Forest Ecology and Management 595 (2025) 122966

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Exotic pine plantations vs. native forests in northern Patagonia: Comparing growth patterns and climate change vulnerability

Ernesto Juan Reiter [a,*], Robert Weigel [a,d], Helge Walentowski [b], Maria Melisa Rago [c,e], Alois Simon [b], Clara Pissolito [c,e], Christoph Leuschner [a]

[a] *Plant Ecology and Ecosystems Research, University of Göttingen, Göttingen, Germany*
[b] *Faculty of Resource Management, University of Applied Sciences and Arts (HAWK), Göttingen, Germany*
[c] *Andean-Patagonian Forestry Research and Extension Center (CIEFAP), Esquel, Argentina*
[d] *Ecological-Botanical Garden, University of Bayreuth, Bayreuth, Germany*
[e] *National Scientific and Technical Research Council (CONICET), Argentina*

ARTICLE INFO

Keywords:
Austrocedrus chilensis
Nothofagus dombeyi
Pine plantations
Tree-ring analysis
Climate sensitivity of growth
Stable isotopes

ABSTRACT

The area planted with exotic conifers has rapidly increased between the 1970s and 2000s in northern Argentinian Patagonia, replacing in many cases native *Nothofagus* and *Austrocedrus* forests. Direct comparisons between pine plantations and native forests with respect to growth patterns, productivity and climate vulnerability are lacking so far. Here, we explore differences in radial growth, climate sensitivity of growth and stomatal regulation between planted exotic (*Pinus ponderosa*, *P. contorta*, *P. radiata*) and neighboring even-aged native stands (*Austrocedrus chilensis*, *Nothofagus dombeyi*) during the stem-exclusion phase (first 32 years) using dendrochronology and stable isotope analysis of stem wood. While all *Pinus* stands reached maximum basal area increment (BAI) earlier than the native species, *Nothofagus dombeyi* was as productive as *Pinus radiata,* the most productive exotic conifer. The main climatic growth constraints were in all five species rainfall deficits and elevated temperatures in late spring/summer, with the most productive species being more sensitive to climate. Stem wood Δ^{13}C and δ^{18}O signatures suggest higher stomatal conductance and transpiration losses of the three exotic *Pinus* species and a recent transpiration increase compared to the native species with an apparently more conservative water use. Our results show that introduced *Pinus* species are not necessarily more productive than native tree species, and their growth may be more vulnerable to climate warming. Since all planted *Pinus* species are invasive in the region and are increasing the fire risk, it is advised in the face of climate change to preferably plant native tree species, where possible, and to reduce the area of conifer plantations.

1. Introduction

The growing global demand for wood and wood-related products (FAO, 2024) together with restoration and carbon markets (Baral et al., 2016; Lindenmayer et al., 2015) have led to increased planting of tree species outside their natural ranges, particularly of fast-growing species in the southern hemisphere (Payn et al., 2015). This process is accompanied by a vital debate about the socio-ecological implications of exotic tree plantations, with a focus on biodiversity loss (Brockerhoff et al., 2008), the alteration of hydrological cycles (Scott, 2005), fire regimes (Mandle et al., 2011), microclimatic (García et al., 2023) and edaphic site conditions (Perdomo-González et al., 2023), and the spoiling of landscapes aesthetics (Williams, 2014). Furthermore, the introduction of exotic tree species may lead to the invasion of neighboring natural habitats (Richardson and Rejmánek, 2011).

From the wood production perspective, the planting of conifers in southern hemispheric temperate climates is driven by three main motivations, (i) to meet the market demand for conifer wood, (ii) to achieve maximum profitability through high productivity, and (iii) to plant tree species with assumed higher drought resistance to cope with climate change (FAO, 2024). Conifer plantations are often established without adequate scientific testing to verify whether the second and third assumptions are met. While several Pinaceae species are highly productive under optimal climatic conditions, it is not well known whether they outperform native species, when planted beyond their natural range. Due to the widely discussed negative impacts of species introductions on

---

* Corresponding author.
E-mail address: ernestojuan.reiter@uni-goettingen.de (E.J. Reiter).

https://doi.org/10.1016/j.foreco.2025.122966
Received 28 April 2025; Received in revised form 30 June 2025; Accepted 1 July 2025

forestry and ecosystem functioning (Braun et al., 2017; Bremer and Farley, 2010; Horák et al., 2019), it is straightforward to compare the growth and yield potential of introduced species with that of productive native tree species in order to assess the potential for closer-to-nature silviculture.

On the eastern slopes of the Andes in northern Argentinian Patagonia, the plantation of exotic tree species as replacement of native forests, mainly of *Austrocedrus chilensis* (D.Don) Pic. Ser. et Bizarri, degraded by fire or after clearance, reached its peak during the 1970s and 1980s, promoted by the government through subsidies (Bava et al., 2015; Gyenge et al., 2010; Pauchard et al., 2016). Since the 1980s, plantations have been established in overgrazed grasslands of the forest-steppe ecotone and in the steppe, where the largest afforestation areas are currently located (CIEFAP, 2017). Nowadays, they cover more than 80.000 ha dominated by the North American species *Pinus ponderosa* Dougl. ex. C. Lawson (CIEFAP, 2017), and to a lesser extent of *Pinus contorta* Douglas ex Loudon, *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus radiata* D. Don. and *Pinus jeffreyi* A. Murray bis (CIEFAP, 2017).

In Argentinian Patagonia, exotic conifer plantations have shown productive timber yields, sometimes exceeding those in their natural distribution range (Gonda, 1998), and faster juvenile growth and higher water use efficiency than native tree species (Gyenge et al., 2008a). However, due to discontinuity in subsidies and relatively long turnover periods, many plantations have been abandoned, and productivity and timber quality have decreased without proper silvicultural management (Bava et al., 2015; CIEFAP, 2017; Raffaele et al., 2015). The accumulated conifer biomass is highly inflammable (Bianchi et al., 2019; Franzese et al., 2022), and can thus alter the fire regime (Paritsis et al., 2018) and increase the invasion risk, as is the case with many pyrophytic species (Franzese and Raffaele, 2017). The three main *Pinus* species introduced to Patagonia possess traits that facilitate fire adaptation: both *P. radiata* and *P. contorta* behave as resilient active pyrophytes, featuring serotinous cones where seed release is triggered by fire (Franzese and Raffaele, 2017), whereas *P. ponderosa* behaves as a resistant passive pyrophyte that can tolerate recurrent low-intensity fires due to adapted bark, crown and root characteristics (Fitzgerald, 2005). All three *Pinus* species have shown to be invasive in Patagonia (Franzese and Raffaele, 2017; Simberloff et al., 2010). Given that fire is the primary disturbance factor that shapes forest composition in northern Patagonia (Kitzberger, 2012) and which has increased in frequency and intensity in recent years due to climate change (Kitzberger et al., 2022), species with fire-adapted traits are favored by this environmental shift.

Concern over plantations replacing native ecosystems in Patagonia has fueled increasing research in exotic species' invasive potential (Franzese and Raffaele, 2017), relevant tree physiological characteristics (Fernández et al., 2014; Gyenge et al., 2012), biodiversity losses (Paritsis and Aizen, 2008; García et al., 2023; Rago et al., 2021), and fire-related risks (Franzese et al., 2022; Paritsis et al., 2018). However, little is known about the climate sensitivity of growth and recent growth trends of exotic tree species in Argentinian Patagonia (Pauchard et al., 2016). The relatively young age of most plantations to date may explain the virtual absence of research on the growth performance and climate vulnerability of these species, since more than half of the plantations are still younger than 25 years (CIEFAP, 2017). On the other hand, many abandoned plantations are now reaching the age of harvest (30–40 years), but are not being cut because of economic reasons. In some cases, the cost of extraction exceeds the value of the wood, and there is no manufacturing sector willing to cover this gap (Bava et al., 2015). In some areas where accessibility is limiting management and harvest operations, such as on steep slopes and at locations above the tree line (>1700 m asl), exotic pines naturalize by invading native forest and non-forest vegetation, which includes protected areas (APN, 2025; Joelson et al., 2025; Simon et al., 2025a). Although the current extent of self-regenerating *Pinus* stands in Patagonia is still limited, the species' ability to quickly invade new, previously unforested habitats and to trigger positive fire-vegetation feedbacks (Franzese et al., 2022), bears the risk of a fast expansion of the area where these exotic species dominate. This warrants studies investigating the growth performance and climate sensitivity of growth of these exotic tree species in order to better understand their economic potential and the associated ecosystem vulnerability to climate change.

Dendrochronological studies have provided valuable insights into the influence of climate on the growth dynamics of major native tree species in northern Argentinian Patagonia (Amoroso et al., 2017; Srur et al., 2020; Suarez et al., 2015). Water deficits and elevated temperatures during the growing season were identified as key climatic factors influencing the growth patterns of the dominant species at low to mid elevations (Reiter et al., 2024). In more humid regions in the west, where the evergreen broadleaf species *Nothofagus dombeyi* (Mirb.) Oerst. dominates, stand-level growth decline and mortality events have been reported in recent decades, linked to increased interannual growth variability and elevated drought sensitivity (Suarez et al., 2004; 2024; Suarez and Kitzberger, 2010). Towards the east, precipitation markedly decreases due to the rain shadow effect of the Andes (Garreaud and Aceituno, 2007), and *N. dombeyi* forms mixed stands with the conifer *Austrocedrus chilensis*. This drought-tolerant species is naturally widespread at the drier eastern edge of the Andean forest belt, being a main constituent of the forest-steppe ecotone. Several studies have demonstrated the strong influence of summer water deficits on the interannual growth variability of *A. chilensis* (Amoroso et al., 2015; Villalba and Veblen, 1997), which are associated with recent growth declines in monospecific stands, particularly at the species' drier limits (Amoroso et al., 2012; Reiter et al., 2024).

Tree-ring studies traditionally focus on dominant trees in mature stands, since these individuals are typically most sensitive to climate and growth is less affected by biological age trends (Biondi and Qeadan, 2008). The growth of juvenile or young trees is influenced not only by climate but by ontogenetic change in growth dynamics and often by intense symmetric or asymmetric competition processes as well, that obscure climatic signals in tree rings (Belmecheri et al., 2022; Du et al., 2021). When dense, even-aged stands (cohorts) close the canopy and the stem exclusion phase begins, growth is often limited by lack of light and soil resources (Bernhardt et al., 2020), leading to vertical stratification of the stand and mortality (Oliver and Larson, 1996). At this stage, the climate sensitivity of growth in combination with other growth-derived metrics such as within-stand growth synchrony and interannual growth variability can provide valuable information about the interactions of stand dynamics and climatic variability early in life (Voelker, 2011). Comparing different species in their climate sensitivity of growth in this stage of life can reveal which species are more susceptible to climate fluctuations, and it may allow assessments of their adaptive potential to climate change. Combining such dendrochronological information with data on isotope signatures in tree rings may allow insights into stomatal responses and patterns of CO_2 and H_2O exchange between the canopy and the atmosphere (Siegwolf et al., 2022). Since ontogeny may have a large influence on the physiology of a tree, species comparisons are best conducted for trees at similar age. This can be done for the introduced conifers in Patagonia only for young trees, as older stands are rare or absent.

Here, we examine in the northern Patagonian Andes in Argentina the growth dynamics and climate sensitivity of radial growth at juvenile age of the three most common exotic *Pinus* species (*P. radiata*, *P. contorta*, *P. ponderosa*) in comparison to that of two native tree species, the broadleaved evergreen species *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*. Specifically, we address the following questions: 1) Are there significant differences in radial growth between native and exotic tree species during the juvenile phase? 2) Do the climatic factors driving radial growth during this life stage differ between native and exotic species? 3) Do native and exotic tree species differ in their stomatal regulation and CO_2 and H_2O gas exchange during the juvenile life stage? To address these questions, we analyzed tree-ring metrics and long-term growth trends, examined the correlation between radial growth and climate, and studied decadal change in stable C and O isotopes in tree rings in neighboring even-aged native and exotic forest stands at three sites with different climatic conditions.

We hypothesized that (1) the three exotic conifers grow faster and have a higher wood production at young age than native tree species, (2) the growth of the exotic conifers is less vulnerable to a warm and dry climate than that of native tree species, and (3) in order to sustain high growth rates, the exotic conifers restrict stomatal conductance with climate drying less than native tree species. Understanding the driving forces and the climate vulnerability of growth during the juvenile phase of these exotic species, as they reach maturity and naturalize in Patagonia, provides a necessary basis for managing these novel ecosystems.

2. Material and methods

2.1. Study area

The study area is located in the Province of Rio Negro in north-western Argentinian Patagonia (71.79°–71.48° W, 41.61°–41.93° S). It spans the transition from the Valdivian Temperate Rainforests in the humid westernmost Argentinean Andes to the drier eastern limits of the forest belt in transition to the Patagonian steppe (Fig. 1). The landscape is characterized by steep slopes and U-shaped valleys formed by multiple glaciation periods (Bouza and Bilmes, 2020). The widespread occurrence of volcanic soils with high water retention capacity (Buduba et al., 2020; Simon et al., 2025b) helps mitigating the strong summer water deficit (Kitzberger, 2012). In the region, the subtropical high-pressure system moves southward during the austral summer (December to February), weakening the prevailing westerly winds which bring moist air from the Pacific Ocean, which results in the transition from an oceanic climate in the west to a Mediterranean-type climate in the east (Paruelo et al., 1998). With decreasing precipitation in the rain shadow of the Andean ridge, seasonality (dry summers and wet winters) increases from west to east (Garreaud and Aceituno, 2007; Simon et al., 2024).

While the study region's natural forest vegetation is predominantly *Nothofagus–Austrocedrus* forest, the species composition varies across the landscape. *Nothofagus dombeyi* thrives in the moister west, while *Nothofagus pumilio* (Poepp. & Endl.) Krasser is more common at higher elevations building up the tree line. In post-fire shrublands and poorly drained soils, *Nothofagus antarctica* (Forst.) Oerst. tends to dominate. Toward the drier east, *Austrocedrus chilensis* becomes more prevalent. The exotic conifers have been increasingly planted in many areas, with their share increasing towards the forest-steppe ecotone (CIEFAP, 2017).

2.2. Sampling design and data collection

We selected three sites with different climatic conditions in the study region (Fig. 1, Table 1), where at least two *Pinus* species and one native species (either *A. chilensis* or *N. dombeyi,* or both) are occurring in close vicinity to each other, in order to directly compare the growth patterns of introduced and native tree species under similar topoclimates at a given site. The stands of native species developed naturally after stand-devastating fires and thus represent more or less cohorts. Across the three sites, we placed sampling plots in each two *Pinus sp.* plantations and in one (or two) nearby native forest stands (*N. dombeyi* or *A. chilensis*), resulting in 10 sampling plots in total (Table 1). Neither the planted conifer stands nor the native stands showed signs of management (thinning or pruning). All sampled plots have a northwestern exposure, with a prevailing slope angle of $< 24°$. At each sampling plot, we recorded during the growing seasons 2021/22–2023/24 the forest structure, analyzed soil properties and selected target trees to be sampled for dendrochronological analysis.

In circular concentric plots in representative sections of the stand, species identity, DBH and total height were registered for all trees with DBH $\geq$ 60 cm in a 1000 m^2 subplot, and for all trees with DBH $\geq$ 7 cm in a 400 m^2 subplot. To compare soil physical properties, we dug a 1 m-deep soil pit close to the plot center, where composite volumetric mineral soil samples of 400 cm^3 were extracted with 100 cm^3 -cores in four depth intervals (0–10 cm, 10–30 cm, 30–60 cm, 60–100 cm). For calculating plant-available water storage capacity (PAWC), we used calibrated pedotransfer functions established for Andosols in the area (Simon et al., 2025b).

For dendrochronological analysis, we extracted wood cores from the 20 dominant and codominant trees closest to the plot center, avoiding damaged and suppressed individuals. Per target tree, two wood cores were extracted at breast height (ca. 1.3 m) in perpendicular directions to each other using a 5 mm-increment borer (Haglöf, Langsele, Sweden), selecting stem sections where reaction wood was assumed to be less pronounced. For measuring ring widths, the increment cores were fixed onto wooden mounts, sanded with increasingly finer grades of sand-paper (200–1200 grains per cm^2), and scanned at a resolution of 2400 dots per inch (dpi) using an Expression 11000XL scanner (EPSON, Japan).

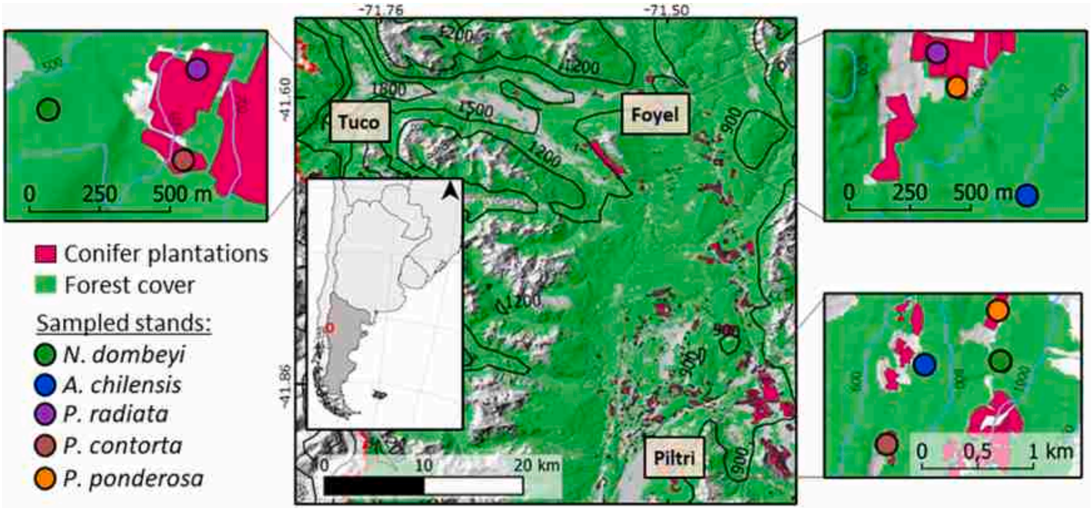

Fig. 1. Map of the study area in Argentinian Patagonia (dark grey in the inlet) and location of sampled stands at the three study sites (Tuco, Foyel and Piltri). Black lines in the center map are isohyets of mean annual precipitation (mm $year^{-1}$; WorldClim 2; Fick and Hijmans, 2017), light-blue lines in side maps indicate elevation above sea level (m a.s.l.).

Table 1
Topographic, climatic, and structural properties of the 10 studied stands. Mean annual temperature (MAT) and mean annual precipitation (MAP) for each site averaged from 6 pixels between 500 and 900 m a.s.l. of the WorldClim 2 dataset (period 1970–2020, Fick and Hijmans, 2017). PAWC (Plant-Available Water Capacity). Species: (n) for native, (e) for exotic. 'Target species' refers to the basal area (BA/ha) and tree density (trees/ha) of the selected species in the stand.

Site	Plot acronym	Elevation (m asl)	Species	MAT (°C)	MAP(mm year^{-1})	PAWC (mm)	Average tree age (years)	Total stand		Target species	
								BA (m^2/ha)	N/ha	BA (m^2/ha)	N/ha
Tuco	TuS1Co	513	*N. dombeyi* (n)	8.4	1709	311	39.5 ± 2.2	61.2	580	59.9	554
	TuS1Pr	603	*P. radiata* (e)			315	36.4 ± 1.5	83.4	411	83.4	411
	TuS1Pc	599	*P. contorta (e)*			-	32.9 ± 1.0	53.5	1093	52.5	989
Foyel	FoS2Ci	713	*A. chilensis* (n)	8.8	1174	101	73.1 ± 4.0	42.1	1036	34.4	363
	FoS2Pr	574	*P. radiata* (e)			249	36.6 ± 2.6	100.3	488	100	462
	FoS2Pp	614	*P. ponderosa* (e)			297	33.1 ± 1.3	60.2	635	39.8	375
Piltri	PiS3Ci	701	*A. chilensis* (n)	8.8	966	295	73.4 ± 6.2	58.4	755	51.3	494
	PiS3Co	901	*N. dombeyi* (n)			222	100.2 ± 4.9	62	742	62	742
	PiS3Pc	674	*P. contorta* (e)			-	33.2 ± 2.2	56.8	722	42.9	303
	PiS3Pp	803	*P. ponderosa* (e)			313	36.8 ± 1.0	58.7	1430	50.4	594

2.3. Stand chronologies and tree ring analysis

We visually dated tree rings under a Stemi 2000 stereomicroscope (Zeiss, Germany) and measured ring width in the scanned images using the CooRecorder V9.5 software (Cybis Elektronik & Data AB, Sweden). The cross-dating of the ring series of a given stand was validated by assessing correlation coefficients (Grissino-Mayer, 2001) and the values of t-tests (Baillie and Pilcher, 1973) using the CDendro V9.5 software (Cybis Elektronik & Data AB, Sweden). For building stand chronologies, we excluded ring series which had an overlapping period of < 30 years, a correlation coefficient < 0.32 or a t-value < 3 (ring series normalized by the P2YrsL method; Cybis Elektronik & Data AB, Sweden).

Our study addresses the early growth of trees which are in the stem-exclusion phase of stand development with strong intraspecific competition, where the ring-width series (RW) typically are influenced by strong nonlinear low-frequency signals that may not reflect fluctuation in environmental factors but result from age and size effects, as well as from biotic interactions (Biondi and Qeadan, 2008). To account for these drivers, we detrended the RW using a flexible 10-year smoothing spline with a 50 % frequency response to generate dimensionless ring-width index series (RWI; Cook and Peters, 1981). This approach minimizes low-frequency signal components resulting from the juvenile growth curve and disturbance effects (e.g. canopy openings due to self-thinning), while enhancing high-frequency signals (e.g. interannual climatic variability). This procedure was together with the subsequent treatment of the chronologies and related quality tests performed with the R package dplR (Bunn, 2008) in R (R Core Team, 2021) in the R studio environment.

We built RWI chronologies for each of the 10 stands by calculating Tukey's bi-weight robust mean across the trees of a stand. The quality of each chronology was assessed by means of the expressed population signal (EPS, the agreement between a limited set of tree samples and a theoretical chronology based on an infinite number of trees; Wigley et al., 1984), the Rbar value (i.e. the average Pearson correlation among all ring series in a chronology), the first-order autocorrelation of the series, and the Gleichläufigkeit (GLK, the proportion of common interannual growth changes between two series; Eckstein and Bauch, 1969). These metrics were calculated for RWI periods, when > 5 ring series were available.

For the further analysis of juvenile growth patterns, we truncated the length of all stand chronologies to the first 32 years, as this was the minimum period length available in all studied stands. To compare stem growth patterns, we calculated basal area increment (BAI) from the tree ring-width series (RW) and the measured diameter at breast height (DBH), computing backwards from the bark (youngest tree ring) to the pith (oldest tree ring) as follows:

$$BAI_t = \pi\left(r_t^2 - r_{t-1}^2\right)$$

where r is the tree radius and t the year of ring formation. The use of BAI as a growth measure is a biologically more meaningful estimate than RW, as it standardizes growth regardless of tree age or diameter, providing clearer insights into growth dynamics (Biondi and Qeadan, 2008).

For further comparing the species' juvenile growth dynamics, we used the Rbar values calculated from the first 32 years of the RWI chronologies as a measure of growth synchrony (the extent of common growth patterns among the tree ring series in a stand). The synchrony of growth reflects, how similar the growth patterns are across the individuals of a population in response to shared environmental factors (Wigley et al., 1984), often tied to a dominant regional climatic signal when calculated in detrended and standardized chronologies (Fritts, 1966). Similarly, we calculated the coefficient of variation (CV) of the RWI chronologies as a measure of relative interannual variability of growth (Cailleret et al., 2019). High CV values point to significant sensitivity to interannual changes, while low CV suggests stability or reduced responsiveness to environmental fluctuations. In light of evidence suggesting that ANOVA is robust to moderate violations of normality and variance homogeneity (Blanca et al., 2017), as observed in our data set, we opted to use ANOVA to test for differences across all groups (sites and species), allowing for consistent and interpretable comparisons across variables.

2.4. Climatic data and climate sensitivity of growth

We used climate data from the nearest meteorological station with long record (Bariloche airport; 41.15°S, 71.16°W; 840 m asl; Fig. 1), where mean monthly precipitation and temperature records are available for the period 1931–2023 (SMN, 2024). Since the first 32 years of the "BoS2Ci" chronology span from 1921 to 1952, and the climate records from Bariloche start just in 1931, the data for the period 1921–1931 was obtained from the CHELSAcruts climate simulations (Karger and Zimmermann, 2018). The climatic data for the period corresponding to each stand's juvenile phase (first 32 years of the chronology) was standardized in order to enable meaningful comparisons of climate-growth correlations. For standardization, monthly values were converted to z-scores (dimensionless numbers) by subtracting the monthly 32-year mean from each value and dividing it by the standard deviation. By doing so, we ensured that the variability is comparable among stands and the different 32-year periods, regardless of the absolute magnitude of the monthly climatic data values, which has varied considerably especially during the last 40 years (Jacques-Coper and Garreaud, 2015). Seasonal drought periods were assessed by calculating the standardized precipitation-evaporation index (SPEI) for each month, which characterizes the water balance (precipitation minus potential evapotranspiration). For calculating SPEI, monthly potential evapotranspiration was estimated with the Thornthwaite formula by means of the R package SPEI v.1.8 (Beguería and Vicente-Serrano, 2011).

For analyzing the climate sensitivity of growth, we correlated the stand chronologies (i.e. the stand averages of the detrended tree-ring series, RWI) with monthly values of average temperature, precipitation and SPEI, using first a static approach over the first 32 years of the chronologies. Preliminary analysis showed the strongest climate-growth correlations when SPEI was averaged over the preceding three months (SPEI3). The regional growing season extends approximately from October to April, spanning two calendar years. We analyzed monthly climate-growth correlations from previous-year October to current April, encompassing the previous and the current growing season over a total of 19 months across three calendar years. Secondly, we analyzed the temporal variability in the climate-growth correlations during the most influential months as derived from the static correlation analyses (current December, January and February) using a 10-year moving window with a 1-year offset for the 32-year period. This window size offered an appropriate balance between temporal resolution and the statistical power required for meaningful inference. To address the reduced sample size in shorter windows, the statistical significance ($p < 0.05$) of correlations was evaluated using a 1000-fold bootstrapped response function within the R package treeclim v2.0.6.0 (Zang and Biondi, 2015).

2.5. Stable isotope analysis

For analyzing long-term trends in the carbon and oxygen isotope signatures of the tree rings, we selected from the 20 wood cores per stand a subsample containing those five cores which showed the tightest correlation to the stand chronology. For each selected core, we sectioned groups of five contiguous annual rings under a binocular using a scalpel, resulting in six wood core sections for the first 30 years of tree life. We then pooled the each five replicate 5-yr-long wood sections of a stand to give a composite sample per period (e.g. 1997–2001, 2002–2006 etc.) and stand, and grounded and homogenized the material using a TS250 centrifugal mill (Siebtechnik, Mülheim, Germany). The isotope composition of C and O in the pulverized wood material and isotope ratios were analyzed by mass-ratio spectroscopy (Delta XP, Thermo Electron, Germany) at the Center for Stable Isotope Research and Analysis (KOSI) of the University of Göttingen. The isotopic signatures are expressed in delta (δ) notation as per mill (‰) deviations to the Vienna Pee Dee Belemnite (C) and Vienna Standard Mean Ocean Water (O) standards (Gonfiantini, 1978):

$$\delta^{13}C = \left(\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{standard}} - 1\right) \times 1000 \qquad \delta^{18}O = \left(\frac{(^{18}O/^{16}O)_{sample}}{(^{18}O/^{16}O)_{standard}} - 1\right) \times 1000$$

From the δ^{13}C values, we calculated fractionation values (Δ^{13}C), which is a more standardized way to interpret $\delta^{1\ 3}$C signatures, since they account for the atmosphere isotopic composition of CO_2 ($\delta^{13}C_{atm}$) and the post-photosynthetic discrimination against ^{13}C in plant tissues (Farquhar et al., 1989; Lavergne et al., 2022). For simplifying the calculation, we assumed no fractionation during photorespiration (Mathias and Hudiburg, 2022), and used the following expression:

$$\Delta^{13}C = \frac{(\delta^{13}C_{atm} - \delta^{13}C_{wood})}{\left(1 + \frac{\delta^{13}C_{wood}}{1000}\right)}$$

where $\delta^{13}C_{wood}$ and $\delta^{13}C_{atm}$ are the δ^{13}C signatures of the tree wood samples and the atmosphere, respectively. Historical records of atmospheric CO_2 concentration (C_a) and $\delta^{13}C_{atm}$ were derived from Belmecheri and Lavergne (2020), available in the isocalcR R package (Mathias and Hudiburg, 2022). Higher Δ^{13}C values indicate larger discrimination against the heavier ^{13}C isotope.

With the Δ^{13}C values, the intrinsic water use efficiency (iWUE) of photosynthesis was calculated through the leaf intercellular CO_2 concentration (C_i):

$$C_i = C_a \frac{\Delta^{13}C - a}{b' - a}$$

where a gives the fractionation during diffusion across the boundary layer and stomata (4.4 ‰; Craig, 1953) and b' the apparent fractionation by Rubisco (25.5 ‰, when derived from wood tissue; Cernusak and Ubierna, 2022). iWUE (i.e. the ratio A/g_s; unit: µmol CO_2 mol^{-1} H_2O) was then received from the C_i values calculated for the 5-year tree ring sections and the corresponding historical C_a records as:

$$iWUE = \frac{C_a - C_i}{1.6}$$

where 1.6 is the H_2O/CO_2 diffusion ratio in air, A is net photosynthesis rate and g_s stomatal conductance for water vapor.

Differences in the means of $\Delta^{13}C$, *iWUE* and $\delta^{18}O$ (averaged over the six 5-year periods for a stand) were compared both within sites for different species and across sites for the same species using ANOVA. Trends in isotopic composition during the 30-year period were tested for significance with the non-parametric Mann-Kendall trend test.

3. Results

3.1. Stand chronologies and juvenile growth metrics

The three introduced *Pinus* species and the two native tree species were represented by each two chronologies located at two different sites, resulting in 10 chronologies in total which base on 310 sampled increment cores. Even though the juvenile stage of growth was covered, all chronologies showed reliable quality indicators (EPS > 0.85 and GLK > 0.65), with Rbar values ranging from 0.36 to 0.74 (Table 2; see also Fig. S3 in the Appendix for running EPS and sample depth).

We found significant differences in juvenile growth metrics between

Table 2

Descriptive statistics of the 10 stand chronologies. EPS: Expressed population signal, Rbar: mean inter-series correlation, GLK: Gleichläufigkeit. Chronology length: Years for which > 5 ring series in a population were available.

Sample plot	No of trees (cores)	Mean DBH (cm)	Average tree height (m)	Chronology length (years)	EPS	Rbar	GLK
TuS1Co	17 (34)	54 ± 9.9	30 ± 2.7	39	0.90	0.36	0.65
TuS1Pr	19 (38)	51 ± 10.5	33.8 ± 5.1	37	0.94	0.47	0.70
TuS1Pc	18 (36)	27.8 ± 4.5	22.6 ± 1.7	32	0.93	0.47	0.69
FoS2Ci	15 (30)	44.9 ± 6.5	16.9 ± 1.5	73	0.97	0.65	0.80
FoS2Pr	19 (38)	53.8 ± 8.2	38.4 ± 3.0	38	0.97	0.62	0.74
FoS2Pp	18 (36)	38.6 ± 9.6	22.7 ± 2.6	33	0.96	0.56	0.72
PiS3Co	15 (30)	55.6 ± 15.4	26.3 ± 4.2	75	0.89	0.35	0.66
PiS3Ci	15 (30)	44.3 ± 9.7	22.3 ± 2.0	102	0.97	0.67	0.79
PiS3Pp	19 (38)	41.7 ± 4.3	22.7 ± 1.4	37	0.98	0.74	0.76
PiS3Pc	17 (34)	39.5 ± 6.8	19.8 ± 1.3	33	0.96	0.56	0.72

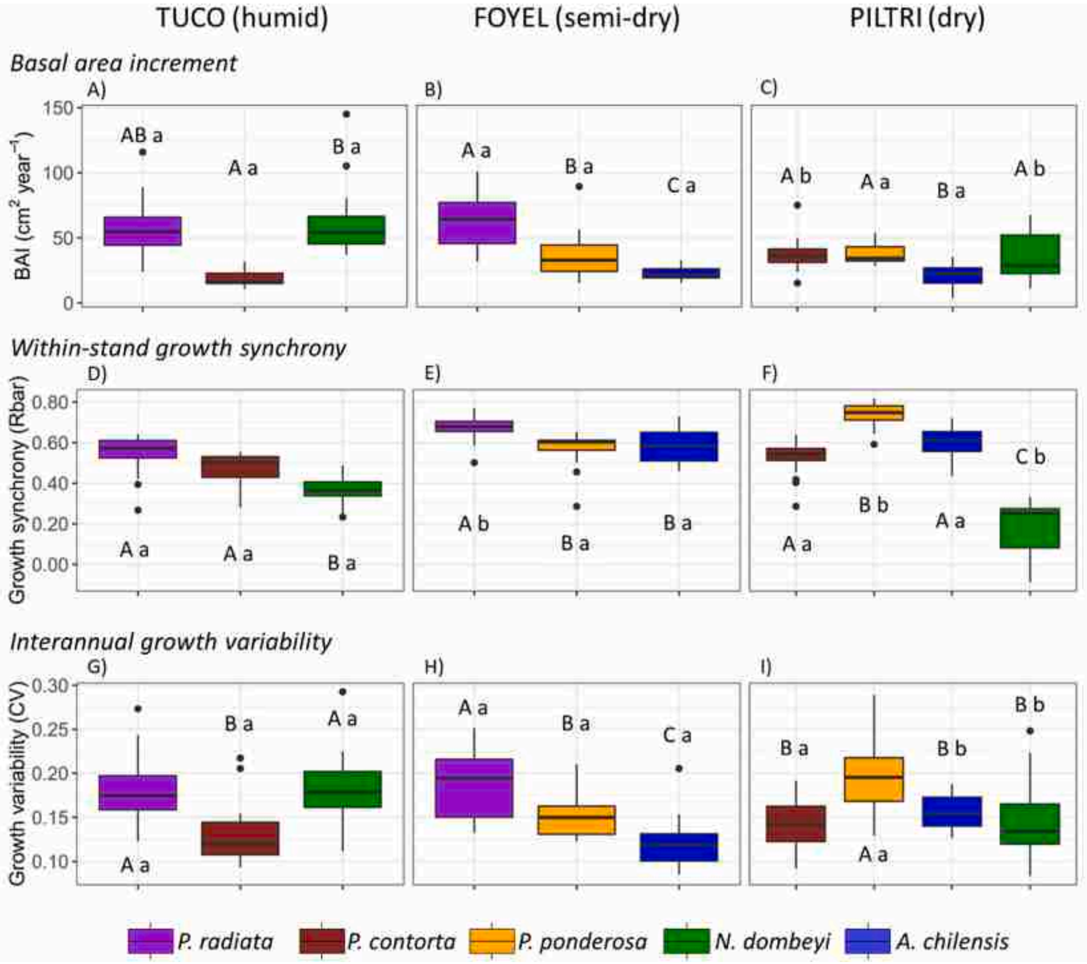

Fig. 2. Stand medians, 25- and 75-percentiles (box) and interquartile range (IQR) (whiskers) of basal area increment (BAI), growth synchrony and interannual growth variability during the first 32 years of growth of the five species at the three sites. Different uppercase letters indicate significant differences between different species at a given site, different lowercase letters indicate significant differences between the sites for a given species ($p < 0.05$).

the five species and three sites. The highest average BAI in the first 32 years of stand growth was registered in *P. radiata* at the semi-dry site (Foyel) (62.9 cm^2 $year^{-1}$; Fig. 2B). Similarly high rates were reached by *N. dombeyi* and *P. radiata* at the humid site (Tuco) (62.4 and 56.0 cm^2 $year^{-1}$, respectively; Fig. 2A), which were significantly higher at this site than that of *P. contorta.* In fact, this conifer reached at this site the lowest BAI recorded for the five species in any of the stands (18.6 cm^2 $year^{-1}$; Fig. 2A). Similarly low growth rates were recorded for *A. chilensis* in the two stands studied, with no significant difference between the sites (Fig. 2B–C). Significant site differences in BAI were only found for *P. contorta* and *N. dombeyi* with opposing trends from humid to dry (Fig. 2A–C).

Average within-stand growth synchrony (Rbar) was generally higher in the four conifer species (in most cases >0.5) than in *N. dombeyi* (0.18 and 0.35). It was highest in the *P. ponderosa* stand at the dry site (0.74; Fig. 2F), significantly differing from the less synchronized *P. ponderosa* population at the semi-dry site (Fig. 2E). High synchronies were also found for *P. radiata* at the humid and semi-dry sites (Fig. 2D and E) and for the two *A. chilensis* stands (Fig. 2E and F). Interannual growth variability (CV) was highest in the *P. ponderosa* stand at the dry site (0.20) and the *P. radiata* stands at the humid and semi-dry sites, but was high also in the *N. dombeyi* stand at the humid site (Fig. 2G – I). Lower CV

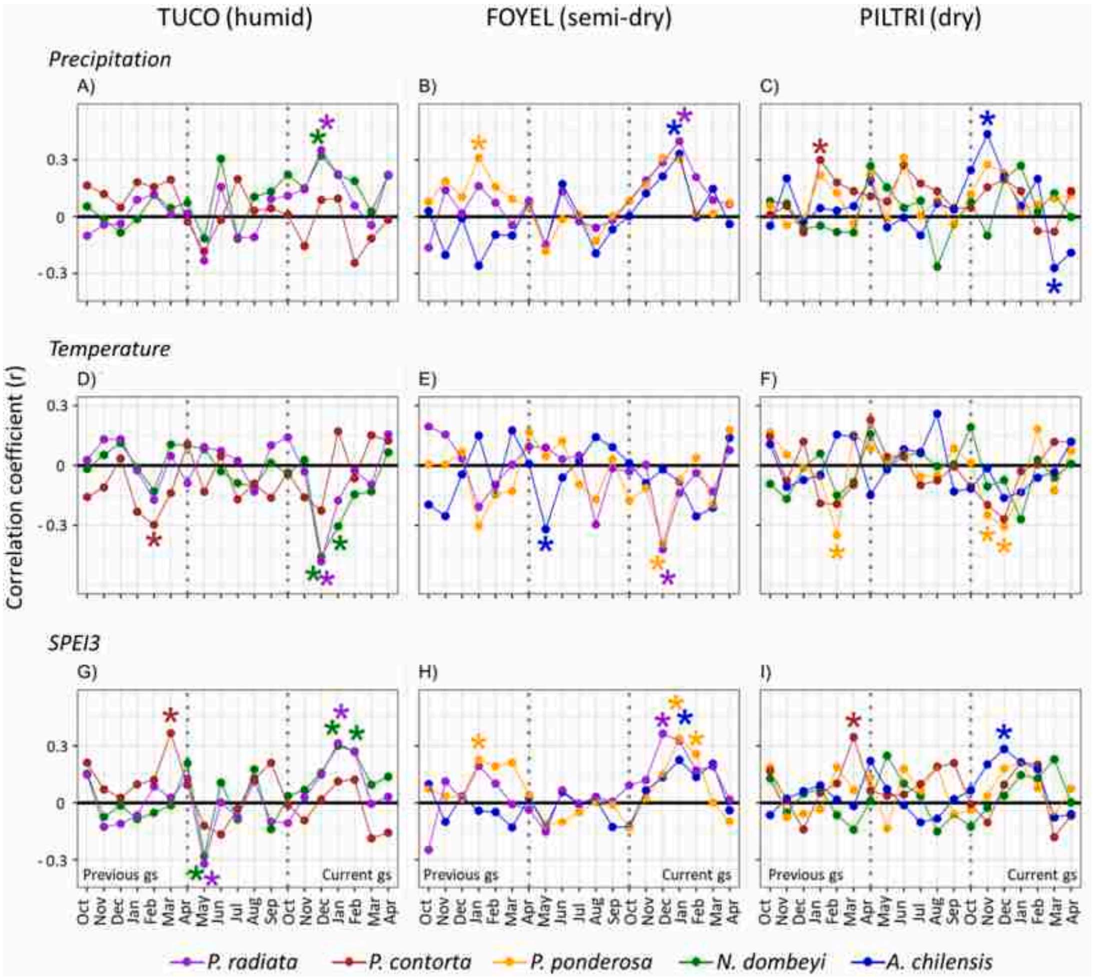

Fig. 3. Pearson correlation coefficients (r) for the relation between standardized ring width (RWI) in the first 32 years of growth and monthly totals or means of precipitation (A to C), temperature (D to F) or SPEI3 (G to I) in the previous growing season (gs, October – April), dormancy period (May – September) and current growing season (October – April) for the five species (different colors) across the three sites (Tuco, Foyel, Piltri). Asterisks indicate significant correlations ($p < 0.05$).

values were recorded for the two *P. contorta* and the two *A. chilensis* stands, and the *N. dombeyi* stand at the dry site. Both native species (*A. chilensis* and *N. dombeyi*) show opposing trends across sites, with *A. chilensis* increasing and *N. dombeyi* decreasing growth variability from the humid to the dry sites (Fig. 2G–I).

3.2. Climate sensitivity of growth and growth trends

All five species showed principally similar climate sensitivities of growth, with a positive growth response to higher precipitation and a higher climatic water balance (SPEI3) in current summer (December – February) and a negative response to elevated temperatures in summer, but only a minor influence of previous summer's weather (Fig. 3). The two most productive species, *N. dombeyi* and *P. radiata*, were particularly sensitive to reduced water availability and higher temperatures at the humid site, whereas *A. chilensis and P. ponderosa* were more sensitive at the drier sites. *N. dombeyi* and *P. radiata* were additionally affected by a dry autumn (May) (Fig. 3G). Interestingly, *A. chilensis* was also restricted by high precipitation in late summer (March) at the dry site, which was not found in the other species (Fig. 3C). *P. ponderosa* showed a marked growth limitation by elevated temperatures in current-summer (November and December) and also in previous summer (February), and this sensitivity was higher at the dry than at the semi-dry site (Fig. 3E and F). *P. contorta* revealed a lower climate sensitivity of growth to current summer weather than the other species, but was primarily affected by a warmer and drier previous summer (Fig. 3D and G).

The basal area increment (BAI) trends in the juvenile stand phase (first 32 years) follow in all five species humped-shaped or (less commonly) bimodal curves, with rapid early increase in growth rate to a first peak reached between 6 (*P. radiata* at Tuco; Fig. 4 A) and 27 years (*A. chilensis* in Foyel, Fig. 4B). At all sites, the exotic species reached their growth peak earlier than the two native species, with *P. radiata* culminating first. Peak BAI rates were as high as 73 – 85 $cm^2\ year^{-1}$ in the two *P. radiata* stands and 82 $cm^2\ year^{-1}$ in the *N. dombeyi* stand at the humid site, while the lowest peak growth rates were recorded in *A. chilensis* (in Piltri: 26.5 $cm^2\ year^{-1}$) and in *P. contorta* (in Tuco: 29.5 $cm^2\ year^{-1}$). The cumulated BAI over the first 32 years was highest in *P. radiata* in the semi-dry and in *N. dombeyi* in the humid sites (around 0.2 m^2) and lowest in *P. contorta* in the humid and in the two *A. chilensis* stands in the drier sites (around 0.06 and 0.07 m^2, respectively; see Table S2 in the Appendix).

According to the moving-window analysis, the growth correlation with precipitation, temperature and climatic water balance increased in most cases during the first decades of life to become significant when BAI peaked or shortly afterwards, and subsequently followed trends that varied among the species and sites (Fig. 4D – I). Marked decreases in precipitation sensitivity after peak growth were observed in *P. contorta* (even a shift from positive to negative influence), *P. ponderosa* (decrease only in most recent years) and *A. chilensis*, but not in *P. radiata* and *N. dombeyi* (Fig. 4D – F). In contrast, the growth sensitivity to elevated summer temperatures has remained in most cases at a similar level after

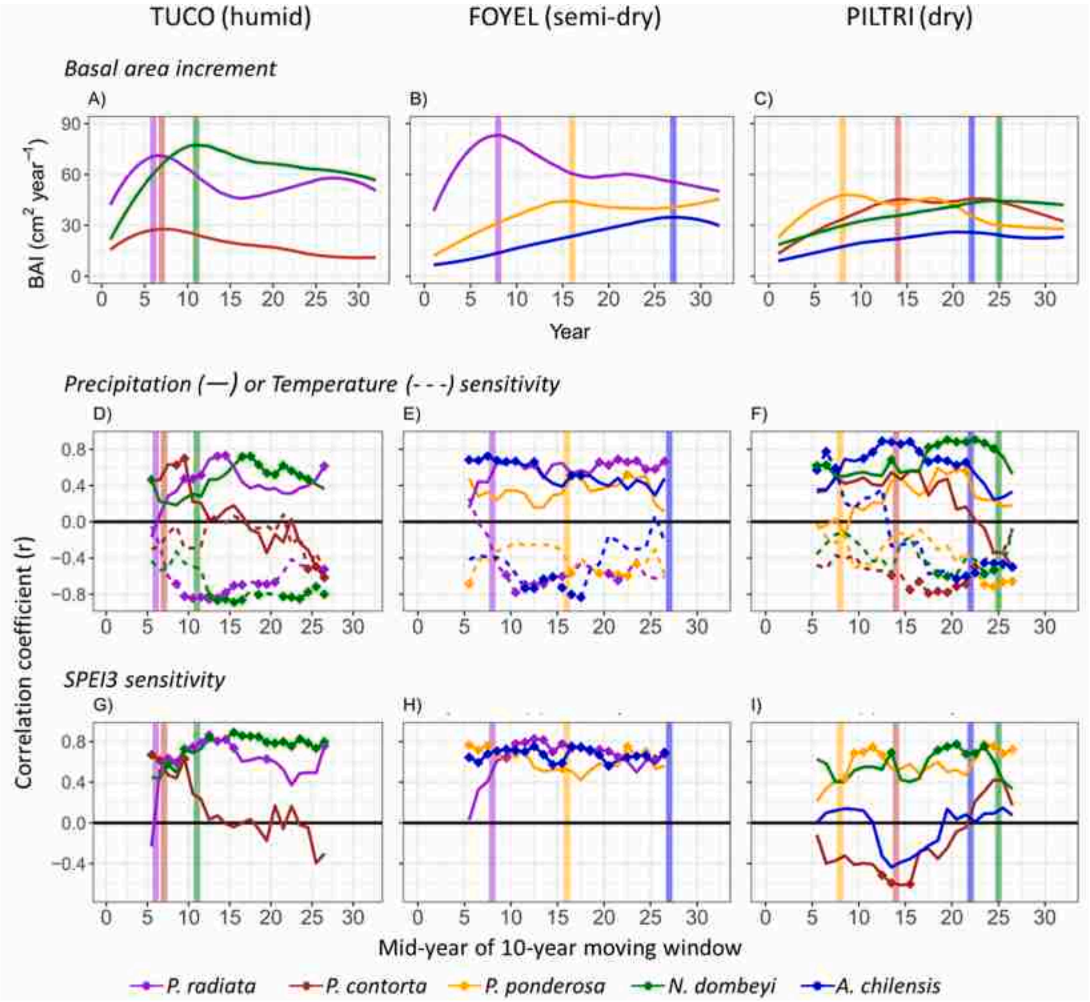

Fig. 4. (A to C) Trends in basal area increment (BAI) during the first 32 years of growth for the five species at the three sites (smoothed splines, 0.5 span, LOESS fit). Peak growth rates are marked with colored vertical lines. (D to F) Interannual variation in Pearson correlation coefficients (r) for the relation between RWI and mid-summer precipitation (P, solid lines; mean of December, January and February) or mid-summer temperature (T, dashed lines) in the first 32 years of growth for the five species (different colors) at the three sites (10-year moving windows). (G to I) Interannual variation in Pearson correlation coefficients (r) for the relation between RWI and mean SPEI3 of the mid-summer in the first 32 years of growth for the five species (different colors) at the three sites (10-year moving windows). Squares in the graphs D to I indicate significant 10-year period correlations.

peak growth (except for a decrease in *A. chilensis* at the semi-dry site) (Fig. 4D – F). Similarly, the BAI sensitivity to SPEI3 varied only little during the first 32 years of growth with the exception of *P. contorta* with a sensitivity shift from positive to negative at the humid site and an opposite shift from negative to positive at the dry site (Fig. 4G and I).

3.3. C and O isotope signatures

^{13}C fractionation (Δ^{13}C) values and δ^{18}O signatures in the stem wood varied considerably among the five species and three sites, when averaged over the 30 years of juvenile growth (Fig. 5). Except for *P. ponderosa*, carbon fractionation was in all species smaller (lower Δ^{13}C) at the drier sites, and fractionation generally decreased from *P. radiata* and *P. contorta* (medians from 16.7 ‰ to 18.3 ‰) to *N. dombeyi* and *P. ponderosa* (16.4–17.7), and finally to *A. chilensis* (15.8 – 15.9; Fig. 5A – C). δ^{18}O in the stem wood was generally higher in the three *Pinus* species (medians of 24.4 ‰ to 26.3 ‰) than in the native species *N. dombeyi* and *A. chilensis* (22.1 – 23.7) (Fig. 5G – I). A significant reduction in δ^{18}O from the humid to the drier sites was observed in *P. ponderosa, N. dombeyi* and *A. chilensis*, but not in *P. radiata* and *P. contorta*. Intrinsic water use efficiency varied less between the species and sites than the two isotope signatures. Differences were not significant except for *P. radiata* and *N. dombeyi* with a higher iWUE at the drier sites (Fig. 5D – F). However, there was a tendency for higher iWUE values at the drier sites (Piltri and Foyel) than at the humid site (Tuco) across the species.

During the 30 years of juvenile growth, Δ^{13}C varied only little in most species at the three sites. The expected long-term decrease in Δ^{13}C as caused by the gradual decrease in $\delta^{13}C_{atm}$ due to fossil fuel burning was visible in our 30-year wood records only in a minority of stands (one *P. contorta* and one *P. ponderosa* stand; Fig. 6A – C). iWUE tended to increase in the three exotic *Pinus* species (significant in *P. ponderosa* and *P. contorta* at each one site), while it remained stable in the two native species (Fig. 6D – F). The iWUE increase is more pronounced at the drier sites. δ^{18}O tended to increase in the 30-year period in all three *Pinus* species (marginally significant in five of the six stands), while it remained stable in *N. dombeyi* and *A. chilensis* (Fig. 6G – I). With growing tree age, the difference in δ^{18}O between the exotic and native species increased progressively (higher in the exotic species).

4. Discussion

To compare native and exotic tree species in their growth patterns and climate sensitivity of growth, we chose a dendrochronological design that compares all species uniformly in their first ~30 years of life.

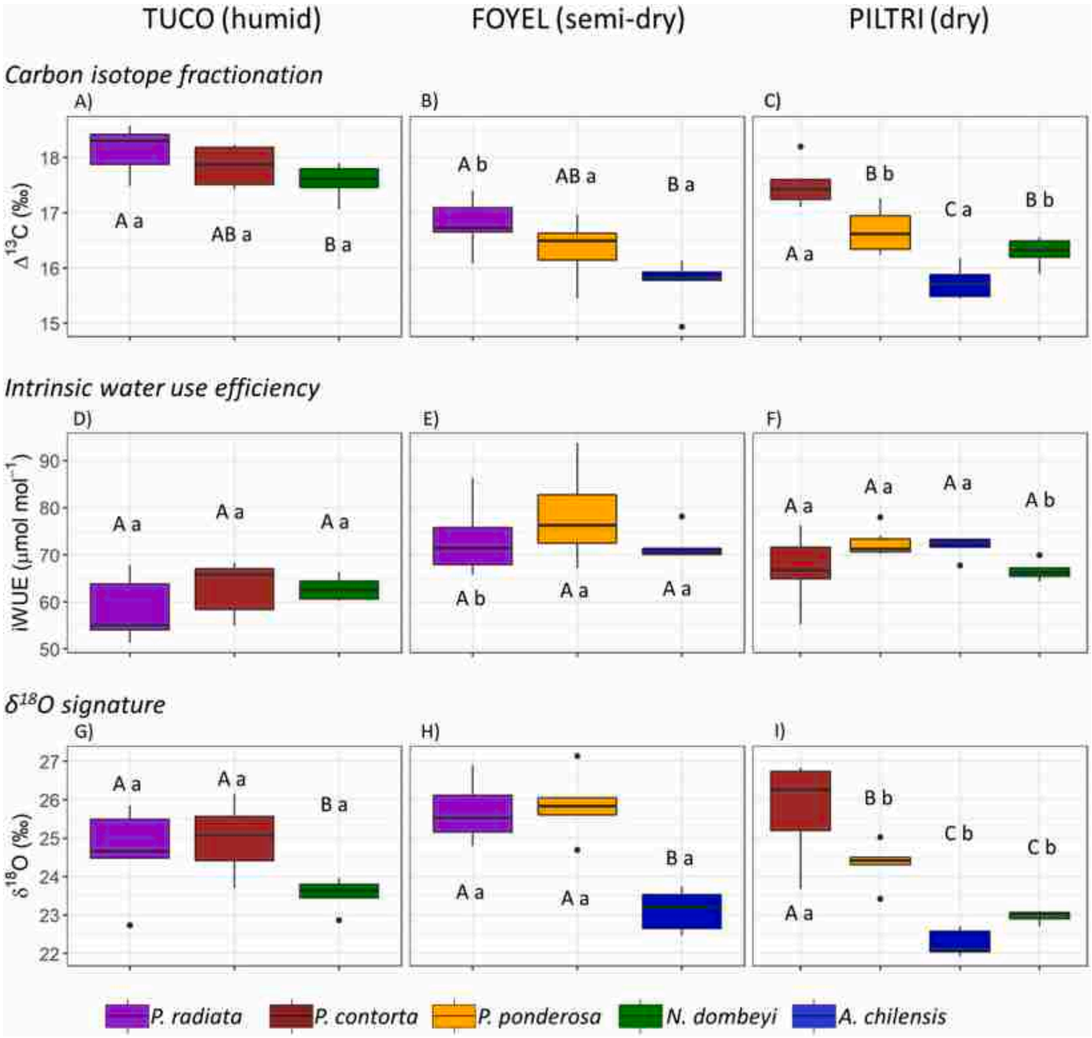

Fig. 5. Stand medians, 25- and 75-percentiles (box) and inter-quartile range (IQR) (whiskers) of carbon isotope fractionation values ($\Delta^{13}C$), intrinsic water use efficiency (iWUE) and $\delta^{18}O$ signatures in the wood mass during the first 30 years of growth (6 periods of each 5 annual rings) for the five species at the three sites. Different uppercase letters indicate significant differences between different species at a given site, different lowercase letters indicate significant differences between the sites for a given species ($p < 0.05$).

This setting differs from most earlier comparisons of native and exotic tree species, where usually stands at different ages were contrasted and ontogenetic effects on growth could thus not be excluded (Gyenge et al., 2008a, 2008b; Laclau, 2003; Licata et al., 2008). In contradiction to our hypotheses (1) and (2), we found that native tree species at juvenile age can be as productive as the fastest growing exotic conifers, and the climate sensitivity of growth of native and exotic tree species is broadly similar in this region.

4.1. Growth rates and vitality indicators

At the moistest site, *N. dombeyi* was as productive as *P. radiata*, the fastest-growing exotic conifer, with comparable growth potential (Navarro et al., 2024), and at the driest site, *N. dombeyi* had a similar mean BAI as *P. contorta* and *P. ponderosa*. The native conifer *A. chilensis*, in contrast, had one of the lowest mean stand-level BAI rates of all species at both sites, and it took longer to reach peak growth rate. However, after 25 years, the species achieved stable growth rates similar to *P. ponderosa*.

With respect to the predicted faster growth of the exotic conifers, our data support hypothesis (1), since the conifers reached peak growth rate already after 6 – 16 years, while the early growth of the two native species culminated somewhat later after 11 – 27 years. However, these results should be interpreted with caution. The *Pinus* species were planted as seedling, whereas all native stands have established from natural post-fire regeneration, i.e. from self-sown seeds (Veblen and Lorenz, 1987). This suggests that when the sampled trees had reached 1.3 m height (i.e. sampling height), competition with post-fire herbaceous and woody vegetation must have been fiercer in the native than in the planted *Pinus* stands, potentially influencing early stem growth and root system development (Dominguez-Lerena et al., 2006). To compare the early growth patterns of native and exotic species under comparable conditions, *Nothofagus* and *Austrocedrus* plantations as well as naturally established *Pinus* forests should be included (e.g., Franzese et al., 2022; Pafundi et al., 2016; Raffaele et al., 2016).

As expected, within-stand growth synchrony and interannual growth variability increased in all conifer species, both native and exotic, from the moister to the drier sites. This reflects the increasing harshness of the climate in terms of high maximum temperatures and high atmospheric saturation deficits, and growing water deficits from west to east in the Patagonian Andes, in linkage to the precipitation gradient. While increasing within-population growth synchrony and growth variability can be interpreted as a sign of climate vulnerability (Cailleret et al., 2019; Schurman et al., 2019; Shestakova et al., 2019), none of the four conifer species showed a significant decrease in average BAI from the moister to the drier sites. Two explanations are plausible. Either the

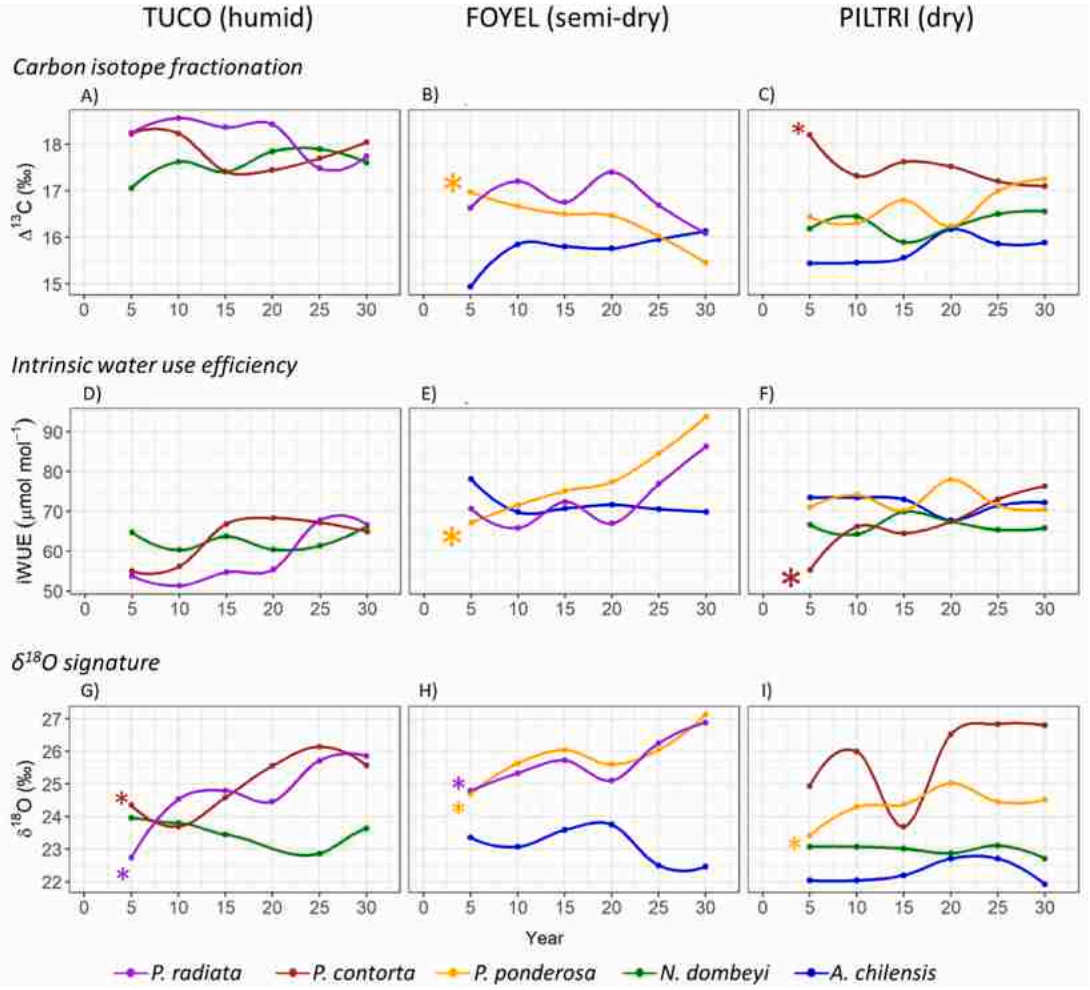

Fig. 6. Long-term change in carbon isotope fractionation ($\Delta^{13}C$), intrinsic water use efficiency (iWUE), and $\delta^{18}O$ signature in the wood mass during the first 30 years of growth (6 periods of each 5 annual rings) for the five species at the three sites (smoothed trends, 0.75-span LOESS fit). Dots indicate means of the pooled previous five annual rings (e.g. year 20 stands for the years 16–20). Large asterisks mark curves with significant trends ($p < 0.05$), small asterisks those with marginally significant trends ($p < 0.1$).

populations at the drier sites have acclimated to the generally higher aridity, or the climate at the drier sites is still within the range of favorable growing conditions for these species. In fact, the long-term average MAP is with 900 – 1700 mm at all three sites still far from the drought limit of the species, and the soil water storage capacity might with > 100 mm at all sites not be limiting growth. For the native conifer *A. chilensis*, a growth optimum in closed monospecific stands in the MAP range of 900 – 1600 mm $year^{-1}$ has been reported, while the species extends with more open stands to precipitation levels of 600 – 900 mm $year^{-1}$ in vicinity of the Patagonian steppe (Dezzotti and Sancholuz, 1991). Among the exotic conifers, *P. radiata* and *P. contorta* plantations have shown vital growth even at MAP levels of 600 mm $year^{-1}$ in Australia (Boardman, 1988) and Patagonia (Sarasola et al., 2006). The most drought tolerant species, *P. ponderosa*, may even grow in Patagonia at 500 mm $year^{-1}$ (Gonda, 1998). Thus, our study sites likely are far from the drought limits of the conifer species, and additional studies at drier sites are needed to explore the species' growth responses to drought and heat and their vulnerability to a future more arid climate (Barros et al., 2015).

The only angiosperm (*N. dombeyi*) differed markedly in that BAI decreased from the moistest to the driest site, and within-population growth synchrony and interannual growth variability were higher at the moister site. This may reflect a greater negative impact of climate on growth at this drier site compared to the conifers, as the reduction in mean annual precipitation from 1709 to 966 mm already appears to expose the species to mild stress. According to Diaz et al. (2020), *N. dombeyi* reaches its hygric distribution limit already at precipitation levels as high as found at the Piltri site. The lower growth synchrony in both *N. dombeyi* stands compared to the conifers could point at a lower sensitivity to climatic stressors, but the fairly high interannual growth variability at the moistest site suggests the opposite. Moreover, earlier research in *N. dombeyi* stands in the region revealed a growing climate vulnerability associated with increasing growth synchrony, interannual growth variability and recent BAI declines in more humid climates (Reiter et al., 2024; Suarez et al., 2004).

Across the five species, growth synchrony and interannual growth variability were higher in the more productive stands, suggesting that higher productivity is usually linked to a higher climate sensitivity of growth. In support, Reiter et al. (2024) found for Argentinian *Nothofagus* species and *A. chilensis* that faster growth at young age increased the probability for vitality decline and negative growth trends at higher age. One explanation could be that faster growing young trees usually develop larger crowns which may render them more susceptible to drought in drier years (Jump et al., 2017). It appears that, in the humid Argentinian Andes, the most productive species (*N. dombeyi* and *P. radiata*) are, according to their high growth synchrony and pronounced interannual growth variability, vulnerable to a warming and drying climate. Thus, management should focus on reducing competition for water by density regulation, particularly at post-disturbance sites with dense stands under higher temperatures (i.e. lower elevation sites). The findings of Fernández et al. (2012) support our statement, since sensitivity to drought decreased with reduced tree density in *P. ponderosa* plantations at more drier sites in the west.

4.2. Climatic drivers of growth

The climate response analysis suggests that the growth of all five species is principally controlled by similar climatic drivers (hypothesis 2), notably precipitation and climatic water balance (SPEI) (positive effect) and elevated temperatures (negative effect) in late spring and early summer of the current year, while the weather of the previous summer and of autumn and winter is less important. Our results align with the findings of previous studies in both native (Reiter et al., 2024; Suarez et al., 2015; Villalba and Veblen, 1997) and exotic tree species (Álvarez et al., 2013; McCullough et al., 2017; McLane et al., 2011). Contrary to expectation, *N. dombeyi* and *P. radiata* showed highest sensitivity to elevated late spring/early summer temperatures at the moistest site, suggesting that heat reduced growth at this site more than at the drier sites, where heat and drought exposure is higher. A possible explanation is better acclimation to heat at the warmer and drier sites in comparison to the faster-growing stands at the moister sites (Jump et al., 2017). This is also indicated by recent observations of elevated drought-induced mortality in *N. dombeyi* stands at moist sites (Suarez et al., 2024). Similarly, drought-induced mortality episodes have been recorded from *P. radiata* plantations across its entire world-wide cultivation area (Carnegie et al., 2022 and citations therein), which are frequently amplified by high stand densities.

The two species dominating the dry forest-steppe ecotone in Argentinian Patagonia, i.e. native *A. chilensis* and planted *P. ponderosa*, differ in their main climatic drivers of growth. *P. ponderosa* appeared as primarily limited by elevated temperatures in current spring/summer (November and December) (and also in previous season's February). In agreement, *P. ponderosa* has been found to develop a large tap root system, which may reduce drought exposure and allow for transpirative cooling (Curtis, 1964; Kolb and Robberecht, 1996). In contrast, *A. chilensis* growth was in our study limited by water scarcity and not high temperatures. This may partly result from the specific conditions under which the species establishes in our region on burnt areas and is growing in the subsequent juvenile period (Urretavizcaya et al., 2012). It usually exists in close contact to other post-fire shrubby vegetation, which hampers its growth through intense competition for light and soil resources, but protects the seedlings from direct insolation, wind, and elevated temperatures (Kitzberger et al., 2000). Intense competition for water with the shrubby post-fire vegetation might explain the stronger growth dependence on precipitation of *A. chilensis* already from the age of 10 years onwards, well before maximum stand density and maximum BAI are reached.

Pinus contorta was the species with the lowest climate sensitivity of growth in our study. Remarkably, all thermal and hygric influences on growth happened in the previous summer and thus carry-over effects likely played an important role in growth regulation. Since the most widely planted provenance in Argentina is *P. contorta* var. *murrayana* (Raffaele et al., 2015) with a natural montane to subalpine distribution, it is likely that this provenance is inherently slower growing (Gundale et al., 2024), and current-year stem growth is partly sustained by stored carbohydrates from previous years. Our results align with previous studies showing a fairly low sensitivity of *P. contorta* growth to climate, and a predominant influence of previous-season effects (Lo et al., 2010), which seems to be characteristic for the species across varied environmental conditions in its natural distribution range (McLane et al., 2011). Our moving-window analysis indicates that the summer temperature sensitivity of *P. contorta* growth has increased with growing age, whereas the dependence on higher summer precipitation has decreased in recent years, which could point on deeper rooting (Ellis et al., 2024), but also at a possible exposure to heat stress at higher age (Marks et al., 2024). In fact, planting a cold-adapted provenance from montane to subalpine origins at lower elevations (600 – 700 m a.s.l. in the study region) might lead to a mis-match of climate adaptation and environmental conditions (Gundale et al., 2024; Lo et al., 2010; Raffaele et al., 2015).

4.3. Stomatal regulation and transpiration losses as inferred from stable isotope analysis

The generally higher mean $\Delta^{13}C$ and $\delta^{18}O$ values in the wood of the exotic conifers, compared to *N. dombeyi* and especially *A. chilensis*, indicate higher stomatal conductance and transpiration rates, supporting hypothesis (3). These results align with previous findings in Patagonia indicating a higher stomatal conductance and longer maintenance of transpiration during drought in *P. ponderosa* than in *A. chilensis* (Gyenge et al., 2008b). The decrease in $\delta^{18}O$ values toward the drier sites in three species (*N. dombeyi, P. ponderosa* and *A. chilensis*) might reflect a higher VPD at these sites, which causes greater enrichment in ^{18}O in the leaves during enhanced transpiration, and this signal is largely maintained in the wood (Saurer et al., 1997). However, since leaf and wood $\delta^{18}O$ is largely dependent on the source water (for which historical data are missing), differences between species at the same site are better comparable than differences between sites.

Clearly, the higher $\delta^{18}O$ values found in the exotic compared to the native species could also indicate that the *Pinus* species are using water sources with higher $\delta^{18}O$ signatures (Song et al., 2022). Due to seasonal shifts in large-scale climatic regimes, the meteoric water stored in the soil before the growing season has a higher $\delta^{18}O$ value than the water that infiltrates during the early summer months (Roig et al., 2006). If in the early stages of the growing season, the *Pinus* species were using the soil water stored during the dormancy months faster than native species (as may be indicated by their higher transpiration rates and faster growth), this could be adding to the higher $\delta^{18}O$ values observed in these species. Further studies have to clarify whether the start of the growing season differs between exotic and native species and thus different components of the soil water reserves are depleted by different species.

In most cases, higher mean $\Delta^{13}C$ values in the wood mass were related to higher mean BAI rates, indicating less stomatal constraints on CO_2 assimilation. A notable exception is *P. contorta* with a fairly low growth rate but high mean $\Delta^{13}C$ and $\delta^{18}O$ values. From the growth response data of this species that suggest enhanced use of stored carbohydrates in radial growth, the relatively high $\Delta^{13}C$ values are difficult to explain, as stored carbohydrate compounds are generally enriched in ^{13}C compared to fresh assimilates (Jäggi et al., 2002), which should lead to lower $\Delta^{13}C$ values. One explanation could be local site factors or species-specific fractionation effects. A possible role might also be played by the mismatch which presumably is experienced by the *P. contorta* proveniences from montane to subalpine origin planted in Patagonia at lower, warmer elevations. Heat and drought stress, insufficient diurnal and seasonal temperature variation or improper dormancy might shift carbohydrate allocation more to stress resistance, root growth, damage repair and defense, thereby reducing the carbon invested in radial growth per unit of carbon fixed in photosynthesis (McDowell et al., 2008; Salmon et al., 2019; Scholz et al., 2014).

The fact that the exotic conifers had similar intrinsic water use efficiencies (iWUE), but in most cases higher $\Delta^{13}C$ and $\delta^{18}O$ values than the native species, suggests that the higher stomatal conductance in the *Pinus* species increased not only CO_2 uptake but also transpiration. Higher transpiration rates support the ideas that the *Pinus* species might be capable of exploiting soil moisture reserves more completely or have access to additional water sources as compared to the native species, as was previously observed for some conifer plantations in the region (Gyenge et al., 2008a; Licata et al., 2011). Even though the three *Pinus* species have increased iWUE in most stands during the 30 years of juvenile growth, likely as a consequence of rising atmospheric CO_2, their transpiration has increased in the same period, probably driven by climate warming and the VPD increase, which must enhance their drought exposure (Sreeman et al., 2010).

5. Conclusion

Our comparative study in northern Patagonia found that the exotic conifers were not principally more productive and not less sensitive in their juvenile growth to climate than the native species. This challenges the assumption that exotic conifers grow faster and are less affected by a warmer and drier climate. In general, the more productive species, when growing under optimal conditions, revealed the highest growth sensitivity to climate. Furthermore, the stable isotope analysis indicates that the exotic conifers are more exposed to drought stress due to higher stomatal conductance and transpiration rates than the native species, and their transpirative water loss likely has risen during the past three decades, further increasing their stress exposure.

Based on these findings and the known negative impacts of *Pinus* species on fire regimes and local biodiversity, it is advised to adopt risk-avoiding silvicultural strategies, which favor native broad-leaved tree species such as *N. dombeyi* and its more heat-adapted relatives *N. alpina* (Poepp. & Endl.) Oerst. and *N. obliqua* (Mirb.) Oerst., as well as native conifers like *A. chilensis*, at all sites where these species thrive. The latter conifer species has the advantage over the pines that it is fairly shade-tolerant and can thus regenerate in the understory of existing stands, allowing to avoid large clear-cuts and to practice continuous-cover forestry in a future warmer and drier climate. In addition, especially at drier sites and in dense stands with elevated deadwood amounts, stem densities should be reduced to lower competition for water, even though timber yield could decrease, and the excess of dead trees should be removed to control the fire risk. The task of establishing sustainable silvicultural systems in the temperate forest region of South America to enhance climate resilience requires more comparative studies on the growth performance and climate sensitivity of native and exotic tree species. This must include research across both humid and dry regions of the Andes, testing ecotypes and varieties with differing climate sensitivity, and should also assess species´performance under exceptional hot-drought events.

CRediT authorship contribution statement

Clara Pissolito: Writing – review & editing, Validation. **Christoph Leuschner:** Writing – original draft, Validation, Supervision, Investigation, Funding acquisition, Conceptualization. **Ernesto Juan Reiter:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maria Melisa Rago:** Writing – review & editing, Validation. **Alois Simon:** Writing – review & editing, Validation, Investigation. **Robert Weigel:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Walentowsky Helge:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition.

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.

Acknowledgments

We are thankful to all the land owners, administrators and workers that allowed us to sample in their forests and plantations. We express our respect for all the native communities that live in and for the forests. We thank Horacio Ivancich for assisting in the contact with the land owners. We further thank all partners of the KLIMNEM project in Argentina and Germany for the fruitful cooperation.

The project is supported by funds of the Federal Ministry of Food and Agriculture (BMEL) based on a decision of the Parliament of the Federal Republic of Germany via the Federal Office for Agriculture and Food (BLE, grant No. 28I-042–01).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122966.

Data Availability

Data will be made available on request.

References

Álvarez, J., Allen, H.L., Albaugh, T.J., Stape, J.L., Bullock, B.P., Song, C., 2013. Factors influencing the growth of radiata pine plantations in Chile. Forestry 86 (1), 13–26. https://doi.org/10.1093/forestry/cps072.

Amoroso, M.M., Daniels, L.D., Larson, B.C., 2012. Temporal patterns of radial growth in declining Austrocedrus chilensis forests in Northern Patagonia: The use of tree-rings as an indicator of forest decline. For. Ecol. Manag. 265, 62–70. https://doi.org/10.1016/j.foreco.2011.10.021.

Amoroso, M.M., Daniels, L.D., Villalba, R., Cherubini, P., 2015. Does drought incite tree decline and death in *Austrocedrus chilensis* forests? J. Veg. Sci. 26 (6), 1171–1183. https://doi.org/10.1111/jvs.12320.

Amoroso, M.M., Daniels, L.D., Baker, P.J., Camarero, J.J. (Eds.), 2017. Dendroecology: Tree-Ring Analyses Applied to Ecological Studies, 231. Springer International Publishing. https://doi.org/10.1007/978-3-319-61669-8.

APN. (2025). Sistema de Información de Biodiversidad (No. Administración de Parques Nacionales) [Dataset]. sib.gob.ar.

Baillie, M.G.L., Pilcher, J.R., 1973. A Simple Crossdating Program for Tree-Ring Research. TreeRing Bull. 33. ⟨https://repository.arizona.edu/handle/10150/260029⟩.

Baral, H., Guariguata, M.R., Keenan, R.J., 2016. A proposed framework for assessing ecosystem goods and services from planted forests. Ecosyst. Serv. 22, 260–268. https://doi.org/10.1016/j.ecoser.2016.10.002.

Barros, V.R., Boninsegna, J.A., Camilloni, I.A., Chidiak, M., Magrín, G.O., Rusticucci, M., 2015. Climate change in Argentina: trends, projections, impacts and adaptation. WIREs Clim. Change 6 (2), 151–169. https://doi.org/10.1002/wcc.316.

Bava, J., Loguercio, G., Salvador, G., 2015. ¿Por qué plantar en Patagonia? Estado actual y el rol futuro de los bosques plantados. Article 2. Ecol. ía Austral 25 (2). https://doi.org/10.25260/EA.16.25.2.0.155.

Beguería, S., & Vicente-Serrano, S.M. (2011). SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index (p. 1.8.1) [Dataset]. https://doi.org/10.32614/CRAN.package.SPEI.

Belmecheri, S., Lavergne, A., 2020. Compiled records of atmospheric CO2 concentrations and stable carbon isotopes to reconstruct climate and derive plant ecophysiological indices from tree rings. Dendrochronologia 63, 125748. https://doi.org/10.1016/j.dendro.2020.125748.

Belmecheri, S., Wright, W.E., Szejner, P., 2022. Sample Collection and Preparation for Annual and Intra-annual Tree-Ring Isotope Chronologies. In: Siegwolf, R.T.W., Brooks, J.R., Roden, J., Saurer, M. (Eds.), Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses. Springer International Publishing, pp. 103–134. https://doi.org/10.1007/978-3-030-92698-4_4.

Bernhardt, J.R., Kratina, P., Pereira, A.L., Tamminen, M., Thomas, M.K., Narwani, A., 2020. The evolution of competitive ability for essential resources. Philos. Trans. R. Soc. B Biol. Sci. 375 (1798), 20190247. https://doi.org/10.1098/rstb.2019.0247.

Bianchi, L.O., Oddi, F.J., Muñoz, M., Defossé, G.E., 2019. Comparison of leaf moisture content and ignition characteristics among native species and exotic conifers in northwestern Patagonia, Argentina. For. Sci. 65 (4), 375–386. https://doi.org/10.1093/forsci/fxy054.

Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. TreeRing Res. 64 (2), 81–96. https://doi.org/10.3959/2008-6.1.

Blanca, M., Alarcón, R., Arnau, J., Bono, R., Bendayan, R., 2017. Non-normal data: Is ANOVA still a valid option? Psicothema 4 (29), 552–557. https://doi.org/10.7334/psicothema2016.383.

Boardman, R., 1988. Living on the edge—The development of silviculture in South Australian pine plantations. Aust. For. 51 (3), 135–156. https://doi.org/10.1080/00049158.1988.10676038.

Bouza, P., & Bilmes, A. (2020). Landscapes and Geology of Patagonia: An Introduction to the Land of Reptiles (pp. 59–83). https://doi.org/10.1007/978-3-030-42752-8_4.

Braun, A.Ch, Troeger, D., Garcia, R., Aguayo, M., Barra, R., Vogt, J., 2017. Assessing the impact of plantation forestry on plant biodiversity. Glob. Ecol. Conserv. 10, 159–172. https://doi.org/10.1016/j.gecco.2017.03.006.

Bremer, L.L., Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodivers. Conserv. 19 (14), 3893–3915. https://doi.org/10.1007/s10531-010-9936-4.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17 (5), 925–951. https://doi.org/10.1007/s10531-008-9380-x.

Buduba, C.G., la Manna, L.A., Irisarri, J.A., 2020. El suelo y el bosque en la Región Andino Patagónica. In *Suelos y vulcanismo*. Asoc. óN. Argent. De. la Cienc. Del. Suelo. 〈https://ri.conicet.gov.ar/handle/11336/194319〉.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26 (2), 115–124. https://doi.org/10.1016/j.dendro.2008.01.002.

Cailleret, M., Dakos, V., Jansen, S., Robert, E.M.R., Aakala, T., Amoroso, M.M., Antos, J. A., Bigler, C., Bugmann, H., Caccianaga, M., Camarero, J.-J., Cherubini, P., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Martínez-Vilalta, J., 2019. Early-warning signals of individual tree mortality based on annual radial growth. Front. Plant Sci. 9, 1964. https://doi.org/10.3389/fpls.2018.01964.

Carnegie, A.J., Kathuria, A., Nagel, M., Mitchell, P.J., Stone, C., Sutton, M., 2022. Current and future risks of drought-induced mortality in Pinus radiata plantations in New South Wales, Australia. Aust. For. 85 (4), 161–177. https://doi.org/10.1080/00049158.2022.2145722.

Cernusak, L.A., Ubierna, N., 2022. Carbon Isotope Effects in Relation to CO2 Assimilation by Tree Canopies. In: Siegwolf, R.T.W., Brooks, J.R., Roden, J., Saurer, M. (Eds.), Stable Isotopes in Tree Rings, 8. Springer International Publishing, pp. 291–310. https://doi.org/10.1007/978-3-030-92698-4_9.

CIEFAP, 2017. Inventario de Plantaciones Forestales en secano - REGION PATAGONIA. Ministerio de Agroindustria, Argentina.

Cook, E., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. TreeRing Bull. 41, 45–53.

Craig, H., 1953. The geochemistry of the stable carbon isotopes. Geochim. Cosmochim. Acta. 3 (2), 53–92. https://doi.org/10.1016/0016-7037(53)90001-5.

Curtis, J.D. (with U. S. Department of Agriculture, N. A. L.). (1964). Roots of a ponderosa pine. Ogden, Utah: Intermountain Forest & Range Experiment Station, Forest Service, U.S. Dept. of Agriculture. 〈http://archive.org/details/rootsofponderosa09curt〉.

Dezzotti, A., Sancholuz, L., 1991. Los bosques de Austrocedrus chilensis en Argentina: Ubicación, estructura y crecimiento. Bosque 12 (2), 43–52. https://doi.org/10.4206/bosque.1991.v12n2-04.

Diaz, D.G., Mathiasen, P., Premoli, A.C., 2020. Subtle precipitation differences yield adaptive adjustments in the mesic *Nothofagus dombeyi*. For. Ecol. Manag. 461, 117931. https://doi.org/10.1016/j.foreco.2020.117931.

Dominguez-Lerena, S., Herrero Sierra, N., Carrasco Manzano, I., Ocaña Bueno, L., Peñuelas Rubira, J.L., Mexal, J.G., 2006. Container characteristics influence *Pinus pinea* seedling development in the nursery and field. For. Ecol. Manag. 221 (1), 63–71. https://doi.org/10.1016/j.foreco.2005.08.031.

Du, H., Li, M.-H., Rixen, C., Zong, S., Stambaugh, M., Huang, L., He, H.S., Wu, Z., 2021. Sensitivity of recruitment and growth of alpine treeline birch to elevated temperature. Agric. For. Meteorol. 304–305, 108403. https://doi.org/10.1016/j.agrformet.2021.108403.

Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwiss. Centralbl. 88 (1), 230–250. https://doi.org/10.1007/BF02741777.

Ellis, E.C., Guy, R.D., Wei, X.A., 2024. Seasonal shifts in depth-to-water uptake by young thinned and overstocked lodgepole pine (*Pinus contorta*) forests under drought conditions in the Okanagan Valley, British Columbia, Canada. Hydrol. Earth Syst. Sci. 28 (20), 4667–4684. https://doi.org/10.5194/hess-28-4667-2024.

FAO, 2024. The State of the World's Forests 2024. FAO. https://doi.org/10.4060/cd1211en.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon Isotope Discrimination and Photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40 (1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443.

Fernández, M., Gyenge, J., de Urquiza, M., Varela, S., 2012. Adaptability to climate change in forestry species: drought effects on growth and wood anatomy of ponderosa pines growing at different competition levels. For. Syst. 21, 162–173. https://doi.org/10.5424/fs/2112211-12586.

Fernández, M.E., Gyenge, J.E., Varela, S., de Urquiza, M., 2014. Effects of the time of drought occurrence within the growing season on growth and survival of Pinus ponderosa seedlings. Trees 28 (3), 745–756. https://doi.org/10.1007/s00468-014-0986-1.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Fitzgerald, S., 2005. Fire ecology of ponderosa pine and the rebuilding of fire-resilient ponderosa pine ecosystems. In: USDA Forest Service Gen. Tech. Rep., PSW-GTR-198. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research, Station.

Franzese, J., Raffaele, E., 2017. Fire as a driver of pine invasions in the Southern Hemisphere: A review. Biol. Invasions 19 (8), 2237–2246. https://doi.org/10.1007/s10530-017-1435-z.

Franzese, J., Raffaele, E., Chiuffo, M.C., Blackhall, M., 2022. The legacy of pine introduction threatens the fuel traits of Patagonian native forests. Biol. Conserv. 267, 109472. https://doi.org/10.1016/j.biocon.2022.109472.

Fritts, H.C., 1966. Growth-rings of trees: their correlation with climate. Science 154 (3752), 973–979. https://doi.org/10.1126/science.154.3752.973.

García, R.A., Fuentes-Lillo, E., Cavieres, L., Cóbar-Carranza, A.J., Davis, K.T., Naour, M., Núñez, M.A., Maxwell, B.D., Lembrechts, J.J., Pauchard, A., 2023. Pinus contorta alters microenvironmental conditions and reduces plant diversity in patagonian ecosystems. Diversity 15 (3), 320. https://doi.org/10.3390/d15030320.

Garreaud, R.D., Aceituno, P., 2007. Atmospheric circulation and climatic variability. Phys. Geogr. South Am. 45, 59.

Gonda, H.E., 1998. Height-diameter and volume equations, growth intercept and needle length site quality indicators, and yield equations for young ponderosa pine plantations in Neuquén, Patagonia, Argentina. Oregon State University.

Gonfiantini, R., 1978. Standards for stable isotope measurements in natural compounds. Nature 271 (5645), 534–536. https://doi.org/10.1038/271534a0.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. TreeRing Res. 57 (2), 205–221.

Gundale, M.J., Lindberg, L., Fajardo, A., Nuñez, M.A., Nilsson, M.-C., Kardol, P., Moyano, J., Nuske, S.J., 2024. Functional traits differ across an invasive tree species' native, introduced, and invasive populations. Biol. Invasions 26 (7), 2295–2311. https://doi.org/10.1007/s10530-024-03316-3.

Gyenge, J., Fernández, M.E., Sarasola, M., Schlichter, T., 2008a. Testing a hypothesis of the relationship between productivity and water use efficiency in Patagonian forests with native and exotic species. For. Ecol. Manag. 255 (8), 3281–3287. https://doi.org/10.1016/j.foreco.2008.01.078.

Gyenge, J., Fernández, M.E., Schlichter, T.M., 2008b. Are differences in productivity between native and exotic trees in N.W. Patagonia related to differences in hydraulic conductance? Trees 22 (4), 483–490. https://doi.org/10.1007/s00468-008-0208-9.

Gyenge, J., Fernández, M., Rusch, V., Sarasola, M., Schlichter, T., 2010. Towards a sustainable forestry development in Patagonia: truths and myths of environmental impacts of plantations with fast growing conifers. Am. J. Plant Sci. Biotechnol. 3, 9–22.

Gyenge, J., Fernández, M.E., Varela, S., 2012. Short- and long-term responses to seasonal drought in ponderosa pines growing at different plantation densities in Patagonia, South America. Trees 26 (6), 1905–1917. https://doi.org/10.1007/s00468-012-0759-7.

Horák, J., Brestovanská, T., Mladenović, S., Kout, J., Bogusch, P., Halda, J.P., Zasadil, P., 2019. Green desert?: biodiversity patterns in forest plantations. For. Ecol. Manag. 433, 343–348. https://doi.org/10.1016/j.foreco.2018.11.019.

Jacques-Coper, M., Garreaud, R.D., 2015. Characterization of the 1970s climate shift in South America. Int. J. Climatol. 35 (8), 2164–2179. https://doi.org/10.1002/joc.4120.

Jäggi, M., Saurer, M., Fuhrer, J., Siegwolf, R., 2002. The relationship between the stable carbon isotope composition of needle bulk material, starch, and tree rings in Picea abies. Oecologia 131 (3), 325–332. https://doi.org/10.1007/s00442-002-0881-0.

Joelson, N.Z., Schneider, E., Heinrichs, S., Zerbe, S., Leuschner, C., Reiter, E.J., Fierke, J., Walentowski, H., 2025. A 50-year perspective on conservation challenges and legacy effects in temperate Patagonian forests. Biol. Conserv. 306, 111124. https://doi.org/10.1016/j.biocon.2025.111124.

Jump, A., Ruiz-Benito, P., Greenwood, S., Allen, C., Kitzberger, T., Fensham, R., Martinez Vilalta, J., Lloret, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Glob. Change Biol. 23, 3742–3757. https://doi.org/10.1111/gcb.13636.

Karger, D.N., & Zimmermann, N.E. (2018). CHELSAcruts—High resolution temperature and precipitation timeseries for the 20th century and beyond (Version 1.0, p. 3298534883328 bytes, NaN) [No Info,application/pdf]. EnviDat. https://doi.org/10.16904/ENVIDAT.159.

Kitzberger, T., 2012. Ecotones as complex arenas of disturbance, climate, and human impacts: The trans-Andean forest-steppe ecotone of northern Patagonia. In: Myster, R.W. (Ed.), Ecotones between forest and grassland. Springer, pp. 59–88.

Kitzberger, T., Steinaker, D.F., Veblen, T.T., 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology 81 (7), 1914–1924. https://doi.org/10.1890/0012-9658(2000)081[1914:EOCVOF]2.0.CO;2.

Kitzberger, T., Tiribelli, F., Barberá, I., Gowda, J.H., Morales, J.M., Zalazar, L., Paritsis, J., 2022. Projections of fire probability and ecosystem vulnerability under 21st century climate across a trans-Andean productivity gradient in Patagonia. Sci. Total Environ. 839, 156303. https://doi.org/10.1016/j.scitotenv.2022.156303.

Kolb, P.F., Robberecht, R., 1996. High temperature and drought stress effects on survival of Pinus ponderosa seedlings. Tree Physiol. 16 (8), 665–672. https://doi.org/10.1093/treephys/16.8.665.

Laclau, P., 2003. Biomass and carbon sequestration of ponderosa pine plantations and native cypress forests in northwest Patagonia. For. Ecol. Manag. 180 (1), 317–333. https://doi.org/10.1016/S0378-1127(02)00580-7.

Lavergne, A., Hemming, D., Prentice, I.C., Guerrieri, R., Oliver, R.J., Graven, H., 2022. Global decadal variability of plant carbon isotope discrimination and its link to gross primary production. Glob. Change Biol. 28 (2), 524–541. https://doi.org/10.1111/gcb.15924.

Licata, J., Pypker, T., Weigandt, M., Unsworth, M., Gyenge, J., Fernández, M., Schlichter, T., Bond, B., 2011. Decreased rainfall interception balances increased transpiration in exotic ponderosa pine plantations compared with native cypress stands in Patagonia, Argentina. Ecohydrology 4, 83–93. https://doi.org/10.1002/eco.125.

Licata, J.A., Gyenge, J.E., Fernández, M.E., Schlichter, T.M., Bond, B.J., 2008. Increased water use by ponderosa pine plantations in northwestern Patagonia, Argentina compared with native forest vegetation. For. Ecol. Manag. 255 (3), 753–764. https://doi.org/10.1016/j.foreco.2007.09.061.

Lindenmayer, D., Messier, C., Paquette, A., Hobbs, R.J., 2015. Managing tree plantations as novel socioecological systems: Australian and North American perspectives. Can. J. For. Res. 45 (10), 1427–1433. https://doi.org/10.1139/cjfr-2015-0072.

Lo, Y.-H., Blanco, J.A., Seely, B., Welham, C., Kimmins, J.P. (Hamish), 2010. Relationships between climate and tree radial growth in interior British Columbia, Canada. For. Ecol. Manag. 259 (5), 932–942. https://doi.org/10.1016/j.foreco.2009.11.033.

Mandle, L., Bufford, J.L., Schmidt, I.B., Daehler, C.C., 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biol. Invasions 13 (8), 1815–1827. https://doi.org/10.1007/s10530-011-0001-3.

Marks, S., Surfleet, C., Malama, B., 2024. Estimating and modeling pinus contorta transpiration in a montane meadow using sap-flow measurements. Forests 15 (10), 1786. https://doi.org/10.3390/f15101786.

Mathias, J.M., Hudiburg, T.W., 2022. isocalcR: An R package to streamline and standardize stable isotope calculations in ecological research. Glob. Change Biol. 28 (24), 7428–7436. https://doi.org/10.1111/gcb.16407.

McCullough, I.M., Davis, F.W., Williams, A.P., 2017. A range of possibilities: assessing geographic variation in climate sensitivity of ponderosa pine using tree rings. For. Ecol. Manag. 402, 223–233. https://doi.org/10.1016/j.foreco.2017.07.025.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178 (4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.

McLane, S.C., Daniels, L.D., Aitken, S.N., 2011. Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. For. Ecol. Manag. 262 (2), 115–123. https://doi.org/10.1016/j.foreco.2011.03.007.

Navarro, C., Donoso, P.J., Soto, D.P., Vásquez-Grandón, A., Esse, C., 2024. Silvicultural systems and estimated profitability of Nothofagus dombeyi plantations: An option for forestry diversification in Chile. New For. 56 (1), 4. https://doi.org/10.1007/s11056-024-10073-7.

Oliver, C., Larson, B., 1996. Forest Stand Dynamics. Wiley.

Pafundi, L., Urretavizcaya, M.F., Defosse, G.E., 2016. Micro-environmental changes induced by shape and size of forest openings: Effects on Austrocedrus chilensis and Nothofagus dombeyi seedlings performance in a Pinus contorta plantation of Patagonia, Argentina. For. Syst. 25 (3), e0.75. https://doi.org/10.5424/fs/2016253-08971.

Paritsis, J., Aizen, M.A., 2008. Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. For. Ecol. Manag. 255 (5), 1575–1583. https://doi.org/10.1016/j.foreco.2007.11.015.

Paritsis, J., Landesmann, J.B., Kitzberger, T., Tiribelli, F., Sasal, Y., Quintero, C., Dimarco, R.D., Barrios-García, M.N., Iglesias, A.L., Diez, J.P., Sarasola, M., Nuñez, M. A., 2018. Pine plantations and invasion alter fuel structure and potential fire behavior in a patagonian forest-steppe ecotone. Forests 9 (3), 117. https://doi.org/10.3390/f9030117.

Paruelo, J., Beltrán, A.B., Jobbágy, E., Sala, O.E., Golluscio, R., 1998. The climate of Patagonia: general patterns and controls on biotic processes. Ecol. Austral 8, 85–101.

Pauchard, A., García, R., Zalba, S., Sarasola, M., Zenni, R., Ziller, S., Nuñez, M.A., 2016. 14. Pine Invasions in South America: Reducing Their Ecological Impacts Through Active Management. In: Canning-Clode, J. (Ed.), Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions. De Gruyter Open, Warsaw/Berlin, pp. 318–342. https://doi.org/10.1515/9783110438666-020.

Payn, T., Carnus, J.-M., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., Orazio, C., Rodriguez, L., Silva, L.N., Wingfield, M.J., 2015. Changes in planted forests and future global implications. For. Ecol. Manag. 352, 57–67. https://doi.org/10.1016/j.foreco.2015.06.021.

Perdomo-González, A., Pérez-Reverón, R., Goberna, M., León-Barrios, M., Fernández-López, M., Villadas, P.J., Reyes-Betancort, J.A., Díaz-Peña, F.J., 2023. How harmful are exotic plantations for soils and its microbiome? A case study in an arid island. Sci. Total Environ. 879, 163030. https://doi.org/10.1016/j.scitotenv.2023.163030.

R Core Team. (2021). R: A language and environment for statistical computing [Computer software]. R Foundation for Statistical Computing. 〈https://www.R-project.org/〉.

Raffaele, E., Núñez, M., Relva, M., 2015. Plantaciones de coníferas exóticas en Patagonia: Los riesgos de plantar sin un manejo adecuado. Article 2 Ecol. ía Austral 25 (2). https://doi.org/10.25260/EA.16.25.2.0.153.

Raffaele, E., Nuñez, M., Eneström, J., Blackhall, M., 2016. Fire as mediator of pine invasion: evidence from Patagonia, Argentina. Biol. Invasions 18. https://doi.org/10.1007/s10530-015-1038-5.

Rago, M.M., Urretavizcaya, M.F., Defossé, G.E., 2021. Relationships among forest structure, solar radiation, and plant community in ponderosa pine plantations in the Patagonian steppe. For. Ecol. Manag. 502, 119749. https://doi.org/10.1016/j.foreco.2021.119749.

Reiter, E.J., Weigel, R., Walentowski, H., Loguercio, G.A., Fierke, J., Winter, A.F.N., Simon, A., Kotowska, M.M., Joelson, N.Z., Caselli, M., Leuschner, C., 2024. Climate vulnerability of Nothofagus pumilio, Nothofagus dombeyi and Austrocedrus chilensis in northern Patagonia's temperate forests. For. Ecol. Manag. 572, 122261. https://doi.org/10.1016/j.foreco.2024.122261.

Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species – a global review. Divers. Distrib. 17 (5), 788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x.

Roig, F.A., Siegwolf, R., Boninsegna, J.A., 2006. Stable oxygen isotopes (δ18O) in Austrocedrus chilensis tree rings reflect climate variability in northwestern Patagonia, Argentina. Int. J. Biometeorol. 51 (2), 97–105. https://doi.org/10.1007/s00484-006-0049-4.

Salmon, Y., Dietrich, L., Sevanto, S., Hölttä, T., Dannoura, M., Epron, D., 2019. Drought impacts on tree phloem: From cell-level responses to ecological significance. Tree Physiol. 39 (2), 173–191. https://doi.org/10.1093/treephys/tpy153.

Sarasola, M.M., Rusch, Verónica, E., Schlichter, T.M., Ghersa, C.M., 2006. Invasión de coníferas forestales en áreas de estepa y bosques de ciprés de la cordillera en la Región Andino Patagónica. Ecol. ía Austral 16 (2). Article 2.

Saurer, M., Aellen, K., Siegwolf, R., 1997. Correlating δ13C and δ18O in cellulose of trees. Plant Cell Environ. 20 (12), 1543–1550. https://doi.org/10.1046/j.1365-3040.1997.d01-53.x.

Scholz, F.G., Bucci, S.J., Goldstein, G., 2014. Strong hydraulic segmentation and leaf senescence due to dehydration may trigger die-back in Nothofagus dombeyi under severe droughts: A comparison with the co-occurring Austrocedrus chilensis. Trees 28 (5), 1475–1487. https://doi.org/10.1007/s00468-014-1050-x.

Schurman, J.S., Babst, F., Björklund, J., Rydval, M., Bače, R., Čada, V., Janda, P., Mikolas, M., Saulnier, M., Trotsiuk, V., Svoboda, M., 2019. The climatic drivers of primary Picea forest growth along the Carpathian arc are changing under rising temperatures. Glob. Change Biol. 25 (9), 3136–3150. https://doi.org/10.1111/gcb.14721.

Scott, D.F., 2005. On the hydrology of industrial timber plantations. Hydrol. Process. 19 (20), 4203–4206. https://doi.org/10.1002/hyp.6104.

Shestakova, T.A., Gutiérrez, E., Valeriano, C., Lapshina, E., Voltas, J., 2019. Recent loss of sensitivity to summer temperature constrains tree growth synchrony among boreal Eurasian forests. Agric. For. Meteorol. 268, 318–330. https://doi.org/10.1016/j.agrformet.2019.01.039.

Siegwolf, R.T.W., Brooks, J.R., Roden, J., Saurer, M. (Eds.), 2022. Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses. Springer International Publishing. https://doi.org/10.1007/978-3-030-92698-4.

Simberloff, D., Nuñez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., Van Wilgen, B.W., Zalba, S.M., Zenni, R.D., Bustamante, R., Peña, E., Ziller, S.R., 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. Austral Ecol. 35 (5), 489–504. https://doi.org/10.1111/j.1442-9993.2009.02058.x.

Simon, A., Fierke, J., Reiter, E., Loguercio, G., Heinrichs, S., Putzenlechner, B., Joelson, N., Walentowski, H., 2024. The interior climate and its microclimatic variation of temperate forests in Northern Patagonia, Argentina. Int. J. Biometeorol. 68. https://doi.org/10.1007/s00484-024-02617-5.

Simon, A., Almeida, P., Geitner, C., Rago, M., Urretavizcaya, M., Walentowski, H., Zerbe, S., 2025a. Soil redistribution and seed availability after fire events in mixed Austrocedrus chilensis forests in Northern Patagonia (Argentina). Fire Ecol. 21. https://doi.org/10.1186/s42408-025-00354-7.

Simon, A., Reiter, E.J., Zehetner, F., Urretavizcaya, M.F., Alonsio, V., Loguercio, G., Ottner, F., & Walentowski, H. (2025b). Unravelling the pedogenetic development of forest soils in Northern Patagonia, Argentina [Manuscript submitted for publication].

SMN. (2024). Bariloche Aeropuerto [Dataset]. Servicio Meteorologico Nacional. 〈https://www.smn.gob.ar/〉.

Song, X., Lorrey, A., Barbour, M.M., 2022. Environmental, Physiological and Biochemical Processes Determining the Oxygen Isotope Ratio of Tree-Ring Cellulose. In: Siegwolf, R.T.W., Brooks, J.R., Roden, J., Saurer, M. (Eds.), Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses. Springer International Publishing, pp. 311–329. https://doi.org/10.1007/978-3-030-92698-4_10.

Sreeman, S., H, B., Ramesh, R., Ganesh, P., Udayakumar, M., 2010. Relationship between 18O enrichment in leaf biomass and stomatal conductance. Isot. Environ. Health Stud. 46, 122–129. https://doi.org/10.1080/10256011003661334.

Srur, A.M., Amoroso, M.M., Mundo, I., Morales, M.S., Rodríguez-Catón, M., Aschero, V., Villalba, R., 2020. Forest dynamics in the Argentinean Patagonian Andes: lessons learned from dendroecology. In: Pompa-García, M., Camarero, J.J. (Eds.), Latin American Dendroecology. Springer International Publishing, pp. 171–201. https://doi.org/10.1007/978-3-030-36930-9_8.

Suarez, M., Sasal, Y., Facciano, L., 2024. Factors driving unexpected drought-induced Nothofagus dombeyi mortality in a valdivian temperate rainforest, Argentina. Forests 15, 1355. https://doi.org/10.3390/f15081355.

Suarez, M.L., Kitzberger, T., 2010. Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. J. Ecol. 98 (5), 1023–1034. https://doi.org/10.1111/j.1365-2745.2010.01698.x.

Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. J. Ecol. 92 (6), 954–966. https://doi.org/10.1111/j.1365-2745.2004.00941.x.

Suarez, M.L., Villalba, R., Mundo, I.A., Schroeder, N., 2015. Sensitivity of Nothofagus dombeyi tree growth to climate changes along a precipitation gradient in northern Patagonia, Argentina. Trees 29 (4), 1053–1067. https://doi.org/10.1007/s00468-015-1184-5.

Urretavizcaya, M.F., Defossé, G.E., Gonda, H.E., 2012. Effect of sowing season, plant cover, and climatic variability on seedling emergence and survival in burned austrocedrus chilensis forests. Restor. Ecol. 20 (1), 131–140. https://doi.org/10.1111/j.1526-100X.2010.00728.x.

Veblen, T.T., Lorenz, D.C., 1987. Post-fire stand development of Austrocedrus-Nothofagus forests in northern Patagonia. Vegetatio 71 (2), 113–126. https://doi.org/10.1007/BF00044825.

Villalba, R., Veblen, T.T., 1997. Spatial and temporal variation in Austrocedrus growth along the forest–steppe ecotone in northern Patagonia. Can. J. For. Res. 27 (4), 580–597. https://doi.org/10.1139/x96-209.

Voelker, S.L., 2011. Age-dependent changes in environmental influences on tree growth and their implications for forest responses to climate change. In: Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds.), Size- and Age-Related Changes in Tree Structure and Function. Springer Netherlands, pp. 455–479. https://doi.org/10.1007/978-94-007-1242-3_17.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23 (2), 201–213. https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.

Williams, K.J.H., 2014. Public acceptance of plantation forestry: implications for policy and practice in Australian rural landscape. Land Use Policy 38, 346–354. https://doi.org/10.1016/j.landusepol.2013.11.023.

Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38 (4), 431–436. https://doi.org/10.1111/ecog.01335.