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Sex-dependent resilience to extreme drought events: implications for climate change adaptation of a South American endangered tree species

Sergio Piraino^{1,2*}, Martín Ariel Hadad³, Yanina Antonia Ribas-Fernández³ and Fidel Alejandro Roig^{1,2,4}

Abstract

Background Recent changes in climatic trends are resulting in an increased frequency and intensity of extreme events, with unknown effect on ecosystem dynamics in the near future. Extreme drought episodes are recognized as disturbance factors capable of modifying forest dynamics and tree growth. Within this context, dioecious tree species may be impacted by climatic extremes, affecting male/female proportions and, consequently, reproductive processes and species persistence. Therefore, there is an urgent need for species-specific assessments of growth tolerance to extreme dry spells in dioecious tree species, to establish effective conservation strategies for these particular natural resources. *Araucaria araucana* (araucaria), an endangered dioecious Patagonian tree species, has recently undergone decay and mortality episodes in response to increasing dry climatic conditions. While sex-dependent tolerance to extreme drought episodes has been assessed in the species' humid distribution range, there is still a lack of information on the gender-based resilience of trees growing in the drier environments of the species' distribution.

Methods We reconstructed, through dendrochronological methods, the sex-dependent response of 105 araucaria individuals (55 female and 50 male trees) to five regional extreme dry spells employing a set of different indices. Resistance, recovery period, and average growth reduction of standardized tree-ring growth were examined, analysing the effect of biotic (sex, pre-drought stem tree growth) and abiotic (local climatic conditions before, during, and after extreme climatic episodes) factors on tree resilience.

Results Sex influences only the species resistance to climatic disturbance, with male individuals showing lower tolerance to extreme drought events. Pre-drought radial growth rates and local meteorological conditions preceding, during, and following extreme dry spells strongly modulated araucaria radial growth resilience regardless of tree sex, influencing the species resistance, recovery period, and average growth reduction.

Conclusions We provide novel and crucial information for the species conservation and management in the current climate change scenario, and contribute to the debate regarding the role of tree sex as a factor influencing woody species growth under particularly adverse climatic conditions. In the face of climate change, an increase in extreme

*Correspondence:

Sergio Piraino

spiraino@mendoza-conicet.gov.ar; spiraino@fca.uncu.edu.ar

Full list of author information is available at the end of the article



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drought events is expected in the easternmost araucaria xeric end distribution area, which will likely decrease the species resilience.

Keywords Araucaria, Climate change, Dendrochronology, Extreme drought event, Resilience

Introduction

Forests cover approximately 42 million km² worldwide, corresponding to 30% of land surface (Bonan 2008). Woodlands globally provide several ecological, economic, and ecosystem services, including biomass production, carbon sequestration, habitat provisioning, and social and cultural values, furthermore playing a pivotal role in various biogeochemical cycles (Brockerhoff et al. 2017; Ellison et al. 2017).

At the global scale, ongoing changing climatic conditions have already impacted forest dynamics, leading to modifications in regeneration, reproduction, health, and growth of these ecosystems (Kirilenko and Sedjo 2007; Beckage et al. 2008; Sturrock et al. 2011; Anderson-Teixeira et al. 2013). In the climate change scenario, extreme drought episodes are considered among the most pressing environmental challenges for trees, especially as the frequency and intensity of dry spells are predicted to increase in the future, along with changes in climate trends (IPCC 2023). Ground-truth information concerning forest resilience to extreme drought events is urgently needed to enhance conservation and management strategies, particularly for endangered species that may be especially vulnerable to climate change-induced dry spells.

Recent studies indicated that forest resilience to extreme dry climatic episodes varies across populations, suggesting that different abiotic and biotic factors may modulate tree ability to cope with water stress. Genetic variation, tree characteristics (age and/or size) and environmental (climatic and topo-edaphic) factors are known to influence forest resilience to extreme droughts (e.g. Merlin et al. 2015; Montwé et al. 2015; Carnicer et al. 2021; Lucas-Borja et al. 2021; Piraino et al. 2022). However, the role of sex as a modulating factor of tree resilience to drought stress have been poorly addressed thus far (but see Rozas et al. 2019). Dioecious species, representing about 6% of total world plants, provide an interesting opportunity for analysing the trade-offs between reproduction and other life-history traits such as growth (Obeso 2002). As climate change continues to escalate, incorporating sex-dependent resilience considerations into future forest conservation and management policies is a mandatory task.

It has been suggested that sex could modulate vulnerability to global warming in dioecious plants, assuming variability between male and female trees in response to changing climatic factors (Tognetti 2012; Hultine et al. 2016). Male and female trees may exhibit different

physiological and xylem anatomical characteristics, leading to diverse responses to environmental stressors and, therefore, to extreme drought events (Obeso 2002; Juvany and Munné-Bosch 2015; Hadad et al. 2021). Theoretical frameworks suggest that female trees may acquire resources more effectively, while males may display higher resource use efficiency, resulting in better survival ability during more stressful periods compared (Obeso 2002). Nevertheless, dioecious tree species do not always exhibit sex-dependent response to unfavourable climatic conditions, with these mechanisms often being associated with species-specific characteristics, leading to mixed results regarding tolerance to stressful events in male or female trees (Juvany and Munné-Bosch 2015). For example, Rozas et al. (2008) claimed that *Juniperus thurifera* female stem growth dynamics showed higher sensitivity to summer precipitation than male individuals. On the other hand, Garcia-Barreda et al. (2022) found no evidence of sex-difference in the species radial growth/climate relationship, and that female trees did not exhibit reduced conservative water use efficiency during extreme drought periods.

Araucaria araucana (Molina) K. Koch (Araucariaceae), also known as araucaria, is an iconic dioecious tree species of Argentinean and Chilean northern Patagonia woodlands (Roig 1998). These forests have faced different natural and anthropogenic disturbances (e.g. fire, logging; Roig et al. 2014), and for this reason, araucaria is nowadays considered an endangered species (International Union for Conservation of Nature; <http://www.iucnredlist.org/>). Recent studies highlighted that *A. araucana* stem growth resilience to extreme dry spells is bioclimatic-dependent, with differences observed among individuals located in mesic and xeric environments (Piraino et al. 2022). In this sense, xeric araucaria woodlands show the worst capacity to withstand climatic stressful episodes (Piraino et al. 2022). However, araucaria sex-dependent resilience has been analysed solely in humid stands, where no differences emerged between male and female individuals concerning stem growth tolerance to extreme drought events (Rozas et al. 2019). Thus, no study has considered sex as a modulating factor on the species resilience to extreme drought episodes in xeric araucaria woodlands. Given the higher sensitivity of these stands to dry spells, analysing the species resilience to extreme drought events in the driest sectors of its distribution would provide useful information on *A. araucana* forests dynamics in the current climate change

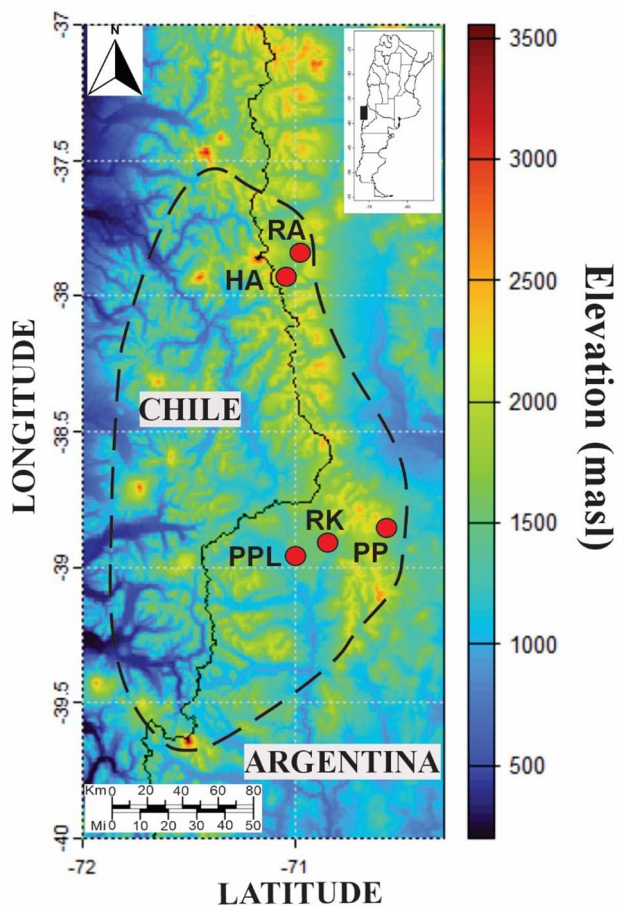


Fig. 1 Location of the study area and analyzed sites. Dotted line indicates *Araucaria araucana* natural forest distribution

scenario (Villalba et al. 2012; Hadad and Roig 2016; Puchi et al. 2022).

In this research we applied dendrochronological techniques to several female and male trees belonging to xeric *A. araucana* woodlands, examining the sex-dependent radial growth resilience to five extreme dry spells occurred during the second half of the 20th century and the beginning of the 21st century. This study aims to contribute to increasing our knowledge of the interactions between sex, drought resilience, and araucaria

persistence in face of climate change. By uncovering sex-specific strategies for coping with extreme drought, we can refine our predictions of how xeric araucaria populations may respond to future environmental challenges. Furthermore, this knowledge could have practical applications in araucaria conservation and management, helping prioritize resources and interventions for the protection of a vulnerable species.

Materials and methods

Study area and dendrochronological sampling

Five sites located in the eastern distribution range (northern Patagonia, Argentina) of *A. araucana* were selected in this study (Fig. 1; Table 1). Sampled forests exhibit the typical physiognomy of xeric araucaria woodlands, characterized by an open, mono-specific tree layer growing on rocky substratum, along with sporadic xerophilous shrubs and steppe-type vegetation (Hadad et al. 2020). Climatically, the examined woodlands are located in an area characterized by Mediterranean-type climate with semi-arid conditions, being mean annual temperature values of 11 °C and total annual rainfall amount of approximately 570 mm (Hadad et al. 2020).

Sampling was focused on dominant and co-dominant adult araucaria individuals, being tree sex determined by identifying the presence and type of the strobiles using a binocular. Two to four wood samples were extracted at breast height (approximately 1.30 m above ground level) from each selected tree with an increment borer. In the laboratory, samples underwent standard dendrochronological techniques, involving air-drying, gluing onto wooden supports, and polishing with progressive finer sandpaper to highlight wood anatomy characteristics (Speer 2010). Calendar years were assigned following the Schulman convention for the Southern Hemisphere (Schulman 1956). Tree-ring widths were measured through the facilities of a Velmex Measuring System (Velmex, INC, NY, USA) with a precision of 0.001 mm, and measurements were statistically checked with COFECHA software (Holmes 1983).

Table 1 Geographical location, number of sampled trees, diameter range, and statistical tree-ring characteristics across the 5 analyzed sites (HA = Hualcupén, PLL = Pampa de Lonco Luan, PP = Primeros Pinos, RA = Río Agrio, RK = Río Kilca). *N* = tree number, where M and F refers to male and female trees, DBH = diameter at breast height (cm), MCV = mean correlation values among individual tree-ring series, EPS = expressed population signal period when value is higher than 0.85 original threshold defined by Wigley et al. (1984)

Site	Latitude	Longitude	<i>N</i> (M/F)	DBH (cm) (M/F)	MCV (M/F)	EPS > 0.85 (M/F)
HA	-37.940000	-71.507500	20 (11/9)	68/70	0.46/0.44	1820/1880
PLL	-38.966944	-71.005833	13 (6/7)	65/64	0.50/0.43	1650/1800
PP	-38.869167	-70.573889	27 (12/15)	81/65	0.47/0.45	1715/1710
RA	-37.833889	-70.977222	25 (12/13)	71/74	0.48/0.45	1800/1620
RK	-38.881389	-70.841944	20 (8/12)	70/66	0.47/0.57	1860/1835

Definition of extreme drought events

In this research, a climatic-based approach was followed to identify extreme drought years. We selected the September–December period (spring) as the time envelope for calculating araucaria sex-dependent resilience, based on previous research (Hadad et al. 2015; Hadad and Roig 2016). A regional series of the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010) of December of the growing year with a timescale of 4 months (hereafter SPEI_4D) was created for the 1902–2017 period. Extreme drought events were defined as those years when SPEI_4D values fell in the lowest 5% percentile distribution. SPEI_4D gridded data were obtained from the KNMI Climate Explorer web page (Trouet and Van Oldenborgh 2013)(<http://climexp.knmi.nl/>).

Calculation of tree resilience indices

This study employed various indices to examine sex-dependent araucaria response to extreme dry spells (Lloret et al. 2011; Thurm et al. 2016; Schwarz et al. 2020). Resilience was assessed considering resistance (R_t), and two different expressions of recovery, that is, recovery period (R_p) and average growth reduction (A_{GR}) (Lloret et al. 2011; Thurm et al. 2016; Schwarz et al. 2020). By combining different approaches in reconstructing forest resilience to stressful climatic episodes, we incorporated reliable metrics concerning tree response to extreme drought events, and thus avoided methodological flaws in resilience analyses (*sensu* Schwarz et al. 2020). Indices were computed based on standardized tree-ring index (TRI) to minimize the influence of factors other than climate (e.g. long-term juvenile age trend, disturbance) on araucaria resilience (Speer 2010; Schwarz et al. 2020). Raw ring measurements were transformed by fitting a negative exponential curve to annual radial increment values, and individual standardized chronologies were obtained through the ARSTAN40c software (Cook and Krusic 2006). Resilience indices were calculated at the tree-level according to the following formulae:

$$\text{Resistance } (R_t) = \text{TRI}_d / \text{TRI}_{pre}$$

$$\text{Recovery period } (R_p) = n \text{ years until } \text{TRI}_{d+n} \geq \text{TRI}_d$$

$$\text{Average growth reduction } (A_{GR}) = G_R / R_p$$

where d refers to drought year, n to the number of years after the extreme event, and pre to the period preceding the dry spell.

R_t defines the ability of tree growth to tolerate the impact of extreme climatic events (Lloret et al. 2011). R_t values below 1.0 indicate low tree resistance to dry spells, while the opposite is true when $R_t > 1.0$ (Lloret et al. 2011). Based on previous research, a three-year window was used in defining the *pre* period in resistance calculation (Piraino et al. 2022). R_p represents the number of years needed by a tree to reach radial growth levels equal

to or higher than those of the pre-drought period (in this study, $pre=3$ years). When tree-ring standardized growth of drought year showed values higher than TRI_{pre} , we arbitrarily set recovery period value as $R_p = 1$. Regarding the A_{GR} index, the G_R variable used in its calculation refers to *growth reduction*, that is, the cumulative growth loss in drought year plus the following years included in the recovery period R_p (Thurm et al. 2016). Similar to R_p , when standardized ring widths did not exhibit a reduction in the year corresponding to extreme dry spells, we arbitrarily set average growth reduction value as $A_{GR} = 0$. We considered a period of 10 years as the maximum length for R_p and A_{GR} calculations, corresponding this window to the time between the first year following the last extreme drought (2008 year; see Results section), and the end of the tree-ring series at one sampled site (2018 year). Finally, the Lloret et al. (2011) recovery index ($R_c = \text{TRI}_{post} / \text{TRI}_d$, with $post=3$ years; Piraino et al. 2022) was estimated to calculate the line of full resilience (Schwarz et al. 2020), according to the following formula: $R_c = 1/R_t$. The line of full resilience compares the observed relationship between resistance and recovery to the hypothetical one characterized by complete resilience, providing an integrated picture of tree species tolerance to extreme dry spells (Schwarz et al. 2020).

Statistical analyses

To disentangle the role of sex as a modulating factor upon araucaria resilience at the dry end of its spatial distribution, separate statistical analyses were conducted for male and female trees. Trees younger than 30 years during the 1956 extreme dry spell were excluded to avoid the influence of juvenile radial growth on resilience calculations. Initially, Spearman rank correlations were calculated to explore possible relationships among resistance, recovery period, and average growth reduction indices. Kruskal-Wallis analysis was then used to investigate significant ($p < 0.05$) sex-dependent differences in resilience indices for each extreme drought year. Finally, generalized linear mixed models (GLMM) (Kuznetsova et al. 2022) were applied to examine the influence of the following biotic and abiotic factors and their interactions on araucaria resilience to extreme drought events: (1) tree sex; (2) mean TRI value of the 5 years preceding extreme dry spells, as a proxy of tree growth (excluding the *pre* window used in R_t calculation; pre_5_TRI); and (3) climatic conditions preceding, during, and following extreme drought episodes (SPEI4_D_{pre} , SPEI4_D_d and SPEI4_D_{post} , respectively; see Fig. S1 for site-dependent annual SPEI4_D trends). SPEI4_D_{pre} was computed as mean SPEI_4D values of three years before the extreme dry spell, while SPEI4_D_{post} was calculated according to the R_p index, computing the SPEI_4D average value of the corresponding number of year that a tree lasted to

reach pre-drought radial growth increments. Regarding R_t , climatic conditions before and during dry spells were included in GLMM, whereas for R_p and A_{GR} , the entire set of abiotic factors was incorporated into statistical modelling. The mentioned biotic and abiotic variables represented fixed factors in GLMM, while site variability, drought year (intra-subject event or repeated measure) and the tree identity were included as random effects. The R_t response variable was square root transformed before analysis. R_p and A_{GR} were modelled following a Poisson and Gamma (log) distribution, respectively. In all cases, we first analysed a full model taking into consideration all main effects and their double interactions and then simplified it to obtain a minimal fitted model, evaluating the change in deviance with Chi-square test ($p < 0.05$) (Crawley 2013). The significance of fixed effects was evaluated with F -test type III deviance analysis (Fox et al. 2023). Finally, the GLMMs coefficients of determination (R^2) were calculated to evaluate the variance of each minimal fitted model (Bartón 2023). Statistical analyses were computed through INFOSTAT and R software (Di Rienzo et al. 2011; R Core Team 2022).

Results

We reconstructed the temporal variability of drought conditions during the September–December period of the year of growth by analyzing the regional SPEI4_D series (Fig. 2). Statistical examination of SPEI4_D

regional fluctuations indicated the occurrence of five extreme regional drought events during the 1902–2017 period: in 1956, 1962, 1983, 1998, and 2008 (Fig. 2). At the site level, tree sample size was similar among the selected stands, ranging from 6 (PLL-male) to 15 (PP-female) individuals in the analysed araucaria woodlands (Table 1). Site sex-dependent ring width chronologies are shown in Fig. S2.

Resistance (R_t) values ranged between 0.84 (1962-male) to 1.08 (1956-female and 1983-male) (Fig. 3). Stem growth rates during drought years were consistently lower than mean values of the three years preceding extreme events, except for female araucarias in the 1956 episode and for male trees in the 1983 dry spell (Fig. 3). On average, female and male trees registered a reduction of 3% and 8%, respectively, in radial growth during dry spells compared to the corresponding three-year previous periods, with male individuals always showing lower R_t than their female counterparts, except for the 1983 extreme drought event (Fig. 3).

Recovery period (R_p) oscillated between 1.92 (1983-male) and 5.11 (1998-female) years (Fig. 3). Overall, male and female trees took about 3 years to recover radial growth rates equal to or higher than the pre-drought period. The fixed maximum window of 10 years used in calculating R_p unlikely underestimated tree growth recovery from extreme drought events, as R_p surpassed this time window in only 10% and 8% of the considered

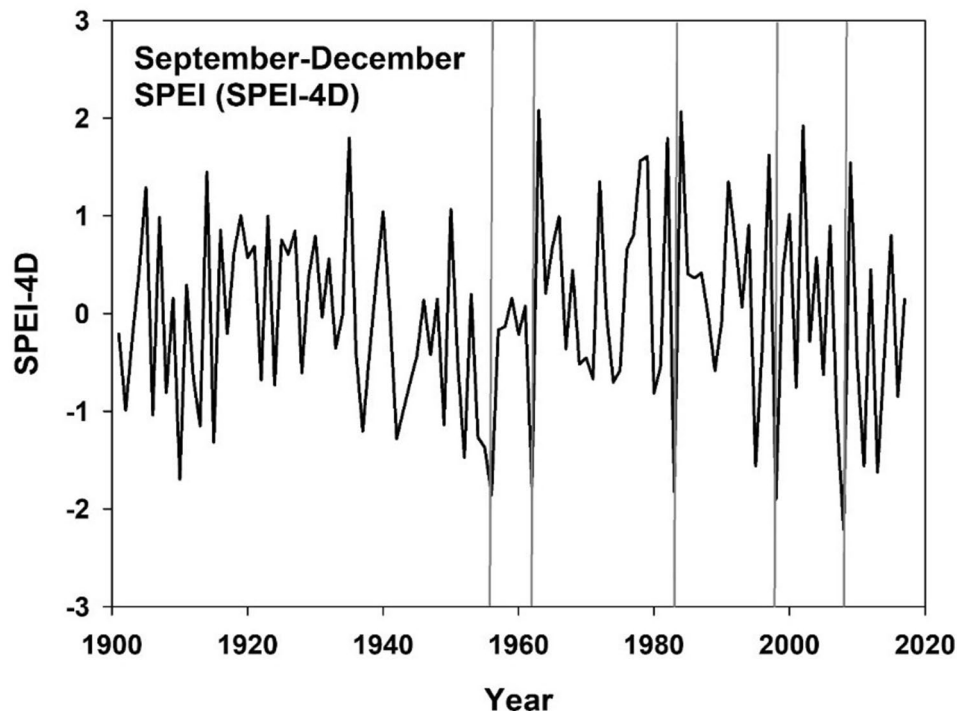


Fig. 2 September–December SPEI of the 1902–2017 period for the studied area (SPEI4_D). Vertical gray lines show the regional extreme drought events

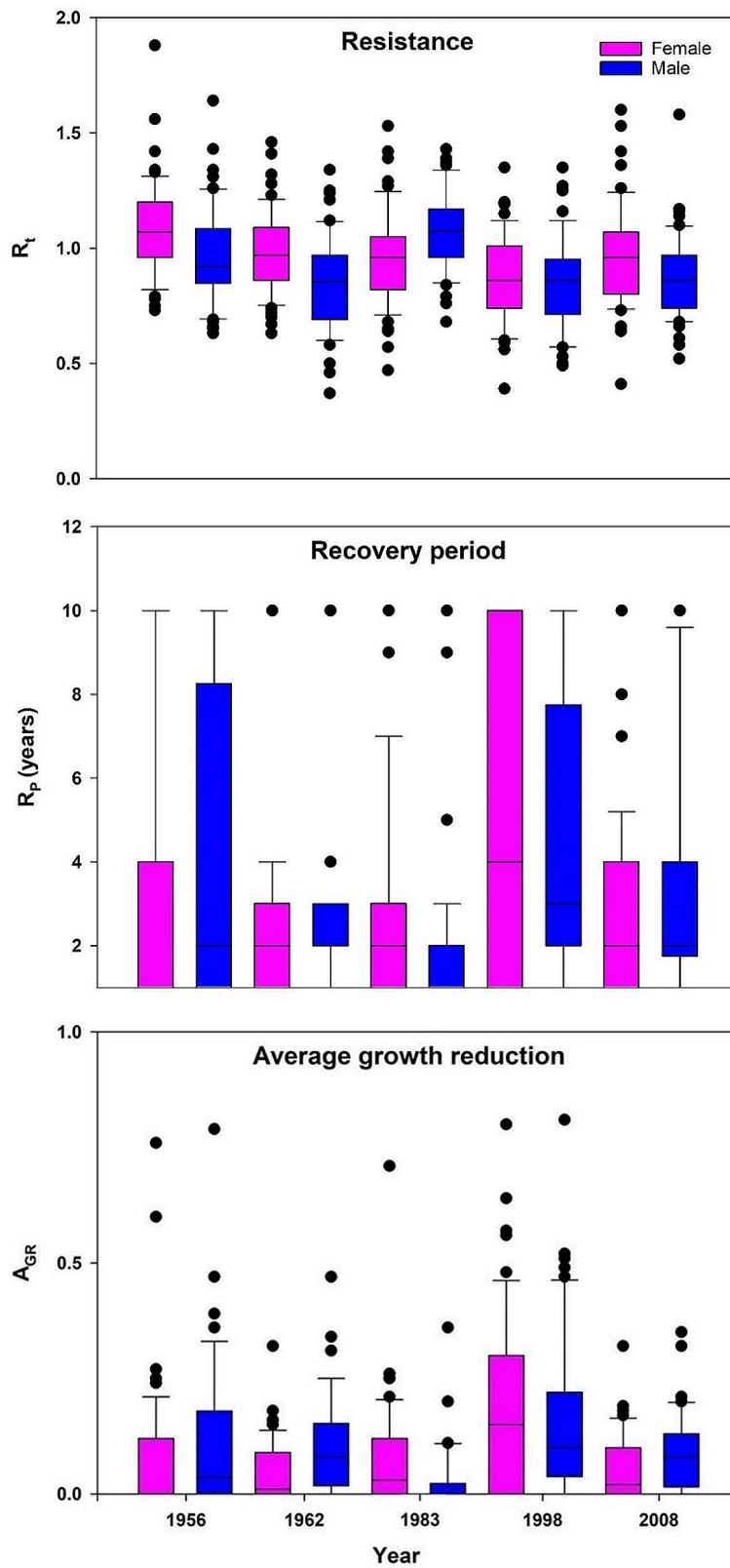


Fig. 3 Box plots for resistance (top), recovery period (middle), and average growth reduction (bottom) of female and male individuals along the examined extreme droughts. Each box shows the values within one interquartile distance (ID 25% above and below the median). The median is shown as a black bar, while whiskers represent values of 1.5 times the IDs and are shown as black lines and circles represent the outliers

cases for male and female trees, respectively (data not shown). Male araucaria individuals exhibited significantly longer recovery period than female trees during the 1956 drought event, while the opposite was true for the 1983 event (Table 2). Regarding the other extreme dry spells, no difference emerged according to tree sex (Table 2).

Average growth reduction (A_{GR}) values fluctuated between 3% (1983-male) and 19% (1998-female) (Fig. 3). Generally, extreme dry spells translated to a post-drought radial growth reduction of 10% (male) and 9% (female), respectively. Male trees presented higher A_{GR} values during the 1956, 1962 and 2008 extreme droughts, and lower values than female individuals for the 1983 dry spell, while the 1998 extreme event affected both sexes equally (Table 2; Fig. 3).

Correlation function analyses revealed that resilience indices are strongly correlated for both male and female araucaria trees, showing significant relations at the $p < 0.0001$ level in all cases (Fig. 4). R_t and R_p exhibited negative relationships ($\rho = -0.71$, $n = 250$; -0.82 , $n = 275$ for males and females, respectively), as well as R_t and A_{GR} ($\rho = -0.89$, $n = 250$; -0.88 , $n = 275$ for males and females, respectively), whereas positive relations emerged between R_p and A_{GR} ($\rho = 0.85$, $n = 250$; 0.93 , $n = 275$ for males and females, respectively).

Calculation of the line of full resilience showed that male and female *A. araucana* trees reacted differently across the selected years to extreme climatic episodes (Fig. 5). In this sense, a higher percentage of male than female trees exhibited full resilience in 1956 (20% vs. 18%), 1962 (76% vs. 69%), and 1998 (24% vs. 16%), while female araucaria individuals performed better than their male counterparts in 1983 (71% vs. 68%) and 2008 (60% vs. 54%) droughts (Fig. 5).

Generalized linear mixed models showed that lower R_t was associated with male individuals, while no sex-differences emerged for R_p and A_{GR} (Tables 3, 4 and 5). Pre-drought growth rates had a negative effect on R_t and a positive one on R_p and A_{GR} , respectively (Tables 3, 4 and 5). Local climatic conditions before and during extreme dry spells were negatively and positively associated with

resistance index, respectively (Table 3). Concerning R_p and A_{GR} , both indices showed a positive relationship with $SPEI4_D_{pre}$, whereas a negative association emerged between recovery period and average growth reduction with $SPEI4_D_d$ and $SPEI4_D_{post}$ values (Tables 4 and 5).

Discussion

In this study, we addressed for the first time the sex-dependent resilience of *A. araucana* to extreme drought events in the eastern semi-arid region of the species distribution, increasing our understanding of this endangered tree species ecology in the current complex climatic change scenario. Although previous investigations explored the modulating effect of sex on araucaria radial growth dynamics in response to extreme dry spells (Rozas et al. 2019), our research further examined the influence of local climatic conditions preceding, during, and following drought events, providing novel information. In this regard, studies reconstructing tree and forest resilience to extreme climatic episodes have only recently begun to consider the effect of climatic envelopes before and after extreme drought events on stem growth resistance and recovery (e.g. Veuillen et al. 2023; Wu et al. 2023; Zhu et al. 2023). Failing to incorporate climatic conditions in both pre- and post-drought periods when modelling tree resilience to extreme dry spells can lead to bias and less reliable information regarding forest growth dynamics in response to this type of disturbance (Schwarz et al. 2020).

The resilience indices adopted in this study were highly statistically correlated, as resistance on one side, and recovery period and average growth reduction on the other, exhibiting negative relationships, while the latter indices were positively related. In this sense, these results suggested that when facing extreme dry spells, trees can prioritize growth during drought years as well invest resources in cambial activity to quickly recover from extreme climatic episodes (high R_t /low R_p and A_{GR}) or, alternatively, be strongly affected by dry spells, due to low tolerance capacity to and recovery ability from drought episodes (low R_t /high R_p and A_{GR}). Regarding the positive relationship between recovery period and average growth reduction, this result was expected since A_{GR} mathematically relies on R_p (Thurm et al. 2016; Schwarz et al. 2020).

Non-parametric statistical analyses, as well as line of full resilience calculations, indicated that differences in male/female response to extreme drought events are not straightforward, as male outperformed females in some years, while females outperformed males during other dry spells. On the other hand, GLMMs suggested that sex modulated only araucaria resistance. These results are, to some extent, consistent with the findings of Rozas et al. (2019), who reported that the resilience of humid araucaria woodlands to extreme drought events was not

Table 2 Results of the non-parametric Kruskal-Wallis test for sex-dependent resistance (R_t), recovery period (R_p) and average growth reduction (A_{GR}), calculated separately for each extreme drought event. Total sample depth is $n = 105$ (male = 50, female = 55). Significant differences in mean resilience indices values at the $p < 0.05$ level are represented in bold characters

Year	R_t (M/F)	R_p (M/F)	A_{GR} (M/F)
1956	0.96/1.08	3.15/4.02	11/7
1962	0.84/0.98	2.20/2.05	10/5
1983	1.08/0.96	1.92/2.65	3/8
1998	0.85/0.87	4.55/5.11	16/19
2008	0.88/0.97	3.16/2.76	9/6

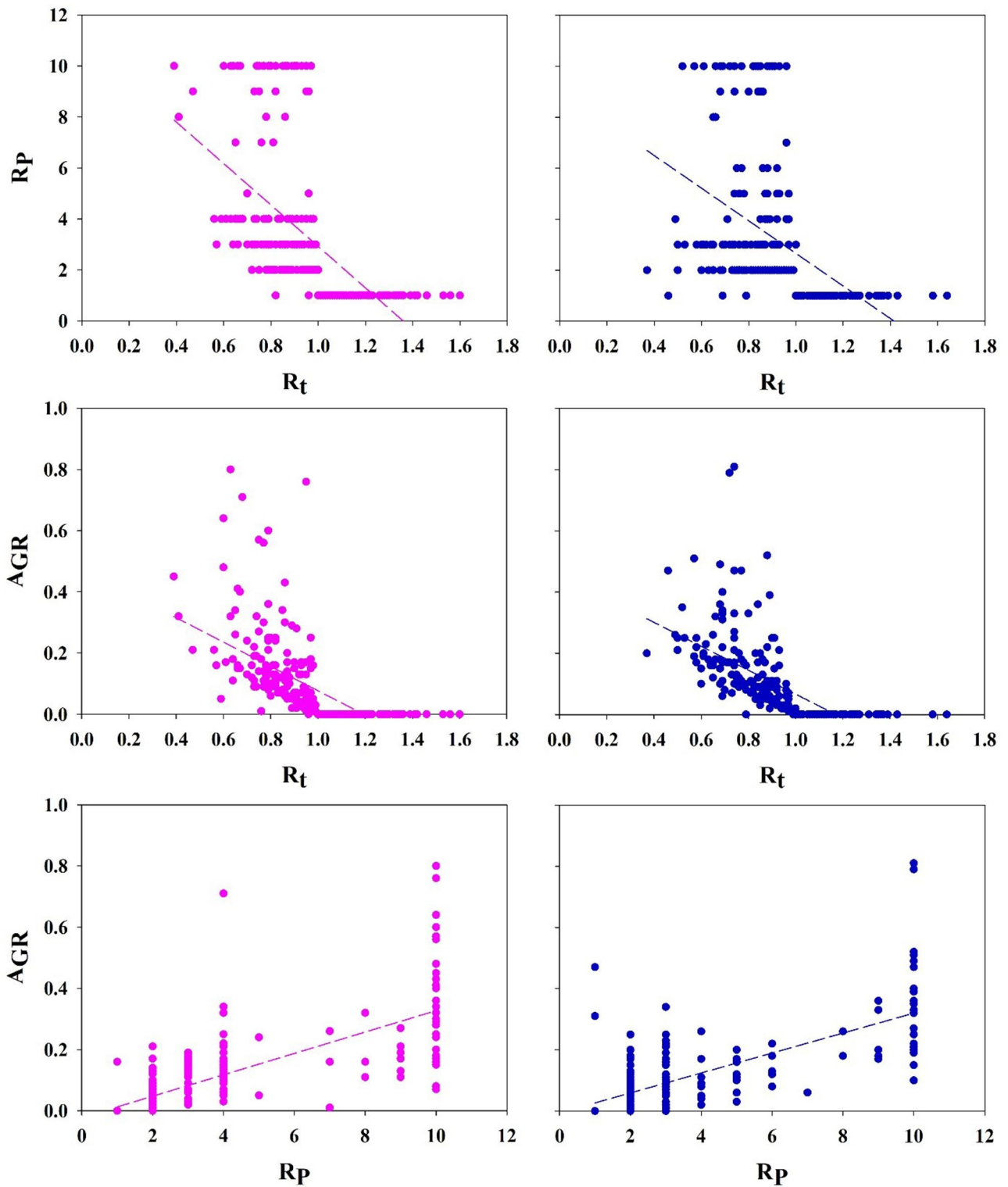


Fig. 4 Relationships between resilience indices for male (left) and female (right) *Araucaria araucana* trees. All linear model slopes are statistically significant at the $p < 0.001$ level. Correlation function values (Pearson r) are indicated in the main text

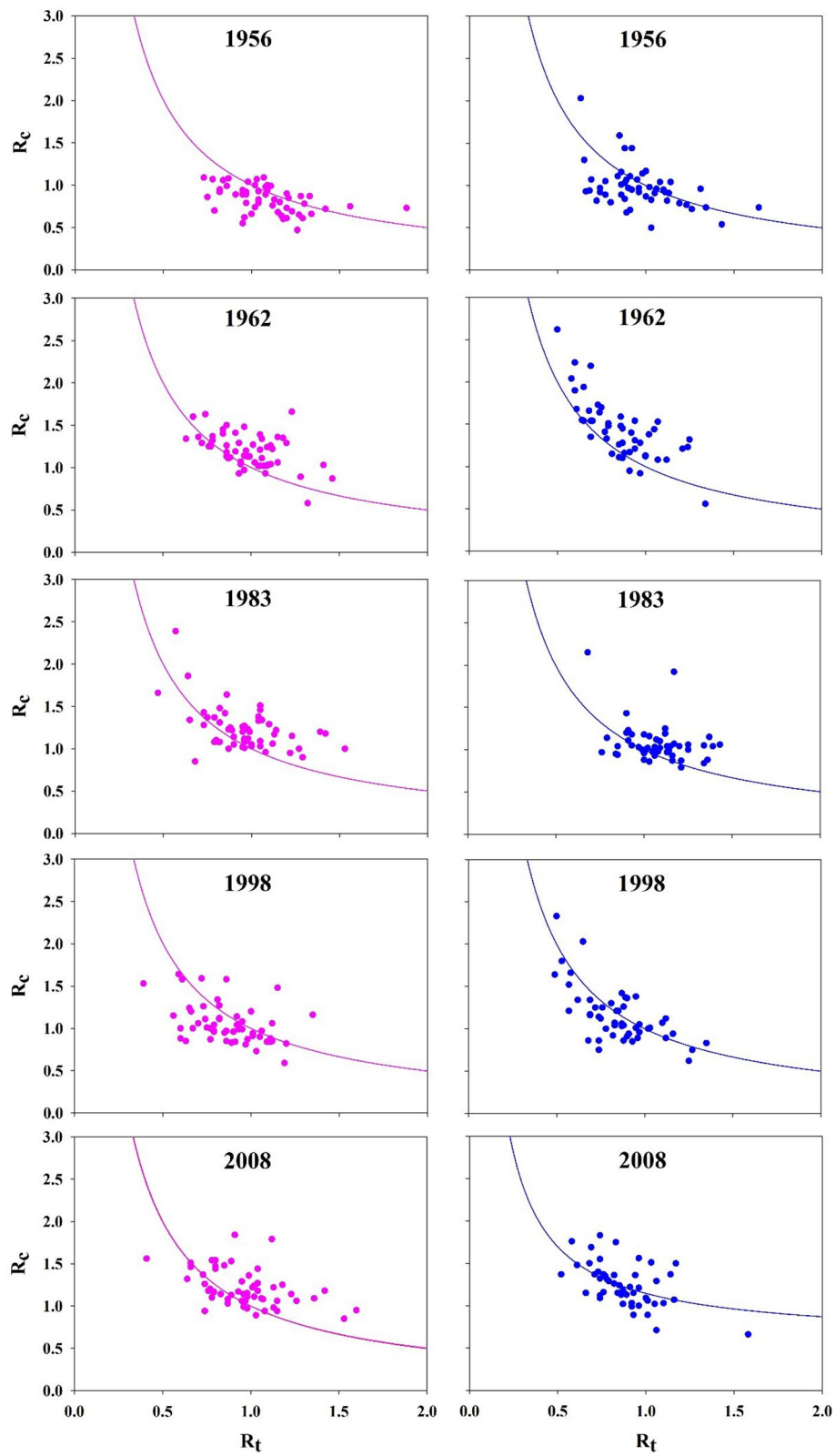


Fig. 5 Comparison of the relationship among the observed tree-level mean R_t and R_c values and the hypothetical function (colored curve) representing the line of full resilience (Resilience = 1.0) at any R_t value for female (left) and male (right) araucaria individuals separately

Table 3 GLMM for the R_t showing the minimal fitted model (adjusted model with significant effects). Fixed factors are represented by: SexM (male), pre_5_TRI (standardized mean stem growth rate prior to extreme drought year), SPEI4_D_{pre} (local climatic conditions of preceding extreme drought year 3-year period), SPEI4_D_d (local climatic conditions corresponding to extreme drought year). Site variability, drought year (intra-subject event) and tree identity represent random effects. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. $R^2 = 0.53$, SE = standard error

Predictor	Estimate	SE	z value	Pr(> z)
Intercept	1.037646	0.049387	21.011	< 0.001***
SexM	-0.029268	0.008864	-3.302	0.00103**
pre_5_TRI	-0.040585	0.016238	-2.499	0.01275*
SPEI4_D _{pre}	-0.075278	0.014148	-5.321	< 0.001***
SPEI4_D _d	0.055803	0.008406	6.638	< 0.001***

Table 4 Results of the GLMM for the R_p showing the minimal fitted model. Fixed factors are represented by: pre_5_TRI (standardized mean stem growth rate prior to extreme drought year), SPEI4_D_{pre} (local climatic conditions of preceding extreme drought year 3-year period), SPEI4_D_{post} (local climatic conditions of post-drought period). Site variability, drought year (intra-subject event) and tree identity represent random effects. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. $R^2 = 0.57$, SE = standard error

Predictor	Estimate	SE	z value	Pr(> z)
Intercept	1.18126	0.13164	8.973	< 0.001***
pre_5_TRI	0.45925	0.0954	4.814	< 0.001***
SPEI4_D _{pre}	0.42954	0.08677	4.95	< 0.001***
SPEI4_D _d	-0.11932	0.04871	-2.449	0.0143*
SPEI4_D _{post}	-1.51448	0.09216	-16.433	< 0.001***

Table 5 Results of the GLMM for the A_{GR} showing the minimal fitted model. Fixed factors are represented by: pre_5_TRI (standardized mean stem growth rate prior to extreme drought year), SPEI4_D_{pre} (local climatic conditions of preceding extreme drought year 3-year period), SPEI4_D_d (local climatic conditions corresponding to extreme drought year), SPEI4_D_{post} (local climatic conditions of post-drought period). Site variability, drought year (intra-subject event) and tree identity represent random effects. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. $R^2 = 0.29$, SE = standard error

Predictor	Estimate	SE	z value	Pr(> z)
Intercept	2.3030005	0.0025391	907.015	< 0.001***
pre_5_TRI	0.012911	0.0018422	7.041	< 0.001***
SPEI4_D _{pre}	0.0070465	0.0017075	4.127	< 0.001***
SPEI4_D _d	-0.002403	0.0009215	-2.608	0.00911**
SPEI4_D _{post}	-0.010471	0.0015902	-6.584	< 0.001***

driven by tree sex. Furthermore, our results also agreed with those of García-Barreda et al. (2022), which showed no sex differences for Mediterranean woody species tolerance to dry periods.

From a physiological perspective, the lower R_t recorded for araucaria male individuals compared to female

trees found in our study can be understood considering that, in the examined woodlands, male radial growth is strictly dependent on current year climatic conditions, while female cambial activity is more closely related to meteorological variability in the year preceding ring width development (Hadad and Roig 2016). Therefore, it could be hypothesized that in xeric araucaria woodlands, the stronger influence of current-year climatic conditions characteristic of male trees could result in a higher reduction in growth rates during extreme drought years, leading to lower resistance values than female araucaria individuals. Future studies incorporating physiological/isotopic techniques can shed light on this specific finding.

Pre-drought growth rates drove the species resilience, as exemplified by their negative (positive) association with R_t (R_p and A_{GR}). This confirmed the findings of previous research conducted in *A. araucana* woodlands across the entire Argentinean distribution range (Piraino et al. 2022). More generally, it is considered that in temperate woodlands, fast-growing trees are likely less adapted than their slow-growing counterparts when facing extreme climatic stressful episodes (Zang et al. 2014). This could be attributed to the higher investment of photosynthetic assimilates in cambial activity in the former, whereas the latter may employ different strategies to cope with dry spells (e.g. increasing root-to-shoot ratio) (Morán-López et al. 2013).

The resilience of xeric araucaria woodlands was influenced by local climatic conditions before, during, and after extreme regional drought episodes. In relation to resistance, the negative association with preceding meteorological conditions and the positive one with the climatic envelope throughout the dry spells reflected both index calculation and possible tree physiological mechanisms. In this sense, as R_t is computed as the ratio between stem growth during extreme event and ring development before a drought episode, it is logical that resistance could show higher values when current climatic conditions are favourable and preceding unfavourable (Lloret et al. 2011; Veuillen et al. 2023). On the other hand, it has been suggested that favourable meteorological conditions preceding a drought event can stimulate an increase in leaf area, potentially rendering trees more susceptible to water stress and consequently affecting their tolerance to dry spells (Zhang et al. 2021; Veuillen et al. 2023). Concerning recovery components, both R_p and A_{GR} were positively associated with local climatic conditions before drought events and negatively with the meteorological envelope during and following extreme dry spells, respectively. The former positive relationship can be understood considering that recovery period, and therefore average growth rate which is mathematically related to R_p , are calculated by comparing post-drought radial growth rates to pre-drought stem increase. In this

sense, improved climatic conditions preceding drought, represented by high SPEI4_D_{pre} values, can enhance tree-ring development prior to the dry spell, implying that ring development must surpass a higher threshold in years following extreme events to fully recover its radial growth. On the other hand, the negative relationship emerged between R_p and A_{GR} and climatic conditions during extreme drought events, can be understood by considering that water stress could be detrimental for post-dry spells cambial activity and therefore radial growth rates, a condition which reflects the “legacy effect” concept regarding tree resilience (Anderegg et al. 2015; Zhu et al. 2023). Finally, the negative association emerged in GLMM between R_p and A_{GR} on one side, and local climatic conditions following extreme episodes on the other, suggested that when post-drought climatic are adverse, narrower ring width will be produced, implying that trees are unlikely to regain growth rates preceding dry spell, as found, for example, for *Pinus halepensis* across its whole distribution area (Veullen et al. 2023).

Conclusions

This research demonstrated that tree sex has a mixed impact on xeric araucaria growth resilience to extreme drought events when compared to other biotic and abiotic factors. Literature on sex-related response to climatic stressors generally asserts that while female trees are physiological superior to their male counterparts when climatic conditions are favourable, during adverse climatic periods male trees can outperform female individuals (Obeso 2002). Nevertheless, as stated in the introduction section, this is only partially true because species-specific studies did not always support this theoretical statement, showing a variety of tree physiological responses to mean and extreme climatic conditions (Juvany and Munné-Bosch 2015). In this context, our findings provided quantitative ground-truth evidence that contributes to the scientific debate concerning the role of sex in tree response to extreme dry spells. The results corresponding to the influence of climatic factors on araucaria resilience to extreme dry spells are particularly relevant, as they clearly indicated that tree resistance and recovery are highly sensitive to local conditions in years preceding, during, and following drought events. As climatic change is expected to exacerbate in the near future in Patagonia territories, we anticipate that the araucaria radial growth resilience will be strongly affected by the predicted increasing adverse climatic conditions for the study area. This finding should be taken into consideration in future management and conservation plans of xeric araucaria woodland.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00505-9>.

Supplementary Material 1

Acknowledgements

We sincerely acknowledge V. Gallardo, S. Papú, A. Hackett-Pain and J. Foest for fieldwork assistance. We also thank the Administración de Parques Nacionales of Argentina for allowing access to sites under protection.

Authors' contributions

Conceptualization: SP. Methodology: SP. Resources: MAH, FAR. Sample collection and preparation: MAH, FAR. Sample analysis: MAH. Data analysis: SP, YAR. Writing: SP. Reviewing: SP, MAH, YAR. FAR. Supervision: FAR.

Funding

This research was supported by the Agencia Nacional de Promoción Científica y Tecnológica of Argentina (PICT-2018-1056 to MAH), Cooperation International Project between CONICET and NSFC-2019 to MAH and Cooperation International Project between CONICET and Royal Society-2019 to FAR.

Data availability

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹Laboratorio de Dendrocronología e Historia Ambiental (IANIGLA CONICET), Av. Dr. Adrian Ruiz Leal, Mendoza, Argentina

²Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Almirte. Brown 52, Luján de Cuyo, Mendoza, Argentina

³Laboratorio de Dendrocronología de Zonas Áridas (CIGEOBIO CONICET), Gabinete de Geología Ambiental (INGEO UNSJ), Av. José Ignacio de la Roza Oeste 727, San Juan, Argentina

⁴Hémera Centro de Observación de la Tierra, Facultad de Ciencias, Universidad Mayor, Camino La Pirámide 5750, Huechuraba, Santiago, Chile

Received: 20 December 2023 / Accepted: 1 March 2024

Published online: 26 March 2024

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