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Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends

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Summary

1 Although climatic variability is a strong driving force for forest dynamics, drought-induced mortality has generally received much less attention than other types of disturbance.

2 In 1998–99 northern Patagonia was affected by one of the most severe droughts of the 20th century, coinciding with a strong La Nina event, and this caused high mortality of *Nothofagus dombeyi* (coihue), the dominant tree species in Nahuel Huapi National Park.

3 Factors involved in determining this mortality of *N. dombeyi* were examined at both patch and tree level. Radial growth characteristics of killed trees and survivors were compared by dendrochronological analyses. Relationships between growth and climate were investigated using response function analysis.

4 At the tree scale, individuals with variable growth were more prone to die from drought than trees with more regular growth. Juveniles whose growth patterns showed sensitivity to climate were particularly likely to die. However, among both killed trees and survivors, older trees were less sensitive to climate.

5 Mean growth rate was a good predictor of mortality in adult trees, showing that trees with slower growth rate were more susceptible to drought. Susceptible trees may have been negatively affected by the drought that affected northern Patagonia in 1956–57.

6 These results underscore the importance of considering drought-induced tree mortality as a non-random mechanism influenced by site, previous stress/disturbance history, ontogeny, vigour, climatic sensitivity and physiology. Spatial patterns of extensive full and partial crown dieback, which are evident in many temperate forests worldwide, may reflect the superposition of these predisposing factors on strong/repeated interannual fluctuations of climate.

Key-words: climatic variation, drought, growth patterns, likelihood to death, *Nothofagus dombeyi*, response function, sensitivity, tree mortality, tree rings

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Introduction

Extreme climatic events such as regional droughts are likely to produce rapid, profound and long-lasting effects on ecosystems and landscapes if large numbers of individuals of dominant or key structural species are killed (IPCC 1996). In tropical forests, drought-related tree mortality can produce important compositional shifts by removing drought-sensitive species (Condit 1998). In temperate broadleaved forests, drought-induced gaps may become the dominant disturbance and therefore be the major mechanism of tree-replacement (Clinton *et al*. 1993). In semi-arid woodlands, drought may cause massive dieoffs that contribute to ecotonal shifts along moisture gradients (Betancourt *et al*. 1993; Allen & Breshears 1998; Swetnam & Betancourt 1998) and accelerate shrub invasion (Grover & Musick 1990).

If global-scale models are to incorporate interannual climatic variability, mechanistic insights will be needed to link climatically anomalous events with physiological or demographic processes (Walker 1996) such as drought-induced tree mortality. Although factors such as environmental stress, biomass allocation patterns, ontogenic changes in susceptibility, growth variability, previous growth trends and genetic variability in drought

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resistance, that predispose adult trees to remain alive or die during severe droughts (Cobb *et al.* 1994), are critical for understanding and predicting community-level responses to altered climatic regimes, they are poorly understood.

Tree mortality events related to increased ENSO-related variability (e.g. the warm events of 1983 and 1997, Condit *et al.* 1995; Williamson *et al.* 2000, respectively) have been monitored in permanent plots in tropical regions. This has allowed quantification of mortality rates and assessment of the resilience of ecosystems to episodic droughts, whereas, in temperate regions, examination of annual rings allows retrospective analysis of the consequences and causes of drought-induced mortality (Cherubini *et al.* 2002). Dating of death and establishment, in combination with live tree ring width data, offers information on mortality and establishment rates as well as on growth responses of trees surviving droughts that occurred more than 100 years ago (e.g. Kitzberger *et al.* 1995; Villalba & Veblen 1997a; Villalba & Veblen 1998). On the other hand, for more recent mortality events, tree rings offer a unique opportunity to compare recent growth conditions and long-term growth patterns between trees that died and those that have survived the drought (Pedersen 1998; Ogle *et al.* 2000; Wyckoff & Clark 2002). Such comparisons provide information on how biomass allocation patterns, drought acclimation, tree decline (expressed as climatic sensitivity) and long-term growth patterns may predispose individual trees to mortality.

Drought may produce instantaneous large-scale water shortage (such that supply falls below the normal range of variability), and thus have an adverse effect on growth. However, plasticity may produce phenotypes that can offset the potential growth-limiting effects of drought, via a range of physiological and morphological process. If instantaneous effects predominate, trees in more water-limited situations will be more prone to die. Predictions at different spatial scales (from coarser to finer) are that trees located at the dry end of a rainfall gradient, on sun-facing slopes, on dry ridges or on shallow soils will be more prone to die, as will exposed individuals. Trees that experience higher interannual growth variability and higher climatic sensitivity are expected to have increased mortality risk. On the other hand, plasticity may lead to drought-induced death occurring more in trees that normally grow in an environment with a relatively constant water supply. These individuals, which develop shallow root systems and have high above/below-ground biomass ratios, may suffer more from extreme water shortage and high temperatures than trees periodically exposed to such shortages. Trees located closer to streams, in deeper, well-developed soils or growing at higher densities would then be expected to suffer higher mortality.

Over a longer time frame, and if background mortality is more diffuse, these processes may interact with overall decline in populations. The decline-disease theory (Manion 1981) suggests that a concatenation of stress factors acting over long periods during a trees' lifetime may be responsible for its death. Integration of the multiple stresses faced by a tree leads to a growth decline and this is proposed to be the main factor involved in the onset of tree weakening and increased susceptibility to subsequent stress (Monserud 1976; Pedersen 1998). Manion's model predicts that factors such as previous droughts or insect attacks may lead to symptoms of decline, including partial crown dieback, insect and hemiparasite infestations, sharp growth declines and slow sustained radial growth, and the affected trees will become susceptible to death from factors such as a new drought. The cumulative effects of repeated drought on tree mortality are important in the context of communities changing in response to changes in mode and amplitude of climatic variability. For example, red oak mortality in the Appalachians during droughts in the 1970s was, in part, related to a prior severe drought in 1925 (Stringer *et al.* 1989).

The forest steppe-ecotones of northern Patagonia are particularly sensitive to interannual climatic variability, which affects tree demography both directly (Villalba & Veblen 1997a, 1998) and, indirectly, via fire regimes (Kitzberger & Veblen 1997; Kitzberger *et al.* 1997; Veblen *et al.* 1999). This has important consequences for community dominance, landscape composition, configuration and shrub/grass encroachment (Veblen & Lorenz 1987; Kitzberger & Veblen 1999). Episodes of massive mortality of *Austrocedrus chilensis* (D. Don) Flor. *et* Boult over the past *c.* 90 years coincide with exceptionally dry springs and summers during the 1910s, in 1943–44 and in the 1950s (Villalba & Veblen 1997a, 1997b, 1998; Villalba *et al.* 1998). Similarly, on the eastern side of the Andes, strong recurring earthquakes affect mixed *Nothofagus dombeyi* (Mirb.) Blume–*A. chilensis* forest and the occurrence of strong seismic events during periods of drought resulted in localized episodic tree mortality on unstable substrates (Kitzberger *et al.* 1995).

Abundant dead-standing trees and partial crown dieback are conspicuous features of northern Patagonian *Nothofagus*-dominated forests (Veblen *et al.* 1996). Although the aetiology of this dieback is not fully understood, decline has been attributed to post-fire cohort senescence in combination with negative effects triggered by seismic events or previous droughts (Veblen *et al.* 1996). Understanding the predisposing causes of drought-induced regional-scale *Nothofagus* mortality in northern Patagonia would allow generation of new conceptual models of forest dynamics that incorporate dieback as a source of opportunity for tree replacement in the context of variable climate and previous disturbances.

During 1998–99, strong La Niña conditions in the western tropical Pacific and an anomalously high polarity of the Antarctic Oscillation (i.e. a strengthened polar vortex; Thompson & Wallace 2000) led to severe drought in northern Patagonia (annual rainfall was the lowest since recordings began in 1905). This climatic event resulted in massive mortality of the 25–40 m tall evergreen tree *Nothofagus dombeyi* (coihue) near its eastern distributional limit towards the Patagonian steppe. In Nahuel Huapi National Park, more than 11 000 ha of forest (*c*. 10% of the *N. dombeyi* forests) had > 25% mortality and *c*. 680 ha had > 75% of trees killed (Bran *et al*. 2001).

We examined the factors involved in determining *Nothofagus* mortality following this drought. At the stand scale, we proposed that if mechanisms related to the instantaneous effects of drought are dominant, episodic mortality would be greatest at the xeric ends of water availability gradients (eastern xeric populations, those with low basal area, on north-facing slopes, rocky ravines or thin soils and non-riparian forests). However, if drought tolerance overcompensates for these effects, we would expect to find higher mortality at intermediate situations (central submesic forests, high basal area, east/west facing slopes, riparian/coastal forests, valley bottoms). If decline predisposes a tree to death, we additionally expected to find higher mortality in forests with evidence of decline (e.g. high density of dead-standing and partially killed trees, heavy infestation with boring insects or mistletoe).

At the individual scale, we expected that more exposed, climatically sensitive trees and trees with large year-to-year growth variation would be more prone to die if instantaneous effects predominated, but trees within closed stands with relatively high leaf area, little climatic sensitivity and low interannual variability in growth would be more affected if drought acclimation was important. On the other hand, if previous decline determines tree death, we expected to find lower mean annual growth and symptoms of decline (insect galleries/woodpecker cavities, partial crown dieback) in trees that died compared with trees that remained alive.

Materials and methods

STUDY AREA

The study area encompasses the foothills of the Andes in the eastern region of Nahuel Huapi National Park (*c*. 40°36′ to 41°32′ S and 71°16′ to 40′ W; Fig. 1). Layers of volcanic ash cover the glacial topography, and soil throughout the region is derived from these parent materials (Andosol type soils). Precipitation in northern Patagonia is seasonally distributed, with approximately 60% falling between May and August At this latitude, mean precipitation decreases abruptly from *c*. 3000 mm year^{-1} at the main Andean cordillera to less than 500 mm year^{-1} only 80 km to the east (De Fina 1972), and vegetation along this gradient changes from

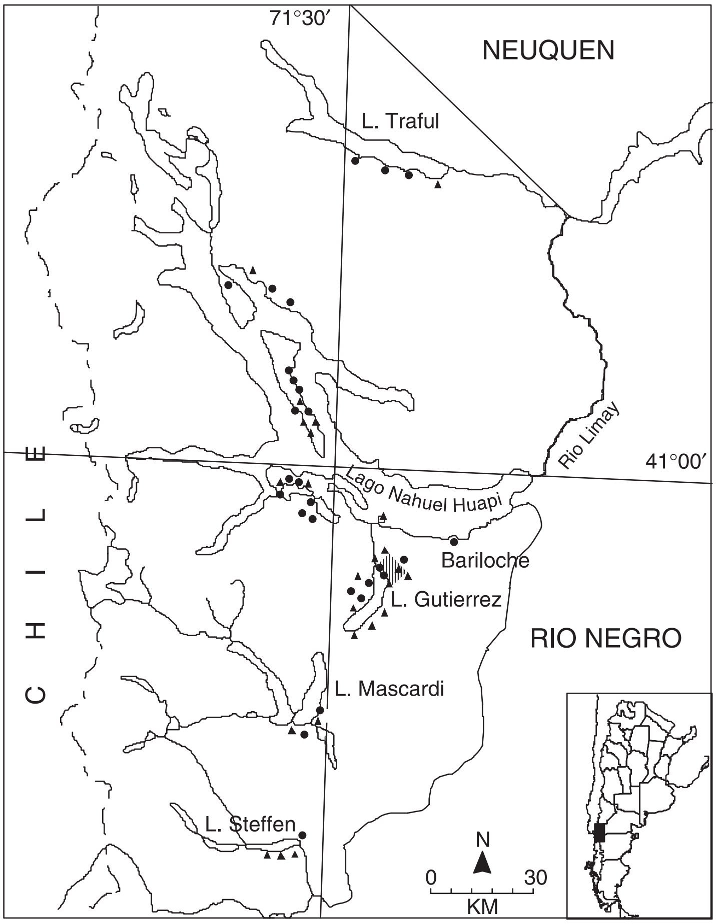

Fig. 1 Location map of the study area showing areas sampled at the stand scale in Nahuel Huapi National Park. High and low mortality stands depicted with triangles and circles, respectively. The area used for individual-scale sampling is shown as shaded.

temperate rain forests to semi-arid steppe. Near the continental divide in Argentina, and on the western slopes of the Andes, rain forests are dominated by tall evergreen *N. dombeyi* and have dense understories of tall bamboos (*Chusquea culeou*) but, as precipitation declines eastwards to *c.* 1500 mm year^{-1}, *A. chilensis* and *N. dombeyi* codominate extensive stands. Nearer the ecotone with steppe, the conifer *A. chilensis* grows as open woodland interspersed with sclerophylous shrublands and, at the eastern limit of tree-dominated communities (*c.* 500 mm year^{-1} rainfall), isolated *A. chilensis* are surrounded by a steppe matrix dominated by cushion shrubs (e.g. *Mulinum spinosum*) and bunchgrasses (e.g. *Stipa* spp. and *Festuca* spp.).

The forests sampled in this study consisted of even-aged, mixed *N. dombeyi–A. chilensis* stands that establish following devastating fire; *N. dombeyi* typically occurs exclusively in the main canopy, whereas *A. chilensis* are partially suppressed in the subcanopy (Veblen & Lorenz 1987).

Instrumental data for the region (1905–99) indicate that annual rainfall in 1998–99 was the lowest on record, as was March–February rainfall (266 mm, *c.* −2.6 standard deviations below the historical mean). In addition, summer (December–February) mean temperature was a record high (1914–2000), +2.1 standard deviations above the historical mean (Bariloche, Airport Station). As the dry, hot summer progressed in 1999, symptoms of water stress, such as leaf wilt and abscission, were more evident and many *N. dombeyi* trees suffered mortality. In the absence of evidence of other causes, we assume that death of *N. dombeyi* is related to the 1998–99 drought.

The most severely affected site, where tree-level factors were studied, was located on a south-west facing slope on Cerro Otto. This was the only forest area with drought-related mortality of > 75% (Bran *et al.* 2001). Elevations range from 800 to 980 m, and mean slope is similar across the site (23%).

PREDISPOSING STAND-LEVEL FACTORS

To assess the influence of drought at the patch level, we randomly selected 52 mixed *N. dombeyi–A. chilensis* stands to represent the ecological diversity of the forest in this area. Opportunities to determine stand mortality due to a particular drought event are rare because rapid sapwood decomposition and leaf abscission prevents assignment of a precise origin to dead stands. At the time of our sampling (2000–01), the dead trees still had brown foliage, which allowed us to assign mortality to the recent drought and to differentiate recent from former mortality (no foliage, partial or no bark). We selected these stands using aerial photographs of the affected area (Bran *et al.* 2001). On each photo, we placed a square grid that represented areas of *c.* 50 × 50 m on the ground. Stands were selected based on a stratified random sampling procedure to give 26 'dead' (> 50% of the trees dead) and 26 'live' sites (< 25% of the trees dead) encompassing the entire area affected by mortality (i.e. most of Nahuel Huapi National Park, *c.* 700 000 ha). At each site, we established a 0.04-ha plot (Elliott & Swank 1994; Pedersen 1998; Pedersen 1999) in which each tree (> 10 cm d.b.h.) was counted, measured for diameter at breast height (d.b.h.) and classified as either healthy or dead, except for long-standing dead trees without bark which were registered as prior mortality. To describe and compare the canopy structure, we measured canopy height, canopy openness (1 = separated, 2 = side by side, 3 = overlapped) and percentage of trees with partial crown dieback. Stand condition was assessed using percentage of trunks with signs of bark beetle or woodpecker attack, and degree of infection by the hemiparasitic mistletoe *Misodendrum* spp. and the pathogenic fungus *Cyttaria* spp. (1 = absence, 2 = isolated infections, 3 ≤ 25% infected trees, 4 = 25–75% infected trees, 5 ≥ 75% trees infected). The abundance of understorey was estimated using four cover classes (1 ≤ 25%, 2 = 25–50%, 3 = 51–75%, 4 ≥ 75%). Site conditions were recorded as slope (°), aspect, altitude, percentage rock cover, stoniness (1 ≥ 75% ground covered by stones, 2 = 25–75%, 3 ≤ 25%, 4 = absence of stones), thickness of the humus layer and proximity of water source.

We used stepwise discriminant function analysis (DFA; STATISTICA package version 5.1) to classify stands into alternative, *a priori* groups (in this case dead and live stands) and to detect sets of stand-level variables that maximized discrimination between live and dead patches.

PREDISPOSING TREE-LEVEL FACTORS

Based on all trees censed in all stands, we examined the association between mortality condition (dead/alive) and d.b.h. classes using a G-test. To examine the vulnerability of trees to death by drought, we selected a relatively homogeneous *N. dombeyi–A. chilensis* stand that had suffered *c.* 75% mortality. We randomly located a 100 m long transect and established five more transects, 60 m apart, parallel to the first transect (Savage 1997). We recorded the condition of the nearest juvenile (10 cm < d.b.h. < 30 cm, < 15 m high) and adult tree (≥ 30 cm d.b.h.) of *N. dombeyi* at 20-m intervals along the transects. For the 56 adults, 29 were dead and 27 live, and of the 55 juveniles located, 27 were dead and 28 live. For each of these, we recorded d.b.h., height (measured with a clinometer), foliage density (1 = high, 2 = intermediate, 3 = low), bole condition (1 = healthy, 2 = partially damaged, 3 = damaged), percentage of crown exposure and distance to nearest neighbouring tree (using the point-centred quarter method, Mueller-Dombois & Ellenberg 1974), and distance to the nearest stump. In addition, for adult trees only, we recorded crown position and degree of crown dieback (1 = healthy crown, 2 = minor branches dead, 3 = major branches dead, 4 = crown nearly dead).

We used DFA to evaluate tree-level factors that predispose an individual to drought-induced mortality by classifying trees into dead and live groups, based on sets of independent variables. This analysis was performed separately for juvenile and adult trees. We applied a stepwise procedure to attain a reduced set of variables that contributed most to the discrimination between groups.

RADIAL GROWTH CHARACTERISTICS AS PREDICTORS OF TREE DEATH

In many tree species, radial growth response to climate varies with age (Szeicz & MacDonald 1993; Ogle *et al.* 2000) and we therefore performed separate analyses on juvenile trees and adult trees. Suppressed trees (trees > 15 m tall but < 30 d.b.h., generally in subcanopy positions) were avoided because of potentially confounding growth responses. From each dead and live *N. dombeyi* tree sampled for predisposing tree-level factors, we used increment borers to extract two cores at breast height. We used standard dendrochronological procedures (Stokes & Smiley 1968; Fritts 1976) for processing all samples. After mounting and sanding smooth, we measured ring widths using a computer-compatible increment tree ring measurer (0.01 mm resolution) and a stereo microscope. Only cores with clearly visible rings and lacking any rotten section were used. Following the convention of Schulman (1956), the date of an annual ring was assigned to the calendar year when growth began. Most individuals exhibited signature years and these were used in cross-dating. Of 222 radii examined, only 161 radii (47 dead and 43 live juveniles, 38 dead and 36 live adults) could be successfully cross-dated.

To remove non-climatic age trends, each ring-width series was standardized using negative exponential and linear regression curves. This standardization transforms the non-stationary ring widths into a new series of stationary, relative tree-ring indices that have a defined mean of 1.0 and a relatively constant variance (Cook & Kairiukstis 1990). We used the CRONOL program from the Dendrochronological Program Library (DPL), and indices were obtained by dividing the raw width for each series by the predicted width given by the fitted model (Delgado 2000).

For all trees, we computed lifetime growth rate (mean ring width), recent (1988–97) and long-term (1973–97) growth rate for adult trees and both recent (1988–97) and long-term (1983–97) growth rate for juvenile trees, as well as sensitivity in mean ring-width index, and age at coring height. Mean sensitivity was calculated as an average of the absolute values of the individual sensitivities in a series following Schweingruber's (1983) equation. For samples that did not reach the pith, we determined the total age using a geometric technique (Duncan 1989; Kitzberger *et al.* 2000).

Because growth variability is not a surrogate for climatic sensitivity, we further investigated the relationship between growth and climate in live and dead trees using response function analysis and correlation functions (Holmes 1992). Response function analysis uses the principal components of monthly climate data as predictors and the ring-width chronology as predictand in a multiple regression analysis (Fritts 1976). Thus, we can estimate the statistical relationship between radial growth and climate. Tree-ring indices of live and dead trees were detrended using a cubic smoothing spline with a weighting factor equal to two-thirds of the series length (Roig Juñet 1991), and autoregressive modelling was performed on each detrended ring-width series. The use of this digital filter ensured that little low-frequency variance was lost in estimating and removing the growth trend (Cook & Kairiukstis 1990). We used the program ARSTAN (Holmes 1992) to develop standard chronologies corresponding to each of the four groups analysed (dead adults, live adults, dead juveniles and live juveniles). Mean monthly temperatures (1914–2001) and mean monthly precipitation data (1904–2001) from Bariloche station were used in the response function analysis and calculation of correlation coefficients. In the analysis we included climate data extending from April of the growth year (t) back to December of the previous growth year ($t - 1$).

Results

N. DOMBEYI MORTALITY AS A RESPONSE TO STAND AND SITE CONDITIONS

Patch-level mortality was best discriminated by a function that included as predictors (in decreasing order of importance) percentage of trees with beetle attack (−0.62), slope (−0.52), canopy height (0.42), and previous mortality (−0.42) (Wilk's Lambda = 0.68, $\chi^2(4) = 18.58$, $P < 0.0009$, see Appendix S1 in Supplementary Material). Note that previous mortality refers to the percentage of dead-standing trees but did not include, and was not related to, the percentage of trees with partial crown dieback. This function predicted high mortality on 73% of the stands with high mortality, and low mortality on 84% of low mortality stands and incorporation of additional variables did not further improve its classificatory power.

High mortality stands had significantly higher previous mortality and a higher percentage of insect attacked and previously dead, barkless trees (Table 1). Other commonly used indicators of dieback, such as partial crown dieback, infection by the pathogenic fungus *Cyttaria* or the hemiparasitic plant *Misodendrum* spp., were not significantly different between dead and live stands. Stand mortality was also independent of size and structure as indicated by similarities in mean diameter, standard deviation of diameter, stand density, canopy openness and understorey abundance. Heavily killed stands were located on significantly steeper, rockier slopes and were less tall than stands with low mortality, but altitude, aspect and proximity to rivers and coasts did not differ (Table 1).

Table 1 Comparison of variables between dead and live *N. dombeyi* stands. Significant differences based on Mann–Whitney *U*-test ($P \leq 0.05$) are shown in bold. §Indicates semi-quantitative predictors

Variables	Stand mortality > 50% (n = 26) Mean ± SD	Stand mortality < 25% (n = 26) Mean ± SD	*P*
d.b.h. (m)	0.47 ± 0.14	0.49 ± 0.13	0.305
SD d.b.h. (m)	3.04 ± 1.04	3.00 ± 0.85	0.816
Trees with partial crown dieback (%)	25.93 ± 15.42	33.69 ± 20.38	0.206
Trees with woodpecker damage (%)	2.56 ± 4.09	2.45 ± 4.09	0.966
Trees with bark beetle damage (%)	16.88 ± 15.55	7.83 ± 7.69	**0.032**
Prior mortality (%)	6.43 ± 6.68	2.25 ± 3.28	**0.011**
Density (trees ha^{-1})	460.20 ± 246.49	492.00 ± 265.16	0.570
Canopy height (m)	22.74 ± 8.19	27.35 ± 5.34	**0.011**
Understorey abundance (%)	70.19 ± 30.21	67.15 ± 32.30	0.824
Canopy openness§	1.65 ± 0.75	1.73 ± 0.53	0.470
Altitude (m)	800.77 ± 101.47	806.31 ± 83.09	0.562
Aspect (angle sine)	0.16 ± 0.71	0.21 ± 0.66	0.832
Slope (°)	17.50 ± 8.55	13.13 ± 8.00	**0.050**
Proximity to water (m)	132.35 ± 179.40	99.92 ± 147.76	0.345
Rockiness§	1.65 ± 0.80	1.23 ± 0.51	**0.021**
Stoniness§	3.23 ± 1.24	3.61 ± 0.90	0.278
Thickness of humus layer (cm)	19.96 ± 10.05	20.48 ± 9.19	0.869

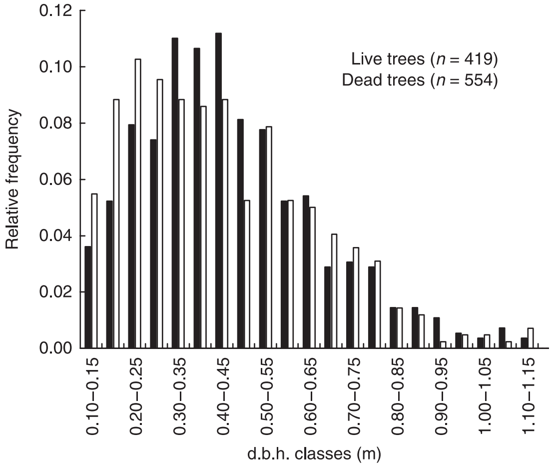

Fig. 2 Frequency distribution of diameter at breast height (d.b.h.) of surviving trees (solid bar) and dead trees (empty bar). Kolmogorov-Smirnov test, $P \geq 0.05$.

PREDISPOSING FACTORS ACTING AT THE TREE SCALE

In contrast to the results at the stand scale, where mortality occurred independently of mean stand structural variables, we found evidence of size-specific tree mortality caused by the drought. Although dead trees were found across the range of all size classes, the d.b.h. distribution of dead trees ($n = 554$) was more left-skewed than that of surviving trees ($n = 419$) (Fig. 2). The condition of trees after the drought (dead/alive) across all stands was dependent on d.b.h. ($G = 45.17$, 3 d.f., $P = 0.05$). Mortality was more frequent than expected by chance in lower size classes (< 30 cm) and less frequent than expected by chance in intermediate size-classes (30–50 cm).

Juvenile trees

Based on the tree-level data collected for juveniles, DF analysis failed to discriminate between dead and live *N. dombeyi* individuals (Wilk's Lambda = 0.83, $\chi^2(9) = 8.90$, $P = 0.44$ for the complete model; Wilks' Lambda = 0.83, $\chi^2(2) = 3.78$, $P = 0.15$ for the stepwise model). Nor did we find significant differences between dead and live trees for any of the predictors considered. Many of the trees (48% of dead and 60% of live individuals) were misclassified by the stepwise model. Although not significant ($P = 0.13$), there seemed to be a tendency towards higher mortality in juvenile trees located in more open microsites (e.g. treefall gaps, edges).

Trends in radial growth patterns did not differ between juveniles that died and those that remained alive after the 1998–99 drought (Fig. 3a). Juvenile trees that died in 1998/99 did not differ from survivors in their lifetime radial growth rate or recent (10 years pre-drought) growth rate (Table 2). However, although the differences were not significant, dead juveniles had grown markedly less in the 30 years prior to the drought than surviving trees, indicating that stressful conditions had probably influenced their growth. In contrast, sensitivity in ring-width index, particularly during the last 15 years, was significantly higher (*c.* 40%) in juveniles that died from the drought compared with those that survived (Table 2). Dead and live juveniles did not differ in total age and these differences in sensitivity in ring-width index could not therefore be due to different tree ages.

Correlation and response function analyses revealed that juveniles that died during the 98–99 drought were more responsive to climatic variability than those that survived (Fig. 4). In general, growth of juveniles that died had higher correlations with monthly climatic

Table 2 Aspects of *Nothofagus dombeyi* juvenile performance that reflect ability to survive drought. Significant differences based on Mann–Whitney *U*-test ($P \le 0.05$) are shown in bold

Variables	Dead juveniles Mean ± SD	Live juveniles Mean ± SD	*P*
Tree age (year)	35.08 ± 15.37	38.96 ± 16.48	0.278
Lifetime radial growth (mm year^{-1})	2.57 ± 0.96	2.56 ± 1.10	0.764
Recent 1988–97 radial growth (mm year^{-1})	2.43 ± 1.07	2.41 ± 1.05	0.969
Sensitivity in mean lifetime ring-width index	0.28 ± 0.08	0.23 ± 0.06	0.123
Sensitivity in mean 1988–97 ring-width index	0.27 ± 0.12	0.23 ± 0.09	0.337
Sensitivity in mean 1980–97 ring-width index	0.26 ± 0.10	0.22 ± 0.06	**0.003**
N° radii	43	44	

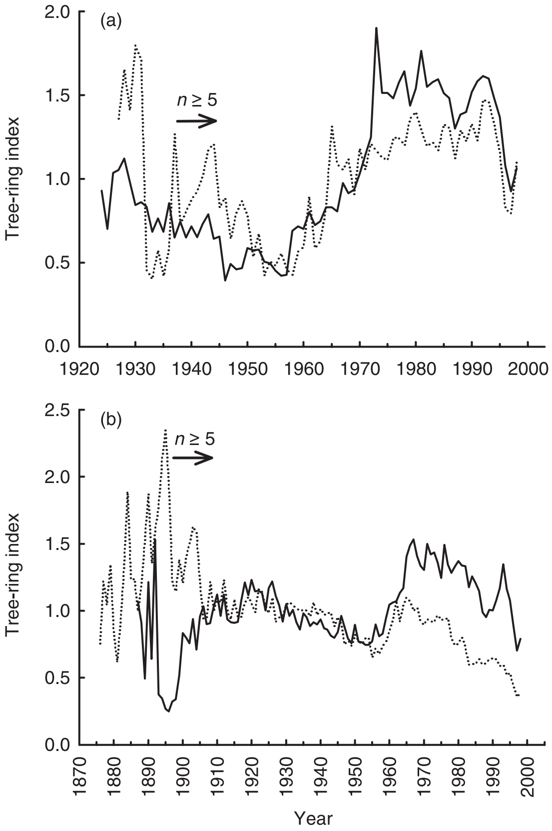

Fig. 3 Non-detrended tree-ring index from surviving (solid line) and dead (dotted line) *N. dombeyi* juvenile (a) and adult (b) trees. Arrows indicate periods for which the number of samples is ≥ 5. The observed ring-width series are fitted to an horizontal line passing through the mean ring width of the series; as the age-size-related trend in ring width has not been removed, this trend decays as a function of increasing radial increment.

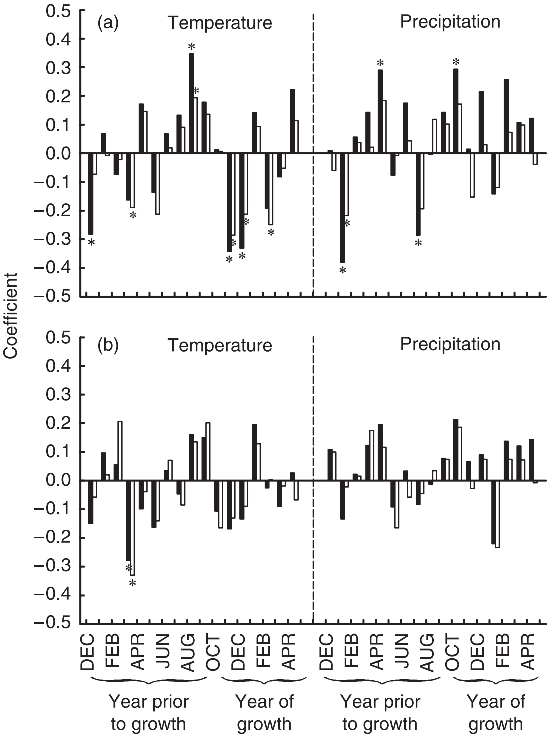

Fig. 4 Correlation function results (solid bars) and response function results (empty bars) for dead *N. dombeyi* juvemiles (a) and surviving *N. dombeyi* juveniles (b). Asterisks indicate response function elements or correlation coefficients significant at 95% confidence level.

variables (in absolute values), particularly in late spring–summer (November–February) of the current growing season, when juveniles that died had two- to threefold lower negative response and correlation coefficients with temperature, than survivors (Fig. 4). In the year of growth, none of the correlation or response coefficients were significant in juveniles that survived, but juveniles that died during the drought, responded significantly to October precipitation (+), July precipitation (–), November, December, February temperature (–) and August temperature (+). For the preceding growing season, juveniles that lived were correlated negatively only with March temperature (–), while juveniles that died responded to April precipitation (+), January precipitation (–), and December and May temperature (–). Overall, the percentage of total variance explained by the multiple regression in the response function analysis was 78% (based on 25 principal components retained) in juveniles that died and 47% (based on 26 principal components retained) in juveniles that survived.

Adult trees

Stepwise DFA revealed that the model that best discriminated between live and dead adult trees contained

Table 3 Predictors comparison among dead and live *N. dombeyi* adult trees. Significant differences based on Mann–Whitney *U*-test ($P \leq 0.05$) are shown in bold. §Indicates semi-quantitative predictors

Variables	Dead adults ($n = 29$) Mean ± SD	Live adults ($n = 27$) Mean ± SD	*P*
d.b.h. (m)	0.46 ± 0.17	0.49 ± 0.17	0.363
Height (m)	21.43 ± 7.81	23.69 ± 6.94	0.186
Partial crown dieback§	1.79 ± 0.93	2.48 ± 1.12	**0.016**
Trunk condition§	1.48 ± 0.77	1.26 ± 0.53	0.255
Distance between crowns (m)	1.31 ± 1.59	0.97 ± 0.89	0.856
Foliage density§	2.72 ± 0.61	2.44 ± 0.64	**0.048**
Crown position§	1.66 ± 0.80	1.89 ± 0.64	0.159
Distance to nearest neighbour (m)	6.47 ± 2.06	7.07 ± 2.14	0.313
Crown exposure§	2.65 ± 1.22	2.04 ± 1.04	**0.044**
Distance to nearest stump (m)	6.35 ± 7.00	5.90 ± 5.30	0.787

Table 4 *Nothofagus dombeyi* adults performance that reflects ability to survive drought. Significant differences based on Mann–Whitney *U*-test ($P \leq 0.05$) are shown in bold

Variables	Dead adults Mean ± SD	Live adults Mean ± SD	*P*
Tree age (year)	84.95 ± 15.58	81.35 ± 19.46	0.6591
Lifetime radial growth (mm year^{-1})	2.04 ± 0.53	2.54 ± 0.80	0.0303
Recent 1988–97 radial growth (mm year^{-1})	1.24 ± 0.67	2.27 ± 0.97	**0.0013**
Recent 1973–97 radial growth (mm year^{-1})	1.54 ± 0.61	2.59 ± 0.91	**0.0004**
Sensitivity in mean lifetime ring-width index	0.28 ± 0.04	0.26 ± 0.06	0.1184
Sensitivity in mean 1988–97 ring-width index	0.33 ± 0.08	0.25 ± 0.06	**0.0038**
Sensitivity in mean 1973–97 ring-width index	0.29 ± 0.06	0.23 ± 0.05	**0.0048**
N° radii	38	36	

two predictors: degree of crown dieback (0.7512) and percentage of crown exposure (−0.5798) (Wilk's Lambda = 0.84, $\chi^2(2) = 8.71$, $P < 0.013$, see Appendix S2), where positive coefficients are associated with surviving trees and negative values with dead trees. Seventy-nine per cent of dead and 64% of the surviving adult trees were correctly classified by the stepwise model. Crowns of trees that survived had noticeably more crown dieback, lower foliage density and less crown exposure than trees that died during the drought (Table 3).

Marked differences in radial growth rate were found between adults that died and those that survived the 98–99 drought (Fig. 3b), with trees that died during the recent drought showing a suppressed growth pattern during the last three to four decades. Dead trees also appear to show early life suppression but low sample numbers limit certainty on this aspect. Mean lifetime growth rates were generally significantly lower in dead *N. dombeyi* adults than in live ones (Table 4). This difference became highly significant when considering growth over the last 25 years and sensitivity in ring-width index was significantly higher in dead trees over the same period (Table 4). Dead and live adult trees did not differ in total age (Table 4).

Survivor and dead adult *N. dombeyi* chronologies showed, respectively, the lowest ($r = 0.37$) and the highest ($r = 0.59$) first-order autocorrelations. Response function analysis indicated that multiple regression models account for only a low amount of the total variance in surviving (38%, 26 principal components retained) and dead (30%, 26 principal components retained) adult trees (Fig. 5). Despite the weak climatic signal, growth was similarly influenced by monthly climatic variables in trees that died and survived the drought. In the former group growth was significantly related to October and December precipitation (+), and August (+) and December (–) temperatures. In the latter group, tree ring responded significantly to September, November and March precipitation (+), August temperature (+) and November and December temperatures (–). For adult trees, we used the period 1914–97 for the response analysis, but because some of the differences between juveniles and adults could be due to using different time periods, we recalculated the response and correlation functions for 1940–97, with similar results (data not shown).

Discussion

REGIONAL DROUGHT AND MORTALITY PATTERNS OF *N. DOMBEYI*

Regional mapping indicated that the highest mortality was restricted to the easternmost and lower altitude areas of the distribution of *N. dombeyi.* Meteorological records show that the 1998–99 drought was not restricted to the area of highest mortality: data from

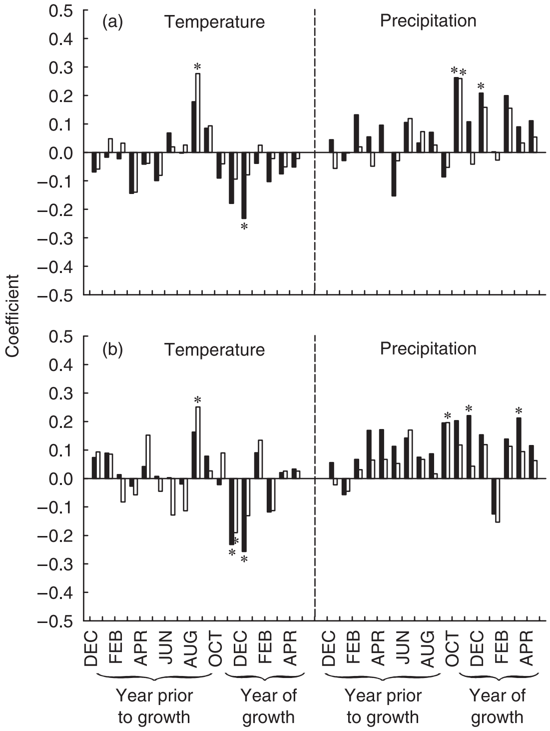

Fig. 5 Correlation function results (solid bars) and response function results (empty bars) for dead *N. dombeyi* adults (a) and surviving *N. dombeyi* adults (b). Asterisks indicate response function elements or correlation coefficients significant at 95% confidence level.

the continental divide, *c.* 100 km NW of Bariloche station (Paso Puyehue, *c.* 3000 mm annual precipitation), show that no precipitation fell during January and February of 1999 and that 1998–99 annual and summer precipitations were 1 SD below the average (APN, unpublished data). We therefore discard the possibility that local characteristics of the drought caused mortality to be restricted to the eastern populations, as the event affected the whole region.

Mortality over large scales appeared to be controlled by the instantaneous effects of the drought rather than by acclimation or plasticity. Other factors, however, may be indirectly involved in making these forests more susceptible during extreme droughts. The easternmost xeric forests were affected by extensive stand-devastating fires during European settlement (Veblen *et al.* 1992), and their canopy trees are therefore *c.* 100-year even-aged cohorts. These forests also have higher cattle loads, have been subjected to logging and may have been affected by previous droughts to a greater extent than more mesic stands. These characteristics make the eastern areas, as a whole, more susceptible and mature old-growth forests to be more resilient to extreme drought. A similar positive feedback between fire and land-use practices was proposed by Laurance & Williamson (2001) for Amazonian forests, but multiple correlations between variables makes it difficult to separate environmental effects from land use or historic legacies.

Although the 1998–99 drought was the strongest in recorded history, it did not affect *Austrocedrus chilensis*, a conifer that coexists with *N. dombeyi* in mixed stands and that spreads as monospecific forests and woodlands further east towards the steppe ecotone. Strikingly, easternmost populations of this species had suffered episodic mortality during the droughts of 1912–13, 1943–44 and 1956–57 (Villalba & Veblen 1998) and it is unclear why the even stronger 1998–99 event did not cause *A. chilensis* mortality.

One possibility is that differences in the timing of the heat shock may cause differential mortality of species with different phenologies. During the 1998–99 drought record temperatures occurred in full summer (January–February temperature was 2.25 SD above the mean), while late spring–early summer was less extreme (+ 1.15 SD for November–December). In contrast, the 1956–57 drought had abnormal temperatures in late spring and early summer (+ 2.78 SD) and a relatively normal full summer (+ 0.45 SD), with a similar, but less extreme pattern in 1943–44. *Austrocedrus chilensis* may be more susceptible to heat shock during the late spring, its period of maximal growth, than in summer, when onset of the dry season has triggered stomatal control and shut off most gas exchange activity. *Nothofagus dombeyi* may have less capacity for uncoupling from environmental conditions as it normally remains active, and thus susceptible to extreme heat and water demand, throughout the summer.

The weaker nature of the 1943 and 1956 droughts (no month as extreme as in 1998) may explain why these did not induce massive *N. dombeyi* mortality, although the 1912 drought, which seemed to have had similar characteristics to the 1998 event, may have produced joint *A. chilensis* and *N. dombeyi* mortality.

MORTALITY-PRONE STANDS

The 1998–99 drought affected a large area of temperate forest in northern Patagonia, but mortality was extremely patchy. The observation that high mortality patches had the highest abundance of dead-standing barkless trees, and trees infested with boring insects, supports the idea that recurring climatic/biotic events make forests more susceptible to subsequent stress. Our results are similar to patterns observed in New Zealand, where cohort structure induced by previous dieback events rendered stands more susceptible to subsequent dieback (Ogden 1988; Ogden *et al.* 1996).

As well as causing immediate mortality, drought may lead both to the presence of weakened trees with declining growth, and to increased canopy heterogeneity (trees with more exposed canopies, due to the gaps created), either of which may predispose trees to mortality during subsequent droughts. Live and dead wood portions of stressed *Nothofagus* individuals are attacked by numerous species of borers, especially *Cerambycidae* and *Curculionidae* (Veblen *et al.* 1996). Such attacks facilitate the entrance of pathogenic fungi and can cause a high degree of trunk rot. The Manion (1981) model proposes that pathogens and herbivorous insects may contribute to loss of vigour of the stand and increase its susceptibility to subsequent stress (e.g. drought). Hanson & Weltzin (2000) found that infection by bark beetle (*Dendroctonus* spp. e *Ips* spp.) was an important predisposing factor for the death of *Pinus ponderosa* forests during the mid-1950s New Mexico drought. Alternatively, bark beetles, opportunistic canker and root rot fungi, and possibly other organisms that specialize in the colonization of weakened plants, may initiate progression towards later death (Mueller-Dombois 1988; Ogden 1988; Elliott & Swank 1994; Swetnam & Betancourt 1998). As drought was very recent, mortality in our *N. dombeyi* forests is unlikely to be the result of beetle attack subsequent to the drought. Nor were other biotic factors, such as infestations by the mistletoes *Misodendrum* spp., not related to *N. dombeyi* mortality. Recent work by Tercero Bucardo (2001) has shown that *Misodendrum* loads increase as a function of passive re-infection on host branches, but this is relatively independent of stress and does not impose a heavy water use burden on their hosts.

We cannot, however, rule out the idea that site factors cause forests to suffer from recurrent drought. Surprisingly, except for slope, no single abiotic variable explained mortality at the stand scale. Severely affected forests were more frequently located on steeper slopes, associated with high rockiness and shallow soils, where suboptimal conditions cause *N. dombeyi* stands to attain lower canopy height (Veblen *et al*. 1996). As canopy height was the only structural variable associated with high mortality stands, separation of causality of structural vs. abiotic factors is again difficult.

MORTALITY-PRONE TREES

Our results confirm the prediction that *N. dombeyi* individuals with more variable growth were more prone to die from the drought than trees with more constant growth. This relationship held for both juveniles and adult trees, and was mainly due to differences in growth variability during the last 10–25 years. However, inter-annual variability in growth does not equate with climatic sensitivity as other endogenous and exogenous non-climatic factors may be influencing tree growth (Fritts 1976). In concordance with similar analyses on pinyon pine mortality in SW North America (Ogle *et al*. 2000), we found that those juveniles that were climatically sensitive were the most prone to die. Growth of juveniles that subsequently died was limited during years of high spring-summer temperatures, but was stimulated during years of higher winter temperatures. These juveniles may have been susceptible because they were located in more exposed positions or had less access to more permanent ground water sources, due to less allocation to roots relative to shoots (Caspersen & Kobe 2001).

Although adult trees that had died showed much more variable past growth than live trees, no substantial quantitative or qualitative differences in the response to climatic variables were found between live and dead individuals. This result contrasts with those of Ogle *et al*. (2000), where trees that died had become much more climatically sensitive with age than trees that survived. In our study, older trees became less sensitive to climate irrespective of their fate after the 1998–99 drought. Higher growth variability in susceptible adult trees may have been driven by biotic factors as insect-attacked trees were more prone to mortality. However, climatic sensitivity in juvenile and adult surviving trees showed a different pattern from that of trees that died. Adult surviving trees were more sensitive than juveniles and their patterns of response to climate (particularly to precipitation) were different with more positive responses to precipitation, and more negative responses to temperature, in the current growing season. This may be due to morphological and physiological changes that accompany ageing, such as increased root/foliage biomass ratios.

Mean growth rate was a good predictor of mortality in adult trees: in support of Manion's (1981) model, adult trees with declining growth were particularly susceptible. Several studies emphasize declining vigour as a prominent characteristic of dying trees (Pedersen 1998; Cherubini *et al*. 2002), with high vigour trees recovering quickly after drought, whereas low vigour trees responded slowly or not at all to improved conditions. Surviving *N. dombeyi* adults recover their normal growth rates after adverse climatic events and some may actually increase their rate of radial growth due to the release of resources as other trees die (Villalba & Veblen 1998). In our study, all dead adult trees had shown a slower growth rate than surviving trees. Manion's model predicts that tree-growth is affected during environmentally stressful years and we therefore looked for sudden and permanent suppression in tree growth rates that coincided with environmental stress (*sensu* Pedersen 1998). We identified 1956–57 as the approximate date when growth trajectories of live and dead adult trees diverged (Fig. 3b) and noted that drought occurred regionally over northern Patagonia at this time (Villalba & Veblen 1998). Without the 1956–57 event, the 1998–99 drought may therefore have induced less severe adult tree mortality. These results emphasize the role of repeated droughts in determining rates of vegetation change that are mediated by fast demographic processes such as tree mortality. Frequency and intensity of extreme climatic events may change as a consequence of anthropogenic global changes (Balling 1996). If drought effects on tree mortality are additive over the lifetime of trees, altered climate may produce strong non-linear changes in ecosystems when critical drought frequency thresholds are surpassed.

Interestingly, trees with former partial canopy dieback showed less mortality during the drought than trees with well-developed crowns. Dieback of upper branches during previous climatic/biotic events may have improved root : shoot ratios, turning them into more drought-resilient trees. Although drought leads to some trees with normally developed and exposed crowns but low growth rates, high interannual growth variability and high risk of death in the next drought event, other trees are partially killed but have more or less constant growth rates. Foliage in these trees is generally located lower and more protected by surrounding canopies and they are therefore more likely to survive the subsequent drought event. Interestingly, although not quantified in this study, the 1998–99 event produced abundant partial crown mortality affecting the top one-third to one-half of trees with formerly normal crowns. This phenomenon has long been known in broadleaved forests (Hursh & Haasis 1931), where many large individuals of *Quercus* spp. showed browning confined to the top-most branches during a drought in the United States.

Although extensive crown dieback has been described for several *Nothofagus* species (Arentz 1988; Veblen *et al*. 1996), and is a conspicuous characteristic of *N. dombeyi* forests, the origin and dynamic maintenance of this pattern has remained unresolved. We suggest that healthy trees that undergo severe drought may respond by shutting off a substantial amount of their upper canopy. Persistence of these trees for extended periods of time may be the result of their higher resilience to subsequent droughts while formerly stressed trees that did not produce partial dieback may be killed. This dynamic scheme may explain the maintenance of both partially killed and dead standing trees in many Patagonian forests. Other non-exclusive explanations are that even-aged cohorts originating from coarse-scale disturbances are simultaneously entering cohort senescence (Mueller-Dombois 1992) or that senescence of populations suffering severe nutrient shortages (Gerrish *et al*. 1988) may be triggered by factors such as pathogen or insect attacks (Veblen *et al*. 1996). The distinctive feature of the first scheme, supported by our results, is that two events are involved, with one causing growth decline and predisposing the tree to a subsequent event that triggers death, rather than partial crown dieback being an accumulative process of increasingly older trees (Veblen *et al*. 1996).

IMPLICATIONS OF DROUGHT MORTALITY FOR FOREST DYNAMICS

Although drought-induced mortality may be an important disturbance event extensively affecting the dynamics of a forest, it has generally received much less attention than tree-falls (Clinton *et al*. 1993). Tree-falls produce discrete openings with abundant coarse woody debris on the gap floor (Clinton *et al*. 1994), whereas drought-induced gaps in species-poor forests generate more diffuse openings in the canopy and do not disturb the forest floor. The lack of understorey disturbance, lower levels of coarse woody debris and apparently low levels of light are all likely to influence seedling regeneration and sapling response. Preliminary data from Suarez (2001) suggest that in mixed *Nothofagus dombeyi*–*Austrocedrus chilensis* forest drought-induced gaps led to strong growth releases of understorey saplings of both tree species but particularly of the shade intolerant *N. dombeyi*. However, drought-induced mortality of these saplings produced a significant thinning of *N. dombeyi*, shifting the diameter distribution towards larger classes and changing the composition of the advance regeneration from *N. dombeyi*-dominated to a more equitable or *A. chilensis*-dominated composition. This suggests that, although *N. dombeyi* will reach the canopy sooner, tree composition will shift to favour the conifer *A. chilensis*. Thus, in contrast to tree-fall gaps, where no compositional changes are expected (Veblen 1989), drought gaps may produce long-term shifts towards forests dominated by more xeric-tolerant species.

Climatic variability is a strong driving force for forest dynamics in northern Patagonia and elsewhere. In northern Patagonian *Nothofagus* forests, climatic variability has indirect effects on fire regimes (Kitzberger *et al*. 1997), which, in turn, are important forces that modify stand structures, as well as landscape composition and configuration (Kitzberger & Veblen 1999). Moreover, changes in the intensity and periodicity of large-scale climatic features, such as ENSO, have been proposed to cause multidecadal changes in regional fire regimes (Kitzberger *et al*. 2001). Similar changes in climatic variability may have affected forest dynamics and composition by modifying the frequency of episodic drought-related mortality and partial crown dieback. Extended periods of low climatic variability may increase the probability of gap-phase replacement without major compositional changes, while periods of higher drought could increase either fire frequency or mass mortality, both processes with important consequences for the future of forest communities and landscapes.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC941/JEC941sm.htm

Appendix S1 Final stepwise model from the discriminant function analysis between dead and live stands.

Appendix S2 Final stepwise model from the discriminant function analysis between individual dead and live adult trees.

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