagonia (Kiladis and Diaz 1989). During La Niña events, pressure over the eastern Pacific is higher and winter precipitation is lower in northern Patagonia (Kiladis and Diaz 1989). Dry and warm summer conditions in northern Patagonia are normally related to more southerly latitudinal positions and increased intensity of the eastern Pacific anticyclone, and to more frequent incursions of continental air masses of subtropical origin (Taljaard 1972, Villalba 1990, 1994).

Long-lasting intervals (i.e., ≥5 years) of dry and warm summers in northern Patagonia have been recorded in instrumental records during this century and in tree ring records over the past several centuries (Villalba 1994, Villalba et al. 1996). During the 20th century, major periods of warmer and drier summers were recorded from 1910 to 1919, from 1957 to 1962, and during the 1980s. Long-lasting anomalies in the climate of Patagonia are also related to large-scale circulation changes. For example, warmer and drier summer conditions in northern Patagonia since the late 1970s are associated with a southward displacement of the subtropical high-pressure belt and a greater influence of subtropical air masses over northern Patagonia (van Loon et al. 1993). During the same period, the tropical Pacific experienced above normal sea surface temperatures and a persistently negative Southern Oscillation index (Trenberth 1990).

Vegetation

Physiographically, from west to east, the northern part of Argentinean Patagonia is subdivided into the main Andean cordillera, the pre-cordillera of foothills and glacial lakes, and the Patagonian plains. Pleistocene glaciers at this latitude retreated 12 000 to 13 000 years BP (Markgraf 1983, 1989). Between 39 and 43° S latitude in the Andes, extensive volcanic ash deposits overlie Pleistocene glacial topography and are the soil-forming parent materials throughout the region. Following the strong precipitation gradient from west to east, there is a dramatic vegetation gradient from temperate rainforests in Chile to the Patagonian steppe in Argentina (Veblen et al. 1995).

In the western area of the Argentinean Andes, the montane slopes are dominated by tall forest of the evergreen *Nothofagus dombeyi.* Further east, where precipitation declines to ~1500 mm, *Austrocedrus chilensis* and *N. dombeyi* form extensive codominant stands. Under the more xeric conditions to the east, *Austrocedrus* forms pure dense stands and then open woodlands codominated by sclerophyllous shrubs and small trees. Further east, *Austrocedrus* disappears and steppe elements such as spiny shrubs and bunchgrasses (*Stipa* spp. and *Festuca* spp.) dominate. The eastern limit and density of *Austrocedrus* woodlands have varied dramatically over the past 100 yr in relation to variations in the frequency of human-set fires (Veblen and Lorenz 1988, Veblen et al. 1992*a*).

METHODS

Field procedures

Cross sections were extracted from dead trees in nine stands at six sites near the forest–steppe ecotone from 39 to 43° S latitude (Fig. 1, Table 1). This was a subset from 26 stands in which all seedlings and trees were aged and mapped for a regional stand-structure study (Villalba and Veblen 1997*a*). The subset chosen for the dating of tree death included the stands with the largest numbers of dead-standing trees where fires had not destroyed evidence of tree mortality. These were open woodlands on relatively xeric sites where the open-grown *Austrocedrus* generally do not exceed 10 m in height. Trees were carefully examined to try to determine probable causes of death. Trees showing evidence of past fires (fire scars or charcoal) were not included. Dead *Austrocedrus* trees uprooted by wind were also excluded. Tree deaths from either burning or windthrow were rare at the sites sampled. Most sample sites are located on rocky, steep slopes, which are not affected by a fungal pathogen that appears to kill trees at some poorly drained sites (Havrylenko et al. 1989).

In each of nine stands, samples were randomly located in areas of homogeneous site, and plots varied in size from 400 to 2700 m^2 to include a minimum of 40 live trees. To increase sample sizes, a few additional samples from dead trees were collected within a 100-m radius of the age-structure plots. For three stands, dead trees were sampled independently of an age-structure plot by sampling all the dead-standing trees within a 100-m radius from a point (Table 1). In each of the nine plots, all dead-standing trees and sound logs were sampled. Although no minimum tree size was set for sampling dead-standing trees, nearly all dead-standing trees were >5 cm diameter at breast height (dbh). The scarcity of smaller dead-standing trees may reflect their more rapid decay due to higher ratios of sapwood to heartwood. Complete or partial cross sections were taken with a manual saw and all samples included ≥ 50 tree rings to facilitate cross dating. Typically, two samples were taken from each tree at different heights to reduce problems associated with missing or partial rings.

Determination of date of death

For those sites where tree mortality was determined, ring-width chronologies were used both to cross date the outermost rings on the dead samples and to describe local patterns of tree growth (Villalba 1995). Twenty-four tree ring chronologies were derived from older *Austrocedrus* sampled at sites near the age-structure sample sites but outside of the sample plots. Locations, site characteristics, and dendrochronological procedures are given in Villalba (1995) and Villalba and Veblen (1997*b*).

Samples of dead trees were segregated into four categories: (1) cross section with bark, (2) cross section without bark but showing no evidence of ring erosion, (3) cross section without bark showing incipient ring erosion, and (4) cross section with pronounced ring erosion. The estimated accuracies of dates of tree deaths associated with these categories are: close to annual accuracy (except where one or two rings were missing prior to death) for the first two categories, 3 to 5 yr for the third, and >5 yr for the fourth. The calendar date of the outermost ring on dead trees was determined by cross dating against master chronologies developed from live trees near each stand sampled for mortality. Both visual cross dating (Stokes and Smiley 1968) and quantitative cross dating (program COFECHA, Holmes 1983) was used to cross date samples of dead trees against master chronologies. The program COFECHA computes correlations between 50-yr segments of the undated series and corresponding segments of the master chronology series. In most cases, we rejected individual series having ≥ 2 segments with correlation values that were not significant at the $P <$ 0.01 level (two-tailed t test; $n = 50$). However, because tree rings contain other clues to cross dating (e.g., light rings, intra-seasonal bands, frost rings) in addition to ring width (Fritts 1976), we also used visual observations in making cross-dating decisions. The death dates of 336 trees were determined, but the total number of dates analyzed was 268 because 68 of the trees died prior to the beginning of the period of analysis (either 1750 or 1850, depending on the site).

Determination of past climatic conditions

Regional climatic records of precipitation and temperature were created by averaging monthly standard deviations from temperature and precipitation records from nearby climate stations. Normalized standard deviations were used so that the weight of each station in the regional average was equal regardless of the raw values. The precipitation record included the Collun-co, San Martín de los Andes, Bariloche, El Condor, Leleque, and Esquel weather stations (Fig. 1). The regional temperature record consists of the Collun-co, Bariloche, and Esquel stations (Villalba 1995). Regional records of temperature and precipitation were grouped into seasonal data sets of 3–6 mo for comparison with tree mortality records. Spring–summer (October through March) showed the strongest association with tree mortality, and, consequently only this monthly combination is presented in the *Results*. A regional moisture index was computed for the period 1906 to 1989 as the difference between the departures (positive or negative standard deviations) from regional spring–summer precipitation and temperature means.

To supplement instrumental climatic records, which sometimes were from stations nearly 100 km distant from the sample sites, *Austrocedrus* ring-width chronologies from trees close to each sample plot were used. Correlation functions indicate that the radial growth of *Austrocedrus* along the forest border in Patagonia is favored by above average precipitation and limited by above average temperature during late spring and summer of the year prior to, and the year of ring formation (Villalba 1990, Villalba and Veblen 1997*b*). Thus, low tree ring indexes of *Austrocedrus* indicate warm-dry springs and summers during the year of ring formation and/or the previous year.

Possible association of mortality events with large-scale synoptic climatic patterns was examined by considering variations in sea level pressure from 1911 to

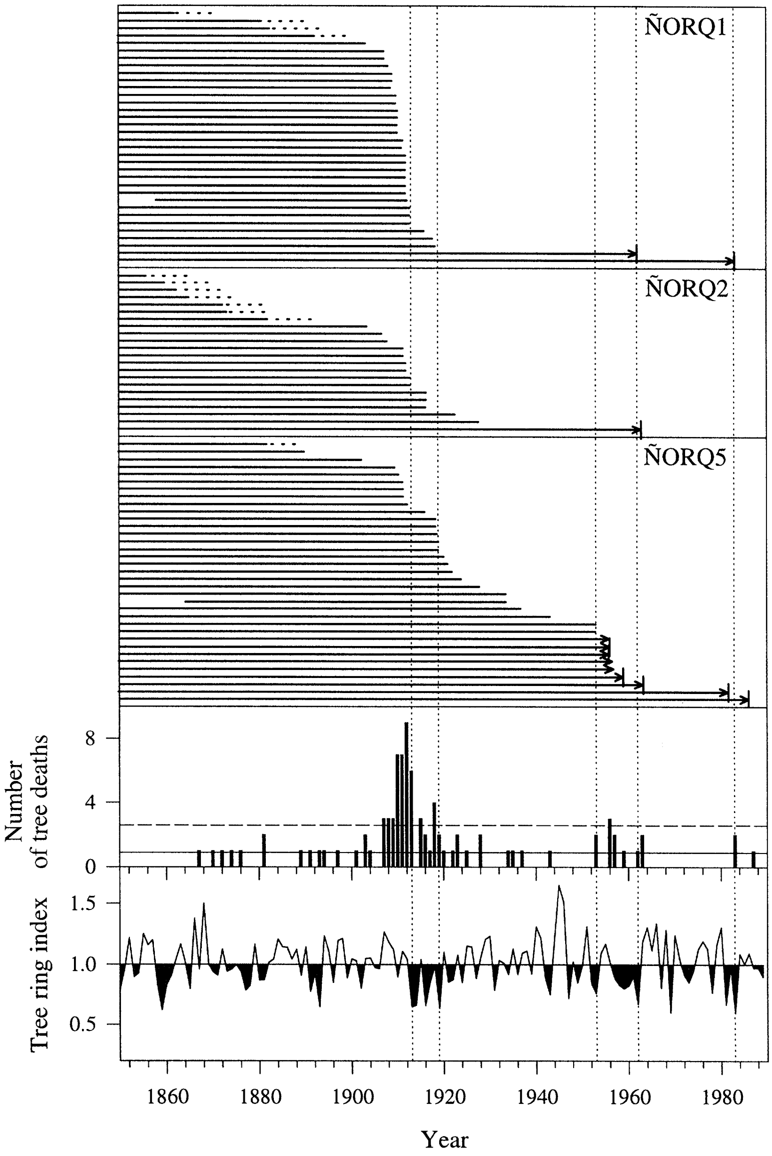

FIG. 2. Results of dendrochronological dating of dead *Austrocedrus* at ÑORQ1, ÑORQ2, and ÑORQ5. The tree ring indexes are from the Ñorquinco chronology ($n = 50$). Samples of dead trees are segregated into four categories: cross sections with bark (→|), cross sections without bark but showing no signs of ring erosion (→), cross sections without bark showing incipient ring erosion (solid line), and cross sections with pronounced ring erosion (dotted line). Dotted vertical lines indicate periods of mortality associated with reduced radial tree growth. In the graph of the number of tree deaths, mean annual tree deaths and +1 SD (for 1900 to 1989) are indicated by a solid and a dashed line, respectively.

1985 for four grid points along the western coast of South America (30–45° S, 70–80° W; Jones 1991). Pressure in this area off the Chilean coast is under the domain of the subtropical high pressure cell of the southeastern Pacific (Pittock 1980*a*, Villalba 1994).

RESULTS

Temporal trends of tree mortality

Dates of tree death are reported in Figs. 2–7 as years of the outermost ring (i.e., without correcting for possible ring erosion or failure of some trees to produce a ring, at the sampling height, the year before death). When considered individually, sample sites show clear episodes of tree mortality, most of which are coincident for nearby stands. For example, in three nearby sites at Lake Ñorquinco (ÑORQ1, 2, and 5) frequency distributions of mortality dates indicate that large percentages of tree deaths occurred in the 1910s (Fig. 2). Cross sections from trees that died in this interval showed only incipient erosion of the outer rings, so that the true dates of death are probably no more than 2 to 10 yr later. The tree ring chronology from this site

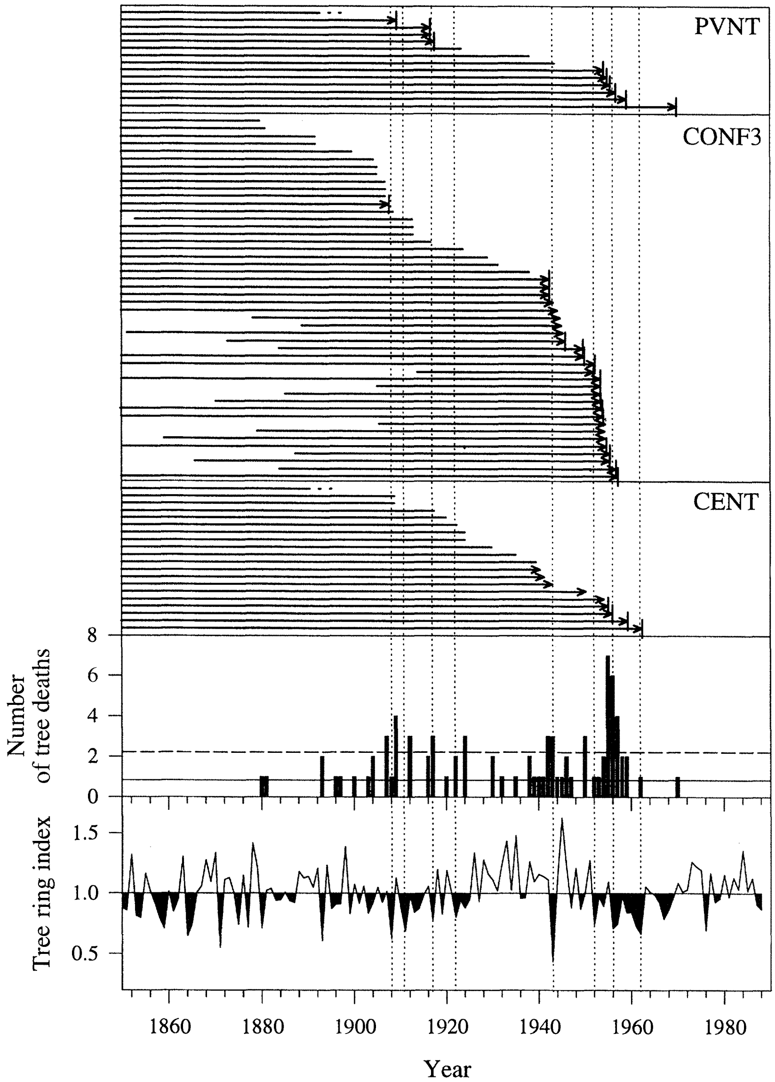

FIG. 3. Results of dendrochronological dating of dead *Austrocedrus* at PVNT, CONF3, and CENT. The tree ring indexes are from the Confluencia chronology (n = 25). Categories and designations are as in Fig. 2.

shows a period of radial tree growth substantially below the long-term mean in 1913–1919, approximately coincident with tree-mortality episode (Fig. 2). Stand ÑORQ5 shows a second period of abundant mortality in 1956–1962 which coincides with one of the periods of lowest rate of radial tree growth during the 20th century (Fig. 2).

Stand PVNT, located ~200 km further south, records increased tree deaths in 1908–1918 and especially in 1954–1959 (Fig. 3). A few kilometers to the east, the Confluencia chronology shows reduced tree growth concurrent with both periods (Fig. 3). At this site, in stand CONF3 there are periods of abundant tree deaths centered on 1907–1912, 1942–1943 and 1953–1957, all of which coincide with reduced radial growth (Fig. 3). In the nearby CENT stand the 1910 to early 1920 period of mortality is less well defined, but above average numbers of trees died about 1940–1943 and 1955–1962 (Fig. 3). In stand CONF7, these three episodes of mortality and reduced radial growth are also recorded; however, in this stand a large number of trees also died during the 18th or early 19th centuries (Fig. 4). Advanced wood decay, however, prevented the precise dating of tree deaths prior to the 20th century.

Stands LCIP and FUTA, located ~280 km further south, record the mortality events of 1942–1943 and 1953–1957 noted in the northern stands (Fig. 5). Tree mortality in these stands, however, was also common in 1969–1970 and 1978–1983. Again, these four periods of mortality coincide with reduced radial growth (Fig. 5).

Tree mortality and climatic fluctuations

When dates of tree death for all nine stands are combined, periods of abundant tree mortality are evident

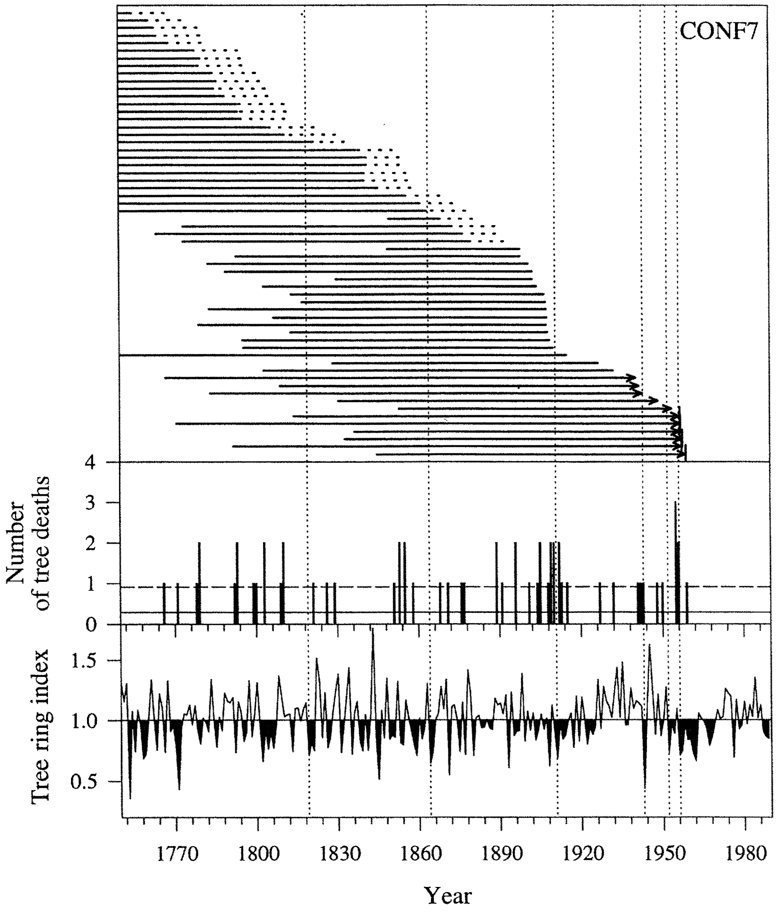

FIG. 4. Results of dendrochronological dating of dead *Austrocedrus* at CONF7. The tree ring indexes are from the Confluencia chronology ($n = 25$). Categories and designations are as in Fig. 2.

in 1907–1918, 1942–1943, and the 1950s (Fig. 6a). For the earliest period, the percentage of cross sections with bark is low (Fig. 6b), and, consequently many of the tree deaths may have occurred a few years later (i.e., many of the 1907–1910 dates may indicate death in ~1912–1914). For the two more recent periods of mortality, high percentages of samples with bark assure relatively precise dating of these events. Periods of abundant tree mortality are consistently associated with drought. The instrumental record shows that the 1910s, 1942–1943, 1953–1954, and 1956–1962 were periods of above average temperatures and below average precipitation during spring and summer (Fig. 6c). Extremely arid conditions were recorded in the springs and summers of 1912–1913, 1942–1943, and 1956 (Fig. 6d). The more precise coincidence of tree mortality and drought for the 1940s and 1950s probably reflects less accurate dating of tree death during the 1910s episode. The occurrence of regional drought during these periods of increased tree mortality is consistent with the reduced radial growth of surviving trees near each site (Figs. 2–5).

To statistically evaluate climatic conditions during periods of graphically determined above average tree mortality, slight deviations between the timing of tree death and its dendrochronological dating must be considered. Consequently, the following algorithm was used to generate a smoothed series of tree death dates (s_t) from the original dates of tree death (d_t):

$$s_t = 0.25(d_{t-2}) + 0.25(d_{t-1}) + 0.5(d_t).$$

This filter partially accounts for imprecisions associated with lack of ring formation during a dry year preceding tree death and erosion of one or two rings following tree death. Its application to the raw tree death dates clearly identifies the years 1912–1913, 1942–1943 and 1956–1957 as three peak periods of high mortality (Fig. 6a). For these objectively identified six years of peak mortality the mean moisture index is −2.89 (SD = 1.16) as opposed to 0.19 (SD = 1.49) for all other years from 1906 to 1989 ($P < 0.0001$; t test).

Intra-regional differences in tree mortality patterns

Despite the general regional synchroneity of climatic variation in northern Patagonia (Villalba 1990, Villalba and Veblen 1997*b*), there are significant north–south

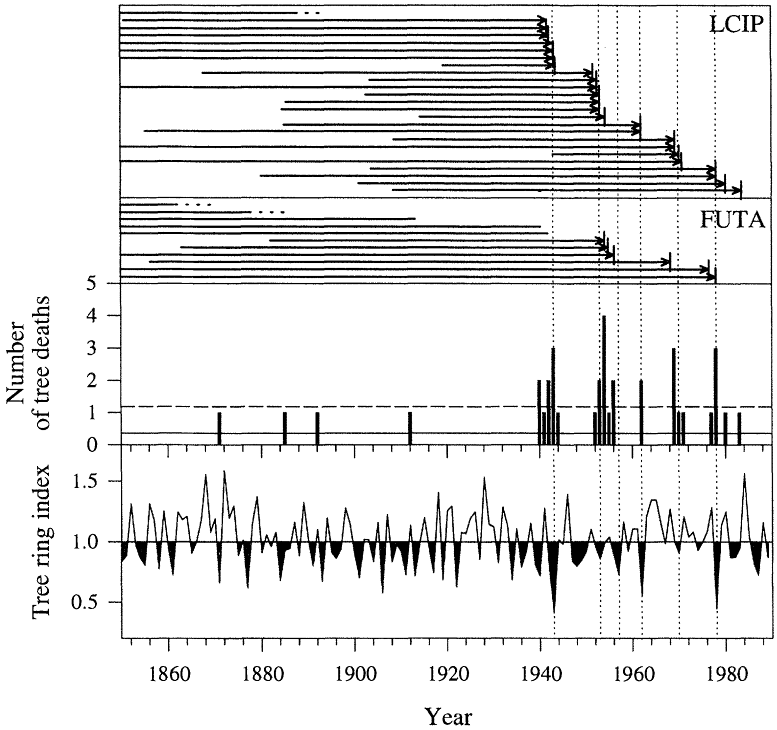

FIG. 5. Results of dendrochronological dating of dead *Austrocedrus* at LCIP and FUTA. The tree ring indexes are from the Nahuel Pan chronology (n = 28). Categories and designations are as in Fig. 2.

differences in the occurrence of mortality episodes. For the northern group (~39° S), the mortality episode of the 1910s is marked but the 1950s episode is relatively minor (Fig. 7). In contrast, the 1910s episode is less striking in the central group (~41° S) and is absent from the southern group (~43° S). The peak in tree mortality in the 1950s is substantially greater for the central and southern groups, and the early 1940s event occurs only in these groups (Fig. 7).

Different intensities of warm–dry climatic conditions along the forest–steppe ecotone appear to explain these differences in timing and intensity of tree mortality events. For the summer of 1912, the departure from the mean temperature at Collun-co (39°58′ S) in the north is substantially greater than that at Esquel (42°54′ S) in the south (Fig. 8). For the same year, precipitation deviation at Collun-co is more negative than that at Bariloche (41°09′ S) in the center. In contrast, the 1956 temperature and precipitation departures are more extreme in the center and the south (Fig. 8). For 1943, precipitation departures are similar at all three latitudes, but the slightly higher temperatures in the center and south imply greater water deficits. A similar north–south pattern of climatic variation is indicated by intra-regional variation in radial growth of *Austrocedrus* during the year following extreme droughts (Fig. 9). However, for the 1912–1913 and 1942–1943 droughts the occurrence of two years of consecutive drought in combination with the autocorrelation of ring widths result in the years of maximum growth reduction being lagged by one year (Villalba and Veblen 1997*b*). In contrast, the 1956 drought occurred mainly in a single year (Fig. 6) and maximum growth reduction occurred in the 1956–1957 growing season (Fig. 9). For 1913–1914, although tree growth is below average over the entire region, the most severe growth reduction in tree growth is in the north (Fig. 9). In contrast, for 1943–1944 and 1956–1957 growth reduction is least in the north.

Inter-tree variations in growth response to drought

Consideration of radial growth patterns of individual trees reveals substantial variation in response to drought (Fig. 10). Depending on drought severity and the physiological condition of the tree, some trees die during the drought and others remain alive a few more years; however, most will recover from the adverse climatic events. Among the trees that die during droughts, there is no unique tree ring pattern that might indicate which trees are predisposed to die. For trees that died during or soon after droughts, the previous tree growth may have been gradually declining, fluctuating around a mean, or increasing (Fig. 10).

A common pattern observed in cross sections from dead trees is the formation of a few extremely narrow rings right after onset of the drought. These trees are not immediately killed by adverse climatic conditions, but many do not recover from the damage caused by

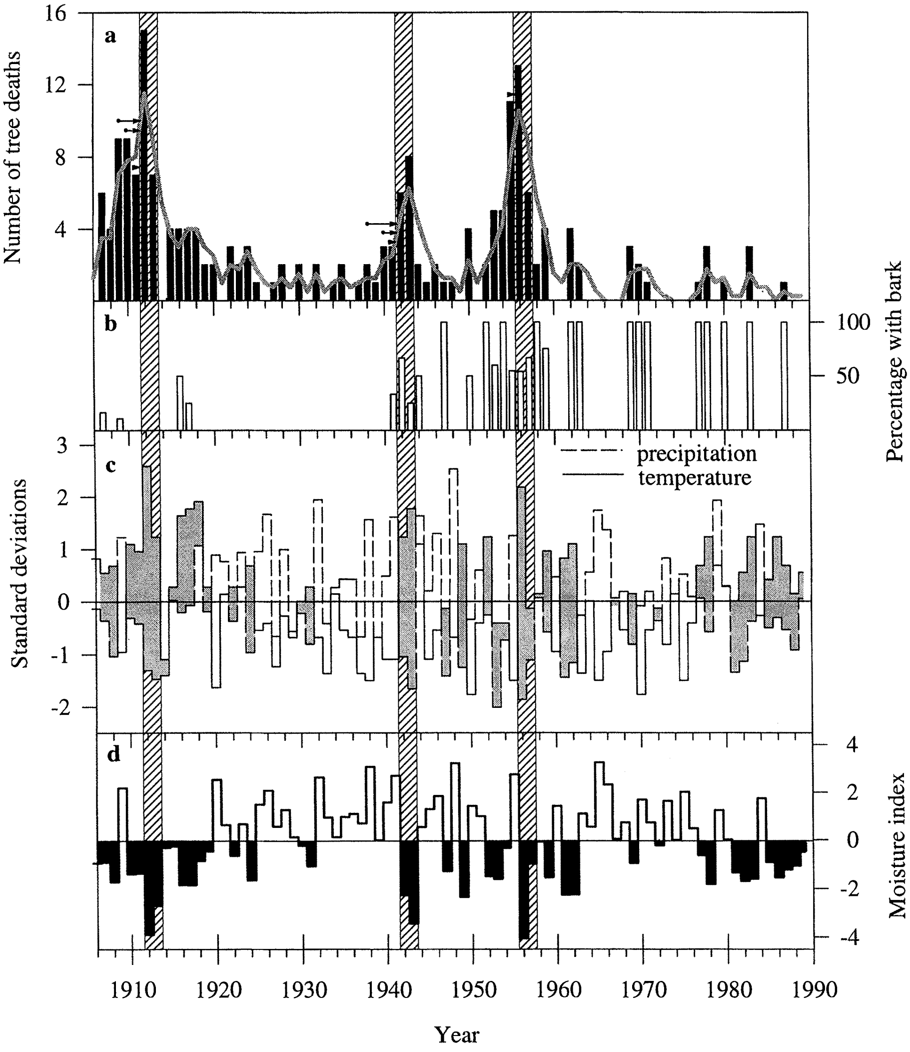

FIG. 6. Number of *Austrocedrus* deaths per year (a), percentage of cross sections with bark for each year (b), regional mean spring–summer (October through March) temperature and precipitation departures (in standard deviations) for 1906–1989 (c), and spring–summer moisture index (d). Slanted lines indicate periods of severe droughts associated with the three most important peaks in tree mortality since 1906. Some mortality dates appear to lead severe droughts by one to several years due to erosion of rings and failure of some trees to produce rings during years of extreme droughts; such dates are joined to the appropriate drought years by horizontal arrows. See the text for the filter used to produce the smoothed line in (a) and the derivation of the moisture index in (d). In (c) shaded areas indicate periods when temperature departures were positive and precipitation departures were negative (i.e., drought). In (d) negative values indicate warm and dry conditions.

the drought and die a few years to a few decades later (Fig. 11). In some trees extreme droughts are followed by stepped declines lasting many decades before the tree dies (Fig. 11c,d). After suffering one or more reductions in growth, trees finally die during a subsequent drought. Most trees, however, recuperate their normal level of growth after adverse climatic events. Indeed, after droughts some trees may increase the rate of radial growth due to the release of resources from the death of other trees (Fig. 11e,f).

Relationship of tree mortality episodes to synoptic climatic patterns

Mean patterns of sea level pressure along the west coast of South America (30–45° S, 70–80° W) differ for years of severe drought (and associated mortality events) and non-drought years (Fig. 12). For years of severe drought, atmospheric pressure is generally higher during the current growing season; during the warmer months (October through March) the differences are statistically significant ($P < 0.001$; *t* test). The higher atmospheric pressure indicates a more intensively developed and southerly located southeastern Pacific subtropical anticyclone during summer. Blockage of the westerly flow by a more southerly located anticyclone reduces the flow of oceanic humid air masses from the west and allows the incursion from the northeast of air masses of continental subtropical origin (Taljaard 1972, Pittock 1980*a*).

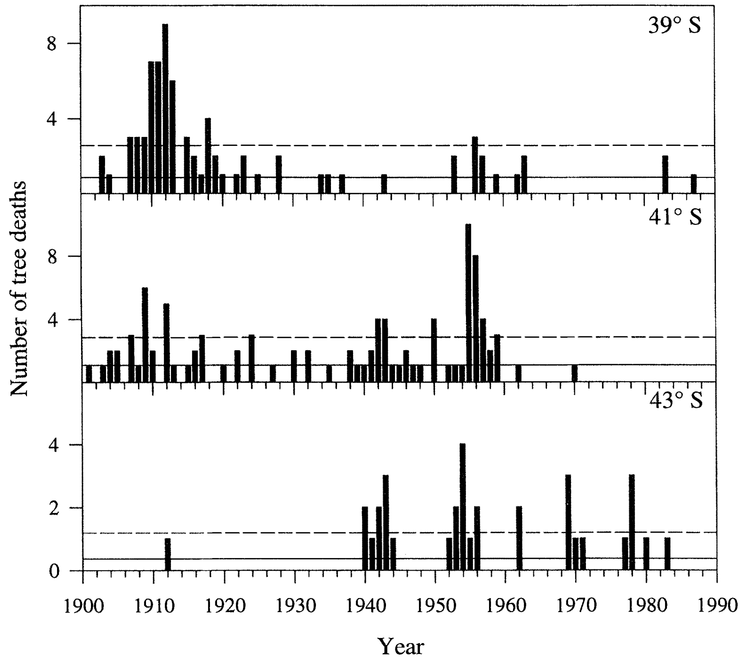

FIG. 7. Number of *Austrocedrus* deaths in the northern stands at 39° S (ÑORQ1, ÑORQ2, and ÑORQ5), the central stands at 41° S (PVNT, CONF3, CONF7, and CENT), and the southern stands at 43° S (LCIP and FUTA). For each sector, mean annual tree deaths and +1 SD (for 1900 to 1989) are indicated by a solid and a dashed line, respectively.

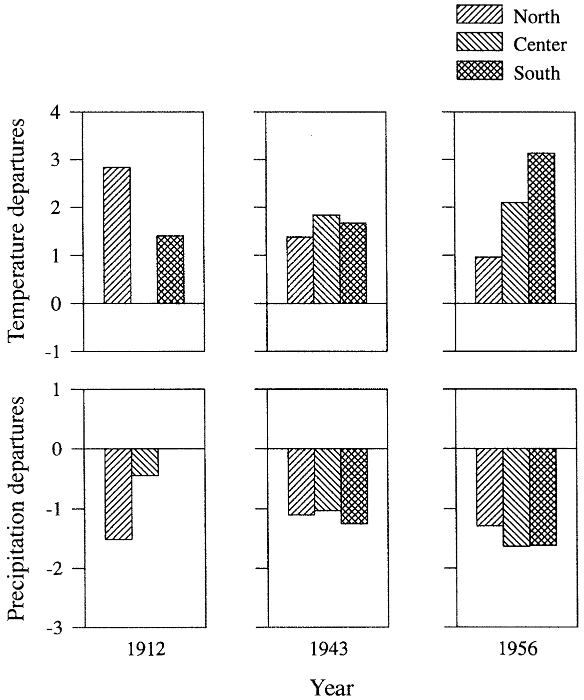

FIG. 8. Normalized departures (standard deviations) from mean spring–summer (October through March) temperature (above) and precipitation (below) for meteorological stations located in the north (Collun-co 39°58′ S), center (Bariloche 41°09′ S), and south (Esquel 42°54′ S) of the area sampled along the forest–steppe ecotone. For 1912, there are no temperature records for the central region and no precipitation records for the southern region.

The strength of the southeast Pacific high pressure cell is closely related to ENSO events (Aceituno 1988, Karoly 1989) that also influence temperature and precipitation in northern Patagonia (Kiladis and Diaz 1989, Villalba 1994). For the interval 1909 to 1981, spring and summer (October to March) temperature variations in Patagonia are significantly correlated with the Southern Oscillation Index (Wright 1989) which is based on sea level pressure differences in the central Pacific Ocean ($r = 0.30$, $P < 0.01$; Fig. 13). However, the strength of this relationship varies greatly during this period as shown by the correlation coefficient for an 11-yr moving average (Fig. 13b). The association between summer temperatures and ENSO is strong during the 1910s to 1920s and again in the 1950s to 1960s, but is nearly absent during the intervening period. The two intervals of high correlation contain two of the major episodes of drought-induced tree mortality (the 1910s and the 1950s) in northern Patagonia (Fig. 13c). The 1942–1943 episode of drought and tree mortality, although not correlated with a change in the Southern Oscillation Index, is associated with an El Niño event.

DISCUSSION

Major episodes of *Austrocedrus* tree mortality in northern Patagonia are centered on the 1910s, 1942–1943, and the 1950s which were all periods of exceptionally warm and dry springs and summers. Although the physiological cause of death cannot be determined by historical techniques, in the absence of any evidence of insect damage or disease we believe that tree death

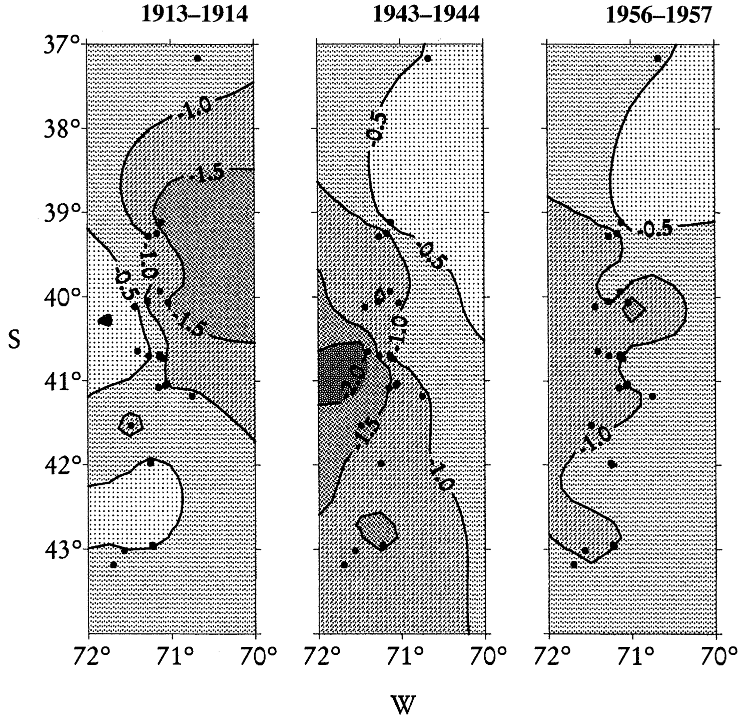

FIG. 9. Maps of mean spatial patterns of *Austrocedrus* radial growth (interpolated from 24 tree ring chronologies; Villalba 1995) for consecutive years associated with major episodes of *Austrocedrus* mortality. Dots indicate chronology sites.

is due directly to moisture stress. Peaks in tree mortality are associated with short (one or two year), extreme droughts. Although the mortality peaks in 1912–1913 and 1956–1957 occurred during the two driest years within decade-long dry periods, the mortality peak in 1942–1943 was encompassed by two wetter intervals. Annual climatic variations, which control year-to-year moisture availability, appear to have greater effects on tree survival than do long-lasting droughts characterized by gradual transitions from previous wet intervals. For example, although dry and warm conditions characterized most of the 1980s, there is no evidence of increased tree morality (Fig. 6).

Good preservation of standing and fallen boles of *Austrocedrus,* probably due to both the relatively dry climate and the high resin content of this species, generally permitted good cross dating of the outermost ring on dead trees. However, erosion of rings and failure of some trees to produce rings for one or two years during severe droughts as they are dying results in some inaccuracies. Thus, in some comparisons of dates of tree death with records of climatic variation (Figs. 2–6), episodes of increased tree mortality appear to lead severe droughts by one to several years. This is more evident in the 1910s because of the larger percentage of dead trees lacking bark. More accurate dating of the death of trees that died since the 1940s was facilitated by the large percentage of samples that retain bark and by the presence of the outermost ring around the entire cross section. Even for trees with bark, missing rings during a year of severe drought results in some imprecision in determining dates of death. For example, on a large number of dead *Austrocedrus* the outermost ring is 1955 even though drought did not occur until 1956. The generally close coincidence between the dates of the outermost rings and severe droughts in 1942–1943 and 1956–1957, however, implies that on most trees rings continue to be produced to within one to two years of death. The use of a filtered series of tree death dates (Fig. 6a) partially overcame the dating inaccuracies and aided in objective identification of peak periods of mortality.

Non-climatic causes of tree death must also be considered in trying to explain episodes of tree mortality. For example, patchy mortality of *Austrocedrus* is also suspected to be caused by root pathogens (Havrylenko et al. 1989), but this type of mortality is limited to higher rainfall areas than our sample areas. Major episodes of tree mortality in northern Patagonia have also been related to the effects of strong earthquakes, particularly at sites of unstable substrate (Veblen et al. 1992*a*, Kitzberger et al. 1995). However, occurrence of extensive earthquake-induced mortality appears to require coincidence with drought (Kitzberger et al. 1995), and in the present study none of the mortality peaks coincide with earthquakes. Thus, in assessing possible causes of episodic mortality of *Austrocedrus* it is important to consider the potential synergistic effects between non-climatic disturbances such as earthquakes and climatic variation. Similarly, past episodes

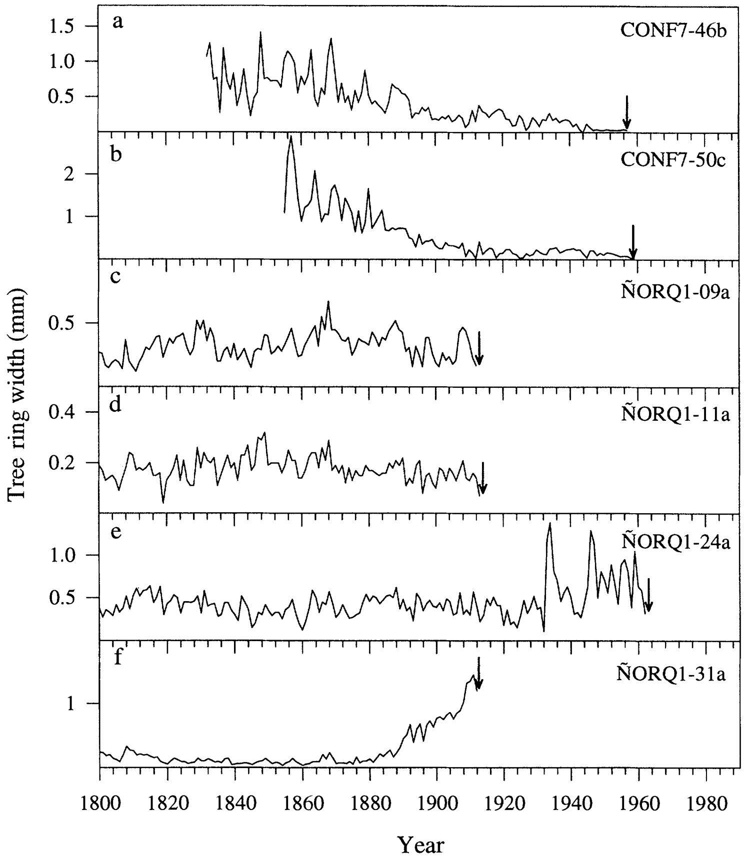

FIG. 10. Selected tree ring series for individual *Austrocedrus* showing variable patterns of growth prior to death. Dates of tree death are indicated by arrows.

of regionally extensive disturbance such as stand-initiating fires could also result in synchroneity of tree mortality over large areas due to a combination of self-thinning and senescence of narrowly even-aged cohorts (Oliver and Larson 1990, Mueller-Dombois 1993). However the *Austrocedrus* stands we studied were all open woodlands where self-thinning is much less intense than in dense stands of mesic habitats. Also, the age structures of these open woodlands indicate that trees established over multi-decadal to multi-centennial time periods so that synchronous mortality due to cohort senescence is unlikely (Villalba and Veblen 1997*a*).

Severe droughts in northern Patagonia, which coincide with major episodes of *Austrocedrus* mortality, are associated with changes in the intensity and latitudinal positions of the southeast Pacific high-pressure cell. During El Niño events, pressure is anomalously low over the eastern sector of the Pacific, particularly in the domain of the subtropical high (Aceituno 1988). In northern Patagonia, positive departures of summer temperature follow the warm El Niño events (Kiladis and Diaz 1989). Conversely, most cold events (La Niña) correspond to cooler summer conditions. However, there are large variations in the effects of ENSO on Patagonian climate depending on the timing, duration, and amplitude of the events (Villalba 1994). Two of the most severe droughts and tree mortality episodes of this century occurred during decades (the 1910s and 1950s) when interannual variations in temperatures in northern Patagonia were highly correlated with the Southern Oscillation Index. During the period of most extended drought in this century in northern Patagonia, moderate ENSO events occurred in 1911–1912 and strong ENSO events occurred in 1913–1915, and 1918–1919 (Quinn and Neal 1992). Similarly, during the 1950s moderate ENSO events occurred in 1951–1953 and a strong event in 1957.

Not all Southern Oscillation events, however, are associated with the regional El Niño (Deser and Wallace 1987, Diaz and Pulwarty 1992). The mortality episode in 1942–1943 is associated with climatic anomalies on the coast of northern Peru equivalent in magnitude to the El Niño events associated with the two other severe drought periods. Even though the year 1943 is not listed as an ENSO event (Diaz and Kiladis 1992), there was a coincidence of high summer temperatures in Patagonia and heavy rain and severe floods along the coastal plain of northern Peru (Deser and Wallace 1987).

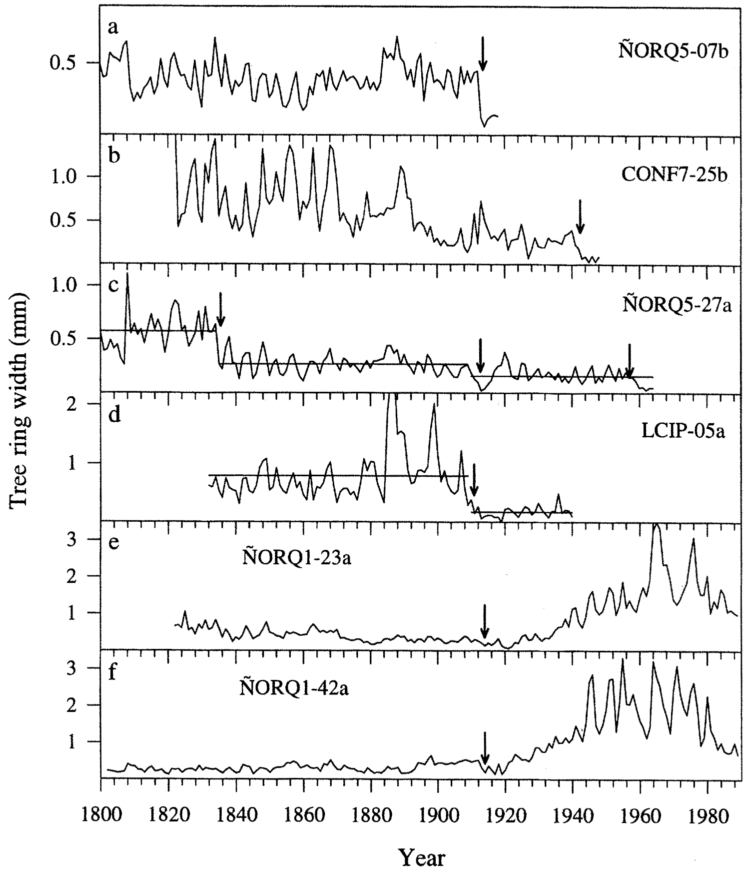

FIG. 11. Selected tree ring series for individual *Austrocedrus* showing variable responses to extremely warm and dry climatic events. Arrows indicate major changes in mean ring-width, and horizontal lines show stepped declines in tree growth rates.

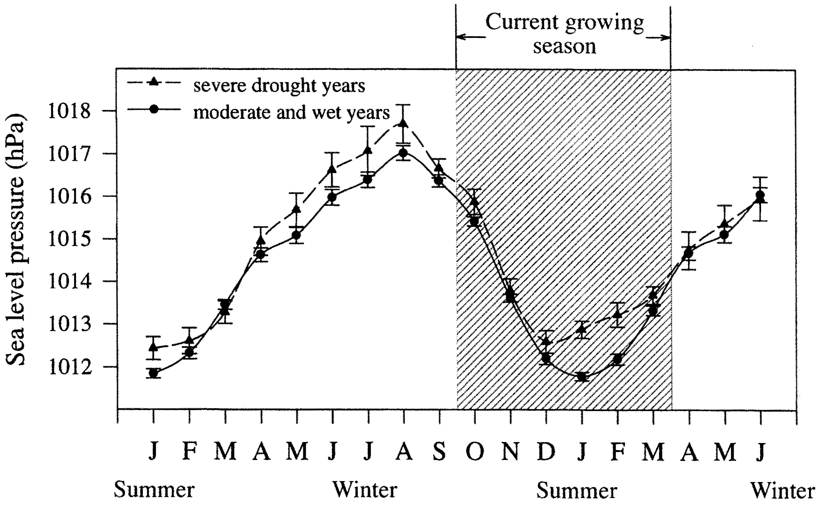

FIG. 12. Mean sea level pressure in hecto-Pascals (hPa) off the Chilean coast (30–45° S, 70–80° W) during summers (October through March) of severe droughts vs. summers of moderate to wet conditions along the forest–steppe ecotone in northern Patagonia for 1911–1985. Severe droughts (1912–1913, 1916–1917, 1942–1943, 1949, 1956, 1961–1962, and 1978) exceed −1.75 SD from the mean moisture index (Fig. 6d). Pressure data are from Jones (1991).

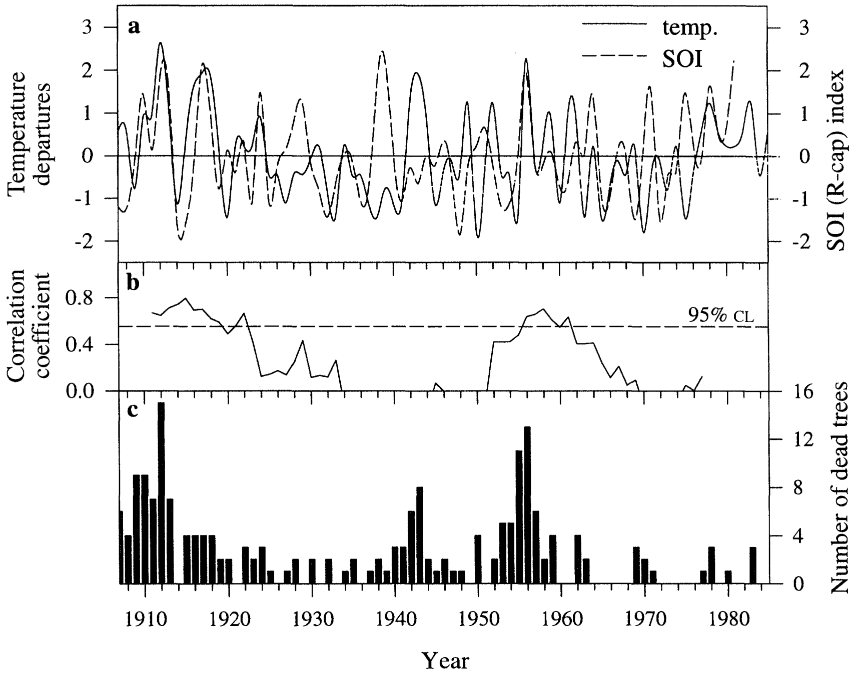

FIG. 13. (a) The Southern Oscillation Index (SOI; R-cap index from Wright 1989) and spring–summer (October through March) temperature departures (standard deviations) in northern Patagonia, (b) moving Pearson correlation coefficients between the SOI and mean spring–summer temperatures plotted on the centroids of 11-yr periods, and (c) number of *Austrocedrus* deaths per year.

Analogous to this study of tree mortality, previous studies have demonstrated strong relationships between variations in the intensity and position of the subtropical high-pressure cell of the southeast Pacific and both fire regimes and *Austrocedrus* seedling establishment in northern Patagonia (Villalba 1995, Kitzberger et al. 1997). Fire occurrence in the *Austrocedrus* woodlands is strongly associated with ENSO events, in particular with the late phases of La Niña events; at longer time scales of ~50 yr, periods of increased ENSO activity coincide with increased fire occurrence (Kitzberger and Veblen, 1997). Successful establishment of *Austrocedrus* seedlings in dry habitats near the steppe is strongly associated with decade or longer periods of cool–wet summers such as 1963 to 1979 (Fig. 14; Villalba and Veblen 1997*a*). In contrast to the effectiveness of short periods (i.e., 2 yr) of drought in causing increased mortality of adult *Austrocedrus,* substantial increases in regeneration appear to depend on periods of cool–wet summers lasting for a decade or more (Villalba and Veblen 1997*a*). Warm–dry summers and a lack of *Austrocedrus* seedling survival in dry habitats since the late 1970s (Fig. 14) is associated with the predominance of the negative mode of the Southern Oscillation (i.e., El Niño conditions) during the same period (Villalba and Veblen 1997*a*). Frequencies and types (cold vs. warm) of ENSO events are likely to continue to vary at decadal scales, as shown by the tree ring record from central Chile and northern Patagonia over the past 800 yr (Villalba 1994). Future increases in intensity and/or frequency of El Niño events is likely to be accompanied by increased episodes of mortality of adult *Austrocedrus* as well as periods of poor seedling survival in drought-prone habitats.

The occurrences of severe droughts as well as periods of above average moisture availability during the present century are important natural experiments for the study of the effects of interannual and interdecadal climatic variability on the population dynamics of *Austrocedrus.* Interpretation of the effects of a period of anomalous climate on forest dynamics needs to consider the potentially confounding influences of the subsequent occurrence of other climatic anomalies as well as disturbances such as fire and grazing. For example, the 1963–1979 period of abundant tree establishment that coincides with cool–wet conditions in northern Patagonia is easily detectable in tree age structures (Fig. 14), because both fire frequency and pressure from livestock have been low during and subsequent to this period (Eriksen 1971, Veblen et al. 1992*a*, Kitzberger et al. 1997). In contrast, cool–wet conditions in the 1920s and 1930s might have also favored increased tree establishment but heavy pressure from livestock that peaked in numbers in the 1930s–1940s (Eriksen 1971) may have prevented their survival. Similarly, regionally extensive droughts in 1942–1943 and 1956–1957 probably would have increased mortality among the trees that established in the 1920s–1930s. This and re-

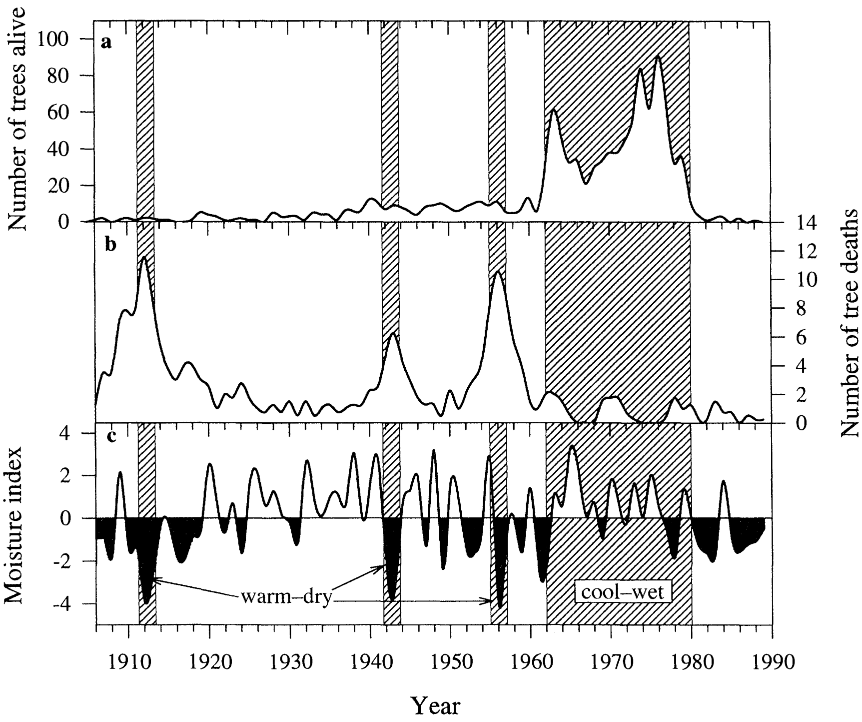

FIG. 14. (a) Composite age-frequency distribution of 1100 *Austrocedrus* trees in 26 stands, (b) numbers of tree deaths in a subset of nine stands from the same 26 stands, and (c) the moisture index for the period 1906–1989. Slanted lines indicate anomalously warm–dry or cool–wet periods associated with peaks in tree mortality or establishment, respectively. Panel (a) is modified from Villalba and Veblen (1997*a*).

lated studies in northern Patagonia (Veblen et al. 1992*a*, *b*, Kitzberger et al. 1997, Villalba and Veblen 1997*a*, *b*, Kitzberger and Veblen, 1997) are revealing the influences of both climatic variation and human activities on ecological processes by examining tree demographic and disturbance patterns across a broad range of spatial and temporal scales.

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