**ORIGINAL ARTICLE**

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# Drought-induced mortality affects understory vegetation: release after death

**Abstract** In recent decades, severe droughts have become an important cause of canopy disturbance in forests, and have shown potential to cause rapid and pronounced vegetation shifts. Under dead canopy, undamaged understory could influence the nature of resource limitation for seedling growth and survival, limiting forest regeneration. We assessed the release response of understory vegetation after a severe drought event in temperate forests of northern Patagonia. Growth trends of dominant tree saplings, and changes in vegetation biodiversity and cover were compared between drought-dead and unaffected canopy. *Nothofagus dombeyi* undergo growth release after the climatic event in affected forests, and the response was evidenced immediately after the disturbance. For *Austrocedrus chilensis*, the growth release response was less evident, due mainly to a difference in age structure. In the understory the release response was barely discernable for some components. There was a tendency towards higher cover of the shrub layer in the understory of drought-affected forests, and an important presence of the exotic shrub *Rosa rubiginosa*. However, the clearest biotic response following drought mortality was the release in growth of understory dominant tree component. Those results strongly suggest that the environment under drought-dead canopy, and the die-off in woody sapling cohorts in a self-thinning process, could favor crown expansion and growth release of understory species that could help predict future forest trajectories in the context of the influence of climatic extreme events.

**Keywords** Drought-dead canopy · Temperate forest · Sapling growth release · Understory vegetation cover · Understory vegetation diversity

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Nomenclature: Ezcurra and Brion (2005) for taxa.

## Introduction

Drought events at both inter-annual and decadal time scales are strong drivers of forest dynamics in several forest types, leaving imprints on the landscape that could persist throughout many years in long-lived forest ecosystems (Allen et al. 2009; Mueller et al. 2005). Moreover, when drought is severe enough to produce massive die-offs, the consequences for forest composition can be considerable. For example, in semi-arid woodlands, drought may cause massive die-offs that contribute to ecotonal shifts along a moisture gradient, and accelerate shrub invasions (Allen and Breshears 1998). In temperate as well as tropical forests, droughts that cause tree mortality produce compositional shifts and diverse death patterns (Clinton et al. 1993, Suarez and Kitzberger 2008) that influence understory vegetation establishment (Beckage et al. 2000; Clinton and Boring 1994).

Global-change-type droughts (Breshears et al. 2005) have become an important source of canopy disturbance in forests and have driven forest vegetation shifts in several climate or habitat types (Elliot and Swank 1994; Fensham and Holman 1999; Lloret and Siscart 1995; Suarez et al. 2004; Williamson et al. 2000). Shifts in forest composition can be attributed to at least two mechanisms. First, direct effects on demography of more drought-sensitive tree species (adult and sapling mortality) cause an immediate reduction in density and change the forest composition in favor of drought-tolerant species (Suarez and Kitzberger 2008). Second and indirectly, post-drought biotic and abiotic changes could affect tree seedling recruitment and understory vegetation performance (Clinton et al. 1993; Royer et al. 2011). A reduction in tree canopy thereby increases near-ground solar radiation, with important primary direct effects on biotic and abiotic processes. Changes in understory light availability and distribution could

influence release dynamics and favor different species. This process could be more relevant in mixed forests where dominant species differ in shade-tolerance. Following understory release, lower light levels reaching the forest floor could negatively influence seedling recruitment and survival of light-demanding species, thereby favoring shade-tolerant species (Suarez and Kitzberger 2008). Consequently, global-change-type droughts can affect biotic and abiotic processes directly, not only at stand level but also at regional scale. Death of overstory trees, and therefore canopy opening, affects processes such as plant physiology, phenology, growth, reproduction, and recruitment success of underneath vegetation. Any alteration of these processes has cascading effects on productivity and diversity, ultimately affecting carbon and water fluxes (Royer et al. 2010).

Under drought-dead canopy, in contrast to tree-fall openings, the mode of tree mortality (standing dead trees) involves little or no damage in the understory, potentially influencing recruitment strategies and favoring species less effective in gap colonization. In addition, a few studies that have included the role of standing dead trees have shown that these might play an influence on native plant colonization and non-native plant invasion (Kane et al. 2011). The intact forest floor and lack of coarse woody debris act as a physical barrier to seedling establishment, particularly for species that require mineral soil for germination or for species whose reproductive strategies depend significantly on "nurse logs" (Beckage et al. 2000; Clinton and Boring 1994). Furthermore, in the absence of forest floor disturbance, pre-existing understory perennial herbs and shrubs could increase in response to increased light conditions, and compete with tree saplings or inhibit seedling establishment (Beckage and Clark 2003; Clinton 2003; Gray and Spies 1997). Although gaps with standing dead trees transmit less light than gaps formed by fallen trees, diffuse shade from standing dead trees may benefit species that respond effectively to temporary sunflecks (Suarez and Kitzberger 2008). Established understory vegetation monopolize water and nutrient resources and increase its cover, thus diminishing resource uptake for new seedling establishment (Coll et al. 2003). In forests where tree-fall dynamics are the main source of disturbance and where no compositional changes are expected within the forest, drought patches may therefore produce long-term compositional shifts that would otherwise be influenced predominantly by wind disturbance. In particular, we might expect increases in xeric and shade-tolerant canopy species. A better understanding of the influence of established understory vegetation is required to elucidate possible trajectories of forest regeneration.

In 1998–1999, strong La Niña conditions occurred in northern Patagonia. This led to severe drought affecting *Nothofagus* forests of the region. The drought was characterized by the lowest annual rainfall in the last 100 years (March–February rainfall 266 mm, ca. −2.6 standard deviation below the historical mean, "Servicio Meteorologico Nacional"). This event resulted in massive mortality of the 25- 40-m-tall evergreen tree *Nothofagus dombeyi* (Mirb.) Blume near its eastern distribution limit. Although drought affected large areas of temperate forest, tree mortality was extremely patchy and created many dead patches. However, we could not rule out the idea that site factors cause dead patches, or that patches were created randomly (Suarez et al. 2004). Furthermore, knowledge of the physiological mechanisms that drove the overstory mortality event, is urgently required to understand the death process that involved only *N. dombeyi* trees at the top of the canopy and some saplings of this species in the understory (Suarez and Kitzberger 2008). Apparently, heat during the growing season contributed to the die-off episodes for *N. dombeyi* forests (Suarez and Kitzberger 2010).

*Nothofagus dombeyi* dominates forests in northern Patagonia; under normal conditions small-scale gap-phase regeneration following tree-fall is common in both monospecific stands and in mixed forests including the evergreen conifer *Austrocedrus chilensis* (D.Don) Flor. et Boult (Veblen 1989). The main goal of this study was to examine forest understory characteristics under drought-dead canopy to assess the short-term effects of the 1998–1999 drought. Regarding the main objective and by comparing drought-dead areas and unaffected areas, we expect to find: (1) a positive effect of open canopy on growth patterns of dominant tree saplings with major release rates in light demanding species (*N. dombeyi*); (2) a change in understory composition and cover following the drought event; and (3) certain species of understory associated with each particular canopy condition. Understory growth performance following loss in overstory canopy cover is an important but sometimes overlooked aspect in the understanding of the positive and negative effects of climate change on forests. Our results emphasize the importance of considering the understory community in the understanding of how dominant species loss can modify the environment and ultimately influence subsequent species recruitment and community persistence.

## Methods

### Study area

The study was conducted in the Nahuel Huapi National Park (NHNP) in northern Patagonia, Argentina. Precipitation in the NHNP is seasonally variable, with approximately 60 % falling between May and August. Due to topography, mean precipitation decreases abruptly from ca. 3,000 mm year$^{-1}$ at the main Andean cordillera to < 500 mm year$^{-1}$ only 80 km to the east (De Fina 1972). Parallel to this precipitation gradient, vegetation changes abruptly from temperate rain forests, dominated by tall evergreen *N. dombeyi*, to semiarid steppe dominated by cushion shrubs and bunchgrasses.

As precipitation decreases to ca. 1,500 mm year$^{-1}$, *N. dombeyi* and *A. chilensis* both form even-aged populations following stand-devastating fires; *N. dombeyi* occurs exclusively in the main canopy, whereas *A. chilensis* is suppressed partially in the subcanopy (Veblen and Lorenz 1987).

This research was conducted across the eastern distribution limit of *N. dombeyi* forests, where drought influence was high enough to produce massive tree die-off. For the dendrochronological inspection of understory growth release, between 2003 and 2005, eight drought-dead canopy patches were selected along the 1,400 mm year$^{-1}$ isohyet in *N. dombeyi–A. chilensis* mixed forests. Drought-dead patches included up to five dead trees in a $20 \times 20$ m plot, resulting in openings of 50–225 m$^2$. Unaffected patches near the drought affected plots were selected according to Bran et al. (2001). Patches were selected avoiding steep slope, burning range, and high herbivorous density areas. The resulting plots were flat, ranging from 6 to 12 % in slope and encompassing almost all aspects, and were placed near lake level (ca. 800 m a.s.l.) where mixed *N. dombeyi–A. chilensis* forest develops. Across the entire affected area in NHNP, post-drought understory biodiversity and cover were analyzed in 41 randomly selected $3 \times 5$ m plots.

Dominant tree sapling release response

Understory release below standing dead trees was compared with growth patterns under unaffected canopy. In early-autumn (April) 2005, at least three saplings ($<10$ m height and 0.05–0.15 m diameter at breast height) of the tree species *N. dombeyi* and *A. chilensis* growing inside each selected patch were chosen randomly and cored. Two cores were obtained for each tree sapling. Cores were taken as low as possible using an increment borer. Standard dendrochronological procedures were used to process all samples (Stokes and Smiley 1968). After mounting and sanding smooth, ring widths were measured (0.01 mm resolution) under a stereomicroscope. Following the convention of Schulman (1956), the date of an annual ring was assigned to the calendar year when growth began (September of the current year in the southern hemisphere). For tree species, crossdating accuracy was checked using visual methods (Yamaguchi 1991).

To examine the mean growth trend of trees sampled, ARS41_win (Cook and Krusic 2006) was used to build chronologies. The observed ring-width series were fitted to a horizontal line passing through the mean ring width of the series, and relative tree-ring indices were calculated by dividing each measure by its expected value (mean). This standardization method filtered out the climatic influence on tree rings (high frequency variability) revealing sustained growth changes (trends). The mean chronology for each species, growing in each condition (drought vs unaffected canopy) was estimated with the biweight robust mean because it discounts the

influence of outliers in computation of the mean by reducing the variance and bias caused by outliers (Cook et al. 1990). Chronology was compared using the 95 % bootstrap confidence limits obtained for each chronology. Both chronologies (by species) were also compared using repeated measures ANOVA, with one between-subject treatment (drought-dead canopy and unaffected canopy) and one within-subject factor (time). The analysis was performed for the last 11 years (1993–2004).

Additionally, ring width was converted into tree basal area increment (BAI) in order to obtain yearly levels of growth unaffected by age trend and to display growth trend clearly. BAI was obtained following the standard formula (Jump et al. 2006). Mean BAI chronologies for each species were built by averaging over all individuals growing under both canopy conditions: drought-dead canopy and unaffected canopy.

Percent of growth change after the drought event was calculated following the Nowacki and Abrams (1997) formula and a 3-year window. Using this procedure, inspection could assess no more than the period 1999–2002 because of blind points at the end of the chronology. With the aim of examining the previous growth pattern of trees that evidenced growth release following the climatic event, we contrasted previous growth (5 years) with the percent in post-drought growth change.

All analyses were done using R software v. 2.8.1 (2008); results were considered significant if the probability of a Type I error was $<0.05$, and marginally significant at probability levels near the threshold.

Understory composition

As shrubs and herbs are not suitable for a dendrochronological inspection, to assess the influence of canopy openness on underneath plant community, we analyzed differences in vegetation biodiversity and cover. Forty-one 15 m$^2$ plots were placed randomly under drought-killed canopy and 15 plots were placed under unaffected forest canopy (as controls). On each plot, three 1 m$^2$ circular quadrats were installed, and we recorded each vascular plant species, its cover using the Braun-Blanquet cover scale, and the number of species (species richness). Midpoints of cover range (%) per species were used in the analysis (Matteuchi and Colma 1982). For further analysis species were grouped into three life-form groups related with vertical stratum in forest understory: herbs, climbers and shrubs (including potential tree in shrub stratum as *Lomatia hirsuta* or *Prunus* sp.). Species richness and life-form cover were compared using a general linear model (GLM). All analyses were done using R software v. 2.8.1 (2008). Results were considered significant if the probability of a Type I error was $<0.05$.

To determine if there were significant differences in understory composition between treatments, we carried out an analysis of compositional similarity (ANOSIM). ANOSIM is a non-parametric permutation procedure

applied to rank similarity matrices underlying sample ordinations (Clarke and Warwick 2001). It produces a global $R$ statistic, which is an absolute measure of distance between groups, and ranges from one, indicating strongly distinct assemblages, to zero, indicating that communities are not separable. Additionally, plant species characteristic of each canopy condition were identified using the Indicator Value method (Dufrêne and Legendre 1997). This method assesses the degree to which a species fulfills the criteria of specificity (uniqueness to a particular habitat) and fidelity (frequency of occurrence). A high indicator value (IndVal, expressed as percentage) indicates that a species can be considered characteristic of a particular habitat or site. Indicator values for each species were calculated based on a species cover matrix, species with significant IndVals > 25 % were considered as species characteristic of the canopy condition. The analysis was done using INDVAL program v 2.0 (Dufrêne and Legendre 1997).

## Results

### Tree sapling release response

The tree species *N. dombeyi* and *A. chilensis*, growing in the understory of drought-dead canopy, showed a release in growth following the climatic event that happened during the summer of 1998–1999. Temporal patterns in radial growth displayed significant differences between *N. dombeyi* saplings growing under dead and unaffected canopy (Figs. 1, 2). Additionally, confidence intervals for recent years separated following the 1998–1999 growing season (Fig. 1a, inset). The analysis of the last 11 years of growth (1993–2004) showed that a sapling growing under dead canopy evidenced higher tree-ring index than a sapling growing under unaffected canopy (Time × Treatment, $F_{10,500} = 2.62$, $P \ll 0.001$), whereas *A. chilensis* ring index chronologies displayed an increase after death of overstory trees—the release in growth showed a tendency though not enough to be highly significant (Fig. 1b). Confidence intervals during the last 10 years showed that the upper and lower confidence interval of both chronologies overlap (Fig. 1b, inset). In the same way, an increase in sapling growth underneath both canopy conditions (Time, $F_{10,500} = 18.79$, $P \ll 0.001$; Time × Treatment, $F_{10,500} = 1.22$, $P = 0.27$) was evidenced in the repeated measures ANOVA run over the last 11 years (1993–2004). Furthermore, *A. chilensis* ring index chronology of saplings growing underneath drought-dead canopy revealed two periods of release during the last 20 years, one following 1980 and other following the 1998 growing season (Fig. 1b).

The BAI growth of both trees species typically followed a sigmoidal pattern, increasing rapidly from young to middle age; except for *A. chilensis* growing underneath unaffected canopy where BAI growth rates were in a plateaus characteristic of middle age (Fig. 2). *Nothofagus dombeyi* growing under unaffected canopy exhibited the highest values in BAI growth, and consequently in diameter, since the time of establishment up to 2004. Although increments in basal area of *N. dombeyi* individuals growing below dead canopy were always lower than the increments evidenced under "not killed" canopy, the relative growth increase following the climatic event was higher. As we standardized (divided by its mean) BAI growth values in order to highlight the growth change pattern, a sudden release in growth was evidenced following 1998–1999 climatic event (Fig. 2a). The two events of increase in growth slightly evidenced in *A. chilensis* tree-ring chronology developed for drought-dead canopy were highly evidenced in BAI trends (Fig. 2b). The onset of BAI chronology separation was around 1980. Whereas BAI trend of saplings growing underneath unaffected forest showed a plateau since that date, saplings growing under dead canopy began an abrupt increase in growth.

In concordance with chronologies and BAI trends, percentage of growth change corresponding to growing seasons following the climatic events showed the same pattern. As we compared prior growth (mean of previous 5 years) in *N. dombeyi* saplings with growth increase during the following growing seasons, the pattern evidenced under drought dead canopy was an increase restricted mainly to the growing season immediately following (Fig. 3a). For the 1999–2000 growing season, the increase rate averaged 130 %, with some individuals reaching 800 % in growth change. During the following seasons, growth stabilized, and very low and moderate release (lower than 50 %) was evidenced. Interestingly, the majority of *N. dombeyi* individuals with higher percentage of growth change were those that had grown at lower rates (0.2–1 mm/year) during the previous 5 years (Fig. 3a). Underneath drought-dead canopy, the percentage in growth change of *A. chilensis* individuals reached on average 68 %, with some individuals reaching 200 %. During the second and third growing seasons, growth stabilized, and only low releases (<25 %) occurred. Higher release events were equally evidenced by individuals growing at lower as well as at higher rates, although these releases (150–200 %) were evidenced in individuals growing at rates reaching 1 mm/year on average prior to the climatic event (Fig. 3b).

### Understory composition

Vegetation richness was barely similar under drought-dead canopy and underneath unaffected canopy [$6.61 \pm 2.28$ and $5.46 \pm 2.17$, $t_{(54)} = 1.68$, $P = 0.09$]. Additionally, the understory species composition was similar under both canopy conditions ($R = -0.03$, $P = 0.64$). However, mean cover of understory vegetation, measured as sum of percentage of cover, varied between the main a priori defined groups: herbs, climbers and shrubs (canopy condition × life-form group, $F_{1,162} = 3.51$, $P \ll 0.03$). While cover of herbs and climbers was similar underneath both canopy conditions (herbs $P = 0.15$; climbers $P = 0.15$); shrub cover tended to be higher under drought-dead
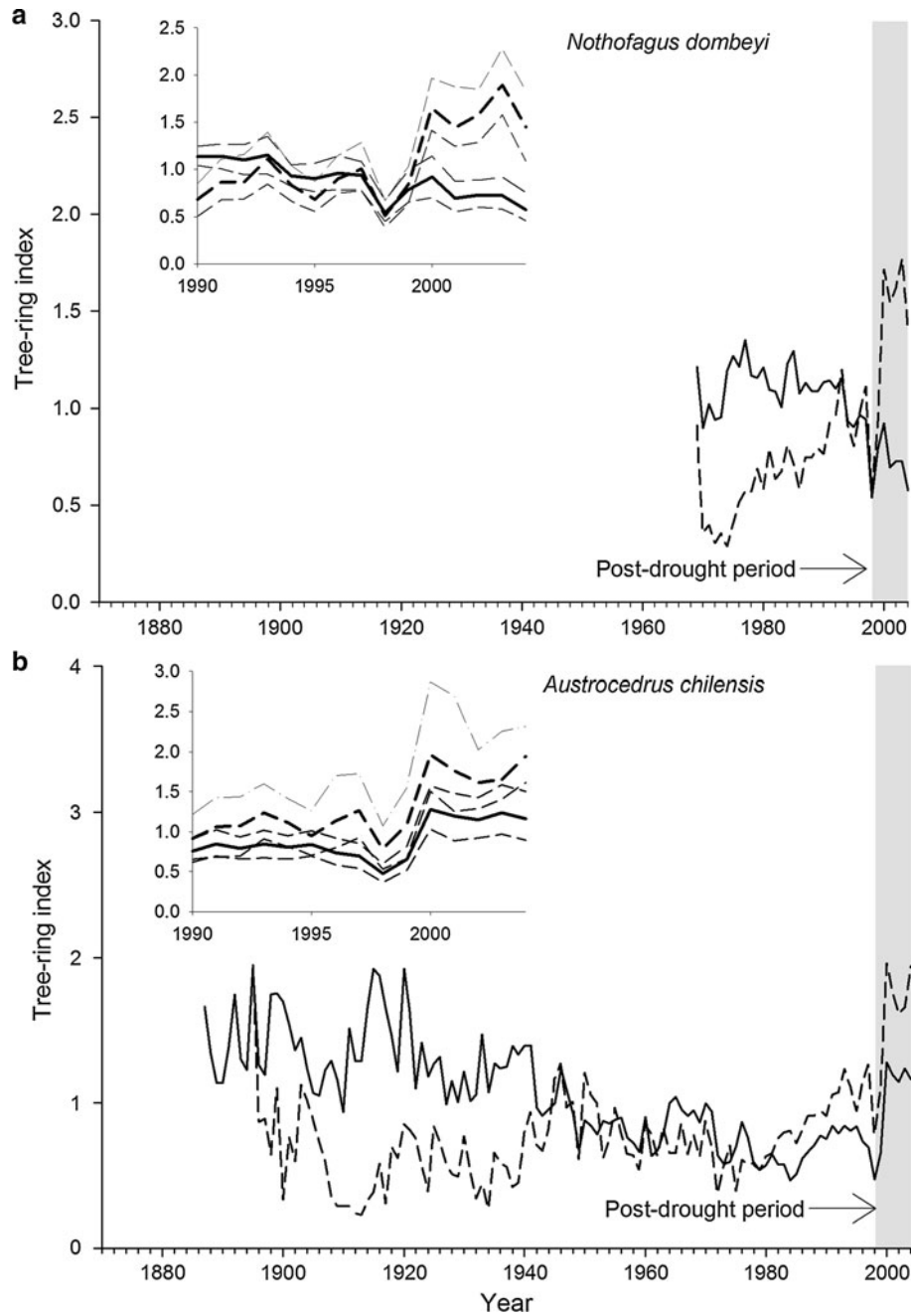
**Fig. 1** Growth pattern measured as tree-ring index for **a** *Nothofagus dombeyi* and **b** *Austrocedrus chilensis* growing under drought-dead canopy (*dashed line*) and under unaffected canopy (*solid line*). The observed ring-width series are fitted to a horizontal line passing through the mean ring width of the series. Chronologies are plotted for the period encompassing more than five series. *Shaded area* Post-drought period (1999–2004). *Insets* Confidence intervals (95 %) for each chronology for the last 15 years

canopy as we expected following a canopy disturbance (drought-dead canopy 47.34 ± 5.17; unaffected canopy 30.61 ± 4.32; $P = 0.06$). At species level, some species could be detected as characteristic of a particular habitat (Fig. 4). The herbs distinctive for unaffected forest canopy were *Osmorhiza chilensis* (I.V. = 69.46, $P = 0.001$), *Alstroemeria aurea* (I.V. = 44.32, $P = 0.04$), and *Taraxacum officinale* (I.V. = 6.67, $P = 0.05$; Fig. 4), and the distinctive shrub was *Ribes magellanicum* (I.V. = 20.40,

$P = 0.02$). In contrast, the indicator value (IV) method showed only one species as characteristic of drought-dead canopy: the shrub *Rosa rubiginosa* (IV = 25.00, $P = 0.04$). However, percent cover of the climber *Mutisia* sp. was also higher under drought-dead canopy ($F_{1,54} = 4.77$, $P = 0.03$). The two dominant shrubs *Schinus patagonica* and *Aristotelia chilensis* had similar cover under both canopy conditions ($F_{1,54} = 2.48$, $P = 0.12$ and $F_{1,54} = 0.04$, $P = 0.84$, respectively).
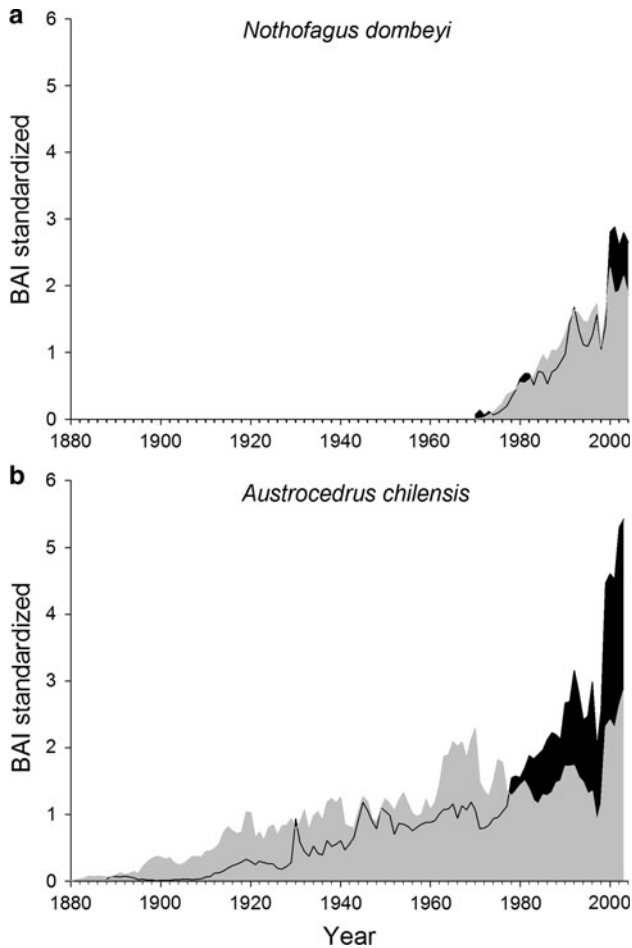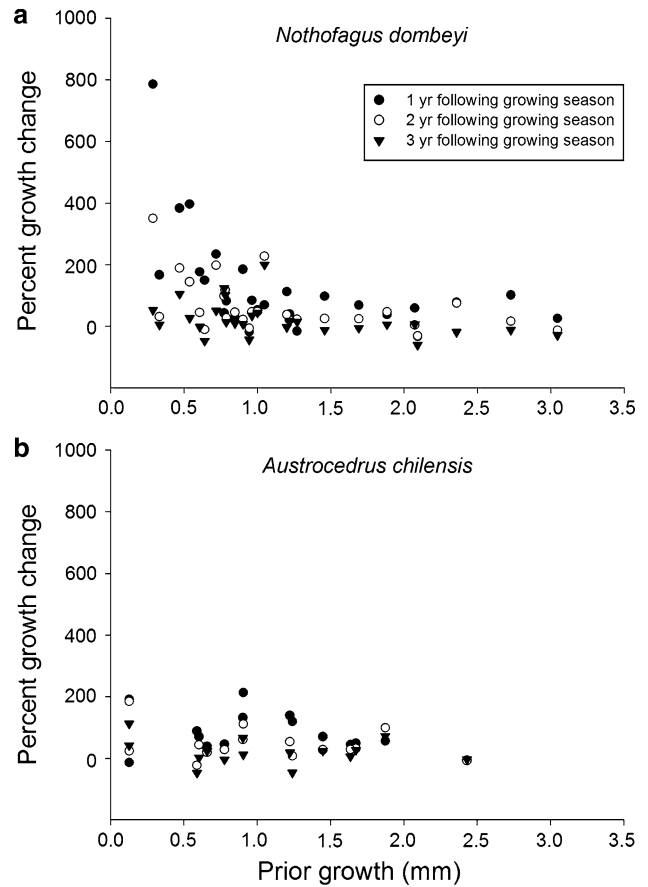
Fig. 2 Growth trends represented as standardized basal area increment **a** for *N. dombeyi* and **b** *A. chilensis* growing under drought-dead canopy (*black area*) and under unaffected canopy (*gray area*)



Fig. 3 Prior growth and percent-growth change relationships for *N. dombeyi* and *A. chilensis* growing under drought-dead canopy

## Discussion

Perhaps the clearest biotic response following canopy mortality was the release in growth of understory components. The presence of a strong release of growth of sapling components suggests that the environment underneath will be influenced by drought-induced death where different abiotic conditions could predominate. This should be taken into account for understanding of the subsequent recruitment patterns of forest species.

Several studies have found that tree mortality induced by drought constitutes a distinctive type of canopy opening and should not be treated as common canopy gaps (Archaux and Wolters 2006; Beckage et al. 2000; Clinton and Boring 1994; Kane et al. 2011; Suarez and Kitzberger 2008). Increased solar radiation and a possible nutrient pulse from leaf shedding by dead canopy trees also produce a substantial release response of pre-established understory vegetation. As found in another study (Suarez and Kitzberger 2008) and in complementary measurements, a high level of forest

floor shading is the main characteristic of drought-dead canopy. Thus, the release response is likely to be more important than new establishments in determining future stand composition. Similarly, Clinton and Boring (1994) and Clinton et al. (1993) have shown that in northern temperate forests, the presence of a dense layer of the evergreen *Rhododendron maximum* in the understory can affect seedling establishment greatly, and determine stand structure under drought-dead canopy. For our stands, Suarez and Kitzberger (2008) reported that, at floor level (0.30 m height), drought-dead canopy was substantially shadier and extremely xeric compared to tree-fall gaps. Although not included in this study, complementary data of light reaching the shrub layer top (1.20 m height) showed that, at this level, the light environment under drought-dead canopy does not differ from that found under natural openings (M.L. Suarez 2008, unpublished data). This data support the idea that a dark forest floor environment is due to a dense shrub layer characteristic of affected areas. The main result of this study is in concordance with this, since a higher release rate of understory components was evidenced under drought-dead canopy. Unfortunately, no other environmental variables, for example nutrient level, were measured during the study that could help explain the nature of release in growth. Additionally, different xeric
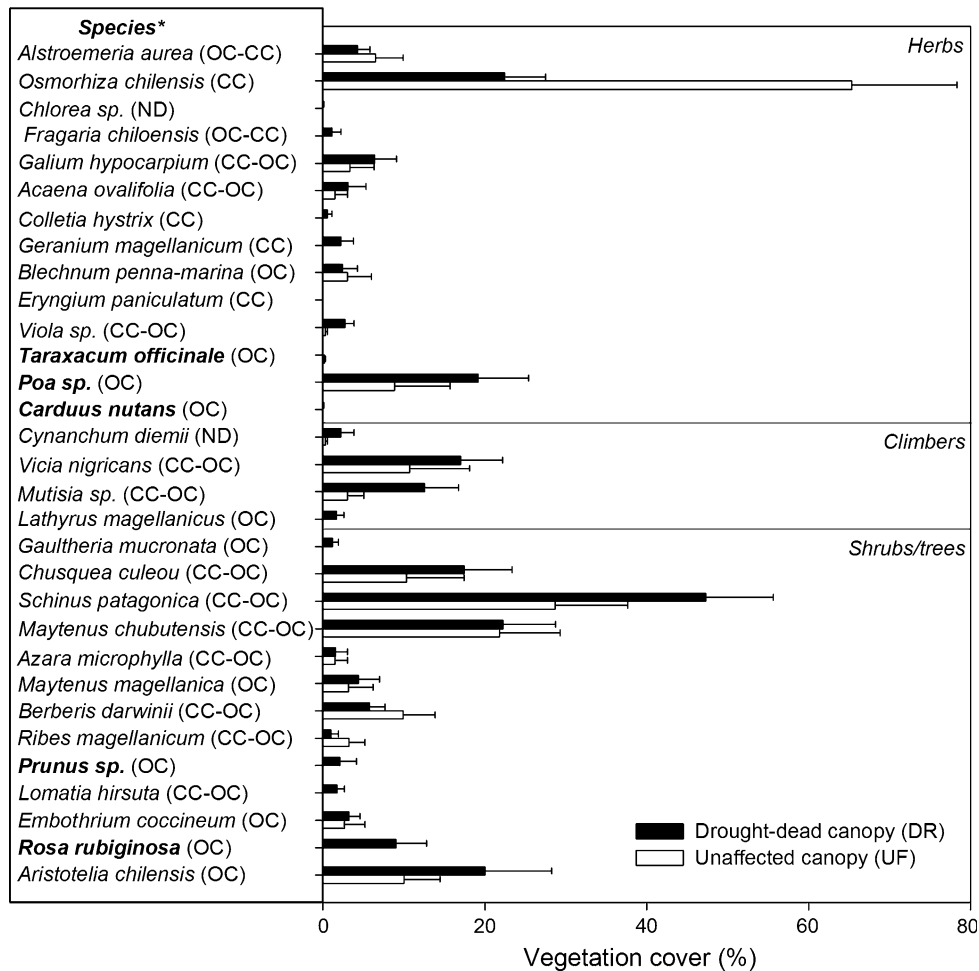
**Fig. 4** Average percentage of vegetation cover of herb, climber and shrub species growing under unaffected (*open bars*) and drought-affected (*filled bars*) forest. Data are observed mean ± standard error. (*Asterisk*) Complete scientific species names: *Alstroemeria aurea* Graham (facultative shade-tolerant, native); *Osmorhiza chilensis* Hook. & Arn.; *Chloraea* sp. (*Chloraea viridiflora* Poepp.); *Fragaria chiloensis* (L.) Duch.; *Galium hypocarpium* (L.) Ende. Ex Grises.; *Acaena ovalifolia* Ruiz & Pav.; *Colletia hystrix* Clos; *Geranium magellanicum* Hook. f.; *Blechnum penna-marina* (Poir.) Kuhn; *Eryngium paniculatum* Cav. & Dombey ex. F. Delaroche; *Calceolaria biflora* Lam.; *Taraxacum officinale* G. Weber ex F.H. Wigg; *Poa* sp.; *Carduus nutans* auct. nonL.; *Cynanchum diemii* T. Mey.; *Vicia nigricans* Hook. & Arn.; *Mutisia* sp. (*Mutisia oligodon* Poepp.& Endl.); *Berberis darwinii* Hook.; *Gaultheria mucronata* (L.f.) Hook. & Arn.; *Chusquea culeou* E. Desv.; *Schinus patagonica* (Phil.) I.M. Johnst. ex Cabrera; *Maytenus chubutensis* (Speg.) Lourteig, O'Donell & Sleumer; *Azara microphylla* Hook. f.; *Maytenus magellanica* (Lam.) Hook. f.; *Lathyrus magellanicus* Lam.; *Ribes magellanicum* Poir.; *Prunus* sp.; *Lomatia hirsuta* (Lam.) Diels ex J.F. Macbr.; *Embothrium coccineum* J.R. Forst. & G. Forst.; *Rosa rubiginosa* L.; *Aristotelia chilensis* (Molina) Stuntz. Habitats used documented for each species are in *parenthesis*: *CC* closed canopy and *OC* open canopy (Damascos and Rapoport 2002; Dezzotti 1996; McAlpine and Jesson 2007; Raffaele et al. 2011; Saldaña et al. 2010). Species names in *bold* indicate exotic species commonly associated with altered environments

conditions under drought-dead canopy should not be responsible for an increase in growth rate. Despite the finding of Suarez and Kitzberger (2008) that drought-induced gaps were more xeric than tree-fall gaps, this characteristic could also be related to different site conditions along the stand. Thus, xeric conditions prevailing under the dead canopy could be attributed to higher density in understory components, which increase water use in the upper horizons (Davis et al. 1999), but are also related to the higher percentage of rock cover that is characteristic of dead patches in comparison to unaffected zones (Suarez et al. 2004).

Since *Nothofagus dombeyi* and *Austrocedrus chilensis* differed in shade tolerance and in sapling ages, a comparison of growth release rates among species underneath each canopy condition was not possible. However, both species evidenced growth release as a consequence of drought, contributing to the knowledge of forest trajectories following an extreme climatic event. Immediately following the extreme climatic event, *N. dombeyi* showed that its percentage of growth increased by eight-fold, but then only doubled from those in previous years as *A. chilensis*. This release response clearly suggests that both species behave similarly as a consequence of canopy openings, and will possibly reach the canopy of forest affected by drought together.

In this study, an unexpected and interesting result was the presence of at least two events of release in *A.*

*chilensis* saplings. The possibility of experiencing more than one event of release in this species is due to the fact that *A. chilensis* individuals were older than *N. dombeyi* saplings. Thus, individuals of *A. chilensis* should not be treated as saplings but as subdominant and/or suppressed trees. Actually, in the study area, the establishment date of the overstory trees has been determined as around 1850 (Suarez 2009), possibly as a consequence of a devastating fire in the NHNP (Veblen et al. 1992). Constant recruitment of overstory of two main trees species was evidenced during a recruitment window of about 70 years (Suarez 2009). Probably, *A. chilensis* individuals analyzed in this study belonged to recruitment events occurring during the last period of the recruitment window. Additionally, *N. dombeyi* saplings were established around 1970. Both the *N. dombeyi* recruitment date and *A. chilensis* previous release event, suggest the presence of a prior event of canopy mortality. Due to the fact that *N. dombeyi* is a shade-intolerant species, its establishment commonly coincides with, or follows the death of, overstory trees (Veblen 1989).

Several studies with artificially created gaps to mimic drought-killed canopy, deal only with the effect of the presence or absence of understory vegetation on forest regeneration (Beckage et al. 2000; Clinton 2003). Here, almost all species were represented equally in both canopy types, and were native and exotic species commonly cited for northern Patagonian forests. In fact, herb species with high cover (and abundance) under unaffected canopy and that have no or low sun preferences were described as understory components in undisturbed mixed *N. dombeyi-A. chilensis* forests [i.e. *Ozmorhiza chilensis*, *Alstroemeria aurea*, *Geranium magellanicum*, *Eryngium paniculatum* (Damascos and Rapoport 2002; Dezzotti 1996)]. Furthermore, all climber species found (cover and presence) were species commonly registered for these forests. Taking into account the higher growth and flowering rates of several climbers (i.e., *Vicia nigricans*) in post-fire environments (Sasal 2009), we expected more climber cover beneath drought-dead canopy since more sunlight reached the understory layer. Accordingly, although only *Mutisia* sp. showed statistically higher cover under dead canopy, all other climber species also had high cover in disturbed sites. Moreover, *Lathyrus magellanicus*, a species commonly found in open canopy conditions, although in low cover and abundance, was registered only for drought-dead patches. Even though the habitat used for each species is in close relation to light tolerance, neither herbs and climbers nor shrub species usually present in the understory of mixed *N. dombeyi–A. chilensis* forest belong to an exclusively light-tolerant group. Nearly all species belong to generalist and facultative shade-tolerant/intolerant groups with higher frequency in one environment over another, but usually cited for closed canopy and gaps (Damascos and Rapoport 2002; Dezzotti 1996; Raffaele et al. 2011).

We barely found a tendency of higher cover of shrub layers underneath dead canopy. Despite our expectations, and based on lower light levels reaching the forest floor of dead-drought canopy (Suarez and Kitzberger 2008), we predicted higher cover of the main shrub species characteristics of *N. dombeyi–A. chilensis* forests. For example, we predicted higher covers of several native large-size shrub species as the heliophilous generalistic *Schinus patagonicus* (Damascos and Rapoport 2002), which develops well under closed canopy but improves its growth due to the increase in light availability; *Lomatia hirsuta*, a small tree which grows well underneath closed and open canopy; and *Aristotelia chilensis*, which has high phenotypic plasticity in response to light (Lusk and del Pozo 2002). Moreover, a dendrochronological preliminary inspection of these three species for their potential use, showed an increase in growth following the 1998–1999 climatic event (M.L. Suarez 2008, unpublished data), supporting the fact that at least this species released growth as a consequence of canopy openings. In addition, all registered shrub species were native to this forest type; however, the exclusive presence of two exotic species (*Prunus* sp. and *Rosa rubiginosa*) under drought-dead canopy agrees with previous studies. Stands prone to be killed by drought were located on unfavorable sites and held higher previous mortality that may possibly be related to previous disturbances favoring the arrival of those species. The presence of *R. rubiginosa* individuals in the affected area should be taking into consideration in futures studies, not only because of its invasive behavior (Damascos and Gallopin 1992), but also as a limiting factor for new recruitment of *N. dombeyi*.

Finally, in this study, the slight evidence of higher shrub covers under drought-dead canopy could be related to the type of growth-response that shrubs undergo. For example, in post-fire ecosystems, large and middle-sized shrubs respond immediately after the disturbance by extending their axis and branches, consequently enlarging their crown area (Bond and Midgley 2001). However, the presence of standing-dead stems retaining twigs and even brown leaves for at least one or two growing seasons, may imply different post-disturbance growth traits in shrub components. Different leaf arrangement and/or an increase in leaf density might be related to lower light levels found in the forest floor by Suarez and Kitzberger (2008), masking an increase in shrub cover as they retain or slightly modify the original cover area.

In a forest dynamic context, releases of tree saplings are commonly taken into account in the analysis of future forest composition after any disturbance (Rentch et al. 2003; Suarez and Kitzberger 2010; Wright et al. 2000). However, only a few studies have researched how overstory death of dominant species can produce changes in understory vegetation through post-disturbance effects involving biotic filters and new distinctive environmental conditions (Kane et al. 2011; Suarez and Kitzberger 2008). These changes in plant community composition that alter regeneration trajectory of the affected species ultimately have a cascading effect on ecosystem functioning. An accurate knowledge of the

behavior of post-disturbance growth trends and vegetation assemblage changes is highly needed in order to assess future forest trajectories.

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