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Climate change-related growth improvements in a wide niche-breadth tree species across contrasting environments

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• **Background and Aims** The vulnerability and responsiveness of forests to drought are immensely variable across biomes. Intraspecific tree responses to drought in species with wide niche breadths that grow across contrasting climatically environments might provide key information regarding forest resistance and changes in species distribution under climate change. Using a species with an exceptionally wide niche breath, we tested the hypothesis that tree populations thriving in dry environments are more resistant to drought than those growing in moist locations.
• **Methods** We determined temporal trends in tree radial growth of 12 tree populations of *Nothofagus antarctica* (Nothofagaceae) located across a sharp precipitation gradient (annual precipitation of 500–2000 mm) in Chile and Argentina. Using dendrochronological methods, we fitted generalized additive mixed-effect models to predict the annual basal area increment as a function of year and dryness (De Martonne aridity index). We also measured carbon and oxygen isotope signals (and estimated intrinsic water-use efficiency) to provide potential physiological causes for tree growth responses to drought.
• **Key Results** We found unexpected improvements in growth during 1980–1998 in moist sites, while growth responses in dry sites were mixed. All populations, independent of site moisture, showed an increase in their intrinsic water-use efficiency in recent decades, a tendency that seemed to be explained by an increase in the photosynthetic rate instead of drought-induced stomatal closure, given that $\delta^{18}O$ did not change with time.
• **Conclusions** The absence of drought-induced negative effects on tree growth in a tree species with a wide niche breadth is promising because it might relate to the causal mechanisms tree species possess to face ongoing drought events. We suggest that the drought resistance of *N. antarctica* might be attributable to its low stature and relatively low growth rate.

Key words: Drought stress, global change ecology, intrinsic water-use efficiency, isotopes, Patagonia, plant–climate interactions, precipitation gradient, tree growth trends.

INTRODUCTION

The vulnerability and responsiveness of forests to drought is immensely variable across biomes (e.g. Babst *et al*., 2019; Batllori *et al*., 2020; Gazol *et al*., 2020). Although tree drought mortality, canopy dieback and growth decline have unfortunately become commonplace in many areas around the globe, in some other regions, well-documented drought events have not led to such drastic effects on trees (Dietrich *et al*., 2019; Fajardo and Piper, 2021). It is difficult to increase our understanding in relationship to how drought can affect forests from stand to biogeographical scales (Clark *et al*., 2016) because drought responses vary greatly among diverse tree species, depending mainly on the severity of the drought and the sensitivity of each species to drought. Although there are some clues regarding which tree

species in a community will be more vulnerable to drought-induced mortality and growth decline (e.g. species with low wood density; Greenwood *et al*., 2017), we do not know which tree populations within a species will be the most vulnerable to drought and other climate extremes (Anderegg *et al*., 2019). This might be of great importance in generalist species with wide niche breadths that are able to thrive in climatically contrasting sites.

Global warming in the Northern Hemisphere is expected to alter tree performance mainly at the edges of their distributions (Cavin and Jump, 2017). Although this is clear, our understanding of which factors enhance tree growth resistance to drought is still limited. This limitation is attributable, in part, to a lack of information at the intraspecific level. Among several

other factors, local adaptation, acclimatization and phenotypic plasticity can strongly alter the resistance of tree species to drought (e.g. Peltier *et al.*, 2016; Sánchez-Salguero *et al.*, 2018), which might explain the high variation in tree growth responses to drought. For example, site productivity can modify phenotypic strategies of trees coping with drought; higher shoot-to-root ratio and height in moist productive sites and the opposite trend in dry, less productive sites. As such, it is intuitive to expect that tree populations thriving in dry and less productive locations will be more resistant and less vulnerable to drought events than those that thrive in moist and more productive locations. Drought might thus act as a selective force by promoting the rate of evolution of drought-adaptive traits (e.g. short stature; Fajardo *et al.*, 2019), especially in widely distributed tree species. Reinforcing this expectation, Cavin and Jump (2017) found that populations of the widespread tree species *Fagus sylvatica* located at the range core of the distribution range showed greater drought-linked growth sensitivity and lower resistance than populations located at the dry-edge limits of its range. However, other studies have found the contrary, that populations located at the driest edge of species geographical ranges have been the most affected by drought. For example, southern tree populations of six species, including *Quercus robur* and *Pinus sylvestris*, located at their distribution edge (the driest part of their range) proved to be vulnerable to drought effects in southern Europe (Camarero *et al.*, 2021). Likewise, Sánchez-Salguero *et al.* (2018) found that trees of *Pinus pinaster* from dry sites were less resistant to drought in terms of growth than trees from wet sites. The determination of which populations are more affected by drought is essential to anticipate tree mortality events and to develop and apply conservation measures.

Tree species distributed across several environmental conditions are said to have a wide niche breadth. The ecological niche breadth of a species is the range or variety of conditions that make up the realized niche of a species (Sexton *et al.*, 2017). Species with wide niche breadths might constitute key system models to study regional-scale patterns of drought-induced tree-growth trends. In principle, we might expect species with wide niche breadths to be less affected by drought because they have evolved ecotypically differentiated subpopulations or simply have high phenotypic plasticity within genotypes, which enables them to thrive in contrasting environmental conditions (Condit *et al.*, 1995; Fajardo and Piper, 2021), such as areas with high or low water availability. Thus far, most current models related to how tree species are affected by climate change generally ignore species niche breadth or intraspecific trait variation in response to environmental stresses (Valladares *et al.*, 2014), which can introduce great uncertainty regarding how forests will ultimately respond to anthropogenic global warming (Anderegg and HilleRisLambers, 2016). Tree species with wide niche breadths are expected to exhibit a higher intraspecific trait variation (most probably attributable to high phenotypic plasticity), and therefore might track environmental fluctuations better (Fajardo and Siefert, 2019). By comparing tree growth rates in response to a climate shift in distinct ecotypically differentiated tree populations across an environmental and productivity gradient (e.g. a precipitation gradient), we can infer whether the ability of a species to cope adequately with drought is represented consistently at the population level. This knowledge is fundamental

for forecasting potential species range shifts (Anderegg and HilleRisLambers, 2016; Cavin and Jump, 2017).

In this study, we assessed temporal trends in tree growth of tree populations located across contrasting climatic conditions, specifically a sharp precipitation gradient in the Chilean and Argentine Patagonia, which should impose strong and directional limitations on tree growth. We benefitted from the existence of an exceptional tree species that grows across a broad niche breadth, *Nothofagus antarctica* (Nothofagaceae), permitting the determination of a growth–climate relationship devoid of spurious comparisons across distantly related clades, which could aid in identifying regional patterns. The ample distribution and niche breadth of this species allowed us to study how populations of the same species respond in growth to prevailing global warming at contrasting hydrological regimes. It is important to note that in addition to global warming, southern South America experienced a strong climatic shift (in the mid-1970s) that modified the climate from cool and humid to warm and dry, with an average increase in temperature of 1.5 °C and an average decrease in precipitation of 40 % (Jacques-Coper and Garreaud, 2015). Considering these antecedents, we tested the hypothesis that tree-growth responses to drought vary across sites with different hydrological regimes. We hypothesized that populations of *N. antarctica* located at the driest extreme of the gradient would be more resistant to drought than populations at the moist extreme, where severe droughts are less frequent. Also, to gain insights into the physiological mechanisms driving tree growth across the precipitation gradient, we assessed the temporal trend in intrinsic water-use efficiency (iWUE) and its relationship with hydrological conditions across locations and during climatically contrasting decades, using tree-ring wood isotopes ($\delta^{13}C$ and $\delta^{18}O$) on a 5-year time scale.

MATERIALS AND METHODS

Species and research sites

Nothofagus antarctica is a deciduous, short-stature tree (mean height of 8 m) that grows throughout a wide latitudinal and longitudinal range in the southern Andes of Chile and Argentina. It covers 1.6×10^6 ha in Chile (Corporación Nacional Forestal, 2016) and 630 000 ha in Argentina (Martínez Pastur *et al.*, 2022). *Nothofagus antarctica* grows across a wide climate gradient (Fig. 1); it can be found thriving in waterlogged soils in hyper-humid locations in western Patagonia (Fajardo and Velázquez, 2021), reaching the elevational treeline in several locations in the southern Andes, and growing in steppe-like environments on the eastern slopes of the Andes in some places in Chile and Argentina (Martínez Pastur *et al.*, 2021). *Nothofagus antarctica* forms discrete stands that can cover several dozen hectares, where it is commonly the dominant species, although it sometimes co-dominates with other Nothofagaceae species (e.g. *N. betuloides* and *N. pumilio*).

We selected 12 sites across a west-to-east sharp precipitation gradient where, owing to the predominant western winds and the Andes Cordillera, precipitation drops rapidly from west to east on the mainland and from south to north on the Fuegian Archipelago. Selected sites included hyper-humid locations near the northern ice field and the Pacific Ocean in southern Chile (Exploradores site), with several sites throughout the
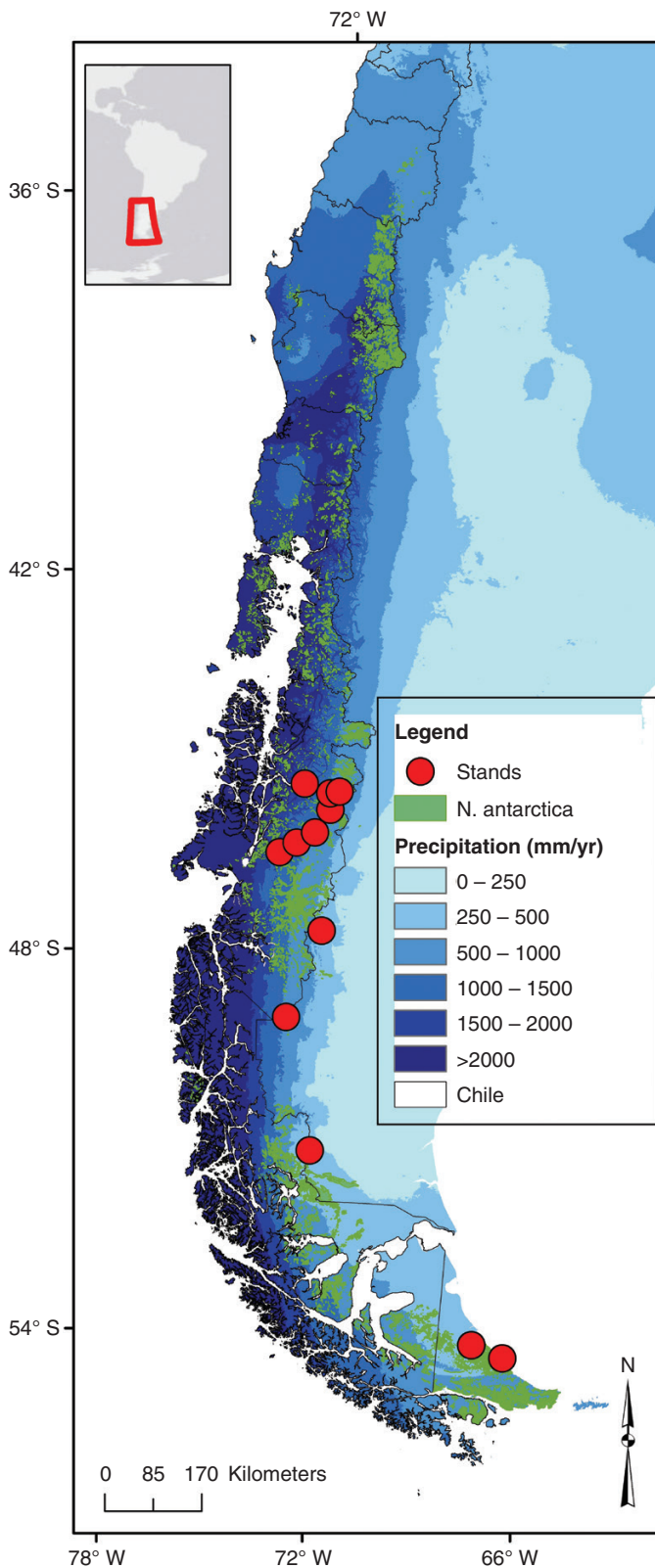
FIG. 1. Regional-scale location of sampled *Nothofagus antarctica* (Nothofagaceae) stands in southern South America, with precipitation isoclines showing the sharp west–east precipitation gradient. Precipitation isoclines are based on data from WorldClim 2 (Harris *et al.*, 2020).

Andes, ending in a couple of locations on the eastern end of Tierra del Fuego, Argentina, facing the Atlantic Ocean (Supplementary data Table S1; Fig. 1).

Field sampling

The field campaign was conducted during the austral growing season of 2019 (from December 2018 to March 2019). Most of these areas had been selected previously for other studies (Fajardo and Piper, 2021; Fajardo and Velázquez, 2021; Martínez Pastur *et al.*, 2021), with the general criterion that stands consist of mature trees, with >90 % dominance of *N. antarctica* and no evident natural (e.g. herbivory) or anthropogenic (e.g. logging) disturbances. At each site, we selected 15–20 dominant trees, devoid of any mechanical damage or apparent generalized fungal infection. Given that this tree species is highly prone to heart rot, we had to try several times before we could finally core a tree in good condition. For each individual, we collected three cores that were extracted perpendicular to the bark using a 5.15 mm increment borer (Haglöf, Långsele, Sweden). We extracted two cores for growth determination at a height of <30 cm, and a third core was extracted for isotope analysis. For each individual, we also measured diameter at coring and breast heights (DBH, 1.35 m) using a diameter tape, and bark depth for both core heights using a bark gauge.

Tree-ring growth measurements

Cores were air-dried, mounted and glued firmly onto grooved wooden blocks, then sanded with successively finer grades of sandpaper until annual rings were clearly distinguished under magnification (×10). Following visual cross-dating, tree-ring widths were measured to the nearest 0.001 mm using a microscope mounted on a dendrochronometer with a Velmex sliding stage (Bloomfield, NY, USA). Cross-dating was checked using the COFECHA software, which calculates correlations among individual and mean site tree-ring series (Holmes, 1983). We then computed the annual basal area increment (BAI) as:

$$\mathrm{BAI} = \left[\pi \left(R_t^2 - R_{t-1}^2 \right) \right],$$

where R_t and R_{t-1} are the radius of the tree stem cross-section in years t and $t-1$. We finally computed an average mean BAI using the BAI values of the two cores.

Drought index

We computed the De Martonne aridity index (I_{DM}; De Martonne, 1926) to characterize the degree of climate dryness at each site location. This index classifies the type of climate in relationship to the soil water availability for plants. The De Martonne aridity index can be expressed as:

$$I_{DM} = P/(T_a + 10),$$

where P is the annual amount of precipitation (in millimetres), and T_a is the mean annual air temperature (in degrees Celsius). The I_{DM} ranges between 15 and 24 for semi-arid site conditions and between 60 and 187 for excessively humid site conditions (Baltas, 2007). The I_{DM} was computed based on temperature and precipitation data for the period 1970–2018. Climate data were

obtained from the 0.5° gridded CRU climate dataset (Harris *et al.*, 2020). In particular, we downloaded monthly temperature, precipitation and potential evapotranspiration data. For each month, the water balance (WB) was calculated as the difference between precipitation and potential evapotranspiration ($P - $ PET). The I_{DM} and the annual WB ($P - $ PET) trend for the period 1970–2018, calculated as the linear regression between WB and year, were negatively related (Supplementary data Fig. S1; i.e. moist sites presented a steeper decrease in the WB than dry sites).

Carbon and oxygen isotope analyses and determination of iWUE

The third core, taken for isotope analyses, was neither sanded nor glued but visually cross-dated. For each of these cores, five-ring sections were homogenized with a centrifugal mill to obtain a particle size of ~1.5 mm (ZM1; Retsch). Cellulose from wood tissue was then isolated and homogenized for $\delta^{13}C$ and $\delta^{18}O$ isotope analyses, following laboratory protocols (Wieloch *et al.*, 2011). Cellulose aliquots of 250 µg for $\delta^{13}C$ (300 µg for $\delta^{18}O$) were weighed on a microbalance (ME36S; Sartorius) in tin (silver for $\delta^{18}O$) foil capsules and converted to CO_2 (CO for $\delta^{18}O$) using a NC 2500 (Carlo Erba) elemental analyser (HT pyrolysis oven, Hekatech, Germany for $\delta^{18}O$) interfaced with a Finnigan DeltaPlus (Delta V Advantage for $\delta^{18}O$) isotope ratio mass spectrometer (Thermo Fisher Scientific Inc.). The $\delta^{13}C$ and $\delta^{18}O$ isotope analyses were conducted at the Stable Isotope Facility of the Institute of Geography, University of Erlangen-Nuremberg, Germany. Stable isotope ratios were expressed as per mille deviations using the δ notation relative to Vienna Pee Dee Belemnite (VPDB) for C and standard mean ocean water (SMOW) for O. The s.d. for repeated analyses was better than 0.2 ‰ for $\delta^{13}C$ and $\delta^{18}O$.

The iWUE of woody plants, which is the ratio between the photosynthetic rate (A) and the stomatal conductance rate (g), i.e. the C fixed per unit of water transpired through stomata, can be determined using the $^{13}C/^{12}C$ ($\delta^{13}C$) isotope ratio from the wood. We inferred iWUE (in micromoles per mole) values from the $\delta^{13}C$ values, following Farquhar *et al.* (1989) and a framework that is about the several causes related to an increase in iWUE, including: (1) a decrease in the stomatal conductance rate (g) along with a constant photosynthesis rate (A); (2) an increase in A along with constant g; or (3) an increase in A along with a decrease in g. The $\delta^{18}O$ signal was used to discriminate among the several causes of the observed increase in iWUE. The $\delta^{18}O$ signal is influenced by water sources, ^{18}O-enrichment of leaf water through transpiration and the back-diffusion of ^{18}O-enriched water owing to site evaporation. Given that $\delta^{18}O$ is more influenced by A than by g, its signal can be used to separate the contributions of A and g to iWUE (Lévesque *et al.*, 2014). According to the dual-isotope conceptual model developed by Scheidegger *et al.* (2000), an increase in $\delta^{18}O$ indicates a decrease in g (e.g. an increase in stomatal closure), in order to minimize water loss along with a constant photosynthesis rate.

Data analysis

All analyses were carried out in the R environment v.4.2.0 (R Development Core Team, 2022). To assess the temporal trends in drought-induced tree growth of *N. antarctica* populations, we initially determined whether tree-ring growth trends for the period

1970–2018 were linear or non-linear. With this aim in mind, we fitted generalized additive mixed-effect models (GAMMs; Wood, 2017), using BAI for each individual tree as the response variable and the interaction between year (trend) and I_{DM} as the fixed factors. GAMM is a flexible semiparametric method that allows for the study of non-linear trends. As in the study by Fajardo and McIntire (2012), we proposed different models in which linear or quadratic functions of year were used in a similar way. We tested whether growth trends are linear or unimodal (second-order polynomial function) and whether such trends vary among sites according to the I_{DM}; for example, we proposed interactions between year (both linear and polynomial) and I_{DM}. We also tested whether growth variability depended on year-to-year variations in WB by including the difference between precipitation and potential evapotranspiration for three different periods (WB_1, whole year; WB_2, November–December; and WB_3, July–December) throughout the 1970–2018 period; that is, we tested whether the BAI series presented a linear polynomial trend (effect of year), depending on drought variations across years (effect of WB), and whether they were different across sites (interactions with I_{DM}). In all the models, we included tree age and diameter (DBH) as covariates. In addition, given that each increment core represents multiple repeated measures of each tree (i.e. temporal autocorrelation), we included tree identity as a random intercept in the analyses and a first-order autocorrelation structure in the models (Ar1). BAI was log-transformed before the analyses. Considering that we were not interested in how tree age and diameter affected growth (e.g. they can be considered confounding factors), we estimated model predictions replacing values of tree age and diameter by the overall mean. Models were fitted with the R/$_{MGCV}$ package (Wood, 2017) using the maximum likelihood approach and default settings for the smooth terms (i.e. for estimated tree age and DBH).

Linear mixed-effect models were used to compare how the iWUE and $\delta^{18}O$ computed for 5-year periods varied across the precipitation gradient in southern South America. Here, site identity was regarded as a random factor to account for the repeated measures performed in each site. The fixed part of the model was composed of the temporal trend (5-year values for the period 1970–2018) and the I_{DM}. Similar to what was carried out with BAI, we considered interactions between time (both linear and quadratic) and the I_{DM} to test for differences in iWUE and $\delta^{18}O$ trajectories among sites. Models were fitted with the R/$_{NLME}$ package (Pinheiro *et al.*, 2021) using the default settings and maximum likelihood estimations. We also computed the conditional (R^2_m) and marginal (R^2_c) values, which account for the variability attributable to fixed effects and fixed plus random effects, respectively (Nakagawa and Schielzeth, 2013). Finally, we selected the final model for each response variable (i.e. BAI, iWUE and $\delta^{18}O$) using the Bayesian information criterion (BIC); that is, we calculated the BIC for the proposed models and chose the one with the lowest value.

RESULTS

Sites across the precipitation gradient

A total of 156 trees and 296 cores were used to compute tree-ring width chronologies that spanned from 38 (PA stand; for

site codes, see Supplementary data Table S1), the minimum, to 113 years (SP stand), the maximum tree age. The I_{DM} varied significantly across sites, showing values from 16 at one of the driest Argentine stands (ET) to 81 at the westernmost, wettest Chilean stand (PA).

In the last five decades, moist sites showed more variable precipitation and WB trends than those found in the dry sites, while temperature was more equally distributed (Supplementary data Fig. S2). Although WB minima depict severe drought events in Patagonia well (1976, 2007 and 2016), moist sites always showed a positive WB (Supplementary data Fig. S2). Apparently, sites located in dry conditions, represented by negative WB values and with I_{DM} < 24, are more stable in their negative WB conditions. Overall, we observed a subtle decrease in precipitation and WB, along with a subtle increase in temperature over time (Supplementary data Fig. S2).

General growth trends

The mean tree-ring width was <4 mm in the humid Chilean sites, and a tree-ring width ≤ 1 mm was observed in the dry Argentine sites. In general, our results show significant differences in the growth trends of *N. antarctica* in relationship to climate across the wide precipitation gradient of southern South America (Fig. 2; Supplementary data Fig. S3). All stands located in moist conditions, with the sole exception of EX, showed monotonic increases in BAI during the last decades (Fig. 2). Negative trends from the 1980s to the present were found in DL, SP, TF and PM (dry sites), whereas no clear trends or even positive trends were found in the driest site (RT). When modelling the BAI, the model with the lowest BIC included a quadratic term of year multiplied by the I_{DM} (Table 1; Supplementary data Table S3). The variation of BAI explained by the quadratic model was relatively high (R^2 = 0.59). Based on this model, BAI clearly increased with time until 1998 and stabilized afterwards (thus, a significantly positive slope on the quadratic year term) at the moister stands, but not at the drier stands, hence the significant year × I_{DM} interaction (see also Fig. 3). The projected trends were created in each site for trees of average DBH and age (26.46 cm² and 67 years, respectively; Supplementary data Fig. S4). The effect of DBH on tree growth trends tended to be more important than the effect of age, in that the former increased with growth up to a point where it stabilized, whereas the latter showed almost no relationship with growth (Supplementary data Fig. S4).

Isotopic signature

Trends in iWUE and δ¹⁸O proved to be significantly associated with year and not with stand location across the precipitation gradient, i.e. they varied independently from I_{DM} (Table 1; Fig. 4; Supplementary data Table S2; Fig. S5). From 1980 onwards, iWUE increased exponentially (best-fitting model contains a quadratic term of year), whereas δ¹⁸O exhibited a slight increase linearly since 1970. The variation in iWUE explained by the quadratic model including year was relatively high (R^2_m = 0.42; R^2_c = 0.48); however, the linear model including year had a poor fit when describing the variation in δ¹⁸O and was not supported by the BIC (Table 1).

DISCUSSION

Based on the sampling of 12 stands of a single species, *N. antarctica*, across a sharp precipitation gradient in southern South America, we found that tree-growth responses to drought varied significantly across sites. The primary patterns of tree growth occurring between 1980 and 1998 exhibited a positive trend in the moist sites, and there was a distinctive turning point in growth at ~1998, showing a clear stabilization in the last two decades (Fig. 3). In contrast, the populations located at the dry sites showed increases or decreases in growth, depending on the site. Accordingly, our best-fitting growth model suggested positive growth trends in the moist populations and rather constant growth trends in the dry populations (Fig. 3). This pattern is somewhat counterintuitive to the increase in temperature and reduction in precipitation observed in the region in recent decades (Supplementary data Fig. S2). We think that this unexpected climate change-related positive growth pattern in the moist sites might be attributable to the fact that these populations never experienced a negative WB (Supplementary data Fig. S2) and that *N. antarctica* is an overall slow-growing species that is not water limited in such moist regions. It is important to note that these results, coming from a wide climatic gradient, prove that tree populations, which are either adapted or acclimatized to differences in water availability, might have different physiological mechanisms or phenotypic strategies, or both, which help them to resist drying conditions and, ultimately, to maintain their current range distribution (see also Fajardo and Piper, 2021). Interestingly, increases in iWUE were observed in all populations during the last two decades, suggesting a physiologically plastic response of trees to cope with less favourable climatic conditions. Whether such plasticity translates into secondary growth differences has proved to be site dependent, at least in part, further suggesting that the decoupling of iWUE and secondary growth varies in space (Kannenberg *et al.*, 2022). Below, we elaborate further on the key implications of these results.

First, the existence of drought, a meteorological event occurring when there is a prolonged time period with lower average precipitation, is a real issue in moist sites that showed significant decreases in annual precipitation, with deficits of ≤60 %, as was the case for the 2016 drought (Garreaud, 2018). However, trees subjected to these drastic reductions in precipitation in the moist sites were never exposed to a negative WB (Supplementary data Fig. S2). Drought periods might imply significantly less cloudiness in these moist locations, which might promote carbon assimilation and growth. Although we did not use cloudiness data to support this explanation directly, the fact that climate has become warmer and drier than before (i.e. the 1970s climatic shift; Jacques-Coper and Garreaud, 2015) necessarily implies less cloudiness. In a few cases, such as boreal and temperate forests of the Northern Hemisphere, drought has also been associated with exceptionally warmer conditions and enhanced tree growth (D'Orangeville *et al.*, 2018). Populations of *N. antarctica* located at the driest extreme of the precipitation gradient showed a constantly stable and negative WB, with positive and negative growth trends. These results suggest that specific drought events have little ecological impact on them. These populations, with low and stable growth patterns throughout
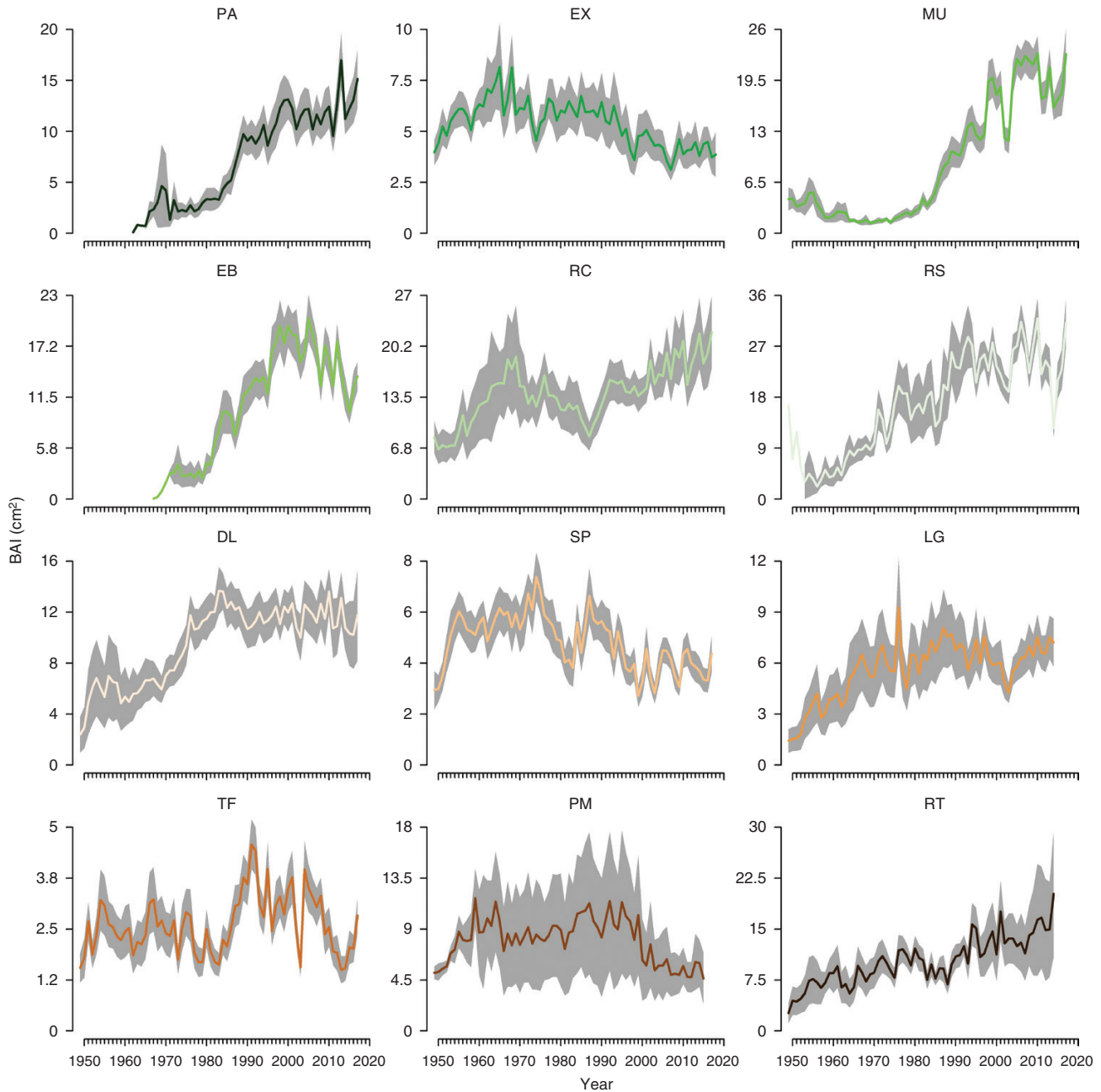
FIG. 2. Basal area increment (BAI; in centimetres squared per year) trends obtained from each site location, which correspond to stands of *Nothofagus antarctica* located across a sharp precipitation gradient in southern South America (Chile and Argentina). The arrangement of panels goes from humid sites/stands with the highest De Martonne aridity index (I_{DM}) at the upper left to dry sites/stands with the lowest I_{DM} at the lower right side of the figure. The shaded area represents the 95 % confidence intervals around the mean of BAI. Codes for the sites are given in Supplementary data Table S1.

time, appear to be acclimatized to extreme climatic situations, including dryness in general. Suffice it to say that no tree mortality events triggered by severe droughts have yet been reported in this species. In a previous study, Fajardo and Piper (2021) found that several tree species, including *N. antarctica*, showed acclimatization to drought (e.g. trees increased both their iWUE and their ratio of soluble sugars to non-structural carbohydrates) and did not reduce their growth during drought periods. Importantly, our results indicate that it is not always possible to predict growth decline from a negative WB,

particularly in dry locations where vegetation is adapted or acclimatized to such conditions. One would expect that vegetation prevailing at moist locations would be at risk of growth decline when drought events occur. However, as seen in the present study, not even the most severe drought in the last 70 years (in 2016) struck so hard as to lead to a negative WB in these moist locations.

Second, *N. antarctica* thrives in the harsh conditions of the Patagonia, including low temperatures, strong winds and a rather short growing season. It is a short-statured and

TABLE 1. *Schwarz's Bayesian information criterion (BIC) ranking of alternative models and statistics relating the year, De Martonne aridity index (I_{DM}) and water balance (WB_1, whole year; WB_2, November–December; and WB_3, July–December) to basal area increment (BAI; in millimetres squared per year), intrinsic water use efficiency (iWUE; in micromoles per mole) and oxygen isotope composition ($\delta^{18}O$; per mille). Stands were located across a sharp precipitation gradient in southern South America (Chile and Argentina). Best models in accordance with the lowest BIC and the highest coefficient of correlation (R^2) appear in bold. In the case of linear mixed-effect models (iWUE and $\delta^{18}O$), the marginal (R^2_m) and conditional (R^2_c) coefficients of correlation are shown. All models predicting BAI included tree age and diameter at breast height (DBH, 1.35 m) as covariates*

Model	BAI		iWUE			$\delta^{18}O$		
	BIC	R^2	BIC	R^2_m	R^2_c	BIC	R^2_m	R^2_c
Null	−8571	0.50	686	0	0	**147**	0	0.72
year	−8711	0.55	663	0.38	0.38	148	0.02	0.78
year^2	−8729	0.56	**660**	**0.42**	**0.48**	151	0.16	0.78
year + I_{DM}	−8709	0.56	666	0.41	0.41	154	0.16	0.80
year * I_{DM}	−8740	0.58	670	0.41	0.41	152	0.02	0.80
year^2 + I_{DM}	−8727	0.57	663	0.45	0.46	155	0.16	0.80
year^2 * I_{DM}	**−8762**	**0.59**	670	0.45	0.52	160	0.17	0.83
year^2 * I_{DM} + WB_1	−8756	0.59	674	0.46	0.52	164	0.17	0.83
year^2 * I_{DM} + WB_2	−8759	0.59	670	0.52	0.58	161	0.19	0.82
year^2 * I_{DM} + WB_3	−8754	0.59	674	0.45	0.52	158	0.27	0.83
year^2 * I_{DM} + WB_1 * I_{DM}	−8744	0.59	679	0.46	0.52	168	0.17	0.84

relatively slow-growing species, which might be beneficial under drought stress and limited resource supplies (Fajardo *et al.*, 2019, 2020). Many tree species from the Northern Hemisphere that have shown growth decline and even mortality under drought stress are rather fast-growing species. Thus, when *N. antarctica* has been exposed to drought, its maintained growth rate could be the consequence of its low resource demands. *Nothofagus antarctica* is a treelet with an average maximum height of ~8 m that can, nonetheless, reach 20 m in very moist locations (Fajardo and Velázquez, 2021). Fajardo *et al.* (2019) have suggested that short stature in trees might be an advantage when coping with the detrimental effects of global climate warming, because short-statured trees have a greater adaptation capacity (i.e. with shorter regeneration times, they should have more opportunities for selection and thus a higher capacity for adaptation) and a higher drought resistance and hydraulic efficiency (i.e. narrow xylem conduits confer embolism resistance, and shorter trees have relatively narrow conduits) than taller tree species. *Nothofagus antarctica* has a wood density of ~0.65 g cm^{-3} (Fajardo, 2022), which is relatively high when all species of the different communities in southern South America are considered. High wood density has been heralded as a trait conferring resistance to drought (Greenwood *et al.*, 2017) and tolerance to competition (Kunstler *et al.*, 2016; Fajardo and Velázquez, 2021). Thus, overall, this species appears to be well equipped to cope with drought, especially in dry environments.

Third, tree species cope with the negative effects of drought via a series of physiological and morphological adjustments (acclimatization), including: leaf shedding, increasing iWUE, stomatal closure, the shrinkage of vascular conduits (Brodribb *et al.*, 2020), the conversion of starch into soluble sugars (Fajardo and Piper, 2021) or the continuous reduction in height

(Fajardo *et al.*, 2019), all ultimately aiming to reduce xylem embolism, carbon starvation (McDowell *et al.*, 2008) or tissue desiccation (Körner, 2019). The $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures and the iWUE trends can shed some light regarding the physiological mechanisms of *N. antarctica* when coping with a reduction in water availability. Both the non-linear significant increase of iWUE and the slight increase of $\delta^{18}O$ occurring in recent decades proved to be independent of site conditions, i.e. they varied independently from I_{DM} (Table 1; Fig. 4; Supplementary data Table S2; Fig. S5). An increase in iWUE has traditionally been interpreted as a signal of water limitation and therefore of stress in trees, which, in most cases, has led to a reduction in tree growth rates (Lévesque *et al.*, 2014; Guerrieri *et al.*, 2022). Here, we used the $\delta^{18}O$ trend to disentangle the effects of stomatal conductance rate (*g*) and photosynthesis rate (*A*) on the increasing iWUE trend, given that $\delta^{18}O$ is independent of variations in *A* and is mainly influenced by water sources (Lévesque *et al.*, 2014). Thus, an increase in $\delta^{18}O$ indicates a decrease in *g*, in accordance with the dual-isotope conceptual model developed by Scheidegger *et al.* (2000). The subtle increase in the $\delta^{18}O$ abundance found in the present study should be related to the near consistence or slight decrease in *g* values. We therefore assert that both the increase in tree growth and the conspicuous and non-linear increase in iWUE in recent decades have most probably been attributable to an increase in the photosynthetic rate (*A*), along with a constant *g*. We suggest that *N. antarctica* populations growing in moist locations experienced a growth release associated with higher temperatures and irradiance (e.g. less cloudiness), and most probably also increased c_a, owing to a general decrease in precipitation coupled with warmer soils. All these factors combined could be responsible for an increase in *A* and, ultimately, an increase in growth rates.
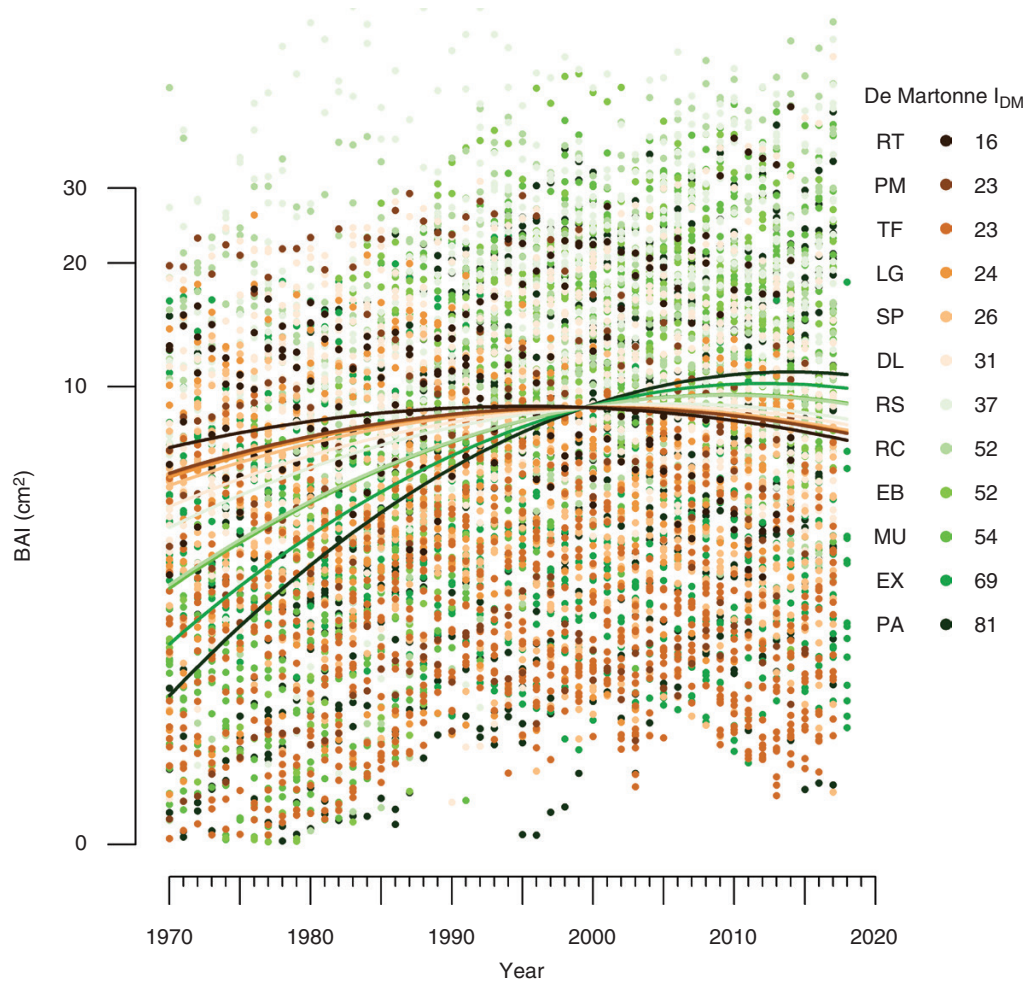
FIG. 3. Basal area increment (BAI; in centimetres squared per year; logarithmic scale) predictions of *Nothofagus antarctica* over time and across aridity (De Martonne aridity index; I_{DM}). Predictions are based on the best-fitting model, which included a quadratic term of year multiplied by the I_{DM} (lowest BCI). Dots represent growth data, and the colour scale ranges from the most humid stands (dark green, in Chile) to the driest stands (dark brown, in Argentina). Lines represent the increasing (positive; mostly for humid stands) or stabilized growth (mostly for dry stands) increments over time at different levels of aridity across the precipitation gradient.

We note, however, that the dual-isotope approach might not always be the most appropriate to make interpretations regarding climate change-related tree physiology (Roden and Siegwolf, 2012). This is because the wood $\delta^{18}O$ signal depends on several factors (water source, leaf water enrichment and the use of stem water during cellulose formation; Cernusak *et al*., 2022). Thus, the subtle increase in the $\delta^{18}O$ abundance might also be attributable to signals related to changes in the water source, because the leaf-derived wood $\delta^{18}O$ signal strengthens when leaf water enrichment and the control played by stomatal conductance are important (Gessler *et al*., 2014).

Conclusions

Predicting drought-induced growth decline and especially forest tree die-off has proved to be difficult. More worrying yet, it has been challenging to secure consensus regarding general patterns of growth decline and mortality worldwide, with most studies reporting drought-induced site-specific responses. In our study, we also found a site-specific response to regional drought, but at the intraspecific level: (1) populations located in areas where the WB remained positive, even when exposed to strong precipitation reductions, showed increases in growth; and likewise (2) in locations constantly subjected to a negative WB, tree populations that are adapted to these harsh conditions showed stable trends in tree growth. The intraspecific variation in growth, as a response to climate change, found here is important because it should shed light on the causes of global cross-species responses to drought and on the resistance mechanisms that tree species must develop to cope with drought. Second, stable growth trends when facing dry conditions (with important increases in growth in moist locations with significant reductions in precipitation) along with an increase in iWUE appear to be related to an increase in the photosynthetic rate rather than an increase in stomatal closure. This is important regarding carbon sequestration in the forests of southern South America. Given that *N. antarctica* is one of the most important and amply distributed tree species in the region, with almost 2×10^6 ha in Chile and Argentina (CONAF, 2016;
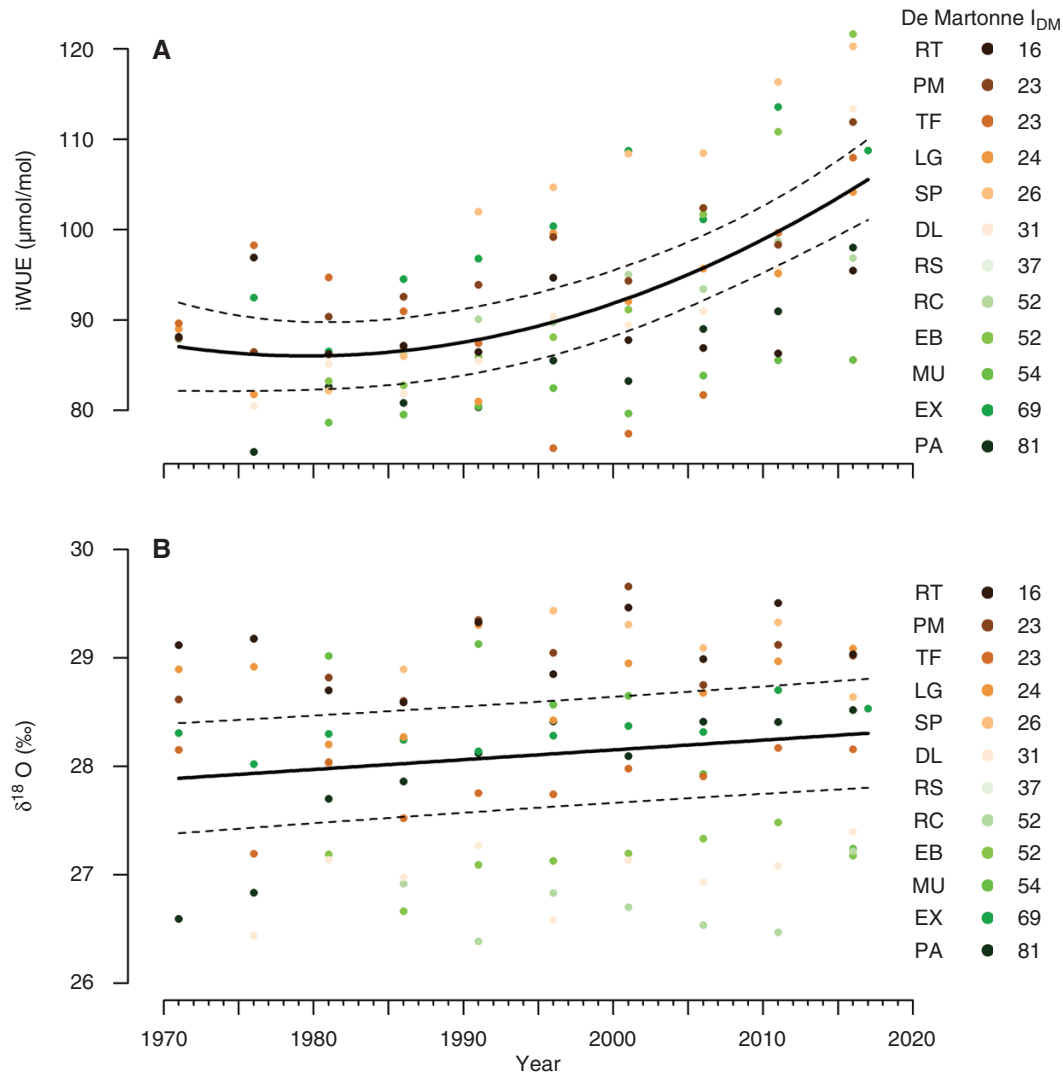
FIG. 4. Water-use efficiency (iWUE; A) and oxygen isotope composition (δ^{18}O; B) across decades for several forest stands of *Nothofagus antarctica* located across a sharp precipitation gradient in southern South America (Chile and Argentina). Dots correspond to isotopic signalling per stand of 5-year rings, ranging from very humid (dark green) to very dry (dark brown) sites. In accordance with statistics, both iWUE (exponential) and δ^{18}O (linear) follow significant increasing trends with time, although δ^{18}O has a low model fit (see Table 1). The key refers to De Martonne aridity index (I_{DM}) values for each stand.

Martínez Pastur *et al*., 2022; Fig. 1), we anticipate that there is a significant potential for carbon sequestration in this region.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following.

Table S1: *Nothofagus antarctica* stands located across a sharp precipitation gradient in southern South America, along with coordinates, elevation, mean annual temperature, total annual precipitation, water balance and its trend, and the current De Martonne index of aridity. Table S2: dendrochronological statistics in the form of tree-ring width of several populations of the tree species *Nothofagus antarctica* located across a sharp precipitation gradient in southern South America from humid to dry locations. Table S3: summary of the selected GAMM of *Nothofagus antarctica* growth. Figure S1: relationship between De Martonne aridity index and the water balance. Figure S2: mean annual temperature, total annual precipitation and water balance during the last 7 decades for 12 stands of *Nothofagus antarctica* in southern South America. Figure S3: growth of *Nothofagus antarctica* trees of different ages and sizes across the aridity gradient. Figure S4: effect of estimated tree age and size according to the GAMM. Figure S5: observed values of intrinsic water-use efficiency and oxygen isotope composition across 5-year periods for forest stands of *Nothofagus antarctica* located across a sharp precipitation gradient in southern South America.

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