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Does competition management improve the ecophysiological response to water shortage of mixed woodland species of North Patagonia?

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ABSTRACT

Globally, the increasing forests vulnerability and drought-induced forest mortality events, extended to a larger scale, may have the potential to rapidly alter forest functioning and the provision of ecosystem services. Patagonian forests in Southern South America constitute an extensive reservoir of wildlife, but at the same time they have high productive potential. These low-mixed forests are composed of co-dominant species that are highly disturbed by local population, both for cattle raising and wood extraction; and different efforts are being dedicated to improve their management. Very little is known about the response of their different woody species to climatic variation, particularly to severe drought in particular, that may guide management strategies to improve productivity and resilience in context of drought stress and climate change. The present study aimed at characterizing the physiological strategies of response to drought to identify the most vulnerable and most resilient species to drought and how they respond under different competition levels. The response of four species of the Andean Patagonian low mixed forest was quantified at three moments of the 2018–2019 growing season in three sites through measurements of the net carbon exchange, vulnerability to xylem cavitation, tissue water relations, and damage of the photosynthetic apparatus. Additionally, records of average monthly values of precipitation and air temperature were used to calculate a standardized precipitation-evapotranspiration index. The normal climatic conditions of NW Patagonia region are characterized by water deficits during the spring-summer growing season, but the studied season presented lower values of standardized precipitation-evapotranspiration index respect to the historical mean values, indicating drier than normal conditions. Analysis of the tissue water relations showed that, in all cases, competition had no effect over the different studied parameters. There were species-specific differences in the models fitted to the vulnerability to cavitation curves; as a whole, all the species differed from each other. Overall, for all the physiological response traits studied, the Site, Species, and Season factors were important predictors in the minimum adequate model. Although there is an effect of competition on the individual annual growth, that effect is not evidenced in physiological variables of punctual measurement. Our results suggest that the effect of summer drought cannot be modulated by density management. The productivity of the species of interest can be improved, but not their adaptability, at least to severe events such as the one of the year of study.

1. Introduction

Temperate forests host the largest and oldest trees and serve as the major source of timber and wood products in the world (Currie and Bergen, 2008). Due to high human-pressure, they present different degrees of degradation, but at the same time, they are possibly the only

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forests with some proven potential for sustainable management (de Gouvenain and Silander, 2017). In addition to the normal climatic variability experienced by temperate forests, current and future projections in the context of climate change suggest that negative impacts on forest functioning are likely to increase in frequency and intensity, mostly due to severe droughts (Choat et al., 2012; Anderegg et al., 2022). In this regard, although increased productivity has been observed in some temperate forests as a result of increased mean temperature and CO_2 atmospheric concentration in the last decades (Hickler et al., 2015), long-term forest decline and forest diebacks have been also reported for temperate forests, particularly in the drier portions of forest distributions (e.g. Camarero, 2021). The increasing forests vulnerability and drought-induced forest mortality events, extended to a larger scale, may have the potential to rapidly alter forest functioning and the provision of ecosystem services, with important implications on the carbon–water balance, plant community composition, and tree population dynamics (Rewald et al., 2020). In mixed forests, different potential responses to climatic drivers by the different codominant species may lead to profound changes in local community composition and species interactions (Thuiller et al., 2005; Bertrand et al., 2011; Morin et al., 2018; Villalba et al., 2022). In this context, it becomes relevant to know how drought affects the productivity and survival of species that coexist in mixed forests, and how forest management results in determining species-specific responses at the community level.

Forest management could play an important role in the mitigation of climatic effects on forests by regulating the thinning intensity and species selection in order to sustain forests compositions of interest (Alvarez et al., 2016; Mina et al., 2017; Morin et al., 2018; Battipaglia et al., 2020). At the same time the reduction of competition for growth resources may allow forests to acclimate to new climatic conditions and enhance the mitigation role played by forest systems (Aldea et al. 2017; Volkova and Weston 2019). In this regard, managing the density of vegetation can induce greater resistance and resilience of growth to drought in the short term on remaining selected broadleaved trees, in opposition to conifer trees (Sohn et al., 2016; Pukkala, 2018). This points out the existence of interactions between management practices and plant functional groups. Promoting mixed forests has also been identified as an adaptation strategy in forest management to cope with climate change (Bolte et al. 2009; Kolström et al. 2011).

Most of the studies dealing with the interaction between drought and management are based on tree growth, through tree dendrochronology or height/radial growth rate analyses (Cotillas et al., 2009; Elkin et al., 2015; Carnwath and Nelson, 2016; Vernon et al., 2018). However, relatively few studies are available on the physiological variables behind the observed growth patterns (Mäkelä et al., 2000), and therefore, integrating these different levels of complexity into actual forest management practices is far from being routine. There is still a gap in knowledge about silvicultural practices' role in the climate-change adaptation of forests (Keenan, 2015; Ammer, 2016; Battipaglia et al., 2020; Nacif et al., 2020). Moreover, the majority of the studies have been focused on North American and European forests, with a lack of knowledge on Southern Hemisphere forests (Návar-Cháidez and González-Elizondo, 2009; Mok et al., 2012; Keenan, 2015; Pasgaard et al., 2015; Nacif et al., 2020).

From a physiological point of view, vegetation removal through thinning may result in higher predawn water potential during drought in non-harvested plants, thus indicating higher access to soil water reserves. Intrinsic water use efficiency (WUEi) could also change in response to thinning, though with large differences according to the species or even without significant changes (e. g. Dinh et al, 2016; Fernandez de Uña et al., 2016; Lechuga et al., 2018). Therefore, the physiological response to thinning seems to be case-specific. Moreover, the effects of management practices would certainly depend on the intensity and/or timing of thinning in addition to the species-specific physiological functioning. Regarding the key physiological traits to focus on, there is consensus about the importance of hydraulic variables to understand the tree responses to severe drought events (Adams et al, 2017; Anderegg et al, 2016). In this regard, the resistance to xylem cavitation is key to discriminating species' ability to tolerate drought (Lens et al 2016; Larter et al 2017), so it is informative to determine the minimum water potential of the plant in relation to cavitation thresholds. On the other hand, at the leaf level, the turgor loss point and the osmotic adjustment capacity have been described as key traits related to drought resistance in woody species (e.g. Lenz et al, 2006; Bartlett et al, 2014; Zhu et al. 2018).

Patagonian forests in Southern South America constitute an extensive reservoir of wildlife, but at the same time, they have high productive potential (Veblen et al., 1996; Pastur et al., 2000). The majority of these lands are covered by secondary forests as a result of human harvest or other human-induced disturbances. The current status of these forests represents considerably altered states of the primary conditions (Currie and Bergen, 2008; Rusch and Varela, 2019). In Patagonia, high forests of coihue *(Nothofagus dombeyi),* lenga *(Nothofagus pumilio)*, Cordillera cypress *(Austrocedrus chilensis)* or ñire *(Nothofagus antarctica)* have suffered profound anthropic disturbances, such as fires, grazing, firewood extraction and replacement by plantations of exotic conifers. The impacts of such disturbances are not thoroughly known (Rusch et al., 2015; Rusch et al., 2017; Rusch and Varela, 2019). In many cases, these alternative states are constituted by mixed forests with lower tree height than the primary forests (low mixed forests), which can play an important role in a successional transition towards reference states (Rusch and Varela, 2019; Nacif et al., 2020). These low-mixed forests are composed of co-dominant species such as *Diostea juncea* (Gillies & Hook.) Miers, *Lomatia hirsuta* (Lam.) Diels ex J.F. Macbr., and *Schinus patagonicus* (Phil.) I.M. Johnst. ex Cabrera); and in some cases, with *Maytenus boaria* on the slopes (Rusch et al., 2015). These forests are highly used by local people, both for cattle raising and wood extraction, and different efforts are being dedicated to improving their management (e.g. Nacif et al. 2020, Goldenberg et al., 2021; Nacif et al. 2021). However, very little is known about the response of their different woody species to climatic variation, and to severe drought in particular, that may guide management strategies to improve productivity and resilience of those forests in a context of drought stress and climate change.

Based on this background, the present study aimed at characterizing the physiological strategies of response to water availability to identify the most vulnerable and most resilient species to drought (the main stress factor in the region), and how they respond under different competition levels. The results are discussed to propose management guidelines for the main woody co-dominant species of the low mixed forests of Northwestern Patagonia aiming to improve their adaptability to climatic stress. We expected to find different physiological responses to drought in the different species, with species being more resistant to drought than others (determined by a lower vulnerability to cavitation and turgor loss point, and the ability to sustain gas exchange during seasonal drought periods), resulting in a different impact of competition management among them. In this regard, we expected a higher positive impact of competition reduction in species more vulnerable to drought than in more resistant ones.

2. Material and methods

2.1. Study sites

The study was carried out in the glaciofluvial valley of El Foyel River, located approximately 80 km South of San Carlos de Bariloche city, in the province of Río Negro, Patagonia, Argentina. The soils are derived from volcanic ashes with sandy loam textures and variable values of organic matter content, resulting in different soil water storage capacity. We selected three sites corresponding to low mixed forest stands (Site 1: El Chucao -ECH-, Site 2: South Foyel -SF-, and Site 3: North Foyel -NF-; Table 1). Each of these low mixed forest stands is the result of the

Table 1

Main characteristics of the studied sites. References: DBH = diameter at breath height. The basal area corresponds to the control situation (with no harvesting).

Site Name	Species Composition	Basal area (m^2 ha^{-1})	Latitude	Longitude	Altitude (m. a. s. l.)	DBH (cm)	Dominant height (m)
South Foyel (SF)	*N. antarctica, D. juncea, S. patagonicus, L. hirsuta Embothrium coccineum*	46.7	41° 38′ 49.7′’ S	71° 30′ 4.9′’ W	760	6.08 (3.18)	4.38
North Foyel (NF)	*N. antarctica, D. juncea, S. patagonicus, Discaria chacaye, F. imbricata, L. hirsuta, E. coccineum, M. boaria*	34.8	41° 38′ 54.6′’ S	71° 30′ 31.4′’ W	800	5.62 (4.92)	3.54
El Chucao (ECH)	*N. antarctica, N. dombeyi, N. pumilio, D. juncea, S. patagonicus, A. chilensis, D. chacaye, L. hirsuta, E. coccineum, M. boaria*	21.9	41° 43′ 41.94′’ S	71° 26′ 40.34′’ W	862	14.5 (7.80)	6.90

m. a. s. l. = meters above sea level.

degradation of the high forests of *N. dombeyi* and *A. chilensis.* El Chucao site was located in a west-facing foothill of Serrucho mountain, while South Foyel and North Foyel correspond to the south and north-facing slopes of a terminal glacier moraine located in the bottom of the valley.

In this region, the climate is cold-temperate. The annual precipitation varies between 920 mm and 1300 mm per year (Bianchi et al., 2016). Mean annual air temperature ranges from 8 °C to 9 °C, with mean annual maximum temperature of 15 °C and minimum of 1.5 °C, and mean annual relative humidity of 65%; frosts are present on average over 120 days a year (Bianchi et al., 2016). Our study sites lie within a Mediterranean climate region, where precipitation follows a strong annual cycle (Aravena and Luckman 2009), in which the bulk of it occurs during the cold semester, resulting in summer drought.

2.2. Silvicultural treatment and competition assessment

To evaluate the interaction between drought response and management we selected a total of 96 trees distributed in the three sites (NF, SF, and ECH) and growing under contrasting inter tree- competition levels, equally distributed among the four studied species (*Nothofagus antarctica*, *Diostea juncea*, *Schinus patagonicus*, and *Lomatia hirsuta*). *Nothofagus antarctica* was the only deciduous species of the four studied. The selected individuals were all adult trees with no signs of canopy dieback, covering a wide range of sizes within each site (trees with a diameter at breast height higher than 10 cm). The measurements were carried out during the 2018–2019 austral growing season (November to April).

In SF and NF sites, tree competition was experimentally modified in 2013 and 2014 by applying different harvest intensities. Within this continuous mixed forest, in May 2013, four increasing levels of harvesting intensities in four replicated plots (31.5 m × 45.0 m each) were applied. The plots were aligned East to West and separated about 30 m between them. Harvesting intensities were quantified as the percentage of removed basal area (30%, 50% and 70%). Harvesting was done along strips of different widths according to the harvesting intensities, across the whole plot. In the treatment with 30% harvesting intensity, the six strips of the plot had a width of 1.5 m (leaving a space of 3.0 m for intact vegetation on the sides); in the treatment with 50% intensity, the six strips of the plot were 2.5 m wide (with 2.0 m wide areas of remaining vegetation); and finally, in the treatment with 70% intensity, the six strips of the plot had 3.5 m width (1.0 m wide areas of remaining vegetation). In the control plot, vegetation was left uncut (0% of basal area removal). Within the harvested strips, all trees and bushes were cut with chainsaws and clearing saws at ground level, leaving them the possibility to regrown as these are mostly sprouting species. For this study, trees for measurement were selected randomly in the non-harvested strips (remaining intact trees) immediately close to the cleared strips of 70% intensity and in the control treatment (the other treatments were further studied for other variables not reported here). The trees measured are supposed to be directly influenced by the openings adjacent to them. These two levels of management were used in order to capture the largest variation within the thinning treatments applied, and for reasons of sampling logistics and subsequent comparison of the data obtained.

In El Chucao forest, we did not apply a similar thinning than in the other sites, but selected trees growing under contrasting competition levels. This site was subjected to a constant low-intensity harvesting by a local farmer, plus two moderate to high wood extraction events (during the 60’s and 90’s decades of XX century). Thus, we took advantage of the management applied in the area to evaluate the response of the individual trees and species.

2.3. Competition indexes and basal area increment (BAI)

For the three sites, a common methodology to quantify and standardize inter-tree competition was applied. For each target tree, a core sample was taken at stump height with an increment borer. Samples were sanded and measured using the software Image Pro-Plus (Version 4.5.0, Media Cybernetics, Inc.) to determine the last year’s ring width (2018–2019 austral growing season), and thus estimate the individual basal area increment of 2018–2019 growing season (BAI_{18-19}). A set of ten competition indexes (Supplementary Material 1) were calculated using relations of tree sizes and distances among the target tree and its four closest neighbors. The calculation of the different competition indices allowed the comparison of information registered in the different sites given the different management practices carried out in each one.

2.4. Climatological analysis

In order to establish whether the 2018–2019 growing season was a dry and/or hot season, records of average monthly values of precipitation and air temperature from 5 meteorological stations near the study area with long historical records (>20 years, Supplementary Material 2) were used to calculate the standardized precipitation-evapotranspiration index (SPEI, Vicente-Serrano et al. 2010). The SPEI is a multi-scalar drought index that can be used for determining the onset, duration and magnitude of drought conditions respect to normal conditions in a site. The SPEI uses the monthly (or weekly) difference between precipitation and potential evapotranspiration (PET) as a measure of the climatic water balance. Particularly, we computed the $SPEI_3$, which is a three-month running mean of the SPEI, for the period 1994–2020 using the package 'SPEI' for R software (Beguería et al. 2014), considering the PET Thornthwaite equation as input (Thornthwaite, 1948).

The weather station records were compared with the values obtained for the 2018–2019 seasons at the studied sites. Subsequently, a comparison was made between values of the $SPEI_3$ index and of temperature for the 2018–2019 growing season (October to May) with historical values (1994–2020).

2.5. Pressure-volume curves for tissue water relations

To obtain basic pressure volume parameters at the species level and under different levels of interspecific competition, pressure–volume (P-V) curves were developed on each of the target trees (twenty-four trees per species, distributed in the three sites and covering a gradient of intra and interspecific competition level), using the free transpiration method, following the protocol "bench dry method" specified by Corcuera (2003). Three to six shoots per target tree with fully developed (expanded) leaves were cut in the field during February of 2018 and taken to the laboratory. For rehydration, the shoots were kept at laboratory temperature (approximately 20 °C) in the dark, submerging their basal portion in water for 24 h. Once rehydrated, the weight of each shoot was obtained with a 1 mg precision scale; then it was introduced into a Schölander-type pressure chamber (PMS M1000; PMS Instrument Company, Albany, USA) and the equilibrium pressure was determined. At regular intervals, the chamber was depressurized and the shoot was left outside of it to dry out under the ambient conditions of the laboratory. Then, its fresh weight and water potential were measured again, and the reduction in the relative water content of the shoot was deduced through successive weighing. The process concluded with the determination of the dry weight of each shoot. The data obtained allowed the construction of the P-V curves, that is, the graphical representation of the inverse of the water potential of the sample against the volume of symplastic water. Based on these curves the following parameters were estimated following the procedure described by Sack and Pasquet-Kok (2010), as well as using the "Pressure volume analysis spreadsheet tool" (PVAST) to analyze data, including testing and correcting for "plateau effects" due to leaf rehydration: osmotic potential at full turgor (π_0); water potential at turgor loss point (Ψ_{tlp}), relative water content (symplastic water) at full hydration (RWC_{ft}), relative water content at turgor loss point (RWC_{tlp}), symplastic water fraction (SWF) at full turgor, the bulk modulus of tissue elasticity (ε), the relative capacitance at full turgor (C_{ft}) and relative capacitance at turgor loss point (C_{tlp}).

2.6. Vulnerability to cavitation (VC) curves

Due to the inherent operational difficulties for the development of vulnerability to cavitation (VC) curves, this variable was studied only at the species level, that is, not including the site and competition index as potential drivers of differences. In general, VC may be considered a conservative trait at the species level, i.e. with low phenotypic plasticity (e.g. Bittencourt et al., 2020; Lübbe et al., 2017; Vander and Pammenter, 1998; Wikberg and Ögren, 2007) and low genetic variability among populations of a species (e.g. Lamy et al, 2014; Lobo et al., 2018), although there are studies showing variation in some species between populations or resources availability (e.g. López et al, 2016; Peguero-Pina et al 2014; Wortemann et al, 2011). For the purpose of this study, we assumed that vulnerability to cavitation is a rather conservative trait in our studied species. This assumption should be, however, be taken with caution since there is an antecedent in *N. antarctica* showing variability in VC between two populations (Bucci et al, 2012), located more distantly between them than our studied sites. The variation as a function of competition and sites was studied through the safety margins variability, the minimum water potential experienced by the individuals in the different treatments being the main driver of potential variability. The '*Cavitron*' device (Cochard 2002; Cochard et al. 2005) was used to construct the curves with the flow-centrifuge method. VC curves were performed using a 42 cm-size rotor according to the maximal vessel length of the studied species (around 20 cm long). The technique consists of spinning xylem segments centered on a rotor to expose them to large negative pressures and then measuring the effect on the hydraulic conductivity (K_h) (Cochard et al., 2005). Five branches per species were measured in total, from samples cut across the three sites (NF, SF and ECH) during the summer 2018–2019, wrapped in wet paper and plastic bags to be sent by express mail to the high-throughput phenotyping platform Phenobois for hydraulic traits in France ("Caviplace", INRAE University of Bordeaux, Pessac, France, and "Cavit-Home", INRAE, Clermont-Ferrand, France). In the lab, measurements were carried out within a week. All the branches were recut under water to obtain 42 cm long samples, whose ends were debarked and inserted into a transparent reservoir containing demineralized and filtered water with 1 mM $CaCl_2$ and 10 mM KCl. The water level in each reservoir differs, thus creating a hydrostatic gradient; as a result, water flows through the sample, which allows K_h to be measured (see Cochard et al. 2005, for further details of this technique). Xylem pressure was first set to a reference pressure (−0.1 MPa), and maximum hydraulic conductivity (K_{hmax}) was measured. The centrifugation speed was then set to a higher value for 3 min to expose the sample to more negative pressure. Conductivity was measured three times for each pressure step, and the average was used to compute the percentage of hydraulic conductivity loss (PLC) at that pressure. The procedure was repeated for at least eight pressure steps until the PLC reached a minimum of 80%. Rotor velocity was monitored with a 10 r.p.m. resolution electronic tachymeter (A2108-LSR232; Compact Instruments, Bolton, UK). We used the Cavisoft software (version 2.0; BIOGECO, University of Bordeaux, Talence, France) for K_h estimation.

We obtained one VC curve per species by pooling the data of the five branches. The data of VC curves were fitted using Prism5 (Graph Pad Software, Inc., San Diego CS, USA), based on the following equation (Pammenter and Van der Willigen, 1998):

$$PLC = 100/(1 + exp((Slope/25)(\Psi - \Psi_{50}))) \tag{1}$$

where Slope is the slope (%) at the inflection point and Ψ_{50} is the inflection point of the curve, which in this case corresponds to the xylem pressure (Ψ) inducing 50% loss of conductivity (Ψ_{50}; MPa). The xylem pressure inducing 12% (Ψ_e) and 88% (Ψ_{88}) loss of hydraulic conductivity were calculated as follows: $\Psi_e = 50 / Slope + \Psi_{50}$ and $\Psi_{88} = -50 / Slope + \Psi_{50}$ (Lamarque et al., 2018).

Values of Ψ_e, Ψ_{50} and the values of minimum daily water potential (Ψ_{min}, MPa) registered in each species, site and date along the 2018–2019 growing season were used to calculate hydraulic safety margins (based on Meinzer et al., 2009; 2016): Ψ_{min}-Ψ_{50}; Ψ_{min}-Ψ_e and Ψ_e-Ψ_{50}). To this end, within the measured minimum water potential values we selected the absolute minimum value of water potential registered in each date, site and species. We also estimated the safety margin concerning the water potential at turgor loss point (Ψ_{min}-Ψ_{tlp}).

2.7. Dynamic ecophysiological variables: gas exchange, minimum leaf water potential, modulated chlorophyll a fluorescence and specific leaf area

Morphological and ecophysiological measurements were performed in each target tree three times along the growing season 2018–2019: late spring, summer and early autumn, corresponding to the time periods: December 17th to 27th; February 7th to 14th; March 25th to 29th. These periods of measurement allow us to analyze the physiological response of the plants during the maximum growth period (late spring); the period of expected maximum drought stress in the studied region (summer); and the potential recovery (early autumn).

Minimum daily water potential (Ψ_{min}, MPa) was registered in the three growth periods per site and species using a Schölander PMS Model 1000 pressure chamber (PMS Instrument Company, Albany, USA) on two leaves per target tree. It was measured between midday and early afternoon. In the same branches, gas exchange measurements were performed using a Li-COR 6400 (IRGA, Li-cor 6400; Li-cor, Lincoln, Nebraska, USA) with a 6400-02B LED source to obtain the leaf net photosynthetic rate at saturating photosynthetic active radiation (PAR) (*Asat*, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}) and leaf transpiration (*E*, mmol m^{-2} s^{-1}). Conditions in the Li-cor 6400 chamber were controlled to 20 °C of air temperature, 1200 μmol m^{-2} s^{-1} of PAR, 400 ppm of air CO_2 concentration, and an airflow of 200 μmol s^{-1}. Air humidity was tracking the ambient air conditions. Each measurement was done using a minimum waiting time of 180 s and a 3% coefficient of variation. Gas exchange measurements (with 2 repetitions per tree) were carried out between 10 A.M. and 5 P.M., taking into account that the gs was kept almost constant along each day, that is, we discarded individual leaves that did not respond to the standard conditions imposed by the Li-cor 6400 chamber. Instantaneous water use efficiency (WUEi, μmol CO_2 mol H_2O^{-1}) was calculated as the ratio of *Asat* to *E*.

The leaves collected for *Asat* measurements were subsequently scanned to obtain their surface area and then left on the stove for 72 h at 60 °C until constant weight for the determination of the specific leaf area (i.e. one-sided area of the fresh leaf divided by the oven-dry mass; SLA; m^2 kg^{-1}).

Additionally, to account for any damage in the photosynthetic apparatus, we measured the modulated fluorescence of chlorophyll *a* expressing the results as the maximum quantum yield of PSII (ratio of variable to maximum fluorescence; Fv/Fm; Maxwell and Johnson, 2000). For this purpose, in the same trees, 2 leaves per tree were sampled, placed in aluminum foil in a cooler to undertake fluorescence measurements after dark acclimation of the leaves, back in the lab, using a Junior PAM fluorometer (Heinz Walz GmbH, Effeltrich, Germany). After applying a pulse of low-intensity light (0.4 μmol photon m^{-2} s^{-1}), we registered the minimum fluorescence yield (F_0). Then we applied a saturating high-intensity light pulse (around 8000 μmol photon m^{-2} s^{-1} for 0.8 s) to induce the temporary closing of PSII, recording the maximum fluorescence yield (Fm); Fv/Fm was then estimated.

3. Statistical analysis

3.1. Competition indexes and basal area increment

We evaluated the effect of the competition index, the Species, the Site, and the tree size (g0, the basal area of the trunk at breast height), for predicting $BAI_{18\text{-}19}$ through linear models, testing all the combinations of these factors and comparing the goodness of fit of the different models using ANOVA. For the selection of the most appropriate competition index, we ranked the R squared resulting from fitting recursively a linear model between $BAI_{18\text{-}19}$ and g0, using different competition indexes as weights (Supplementary Material 3). For the statistical fitting, we used the “lm” function from the package “stats” from R software (R Core Team, 2021).

3.2. Pressure-volume curves analysis

To determine differences in tissue osmotic and elastic parameters we fitted a linear model using Site and Species, including its interaction, as explanatory variables, and competition index as weights as described in previous paragraphs. The fitting procedure was carried out using the “lm” function of the “stats” R’s package. Model coefficients and intercepts were tested for statistical differences.

3.3. VC curve and safety margins analysis

For the VC curves, the accuracy of the fitted parameters was examined via the ratios between the standard errors of estimate (SEE) and the best-fitted values (Zar, 1999). We used global fitting (Motulsky and Christopoulos, 2004) to compare the fitted parameters between each pair of species. In each case, we report the evidence ratio (ER) in favor of the better model (i.e., global vs. separate fitting to the data; Motulsky and Christopoulos, 2004). We performed these analyses using Graph Pad Prism 5 Software (Graph Pad Software, Inc. San Diego, USA).

The significance of differences and the relationship between Ψ_e or $\Psi_{min,}$ with Ψ_{50} (safety margins) between species were compared using two-way ANOVA (using the Species and Time as factors) and correlation analysis. In each case, the assumptions of the model were checked. Normality was tested using the Shapiro–Wilk tests or graphically using QQ plots. Homoscedasticity was checked using Levene’s test, with a significance level of $\alpha = 0.05$. We performed these analyses in R Software Version 4.1.0 using the *rstatix* and *emmeans* packages.

3.4. Effects of site, species, and competition on dynamic physiological traits

The multi-model inferential framework following Burnham et al. (2011) was used to select the best model to analyze how plant physiological responses were affected by Site, Species, Competition level, Time of the growing season and their interactions. This framework was implemented in R Software, using the function “dredge” (package MuMIn, Barton 2022), which performs an automated fitting of a global model and select the best particular explanation (combinations of predictors), using the lowest AICc model value (a corrected form of the Akaike Information Criteria) and selecting posteriorly the minimum adequate model.

Global model:

$$y = X\beta + Zu + \varepsilon \tag{2}$$

where:

y: $N \times 1$ column vector, the outcome physiological variable, alternatively: *Asat*, *gs*, *E*, WUEi, Ψ_{min}, Fv/Fm and SLA.

X: $N \times p$ matrix of the *p* predictor variables: Site, Species, Time of the season, Competition index.

β: is a $p \times 1$ column vector of fixed-effects regression coefficients.

Z: is the $N \times qJ$ design matrix for the *q* random effects and *J* groups: Season nested in tree.

u: is a $qJ \times 1$ vector of *q* random effects for *J* groups.

ε: is a $N \times 1$ column vector of the residuals.

J: groups of cases: 96 trees.

N: number of cases (596 measurements).

The predictor variable with the largest predictor weight is thus estimated to be the most important of the predictors, and it begins to be considered important with values equal or greater than 0.4 (Burnham and Anderson, 2002). We calculated the relative importance value for each predictor variable with the *importance* function in the package MuMin, which sums the ‘Akaike weights’ over all the models that include the predictor variable. All the assumptions regarding the multimodel inference framework were tested (homoscedasticity, residual normality, non-collinearity, and independence of the variables).

All the independent ecophysiological variables were continuous and unimodally distributed. In terms of the moment coefficient of skewness, *Asat*, *E*, and WUEi were positively and moderately skewed (1.51, 2.09, 1.66, respectively). The gs was exponentially distributed with a very high positive skewness coefficient (25.89). Besides, Ψ_{min} presented a near–symmetric distribution around its mean (-0.15), while Fv/Fm was moderate and negatively skewed (-0.95).

The intercept of the model is the predicted value of the dependent variable when all independent variables are zero. It is the reference value of the model, that is, the fixed effects for which an effect (a coefficient) is not estimated because it is within the reference line. If its value is different from zero, it means that it affects the response variable. In the same way, those factors or factor levels that are different from zero have an effect on the response variable.

4. Results

4.1. Competition indexes and basal area increment (BAI)

The Alemdag index, a distance-dependent index, was selected from among all the indices of competition (see Supplementary Material 1 for its formula and Supplementary 3 for ranked goodness of fit; r^2 values) and considered as a factor within the multi-model inference framework (see below). Supplementary Material 4 summarized the results of the comparison between all the considered models of the relationship between $BAI_{18\text{-}19}$ and the area of the trunk (g0), the competition index, Species, and Site factors. A marked effect of g0 could be seen as an explanatory variable of BAI (Supplementary Material 4). All the considered factors were shown to affect the current tree growth. From the comparison of the adjusted r^2 values, it can be seen that the best model was the one that considers all the factors as explanatory variables ($BAI_{18\text{-}19} \sim g0 * Species * Site * Alemdag$; $r^2 = 0.870$).

The two species with the highest $BAI_{18\text{-}19}$ were *N. antarctica* and *L. hirsuta*. In general, all the species grew more in El Chucao site in relation to the other two sites (Supplementary Material 5).

4.2. Climatological analysis

The evolution of the $SPEI_3$ during the 2018–2019 growing season (October to May), along with the comparison with historical values (1994–2020), is depicted in Fig. 1 (upper panel). To identify the role of the different climate variables behind the fluctuations of the $SPEI_3$, three-month moving averages of temperature (Fig. 1, middle panel) and three-month cumulated precipitation (Fig. 1, lower panel) were also included. Broadly, the temporal evolution of the $SPEI_3$ can be explained by the evolution of the precipitation. The studied season began with a low value of $SPEI_3$ (below the 25% percentile); then it showed a recovery for the next three months (November, December and January), probably responding to a pulse in precipitation. Both $SPEI_3$ and precipitation showed low values for the remaining months of the growing season (both below the 25% percentile). Temperature showed a much more stable temporal behavior, with values above the long-term averages during the whole period. Especially during the first four months, temperatures were above the 75% percentile, even reaching the historical maximums during November and December. Although these high temperatures likely contributed to the overall low values of $SPEI_3$ during the 2018–2019 season, they do not explain the sub-seasonal variations described above. As a whole, the studied growing season was characterized by precipitation below the mean values and temperatures above the maximum values, thus, representing severe hot-drought conditions for the plants acclimated to the regional climate.

4.3. Pressure-volume curves

Analysis of the tissue water relations showed that, in all cases, the competition did not affect the different studied parameters. *Diostea juncea* and El Chucao site were retained in the intercept of the model and they were significantly different from zero (Table 2, Supplementary Material 6).

Nothofagus antarctica had lower osmotic potential at full saturation and water potential at turgor loss than *D. juncea*, although they did not differ in the modulus of elasticity of cell walls. *Diostea juncea* showed higher symplastic water content at full turgor (SWF) in relation to *L. hirsuta* and *N. antarctica*. Regarding the modulus of elasticity of the cell walls, *S. patagonicus* showed higher values than *D. juncea* ($p < 0.001$), which means more rigid cell walls. Finally, *S. patagonicus* and *L. hirsuta* showed lower values of tissue capacitance at full turgor (Cft) compared to *D. juncea* ($p = 0.01$ and 0.03, respectively).

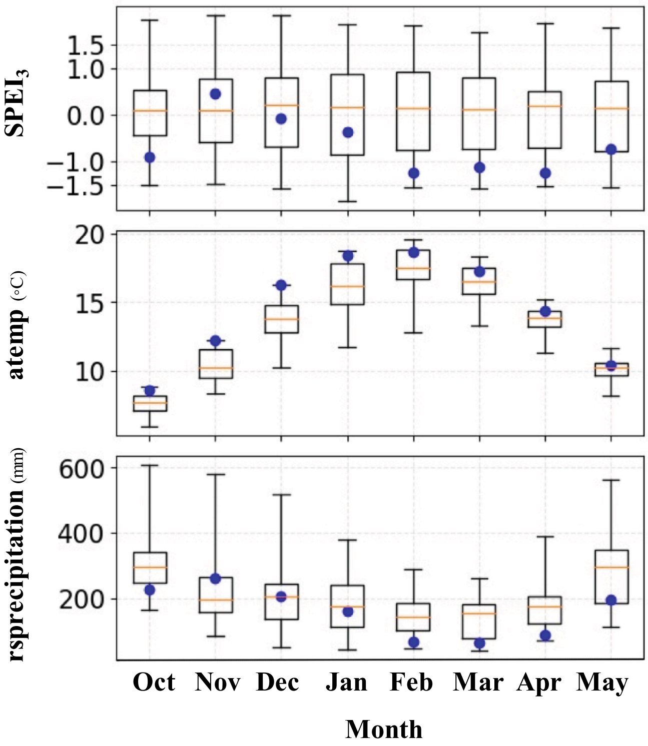

Fig. 1. Boxplot diagrams of historical distributions of the $SPEI_3$ index (upper panel), three-month moving averages of temperature (atemp, middle panel) and three-month moving cumulated precipitation (rsprecipitation, lower panel), for each month during the 1994–2020 period. Whiskers represent minimum and maximum values of the distributions, the boxes represent the interquartile ranges, and the orange lines the means. Values for the 2018–2019 season are depicted in blue dots.

For the four species, some of the parameters displayed some degree of plasticity comparing their values among sites. In this regard, plants in South Foyel showed lower values of πo and Ψ_{tlp} compared with those growing in El Chucao ($p = 0.01$ and 0.02, respectively). However, in general terms, the studied species did not differ markedly in the parameters of the PV curves, and none stood out for having values that clearly distinguish it from the others.

4.4. Vulnerability to cavitation curves and safety margins

The estimated parameters of the VC curves for the different species are presented in Fig. 2 and hydraulic safety margins are presented in Table 3. Overall, the species studied presented a limited range of embolism resistance (i.e. Ψ_{50} values ranged from to − 2.1 to − 3.7 MPa for *N. antarctica* and *D. juncea*, respectively; with even a lower range of variation in Ψ_{tlp} seen in the previous section).

There were species-specific differences in the models fitted to the VC curves; as a whole, all the species differed from each other (ER = tending to infinity; Fig. 2). In contrast to the leaf water relations parameters (previous section), the most resistant to cavitation species was *D. juncea* (with the lowest slope and Ψ_{50}) and the most vulnerable was *N. antarctica*, with the highest slope and Ψ_{50} (although not significantly

Table 2

Mean values (± s. d.) of the estimated parameters obtained from pressure-volume curves for each Species and Site. The few statistical differences are indicated in the text and are presented in detail in Supplementary Material 6. References: relative capacitance at turgor loss point = C_{tlp}; relative capacitance at full turgor = C_{ft}; bulk modulus of tissue elasticity = ε; relative water content (symplastic water) at turgor loss point = RWC_{tlp}; symplastic water fraction at full turgor = SWF; osmotic potential at full turgor = π_0; water potential at turgor loss point = Ψ_{tlp}.

Species/Site	C_{tlp} (%)	C_{ft} (%)	ε (MPa)	RWC_{tlp} (%)	SWF (%)	Πo (MPa)	Ψ_{tlp} (MPa)
S. patagonicus	0.11 ± 0.05	0.06 ± 0.03	15.99 ± 15.58	90.53 ± 4.24	1.61 ± 0.46	−1.10 ± 0.35	−1.54 ± 0.38
N. antarctica	0.11 ± 0.06	0.08 ± 0.02	9.08 ± 3.25	85.94 ± 3.27	1.33 ± 0.18	−1.25 ± 0.27	−1.87 ± 0.45
L. hirsuta	0.13 ± 0.05	0.06 ± 0.02	12.22 ± 3.04	90.77 ± 3.05	1.67 ± 0.44	−1.06 ± 0.25	−1.44 ± 0.29
D. juncea	0.14 ± 0.09	0.10 ± 0.04	8.71 ± 5.72	88.81 ± 4.94	2.07 ± 0.56	−0.80 ± 0.33	−1.17 ± 0.33
El Chucao	0.12 ± 0.05	0.07 ± 0.03	13.2 ± 13.65	90.19 ± 4.62	1.74 ± 0.49	−0.93 ± 0.24	−1.33 ± 0.33
North Foyel	0.13 ± 0.06	0.08 ± 0.03	10.28 ± 4.26	88.88 ± 3.53	1.76 ± 0.56	−1.05 ± 0.31	−1.49 ± 0.43
South Foyel	0.12 ± 0.08	0.08 ± 0.03	10.98 ± 6.10	87.87 ± 4.64	1.51 ± 0.44	−1.19 ± 0.37	−1.71 ± 0.48

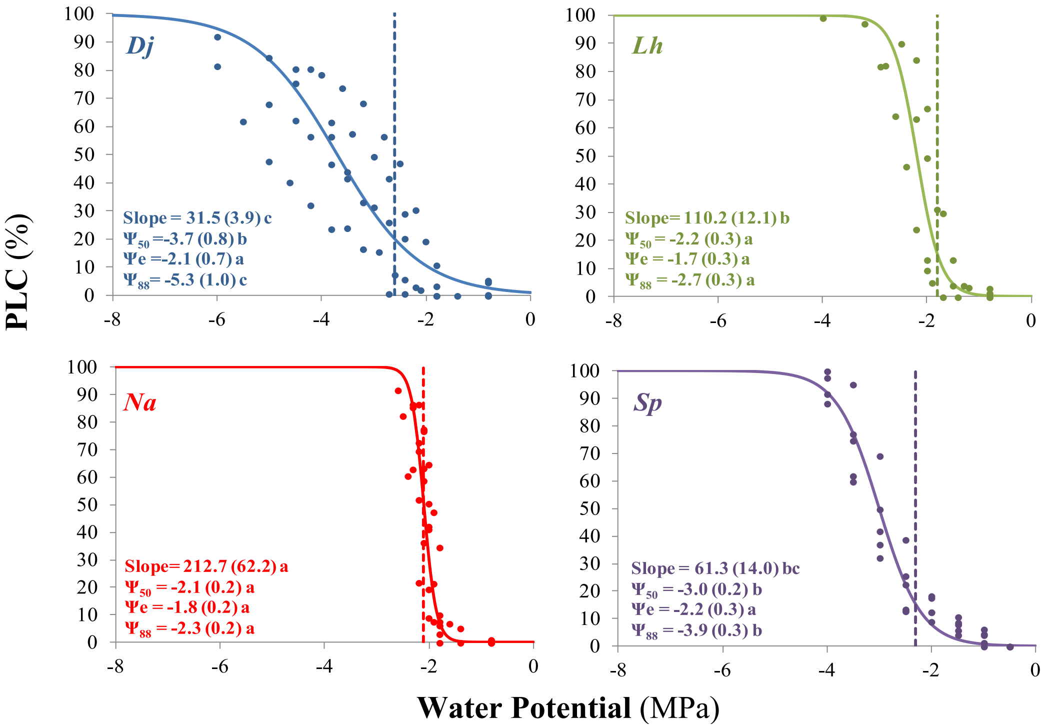

Fig. 2. Vulnerability to cavitation curves of each species depicting the percent loss of hydraulic conductivity (PLC, %) vs. the water potential (MPa). The following parameters of the curves are indicated for each species within the corresponding panels: slope (± s. d.), water potential (MPa) at air entry (Ψe; *sensu* Meinzer et al., 2009; 2016), and water potential (MPa) inducing 50% and 88% loss of conductivity (Ψ50 and Ψ88 (±s. d.)). Different lowercase letters indicate differences among Species for each parameter by means of one-way ANOVA, *p* = 0.05. The vertical dashed line in each panel shows the Ψ_{min} absolute value of each species measured in the field. *Dj* = *Diostea juncea*; *Lh* = *Lomatia hirsuta*; *Na* = *Nothofagus antarctica*; *Sp* = *Schinus patagonicus*.

different than the Ψ_{50} of *L. hirsuta*) (Fig. 2).

Regarding the safety margins, some differences were observed between the different species and time of the season, without interaction effect between factors (two-way ANOVA; Table 3). Considering the turgor loss point safety factor (Ψ_{min}-Ψ_{tlp}), *D. juncea* and *S. patagonicus* presented always negative values, whereas *L. hirsuta* and *N. antarctica* presented average positive safety margins, but with negative values in some sites or times of the year (see standard deviation in Table 3).

The safety margins relative to the initiation of the cavitation process (Ψ_{min}-Ψ_e) were lower in summer compared to the spring and autumn values in all the species, including negative values in some situations (see standard deviation in Table 3), with no significant differences between the species. In relation to a higher degree of xylem cavitation (Ψ_{min}-Ψ_{50}), the largest margins were recorded in *D. juncea,* followed by *L. hirsuta* and *S. patagonicus,* whereas *N. antarctica* presented the lowest values. No differences were observed between periods of the growing season.

No significant correlation was observed between mean values of Ψ_{50} and Ψ_{tlp} across species (p = 0.22). Moreover, no correlation was observed between Ψ_{min}-Ψ_{tlp} and Ψ_{min}-Ψ_e (Pearson coefficient of correlation ρ = 0.12, p = 0.71), but a high and negative correlation was found between Ψ_{min}-Ψ_{tlp} and Ψ_{tlp}- Ψ_{50} (ρ = -0.7, p = 0.01). From the measured absolute minimum water potential values and the VC curves, it seems that, in general terms, none of the species reached critical K_h losses under a severe summer drought as the one measured.

4.5. *Effects of Site, Species, and competition on dynamic physiological traits*

Overall, for all the physiological response traits, the Site, the Species, and the Season were important predictors in the minimum adequate models (see estimated fixed–effects coefficients of the models and relative importance in Tables 4 and 5), whereas the competition index did not have a significant effect on the studied variables. Since the intercept of a mixed-effects model constitutes a baseline, some factor levels were not explicitly declared in the table of model coefficients but were included in the intercept estimations by the fitting process. These levels were for the Species: *D. juncea*, for the Site: El Chucao, and for the Season: Spring, and they all were significantly different from zero.

In addition, the interactions of Species * Season and Site * Season were significant for all the variables, while for SLA, the Site * Species interaction was also significant (Table 6).

The minimum adequate models were composed of 18 fixed – coefficients (levels of factors plus interactions) but not all of them were

Table 3
Mean safety margins (± s. d.) of each species (based on Meinzer et al., 2009; 2016). Different lowercase letters indicate differences among Species for each safety margin by means of two-way ANOVA ($p < 0.05$). Different capital letters indicate differences among Times for each safety margin by means of two-way ANOVA ($p < 0.05$).

Time	Species	Ψ_{min}-Ψ_{tlp} (MPa)	Ψ_{min}-Ψ_{e} (MPa)	Ψ_{min}-Ψ_{50} (MPa)	Ψ_{e}-Ψ_{50} (MPa)
Spring	*Dj*	−0.36 ± 0.15 bA	0.57 ± 0.15 aA	2.17 ± 0.15 aA	–
	Lh	0.06 ± 0.18 aA	0.32 ± 0.18 aA	0.82 ± 0.18 bA	–
	Na	0.15 ± 0.18 aA	0.08 ± 0.18 aA	0.38 ± 0.18 cA	–
	Sp	−0.28 ± 0.15 bA	0.38 ± 0.15 aA	1.18 ± 0.15 bA	–
Summer	*Dj*	−0.88 ± 0.35 bA	0.05 ± 0.35 aB	1.65 ± 0.35 aA	1.61 ± 0.19a
	Lh	0.07 ± 0.15 aA	0.33 ± 0.15 aB	0.83 ± 0.15 bA	0.46 ± 0.06c
	Na	−0.01 ± 0.18 aA	0.08 ± 0.18 aB	0.22 ± 0.18 cA	0.25 ± 0.06c
	Sp	−0.61 ± 0.09 bA	0.05 ± 0.09 aB	0.85 ± 0.09 bA	0.90 ± 0.23b
Autumn	*Dj*	−0.58 ± 0.38 bA	0.35 ± 0.38 aA	1.95 ± 0.38 aA	–
	Lh	0.14 ± 0.09 aA	0.40 ± 0.09 aA	0.90 ± 0.09 bA	–
	Na	0.27 ± 0.05 aA	0.20 ± 005 aA	0.50 ± 0.05 cA	–
	Sp	−0.31 ± 0.09 bA	0.35 ± 0.09 aA	1.15 ± 0.09 bA	–

Table 4
Models that minimize information loss from data for each physiological response variable, formula, weights, and degrees of freedom (d. f). References: *Asat* = leaf net photosynthetic rate at saturating photosynthetic active radiation (μmol CO_2 m^{-2} s^{-1}), *gs* = stomatal conductance (mol H_2O m^{-2} s^{-1}) *E* = leaf transpiration (mmol H_2O m^{-2} s^{-1}), WUEi = intrinsic water use efficiency (*Asat/E*), Ψmin = midday water potential (MPa), Fv/Fm = maximum quantum yield of PSII. SLA = Specific Leaf Area (m^2 kg^{-1}). Models are sorted in descending order by weight.

Model formula	Weight	d. f.
Ψ_{min} = Season + Site + Species + (1 | tree: Season) + Season: Site + Season: Species	0.727	20
E = Season + Site + Species + (1 | tree: Season) + Season: Site + Season: Species	0.711	20
Fv/Fm = Season + Site + Species + (1 | tree: Season) + Season: Site + Season: Species	0.681	20
Asat = Season + Site + Species + (1 | tree: Season) + Season: Site + Season: Species	0.625	20
gs = Season + Site + Species + (1 | tree: Season) + Season: Site + Season: Species	0.492	20
WUEi = Season + Site + Species + (1 | tree: Season) + Season: Site + Season: Species	0.222	20
SLA = Season + Site + Species + (tree: Season) + Season: Site + Site: Species	0.212	20

significantly different from zero. For example, *Asat* presented 16 significant coefficients, 15 for E, 17 for *gs*, 6 for WUEi, 14 for Ψ_{min}, 10 for Fv/Fm, and 11 coefficients for SLA (Table 6). This means that there are ecophysiological variables that are better explained by the factors (e.g. Species, Site, or Season) or by their interactions (e.g. Site * Season, Species * Season, or Species * Site) than others.

Fig. 3 and Supplementary 7 illustrated the variability of physiological traits among Sites, Species and Seasons. For *Asat, gs* and *E*, *D. juncea* trees presented a different pattern compared to the other species along the growing season (Fig. 3), as well as El Chucao site presented a different general pattern compared to both North and South Foyel (Table 6; Fig. 3 and Supplementary 7).

Broadly, the *Asat* showed a marked reduction pattern during the Summer in all the species in North Foyel and particularly for *D. juncea* in North and South Foyel sites (Fig. 3 and Supplementary 7). This reduction was accompanied by a similar pattern in *gs*, and consequently, in leaf transpiration (Fig. 3 and Supplementary 7). As mentioned before, *D. juncea* trees showed differences throughout the season compared to the rest of the species. They presented a pattern of reduction in gas exchange during summer drought, which was not observed, however, in El Chucao site, where for all the species the pattern was of an increasing trend throughout the growing season (Spring to Autumn). The decrease in gas exchange in North and South Foyel sites was not permanent, but stopped during Autumn, within the same growing season (Supplementary 7). Unlike the observed variation in *Asat* and *E* in some species and sites, the WUEi was almost constant along the growing season in all the studied species (Fig. 3 and Supplementary 7).

Concerning the Ψ_{min} values, particularly in North Foyel, a consistent pattern of reduction was observed in *D. juncea* and *L. hirsuta,* and in the case of South Foyel, in *D. juncea* and *S. patagonicus.* The remaining species did not significantly vary its Ψ_{min} values within each site or even increased it during the growing season (Fig. 3 and Supplementary 7). In relation to the SLA values, almost no variation between sites was observed. *D. juncea* and *N. antarctica* values were higher than in the two other species. A consistent pattern during the growing season was observed for all species with maximum values of SLA during the summer.

In relation to the Fv/Fm ratio, the pattern was consistent for all the species: the maximum values of Fv/Fm occurred during summer (Fig. 3 and Supplementary 7), that is, not only there was no damage to the photosynthetic apparatus as a result of the drought, but in that period they presented the maximum photosynthetic capacity at a biochemical level, which indicates that the decrease in *Asat* observed in some situations (species or sites) during the summer drought was due to temporary stomatal closure.

5. Discussion

The present study aimed at determining the differential physiological response of four woody species of low-mixed Patagonian forests to environmental factors, in particular, to the seasonal variation characterized by severe summer drought, and how they respond under different competition levels. As we expected, some different physiological responses to drought were found among the different species considered, but as a whole, they did not present marked differences in their general responses to drought. In this regard, only one of them, *Diostea juncea*, showed a marked decrease in gas exchange during the summer drought, but with no medium-term consequences in its functioning. Surprisingly, this species was the most resistant to xylem cavitation of the studied species, but also the most intolerant to dehydration in terms of shootś water relations (parameters of the pressure–volume curves), suggesting that these leaf parameters are more suitable to explain seasonal patterns and gas exchange limitations under drought in the studied ecosystem than the xylem hydraulic parameters. However, more studies of vulnerability to cavitation are needed, taking into account the potential variability among sites, dates or even individuals,

Table 5

Relative importance of each predictor variable. Bold letters indicate variables or variable interactions included in the minimum adequate model ("*mam*"). References: Alemdag = competition index of Alemdag; *Asat* = leaf net photosynthetic rate at saturating photosynthetic active radiation; *gs* = stomatal conductance; *E* = leaf transpiration; WUEi = intrinsic water use efficiency (*Asat/E*); Ψ_{min} = minimum daily water potential; Fv/Fm = maximum quantum yield of PSII; SLA = Specific Leaf Area. Numbers in parentheses indicate the number of models in the dredging table that contain each factor as an explanatory variable.

Variable	**Season** (28)	**Species** (28)	**Season* Species** (12)	**Site** (28)	**Season* Site** (12)	**Alemdag** (19)	**Site* Species** (12)	**Season*: Site* Species** (2)
Asat	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.27	0.14	<0.01
gs	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.27	0.31	0.08
E	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.27	0.03	<0.01
WUEi	**0.96**	**0.82**	0.39	**0.98**	**0.72**	0.26	<0.01	<0.01
Ψ_{min}	**1.00**	**1.00**	**0.99**	**1.00**	**0.99**	0.26	0.02	<0.01
Fv/Fm	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	0.27	0.07	<0.01
SLA	**1.00**	**1.00**	0.42	**1.00**	0.53	0.30	0.99	<0.01

Table 6

Estimated fixed-effect coefficients of the minimum adequate model. Asterisks show the significance level (*=<0.05; **=<0.01; ***=<0.001). References: NF = North Foyel Site; SF = South Foyel Site; ECH = El Chucao Site; *Na* = *N. antarctica*; *Lh* = *L. hirsuta*; *Dj* = *D. juncea*; Sum. = summer; Aut. = autumn.

Factors/Interactions	**Factor level**	***Asat***	***E***	***gs***	**WUEi**	**Ψmin**	***Fv/Fm***	***SLA***
Intercept		12.516 ***	1.575 ***	0.136 ***	7.984 ***	−1.103 ***	0.704 ***	8.383e−03 ***
Site	NF	4.625 ***	0.391 **	0.078 ***	1.490 **	−0.126 *	0.031	−7.340e−04
	SF	2.446 **	0.248 *	0.050 ***	0.619	−0.107	0.042 *	−2.228e−03 ***
Species	*Na*	−10.063 ***	−1.172 ***	−0.134 ***	−0.854	−0.180 *	−0.003	8.378e−04
	Lh	−6.614 ***	−0.875 ***	−0.101 ***	0.228	0.164 *	−0.159 ***	−5.088e−03 ***
	Sp	−8.956 ***	−1.158 ***	−0.130 ***	0.783	−0.158 *	−0.072 ***	−4.494e−03 ***
Season	Sum.	−5.581 ***	−0.735 ***	−0.080 ***	0.265	−0.495 ***	0.046 *	2.459e−03 ***
	Aut.	−0.7379	0.211	−0.015	−0.898	−0.315 ***	0.036	1.788e−03 ***
Site * Season	NF * Sum.	−6.579 ***	−0.633 ***	−0.098 ***	−1.395	−0.010	0.022	−1.315e−03 *
	SF * Sum.	−3.740 **	−0.450 *	−0.066 ***	0.792	0.151	−0.067 **	2.387e−04
	NF * Aut.	−4.952 ***	−0.406 *	−0.094 ***	−1.603 *	0.287 **	−0.075 **	−1.250e−03
	SF * Aut.	−4.996 ***	−0.700 ***	−0.092 ***	0.439	0.304 ***	−0.098 ***	−7.776e−04
Species * Season	*Na* * Sum.	7.471 ***	0.844 ***	0.113 ***	1.891 *	0.352 ***	0.009	–
	Lh * Sum.	7.280 ***	0.927 ***	0.112 ***	0.225	0.337 ***	0.123 ***	–
	Sp * Sum.	7.351 ***	0.936 ***	−0.118 ***	0.085	0.200 *	0.032	–
	Na * Aut.	6.093 ***	0.322	0.077 ***	2.328 **	0.344 ***	0.052	–
	Lh * Aut.	2.555	0.007	0.0489 *	1.752 *	0.238 *	0.131 ***	–
	Sp * Aut.	5.195 ***	0.399 *	0.082 ***	0.326	0.036	0.052	–
Site * Species	*NF * Lh*	–	–	–	–	–	–	1.800e−03 *
	*SF * Lh*	–	–	–	–	–	–	2.941e−03 ***
	*NF * Na*	–	–	–	–	–	–	−6.534e−05
	*SF * Na*	–	–	–	–	–	–	2.244e−03 **
	*NF * Sp*	–	–	–	–	–	–	8.975e−04
	*SF * Sp*	–	–	–	–	–	–	2.611e−03 ***

particularly in the case of *D. juncea*, which was the species with highest dispersion in the observed data.

Understanding how competition influences tree growth response to drought is essential for forest management aiming at climate change adaptation. However, published results from individual case studies are heterogeneous and sometimes contradictory (Gazol and Camarero, 2016; Serra-Maluquer et al. 2018; Mausolf et al. 2018; van Mantgem et al. 2020). The review and *meta*-analysis conducted by Castagneri et al. (2021) showed that competition does not affect the response of tree growth to drought in a unidirectional and universal way. Moreover, although density reduction (thinning) may alleviate growth declines during drought, the effects on growth after stress are uncertain. The large variability among investigated cases suggests that local-scale processes play a crucial role in determining such responses and should be explicitly evaluated and integrated into specific strategies for adaptation of forests to climate change (Castagneri et al., 2021). In our study, regarding the effect of competition, and therefore the possibility of managing the plants response to drought, although an improvement effect was noted on the values of the residuals of the models when using the Alemdag competition index as a weight, in no case there was evidence of a significant effect of this factor in the structure of the different models. This suggests that, at least under the climatic conditions of the studied year (characterized by a severe drought) and the environmental and management conditions of the three studied sites, the measured physiological short-term response to drought of the species is independent of the competition level. Although we cannot rule out the possibility that other physiological variables are not affected by competition, it seems that there is not a limitation imposed by the occupation of the space and the shared resource use by the different individuals, but to intrinsic physiological characteristics of each species. Notwithstanding this, our results indicate a good correlation between the current radial growth (radial growth of the last growth season, BAI) and the different competition indices considered (Table 4), suggesting that, beyond the response to summer drought, individual tree growth -which is probably concentrated in the spring season where water availability is relatively high in this Mediterranean-type climate- is modulated by the presence of other individuals and may be optimized by management. In this regard, soil water content is highly affected by the basal area of the stands, even in humid periods and seasons, as has been measured in other sites of Patagonia (e.g. Martínez-Meier et al., 2015). It could also be possible that unmeasured ecophysiological variables explaining growth would have been affected differentially by competition.

Considering the species-specific differences, *Diostea juncea* was the species with the highest potential for CO_2 fixation per unit leaf area, but also with the highest reduction in gas exchange due to the decrease in soil moisture values and/or increases in vapor pressure deficit (VPD) that occur in summer in the study region (Gyenge et al, 2009). This was probably due to its more negative safety margins concerning cell turgor

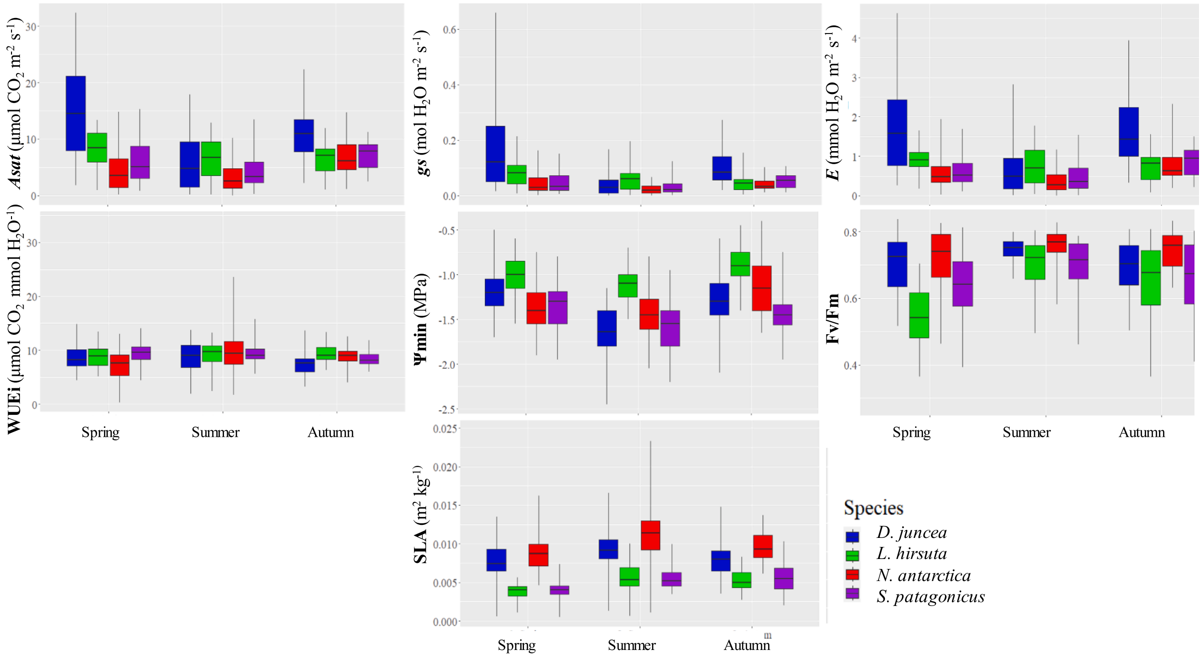

Fig. 3. Observed values Boxplots of eco-physiological variables in the different Seasons by Species. Variables: *Asat* = leaf net photosynthetic rate at saturating photosynthetic active radiation, *gs* = stomatal conductance, *E* = leaf transpiration, WUEi = intrinsic water use efficiency, Ψ_{min} = minimum water potential, Fv/Fm = maximum quantum yield of PSII, SLA = Specific Leaf Area. Units of each variable are indicated in the y-axis.

that constrain its stomatal conductance and water loss, a behavior common to a conservative strategy of water use. The observed high gas exchange capacity at the leaf level in this species is in agreement with the high canopy conductance measured at the whole plant level from sapflow measurements, which was also higher than in the codominant species in mixed forests (Fernández et al, 2009). It is important to note, however, that this species has a low leaf area index and sapwood area (Gyenge et al, 2009), which in conjunction with its high sensitivity to water deficit (this study; Fernández et al, 2009), may result in a relatively low contribution to the whole forest carbon fixation and transpiration. As mentioned earlier, it is interesting to note that this high (but short-term) sensitivity to water deficit is observed in the most-resistant to cavitation species of the four studied.

Studies within communities (e.g. Brodribb et al, 2003) and across biomes (Zhu et al, 2018) show that there is a weak or no direct correlation between the water potential at turgor loss point and the water potential at 50% of xylem conductivity loss (Ψ_{50}) in woody species.

Our results are in agreement with this lack of relationship between these traits. In addition, we did not find a significant correlation between the safety margins relative to the turgor loss point and the initiation of the cavitation process. However, we did find a strong and inverse relationship (correlation coefficient: −0.7; $p = 0.01$) between the safety margins relating the turgor loss point and the Ψ_{50}. This means that within the studied communities, the species losing more cell turgor in the field were those with the highest margins respect to critical losses of hydraulic conductivity (Ψ_{min}-Ψ_{50}), and *vice versa*. Therefore, this mixed forest seems to host species with a more conservative behavior operating far from important K_h losses, such as *D. juncea* (and *S. patagonicus* in lesser degree), and species with a riskier strategy, such as *N. antarctica* (and *L. hirsuta* in lesser degree), which maintains high gas exchange at the expense of hydraulic losses (as assumed based on minimum water potential measured and the VC curves). In *N. antarctica*, the species that presented the highest vulnerability to cavitation, which was even higher than previous antecedents in two other populations of the species (Bucci et al 2012), the lowest values of osmotic potential at full turgor and water potential at turgor loss would allow it to keep its stomata open and absorbing water at low soil water potential and, consequently, maintaining the physiological activity and growth (Jones and Turner, 1980; Schonfeld et al., 1988). On the other hand, our results suggest that the four species lose leaf turgor during the afternoon (with some species, and in some sites and times of the season, more limited than in others), the moment of minimum water potential and maximum VPD. This is in agreement with previous studies of canopy conductance of the studied species (Fernández et al, 2009), showing that the maximum stomatal activity was developed during the morning, and all species partially closed their stomata as daily VPD increased. In the short term, none of the observed strategies seem to have affected differentially the response of the studied species to a particularly severe summer drought. However, more studies are needed to determine the influence of these alternative behaviors in response to recurrent (or more frequent) and severe droughts as those measured in the last years in the studied region (Castellanos et al., 2022). Notwithstanding this, it is important to notice the limitations in our estimations of safety margins. Firstly, in this study we did not measure vulnerability to cavitation at the individual level, as we did with the other variables, so there may be some variation in the real individual Ψ_{50} values, whose effect could not be evaluated. Secondly, the absolute values of the estimated safety margins should be taken with caution because we used for its calculation the minimum water potential al leaf level and the vulnerability to cavitation parameters of the stem wood. Since there is a disequilibrium in water status of the plants organs during the transpiration process (e.g. Johnson et al, 2011), with leaves having more negative water potential than stems, the safety margins could be somewhat underestimated. We consider, however, that the ranking of values among species would be the same.

Our measurements carried out in three periods along the growing season (including the dry summer period), allowed us to determine that a severe drought summer did not affect the physiological integrity of the studied species in the studied season, even when a decrease in gas exchange, turgor or xylem conductivity losses of different magnitude were detected in some of them. However, all species presented high gas exchange performance after the summer drought, indicating high drought tolerance and resilience, irrespective of the site, the species and the competition level. The lack of effect of competition reduction on the physiological response to drought contrasts with studies that propose thinning as a way to improve water status and gas exchange of remaining individuals by means of increased water and nutrient availability (e.g. Dinh et al, 2016). However, thinning not always results in higher water content, in particular where grasses increase also their cover in openings (e.g. Bahamonde et al, 2018). In addition to understory water use, the thinning can also increase soil evaporation.

5.1. Conclusions and management implications

From the results of the present study, it was seen that inter-tree competition does not affect the physiological response of the four studied species to summer drought, but it does affect their individual growth, albeit to a small extent. These results suggest that the effect of summer drought response cannot be mitigated by density management. In other words, the productivity of the species of interest can be improved, but not their adaptability, at least to severe events such as the one of the year of study.

According to our results and those by Gyenge et al. (2008), *N. antarctica* and *L. hirsuta* have comparatively higher growth rates and the possibility to reach larger sizes (more than 25 cm in diameter) in comparison to the other two species considered in the present study. This is in agreement with their riskier strategy in terms of hydraulic safety margins (i.e. they maximize carbon gain at the expense of some losses of hydraulic conductance). Moreover, Sarasola et al. (2008) and Goldenberg et al. (2020) confirmed a high growth response in *N. antarctica* growing in stands subject to thinning, which means that it can take advantage of released resources. These results suggest that thinning could differentially favor *N. antarctica* and *L. hirsuta* at the expense of the more conservative species of the community. Furthermore, Gyenge et al. (2008) also mention that the species with higher productivity (in this case, *L. hirsuta* and *N. antarctica*) have greater efficiency in water use than those with lower productivity. In this way, selectively extracting low-productivity species could increase the individual growth rate of remaining trees, increasing their potential commercial value, and at the same time, optimizing the water use efficiency at stand level (Gyenge et al. 2008). However, the impact of removing individuals of one species or another in terms of resources release and capture by remaining species still needs to be studied.

In spite of the potential positive impact of thinning on treeś growth (but not on their drought adaptability), partial openings of low-mixed forests have also recently been shown to offer ecological benefits and provision of ecosystem services (Coulin et al. 2019, Chillo et al. 2020, Nacif et al. 2021). However, the natural regeneration dynamics of these systems would change in response to cover management, probably affecting differently the survivorship of young seedlings of the different species in open areas, particularly in dry summer (as has been observed as a result of openings produced after canopy mortality events due to extreme droughts in other Patagonian forests (Suarez and Kitzbrger, 2008). Therefore, management interventions that involve the extraction of individuals in these mixed forests should analyze the dynamics (and eventually, the planting) of saplings of key species that may be affected due to the change in forest structure.

CRediT authorship contribution statement

S.A. Varela: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **J.P. Diez:** Methodology, Investigation, Writing – original draft, Writing – review & editing. **F. Letourneau:** Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **E. Bianchi:** Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **M. Weigandt:** Conceptualization, Methodology, Visualization, Writing – review & editing. **A.J. Porté:** Conceptualization, Methodology, Visualization, Writing – review & editing. **A.S. Sergent:** Conceptualization, Methodology, Visualization, Writing – review & editing. **M.E. Nacif:** Conceptualization, Writing – review & editing. **L.A. Garibaldi:** Conceptualization, Writing – review & editing. **M.E. Fernández:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121039.

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