Forest Ecology and Management 597 (2025) 123165

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Intraspecific variation in drought tolerance traits in a *Nothofagus* species (southern beech) in southern South America

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ARTICLE INFO

Keywords:
Functional traits
Temperate forests
Common garden
Latitudinal gradient
Assisted migration

ABSTRACT

Latitudinal gradients have commonly been used to evaluate intraspecific trait variation. However, studies assessing the mechanisms underlying this variability (i.e., genetic differentiation and/or phenotypic plasticity) are highly limited for tree species, especially for those from the Southern Hemisphere. The aim of this study was to evaluate intraspecific variability in functional traits related to drought tolerance and the underlying mechanisms in *Nothofagus obliqua* (Mirb.) Oerst. (southern beech), an ecologically and economically important tree species in Chile. We measured 11 functional traits and tree radial growth in six populations growing in a common garden and at their site of origin across a latitudinal gradient in the Andean and Coastal Cordilleras of south-central Chile. There were significant differences in most of the evaluated drought tolerance traits across the gradient, although few of them exhibited a clinal trend. From the studied populations, two located in the northern and southern limits of the Coastal Range were the most drought tolerant, probably due to restrictive site-specific conditions. Only two traits, wood vessel proportion and tree-radial growth, were genetically differentiated with the wettest population having the largest radial growth. Plasticity to local environmental conditions is likely to be the key mechanism for *Nothofagus obliqua* adaptation to climate change. Finally, a weak but significant trade-off between growth and safety was found across the gradient, with populations from wetter environments growing faster and being less drought-tolerant than populations from drier sites. This is the first study of this type carried out in adult trees of the temperate forests of South America. In a climate change adaptation context, our results demonstrated that assisted migration of provenances cannot be broadly recommended, as some northern populations perform poorly when planted in the south.

1. Introduction

Droughts are predicted to be more frequent and intense in some regions (IPCC, 2021); with sustained warming and water deficit leading to increases in atmospheric vapor pressure deficits (VPD) (Grossiord et al., 2020; McDowell et al., 2022), which are affecting the growth and physiology of trees around the world (Allen et al., 2010; Anderegg et al., 2012; Breshears et al., 2013; Grossiord et al., 2020; Hartmann et al., 2018). In fact, tree mortality has been observed in different regions (Allen et al., 2010, 2015), including temperate forests (Crouchet et al., 2019; Schuldt et al., 2020; Suarez et al., 2004). The Mediterranean-type and Temperate climate regions of southern South America have

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https://doi.org/10.1016/j.foreco.2025.123165
Received 15 July 2025; Received in revised form 29 August 2025; Accepted 9 September 2025
Available online 18 September 2025
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experienced moderate warming, but also a persistent precipitation decline during recent decades (Falvey and Garreaud, 2009; Lara et al., 2020; Morales et al., 2020; Villamayor et al., 2021). In fact, the longest-lasting megadrought recorded in south-central Chile, occurred recently between 2010 and 2022 (Barichivich et al., 2020; Garreaud et al., 2019; SEGRA, 2020).

There is an increasing need to understand how different tree populations respond to droughts to predict forests responses to climate change (Gazol et al., 2023). Traits have been useful to understand variations in plant functioning (Violle et al., 2007), as well as to predict the tolerance of species to droughts (Bussotti et al., 2015; Maherali et al., 2004). Foremost among these traits are those related to the water transport system, including xylem vulnerability to embolism (xylem water potential at which 50 % of hydraulic conductivity is lost: P_{50}), the hydraulic safety margin (Anderegg et al., 2016; Choat et al., 2012), and vessel size and density (Martínez-Vilalta et al., 2023), as well as leaf traits related to gas exchange and resource acquisition, such as leaf mass per area (LMA, Greenwood et al., 2017, Savi et al., 2017) and carbon (C) isotope composition ($\delta^{13}C$, (Rosas et al., 2019)).

The state of the art within the study of functional traits has revealed hydraulic trade-offs between efficiency and safety (Pritzkow et al., 2020). More drought tolerant species often grow slower than less tolerant species due to the carbon costs related to building a more tolerant architecture (Kerr et al., 2023). Thus, growth versus stress tolerance trade-offs are expected to characterize trait variation in trees (Adler et al., 2014; Reich, 2014).

Most studies have assessed functional trait differences between species (Anderegg, 2015), and only a few studies have delved into the underlying mechanisms of intraspecific trait variability, such as phenotypic plasticity and genetic differentiation (Benomar et al., 2016; Kerr et al., 2023; Pritzkow et al., 2020; Skelton et al., 2019). Yet, genetic differentiation and local adaptation can influence forest survival in the future and provide targets for artificial selection (David-Schwartz et al., 2016; Nicotra et al., 2010). Over shorter time scales, phenotypic plasticity could allow individuals to better respond and be resilient to changes *in situ* (Nicotra et al., 2010).

Common gardens (progeny-provenance trials) can help to examine traits´ genetic underpinning and degree of plasticity, and therefore, represent a useful tool to test hypotheses associated with climate adaptation (Mátyás, 1996). Results for different species reveal that traits can vary from having limited genetic differentiation and phenotypic plasticity (Lamy et al., 2014) to high phenotypic plasticity (Blackman et al., 2017; López et al., 2016; Pritzkow et al., 2020; Stojnic et al., 2017), or genetic variation (Hajek et al., 2016). Latitudinal gradients have also commonly been used to assess intraspecific trait variation, helping to understand the potential of species to adapt to water scarcity (Anderegg and Hillerislambers, 2016; García-Cervigón et al., 2020; López et al., 2021). Although trait variation across gradients can be highly trait and species-specific (Vilà-Cabrera et al., 2015, Rosas et al., 2019), functional traits most often vary in a predictable manner. Thus, trees from drier areas tend to follow a resource-conservative strategy, investing in traits that provide stress tolerance, such as smaller vessels (Schuldt et al., 2016), a less vulnerable xylem (Stojnic et al., 2017), deeper roots (Laughlin et al., 2023) and higher LMA (Warren et al., 2005), than trees from wetter environments.

Studies on intraspecific trait variability are highly limited for non-European species, especially across gradients (Gazol et al., 2023). Here, we examined intraspecific variation in traits of adult *Nothofagus obliqua* (Mirb.) Oerst. (southern beech), an ecologically and economically important tree species in Chile. The few studies developed in a common garden and reciprocal transplants in *Nothofagus* spp., were developed for seedlings of *N. obliqua* (Aparicio et al., 2015, Duboscq-Carra et al., 2018) and seedlings and saplings of other *Nothofagus* species (Premoli and Brewer, 2007, Premoli et al., 2007, Premoli and Mathiasen, 2011, Duboscq-Carra et al., 2020). *Nothofagus obliqua* dominates most of the native forests of Chile (Ramírez, 1987) and has a reduced presence in southern Argentina, spanning a latitudinal gradient from Mediterranean to Temperate climate in Chile (Donoso et al., 2006). Individuals of this species can be over 300 years old and secondary stands are commercially important, but also the ecological baseline for multi-species mature forests that provide essential ecosystem services (Lara et al., 2003). Similar to most native tree species in Chile, there is limited information concerning functional trait variation across its distribution (but see, Donoso, 1979; Donoso et al., 2004), especially on drought tolerance traits.

The main objective of this study was to evaluate intraspecific variability in functional traits related to drought tolerance in *N. obliqua,* as well as the degree of genetic differentiation and plasticity across the species gradient. To reach this objective, we measured *N. obliqua* traits from six populations growing in a two-decade old common garden located in southern Chile, as well as from the same populations growing along its geographic distribution. We hypothesized that there would be clinal variation in drought tolerance traits and radial growth in the field, with northern (drier) populations being more drought tolerant and slower growing compared to southern (wetter) populations.

2. Materials and methods

2.1. *Nothofagus obliqua* in Chile and study sites

Nothofagus obliqua is a deciduous species that grows along an environmental gradient from 35°S to 41° S in the Coastal Range, Central Depression and Andean Cordillera of Chile (Donoso et al., 2006). The climate in the northern part of the geographic distribution is a Mediterranean-type characterized by warm, dry and long summers. At the northern latitudes the species occurs at elevations ranging between 400 and 2000 m a.s.l. (Donoso et al., 2006, Vergara, 2011). To the south, *N. obliqua* grows from sea level to around 400 m a.s.l., where the climate is cooler and wetter, and the summers are shorter, although the Mediterranean-type influence is still present (Donoso et al., 2006, Vergara, 2011). Mean annual temperature (MAT) associated with sites where *N. obliqua* occurs varies across its geographic distribution, decreasing from 15 °C in more northern sites to 10 °C in more southern sites. Mean annual precipitation (MAP) associated with the sites varies with latitude and elevation, ranging from ~500 mm to 1500 mm. In the south, precipitation ranges from 1000 mm in the valleys to 3500 mm in the higher reaches of the Andes Mountains (Di Castri and Hajek, 1976; Donoso et al., 2006).

To evaluate variation in drought tolerance traits and the degree of genetic differentiation and plasticity across the species gradient, we selected six out of the 31 *N. obliqua* populations belonging to 14 provenance zones (Vergara, 2011), planted in a progeny-provenance trial in Fundo Arquilhue, Los Rios Region (40.24°S, 72.05°W, 266 m a.s.l., UACH and INFOR, 2001). The progeny-provenance trial Arquilhue was planted in 2000, and consisted of five random blocks, at a density of 4 × 2 m in a south-facing area with 8 % slope. The trial is located less than one km from a lake.

The six populations considered provenances from the northern and southern limits of *N. obliqua*'s distribution (Table 1, Fig. 1), avoiding selecting provenances of *Nothofagus macrocarpa* (A. DC.) F.M. Vázquez & R. Rodr. that grow mostly north of *N. obliqua*. *N. macrocarpa* was considered a variety of *N. obliqua* at the time of the common garden installation (UACH and INFOR, 2001). The provenances chosen from Maule to Los Ríos Region are presented in Fig. 1 and were the following: Vilches from the Andean Range of the Maule Region (35.58° S- 71.12° W), Quirihue from the Coastal Range of the Ñuble Region (36.32° S, 72.47° W), Recinto from the Andean Range of the Ñuble Region (36.82° S, 71.75° W), Lago Colico from the Andean Range of the Araucanía Region (39.02° S, 72.01° W), Lliflén from the Andean Range of Los Ríos Region (located at 15 km from the common garden at 40.21° S, 72.23° W) and Llancacura from the Coastal Range of Los Ríos Region (40.31° S, 73.37° W, Table 1, Fig. 1). These populations were also sampled from

Table 1
Location of the study sites and common garden and climate conditions in each of them. Annual, and summer precipitation, summer vapor pressure deficit (VPD), as well as minimum (Tmin) and maximum temperatures (Tmax) in winter and summer, respectively, are shown. Climate data were obtained from the gridded dataset CR2met (https://www.cr2.cl/downloads/cr2met/) and VPD was calculated using temperature data from the ERA 5 Land product (https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview). Mean climate data was calculated for the period 1960–2021.

Site	Southern latitude (°)	Western longitude (°)	Altitude (m)	Winter Tmin (°C)	Summer Tmax (°C)	Annual precipitation (mm)	Summer precipitation (mm)	Summer VPD (kPa)
Vilches	35.58	71.12	832	2.1	24.3	1555	103	0.55
Quirihue	36.32	72.47	893	2.9	24.6	1002	54.6	0.78
Recinto	36.82	71.75	707	2.7	23.7	1911	157	0.63
Colico	39.02	72.01	401	2.9	21.8	2280	345	0.41
Llifén	40.21	72.23	102	3.4	20.3	2458	448	0.34
Llancacura	40.31	73.37	446	3.4	20.9	1891	260	0.48
Common Garden Arquilhue	40.24	72.05	266	3.4	20.3	2458	448	0.34

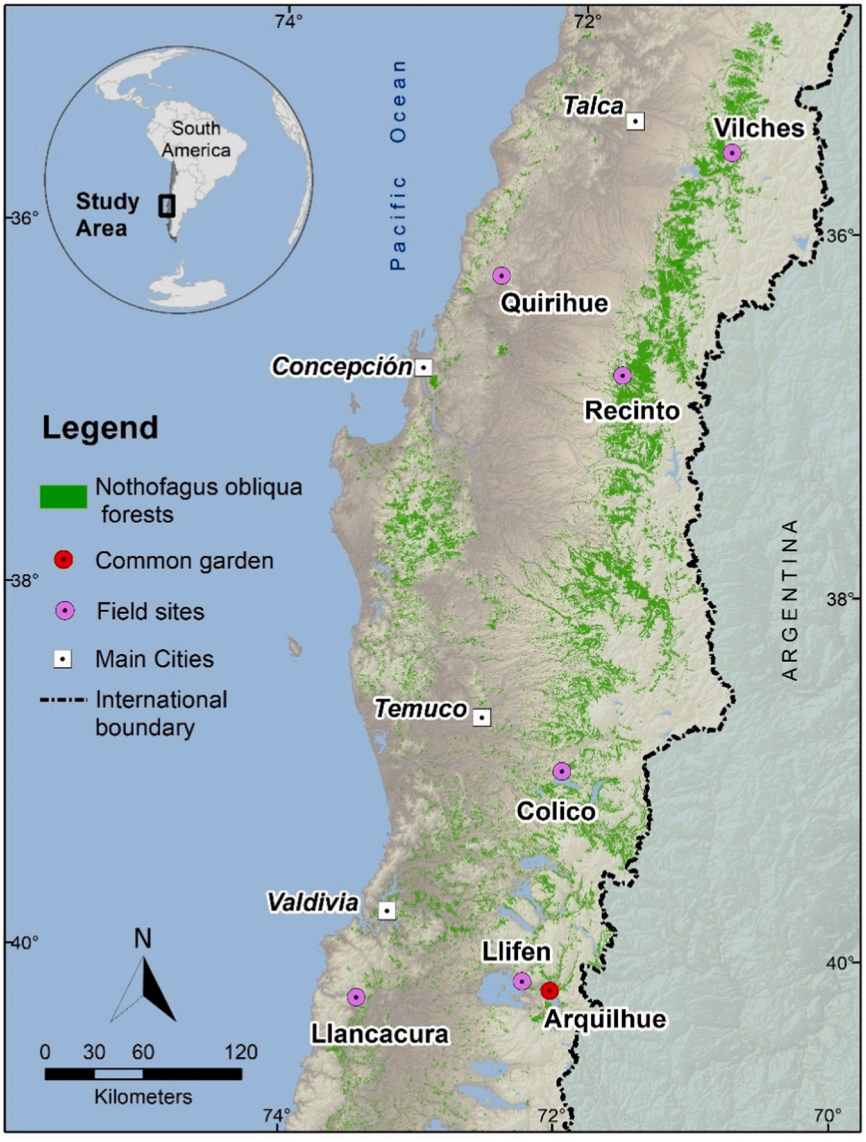


Fig. 1. Location of the six *Nothofagus obliqua* populations across the latitudinal gradient and the common garden.

the site from where the seeds were collected for the original progeny-provenance trial. In cases where the forests no longer existed (Colico and Llancacura), the closest possible forest patch was considered. In all cases, the sampled forests were unmanaged. To minimize the potential variation given by tree size, sampled individuals in the common garden and field populations ranged between 25 and 45 cm diameter at breast height (1.3 m above ground, dbh).

From each population in the field, as well as in the common garden we sampled the following traits: a) vulnerability to xylem embolism through the water potential at which 50 % of the hydraulic conductivity is lost (P_{50}) and the water potential at which 88 % of the hydraulic conductivity is lost (P_{88}), which is considered a point of no return that

can potentially lead to tree mortality (Urli et al., 2013) b) xylem safety margin, c) wood density (WD), d) xylem vessel diameter, e) vessel area, f) vessel density, g) vessel proportion, h) potential stem conductivity, i) mean tree growth of the last five years j) leaf area and k) leaf mass per area (LMA). In the case of the field populations the leaf carbon isotopic composition ($\delta^{13}C$) was also measured. Each of these traits was sampled from five trees per population in the common garden and the field (site of origin or *in situ*), except for the Vilches population at the common garden, where only four trees could be sampled. Several studies that have assessed ecophysiological traits in forests have been published using a similar number of sample trees (Bongers et al., 2017, David-Schwartz et al., 2016, Eilmann et al., 2014, Pritzkow et al., 2020, Kerr et al., 2023).

The main climate characteristics of each field site and the common garden are presented in Table 1. The climate gradient across the sampled sites (latitudinal gradient) is shown in Figure S1.

2.2. Xylem vulnerability to water scarcity

The resistance to hydraulic failure of each population was determined by generating xylem vulnerability to embolism curves using the pneumatic method (Pereira et al., 2016, 2019). These curves capture the relationship between xylem water potential and percent loss of hydraulic function (or, more accurately, the percentage of air discharged). Long branches of at least 1.2 m length were collected early in the morning from the top or sun-exposed areas of the trees using a big shot (line launcher) and a handmade V shape cutting knife. Branches were transported to the lab in a black plastic bag with the base of the branch covered with wet paper towels to avoid dehydration. Once in the lab, a short length (~60–90 cm) from the longer sample branch was recut under water and kept within a black bag in the dark for 30 min for stabilization. Any damage or rip in the branch was sealed with liquid PVA glue. After the stabilization period, the base of the branch was connected to a pneumatron apparatus V 1.0, to record the air flowing out of the stem (Pereira et al., 2016, 2019). This air was measured as pressure changes in a vacuum reservoir. At the same time, the water potential of the branch was measured from a small twig (cut from the branch) using a Scholander-type pressure bomb (PMS Instruments, OR, USA). After the first measurement, branches were left to dry for increasing time intervals (15 min, 30 min and up to one hour) between measurements. After each dehydrating time and before each air flow and water potential measurement, branches were left to stabilize for 30 min within a black plastic bag. The formulas used to calculate the percentage of air discharged are described in the Supplementary Information (SI).

A sigmoidal curve was used to fit the data and calculate the P_{50} and P_{88} for each tree (Pereira et al., 2016). Examples of vulnerability curves for each population are presented in the SI (Figures S2 and S3). The hydraulic safety margin (MPa) was calculated as the water potential difference between the stem P_{50} and the minimum xylem water potential measured in the common garden and field populations. The minimum water potential was measured at the end of summer (end of February) in the common garden and field populations.

2.3. Wood density and wood anatomical traits

Additional similar branches were collected to evaluate anatomical traits. From each branch, we collected a section that was 5 cm long with a diameter of approximately 1 cm, for WD estimates. WD was determined using the water displacement method after the bark had been removed (Osazuwa-Peters and Zanne., 2010).

From the same branches, we also collected sections that were 10–15 cm long and ~1 cm diameter for measurements of vessel area (μm^2), vessel diameter (μm), vessel density (number/mm^2), vessel proportion or coverage (%), which corresponds to the area covered by vessels, and potential conductivity (kg m^{-1} MPa^{-1} s^{-1}, see the formula in the SI). Vessel diameter was calculated from vessel area using the area of a circle. Cross sections 25 μm width were obtained using a rotation microtome Accu-Cut SRM 200 and they were prepared, mounted and photographed according to details shown in the SI.

2.4. Leaf traits

Leaf area and LMA were measured for 15 leaves per tree. Leaf area was measured immediately after collection using an EPSON V850 scanner and the ImageJ software. Once in the laboratory, leaves were dried in an oven at 70 °C for 48 h, after which their dry weight was recorded.

In the case of field populations, several leaves were collected from the five sampled trees to determine the leaf C isotopic composition. Analyses were done at the Laboratory of Biogeochemistry and Applied Stable Isotopes at Pontificia Universidad Católica de Chile.

2.5. Tree growth

Tree-ring cores were obtained from all the studied trees from the field and the common garden using an increment borer (at dbh). Cores were mounted and sanded until the rings were visible. Then, cores were scanned, and tree-ring width was measured using the program CooRecorder 9.5 (Cybis Elektronik & Data AB). The mean width of the last five complete years was considered for subsequent analyses. In the case of field populations, at least 15 trees were sampled to cross-date the series and build tree-ring chronologies (these 15 individuals included the trees sampled for other traits).

2.6. Statistical analyses

To evaluate traits' intraspecific variability across the field gradient, as well as to evaluate which traits are genetically differentiated within the common garden, one-way ANOVA analyses with Tukey as a post-hoc test were run using R software (R Development Core T, 2014).

Moreover, to have an approximation of the degree of trait plasticity, we run T-tests to compare trait values between the field and the common garden for each population. Data normality was checked using the Shapiro-Wilk Test, and in case of no normality, the non-parametric Wilcoxon test was run in R software (R Development Core T, 2014).

Linear regressions were carried out between traits measured in the common garden and climate at the populations' origin. These relationships are necessary because some traits can be under genetic predisposition, even when no significant differences are found between populations (Hajek et al., 2016). Seasonal climate (precipitation, maximum temperature and vapor pressure deficit (VPD)), as well as soil moisture were used. Finally, linear regressions were run to evaluate if there is any relationship between the different traits measured in the field and tree growth during the last five years.

Climate data was obtained from the CR2MET gridded dataset (https://www.cr2.cl/datos-productos-grillados/). The ERA5 Land dataset was used to derive VPD, and gridded soil moisture data were obtained from (https://ldas.gsfc.nasa.gov/fldas). See more details in the SI.

3. Results

3.1. Intraspecific trait variation across the latitudinal gradient

Most traits (ten of 13 traits), including tree growth, differed between populations across the gradient (Fig. 2). *In-situ* populations across the latitudinal gradient differed significantly in xylem tolerance to water deficit ($p = 3.882e^{-05}$ for P_{50} and $p = 0.0034$ for P_{88}). However, these traits did not exhibit a clinal trend across the gradient, with Llifén ($P_{50} = -2.2$ MPa) and Llancacura ($P_{50} = -3.5$ MPa), the two southernmost populations, having the least and most resistant xylem, respectively (Fig. 2 A, B). Llancacura was also the population with the largest safety margin (Fig. 2 C). Vessel diameter and vessel area were the lowest at

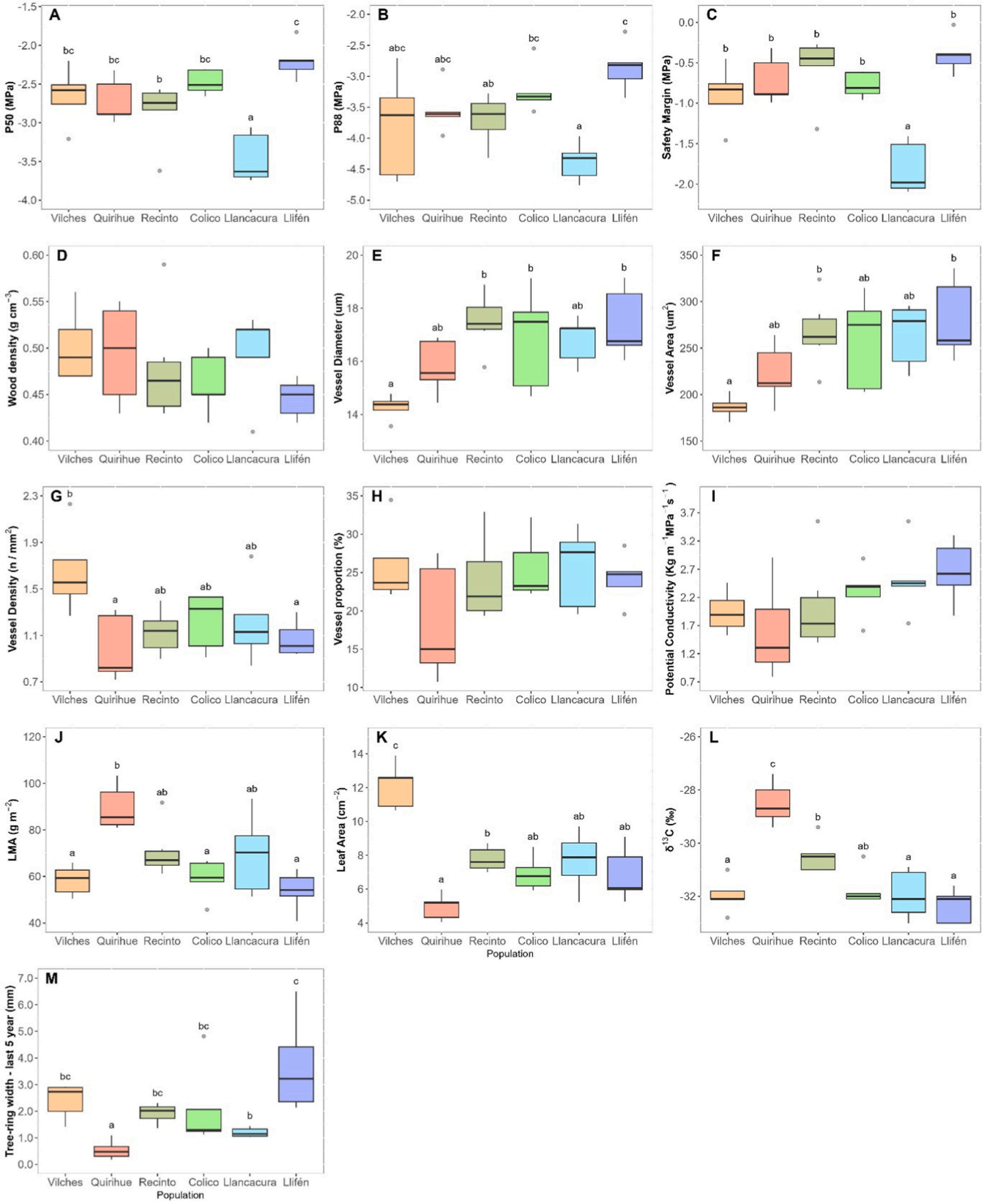


Fig. 2. Box plots of stem and leaf traits for the different *Nothofagus obliqua* provenances growing in the field. Sites are ordered from north to south. Significant differences found through a one-way ANOVA and the Tukey post-hoc test are shown as letters.

Vilches, the northernmost population (Fig. 2 E,F), and there was a gradient from smaller to larger vessels, and/or from lower to higher potential conductivity from north to south, although differences were not significant in this last trait (Fig. 2 E,F,I). There was a decreasing trend in LMA and $\delta^{13}C$ values from north to south, except for Vilches the northernmost population, which displayed the lowest LMA and the most negative foliar $\delta^{13}C$ values (Fig. 2 J, L). Leaf area did not show a clear pattern of variation across populations, with the two northernmost populations (Vilches and Quirihue) possessing the highest and lowest leaf area values, respectively (Fig. 2 K). We found no significant differences among populations in WD, vessel proportion and potential conductivity (Fig. 2 D,H,I). Growth was the highest in Llifén, the southernmost Andean population, and the lowest in Quirihue, the northernmost Coastal population, with the second lowest growth observed in the southern Llancacura population (Fig. 2M).

3.2. Intraspecific trait variation within the common garden

In the common garden, only vessel proportion ($p = 0.024$) and tree growth during the last five years ($p = 0.001$) differed significantly among populations. Vessel proportion was higher in Llifén than in Quirihue (Fig. 3H), whereas tree growth was higher in Llifén compared to all other populations, except Colico (Fig. 3L).

3.3. Plasticity on a provenance-by-provenance basis

When comparing trait values between the field and common garden for each population, Vilches, the northernmost provenance, was the one with the largest number of traits that showed plasticity (leaf area, WD, vessel area, vessel diameter and tree growth, Fig. 4). Leaf area, WD and tree growth were higher in the field than in the common garden, while the contrary was found for vessel parameters (Fig. 4). In the case of Quirihue, leaf area and LMA exhibited plasticity, with smaller leaf area and larger LMA values in the field compared to the common garden. In this population, growth also showed plasticity, being higher in the common garden than in the field. The mid-gradient Recinto population did not show plasticity in any of the traits, and Colico and Llancacura showed plasticity in xylem safety margin and P_{50}, respectively. Trees from Colico were safer when growing in the wet common garden conditions, and trees from Llancacura showed the safest xylem in the field. Finally, the southern population Llifén exhibited plasticity in safety margin and vessel density, with trees having a safer xylem and higher vessel density in the common garden compared to the field.

3.4. Relationships between functional traits in the common garden and climate at the populations' origin

For the common garden, only two significant relationships were found between traits and climate at the site of origin (Fig. 5). Vessel proportion was negatively related to summer VPD ($p = 0.013$, Fig. 5A), whereas tree growth was positively related to summer precipitation ($p = 0.045$, Fig. 5B).

3.5. Relationships between functional traits and radial growth across the gradient

The only significant relationship between five-year growth rate and any of the functional traits across the gradient was with P_{88} ($p = 0.015$), indicating that individuals and populations with greater drought tolerance exhibit a lower growth rate (Fig. 6).

4. Discussion

Our results reveal a substantial intraspecific variation in drought tolerance traits among adult *Nothofagus obliqua* populations growing in field sites across south-central Chile. Ten of the 13 traits (including tree growth) showed population-level differences in the field. However, only two traits (i.e., vessel proportion and tree growth) differed between populations grown in a common garden. When evaluating plasticity on a provenance-by-provenance basis, the population that showed a higher number of plastic traits was the northernmost one, and the mid-gradient population did not show plasticity in any of the traits evaluated. Although a complete assessment of phenotypic plasticity could not be performed with the available data, our results suggest that intraspecific trait variation in *N. obliqua* may be primarily driven by phenotypic plasticity rather than by local adaptation. We also found evidence for a weak trade-off between growth and drought tolerance in this species.

4.1. Intraspecific variability in drought tolerance traits of N. obliqua

Our findings revealed intraspecific variation in the capacity to withstand drought, expressed as P_{50} and P_{88}, although this trait was not genetically differentiated. These results agree with what was reported for P_{50} (but not for P_{88}) in *Fagus sylvatica* L. (European beech) (Hajek et al., 2016), and in other studies (Wortemann et al., 2011, Aranda et al., 2014). They also agree with what was reported for conifers (Lamy et al., 2014, Sáenz-Romero et al., 2013), where no genetic differentiation was found among populations, indicating that probably this trait was canalized and "uniformly selected" (Lamy et al., 2011). Furthermore, the field variation in xylem vulnerability was not predictable from the climatic differences, departing from the expectation that the most drought tolerant populations would be located at the driest end of the gradient (e.g., Aranda et al., 2014; Choat et al., 2007; López et al., 2016; Stojnic et al., 2017). While trees from the wettest site Llifén have the least tolerant xylem, trees from Llancacura, which has a moderate climate, have the highest drought tolerance. This result could be explained due to soil site differences between the Coastal Range and the Andes Cordillera, which have been described at similar latitudes (Urrutia-Jalabert et al., 2015a, 2015b, Peralta, 1976). Soil moisture, as well as local pedo-climate conditions, including nutrient availability, influence cavitation resistance in different species (Awad et al., 2010; Beikircher and Mayr, 2009; Cary et al., 2020; Wortemann et al., 2011). Soils in the Coastal Range are shallow, of metamorphic origin (Peralta, 1976), and have a low water retention capacity, which can strongly influence tree species growth and forest dynamics (Urrutia-Jalabert et al., 2015c, 2017). Another factor that could explain the greater drought tolerance of Llancacura than that of Llifén, is the persistence of the species in glacial refugia in the Coastal Range (Azpilicueta et al., 2009).

Overall, all *N. obliqua* populations except Llancacura (which exhibited a highly resistant xylem) showed narrow safety margins from P_{50} (< 1 MPa; Choat et al., 2012). Two populations from the south (Colico and Llifén) showed plasticity in this trait, with trees having a safer xylem in the wetter common garden, where they experience less negative minimum water potentials, compared to the field. Moreover, Llancacura showed plasticity in its P_{50}, investing in a less resistant xylem when growing under better site conditions in the common garden.

We observed a significant variation in vessel size across the gradient, with populations growing in wetter conditions tending to have larger vessels. The northernmost population (Vilches) showed the smallest vessel diameters, in line with our prediction that the driest sites would display a resource-conservative strategy. Interestingly, we cannot discern if this is driven by freeze-thaw or by drought-induced embolism avoidance, because the Vilches locality has the lowest minimum temperature of the gradient. Small diameter vessels have been reported to be more resistant to freezing-induced cavitation than large diameter vessels (Hacke and Sperry, 2001, Davis et al., 1999). Vessel size is a plastic trait in this population, so trees from this provenance are able to increase their vessel size under the wetter common garden conditions (Tyree and Zimmermann, 2002).

Trees at Quirihue (the coastal northern population) had the largest LMA and the highest water use efficiency in the field (lowest discrimination), reflecting that this population had adaptations at the foliar level

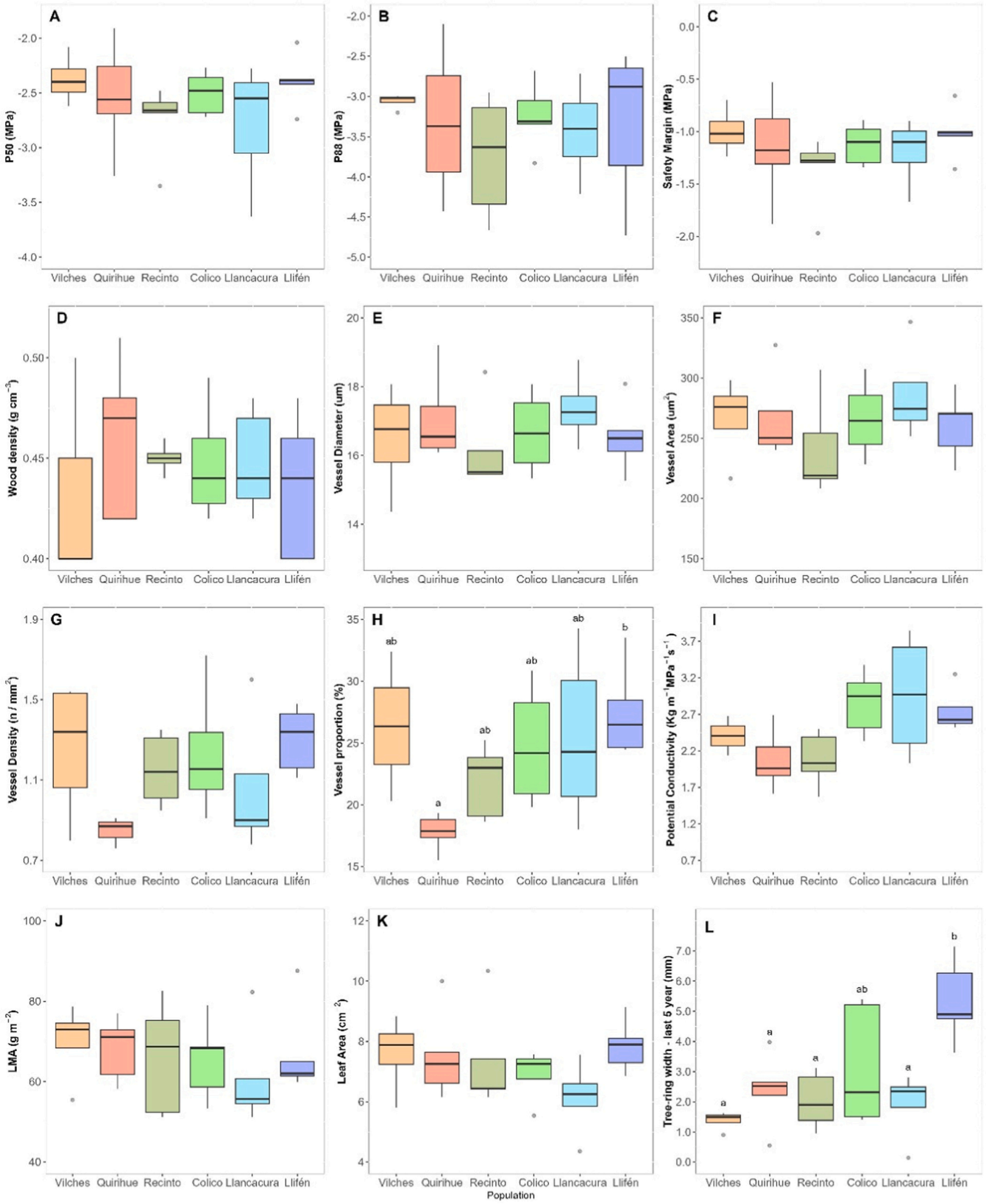


Fig. 3. Box plots of stem and leaf traits for the different *Nothofagus obliqua* provenances growing in the common garden. Sites are ordered from north to south. Significant differences between populations found through a one-way ANOVA and the Tukey post-hoc test are shown as letters.

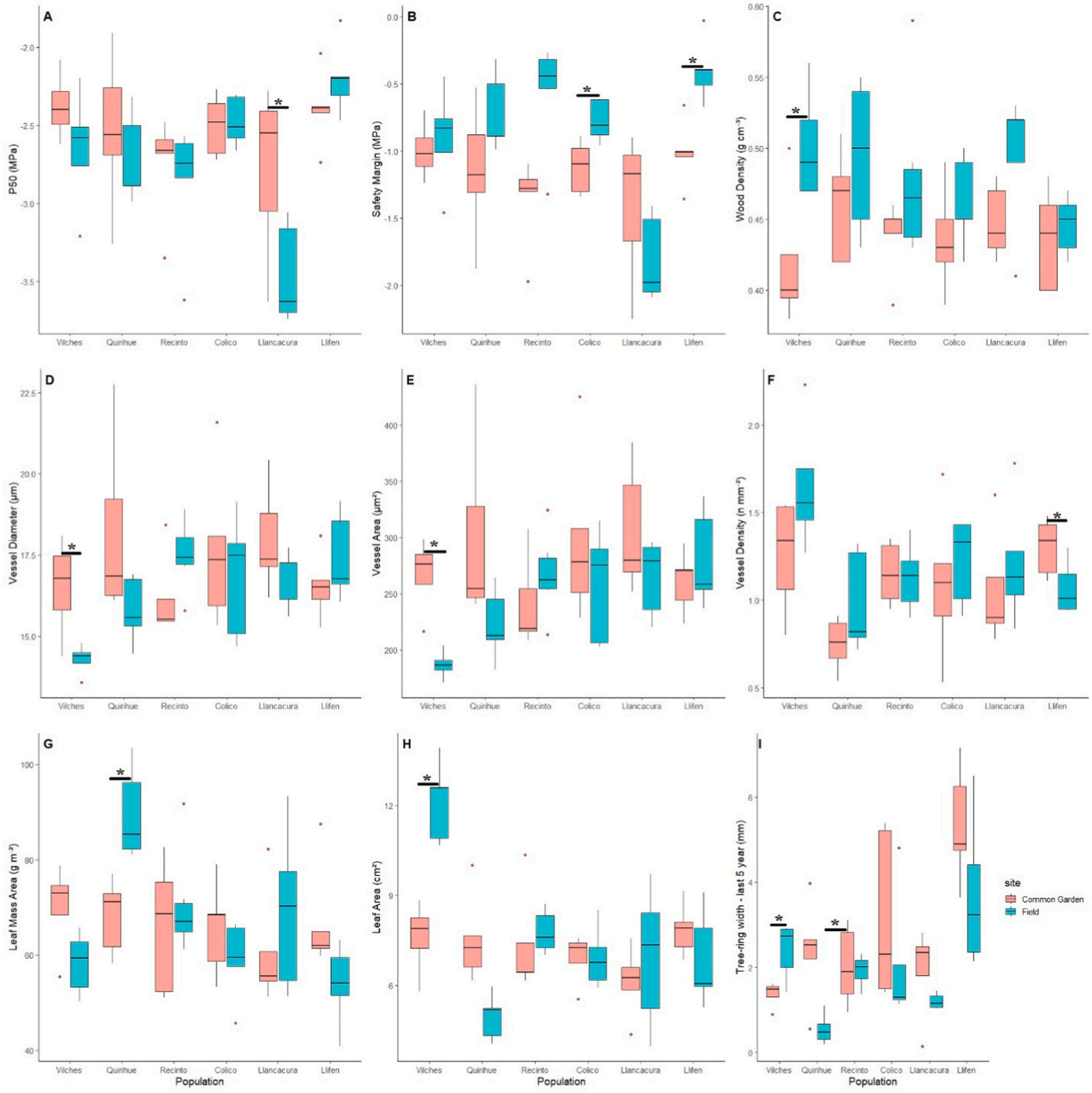


Fig. 4. Box plots comparing trait values measured in the common garden and the field for the different populations. Only traits for which a significant difference was found are shown. Significant differences are shown with an asterisk.

to be more conservative in the use of water (Wright et al., 2005). Higher LMA values in dry sites are a drought stress adaptation, as higher LMA confers a higher wilting resistance or higher tolerance to low water potentials (Schulze et al., 1998, Cunningham et al., 1999, Wright et al., 2005). Leaf area and LMA are plastic traits in this population, enabling trees from this provenance to adopt a faster resource-acquisition strategy under wetter conditions (Reich, 2014).

WD, vessel proportion and potential conductivity were the only traits that did not significantly vary across the gradient. This result surprisingly differs from other studies that found increases in WD with drier conditions, at both intra- and interspecific level (Fajardo and Piper, 2011). However, this trait was plastic in the northernmost population Vilches, and as it can be expected, higher WD values were found in the drier field conditions than in the common garden, as WD can promote plant tolerance to droughts (Hacke et al., 2001; Willson et al., 2008, but see (Hoffmann and Sgrò 2011)).

Although vessel proportion did not differ among field sites, it was differentiated by population in the common garden. Hajek et al. (2016) reported population differences in vessel density for beech across its distribution and Eilmann et al. (2014) reported population differences for wood properties related to vessel size in the same species. Moreover, the significant relationship between vessel proportion and summer VPD at the populations' origin, with the lowest vessel proportion at the driest population Quirihue, further supports that this trait is under genetic differentiation (Hajek et al., 2016). A lower vessel proportion could function to isolate xylem vessels, providing safety from embolism

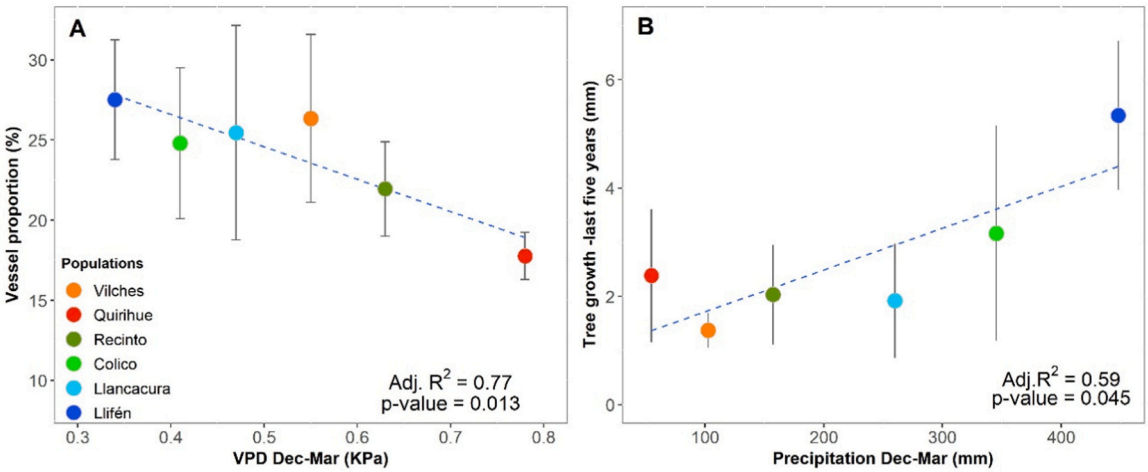


Fig. 5. Relationships between functional traits at the common garden and climate at the populations' origin. A) Vessel proportion related to summer (December-March) VPD, and B) tree growth over the past five years related to summer precipitation (December-March). The adjusted R^2 and the significant p-values are shown. Bars correspond to standard deviations of the sample at each site.

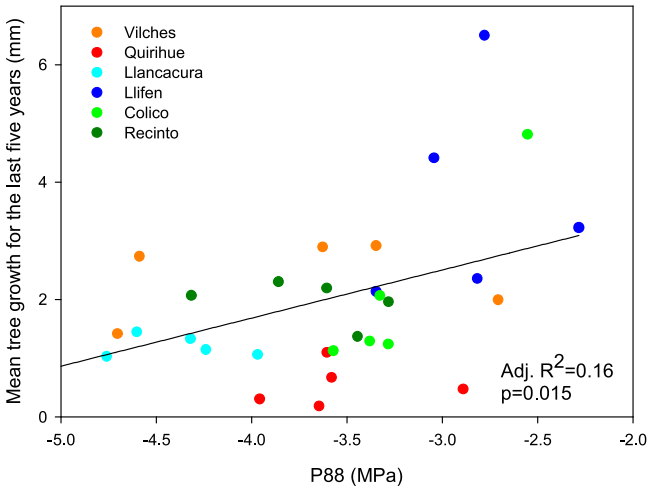


Fig. 6. Relationship between xylem vulnerability to water deficit (expressed as the P_{88}) and mean tree growth during the last five years in the field populations. The adjusted R^2 and p-value are shown.

propagation. It also remains possible that other non-measured anatomical attributes are playing a role, since thicker fiber walls may also contribute to lower vessel proportions, conferring a higher resistance to embolism (Jacobsen et al., 2005, Janssen et al., 2020). The lowest vessel proportion in the driest site is consistent with our prediction that dry populations have a more conservative hydraulic strategy.

Tree-growth rates were also genetically differentiated among populations, and there was a positive relationship between growth rates and summer precipitation at the sites of origin, with lower growth rates in the driest populations. This is in overall agreement with what was reported by Urrutia-Jalabert et al. (2021) for *N. obliqua* across a similar latitudinal gradient from drier to wetter sites in the Andes. These overall results suggest that growth rates and vessel proportion evolved to local climate pressures (Hajek et al., 2016). Moreover, it is important to mention that although tree growth was genetically defined to be higher in trees from Llifén than in trees from most populations, this trait was plastic in the two northernmost populations Vilches and Quirihue. In the case of Quirihue, and as it can be expected, growth was higher in the wet common garden than in the field, and the opposite was found for Vilches (see more details in Section 4.4).

Considering all provenances, Quirihue and Llancacura both populations from the Coastal Range, located at two different latitudes, were the two most tolerant to droughts, because of different traits associated to leaves and stems, respectively.

4.2. Growth-tolerance trade-off

A significant positive relationship between five-year radial growth and P_{88} across the gradient, was consistent with our prediction that the wetter populations (e.g. Llifén) would grow faster and be less drought tolerant compared to the trees growing at drier sites (Cochard et al., 2007, García-Valdés et al., 2021). This finding is also in accordance with the "fast-slow" plant economics spectrum, where conservative species, or in this case conservative populations, are more drought-tolerant, but have lower rates of resource gain than the acquisitive (and more vulnerable) ones (Reich, 2014). Although this trade-off has been proposed to operate within populations in a conifer species – where faster shoot growth leads to longer, less air-resistant xylem (Johnson and Brodribb, 2023), such a relationship has not previously been demonstrated in an angiosperm. Nevertheless, the fact that we did not observe a relationship between growth rate and other hydraulic traits suggests that the trade-off is likely to be weak.

4.3. Study limitations

A limitation of this study is that populations sampled in the field had different life histories and trees were generally older than those growing in the common garden. Another limitation is that a common garden in a dry site does not currently exist in Chile, so it is not possible to have the complete set of environmental conditions that populations can have. This prevents the assessment of the populations ability to adapt to conditions that are drier than at their site of origin. Moreover, due to the absence of this common garden, we cannot completely assess the contribution of genetic differentiation, phenotypic plasticity, and/or their interaction on the different studied traits. Nevertheless, our study setting was the best available to comprehensively assess intraspecific variation in drought tolerance traits and infer its underlying mechanisms (i.e., plasticity and genetic differentiation) in adult individuals of *N. obliqua* in southern South America.

4.4. N. obliqua forests under the drying climate in Chile

Considering our main findings, it appears that plasticity to local environmental conditions is likely the key mechanism for *Nothofagus obliqua* adaptation to environmental variation (Carvajal et al., 2017;

Valladares et al., 2014). Only trees from Recinto did not show plasticity in any of the studied traits under wetter conditions, so their ability to adapt to drier conditions remains uncertain.

Another important finding of our study was that the wettest population Llifén had the highest radial growth, and the northernmost Vilches population had the lowest growth when grown in the same wet environment. This finding implies that planting northern/drier *N. obliqua* populations in the wet south for any purpose cannot be broadly recommended, as the low growth of the Vilches population was also associated with the lowest WD and the most vulnerable xylem in the common garden. The low productivity of a drier provenance in a wet environment was also reported for some beech populations in Europe (Eilmann et al., 2014), so assisted migration for production purposes must be carefully evaluated.

Provenances from wet areas, such as Llifén, which grow fast, but did not show drought tolerance at its site of origin, should not be considered for future restoration programs, as it is uncertain if trees can resist future drier conditions. On the other hand, the southernmost coastal population Llancacura, was the most drought tolerant and could be considered for future restoration programs, although its growth rate was among the lowest. The northernmost coastal population Quirihue also appears as a possibility, with higher growth rates than Llancacura, a relatively safe xylem and plastic leaf traits.

5. Conclusions

This study demonstrated that the drought tolerance of *N. obliqua* varied across its distribution and was mostly driven by phenotypic plasticity, as only two of the studied traits showed genetic differentiation. Two populations located in the northern and southern limits of the Coastal Range were the most drought tolerant, which was probably associated with restrictive site-specific conditions. Planting northern/drier *N. obliqua* populations in the wet south cannot be broadly recommended, as the low growth of the northernmost Vilches population was also associated with a vulnerable xylem. The wettest population Llifén had the highest radial growth, but this was associated with the lowest drought tolerance of the gradient.

As this study was performed utilizing adult trees, further studies should evaluate functional traits within seedlings and saplings, as there can be ontogenic changes that influence the species' tolerance to water stress.

Funding

R.U-J thanks the Fondecyt Regular Grant 1240500 and Fondecyt of initiation Grant 11200710, the ANID/FONDAP 1523A0002 project (Center for Climate and Resilience Research CR2) and the ANID- Millennium Science Initiative- Center Code NCN2024_040. D.E.C. thanks the Fondecyt postdoctoral Grant 3230154 and Proyecto Basal FB210006 (Instituto de Ecología y Biodiversidad, IEB). R.I acknowledges the FONDEF Project D96I1052 "Mejoramiento genético para especies de *Nothofagus* de interés económico".

CRediT authorship contribution statement

Rocío Urrutia-Jalabert: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Conceptualization. **Braulio Gutiérrez:** Writing – review & editing. **Alejandro Cárdenas:** Writing – review & editing, Formal analysis. **Roberto Ipinza:** Writing – review & editing. **Robert Skelton:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Danny E. Carvajal:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **María Paz Peña:** Writing – review & editing, Formal analysis. **Jarmila Pittermann:** Writing – review & editing, Investigation.

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

The authors acknowledge the Instituto Forestal INFOR for facilitating the use of the common garden, that was established thanks to the FONDEF D96/1052 UACH-INFOR project. Special thanks to the technician Mr. Mauricio Navarrete for his invaluable support in selecting and finding the study sites. We thank the following landowners that kindly allowed us to work in their properties: Patricio Roa, administrator of Fundo Arquilhue and the Empresa Sociedad Agricola y Forestal Taquihue S.A., Olga Roa from Vilches, Daniel Urrutia from Recinto and Miguel Provoste from Fundo Chollinco, Llifén. Finally, we thank Victor Castillo for helping in fieldwork, Aldo Farías for making the map of the study area and Carmen Gloria Rodriguez for dating and measuring the tree-ring samples.

Authors' contributions

Rocío Urrutia-Jalabert (R.U-J) planned and designed the research; Danny E. Carvajal (D.E.C) helped to refine research questions and design. D.E.C, Robert Skelton and Jarmila Pittermann contributed ideas and analyses and wrote and reviewed the paper. Alejandro Cárdenas (A. C), D.E.C and R.U-J performed the measurements in the field and Laboratory analyses. María Paz Peña, R.U-J, D.E.C and A.C analyzed the data. Braulio Gutiérrez and Roberto Ipinza contributed fundamental information about the common garden and field sites and reviewed the paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123165.

Data availability

Data will be made available on request.

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