Dendrochronologia 92 (2025) 126360

Contents lists available at ScienceDirect

Dendrochronologia

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

Variation in radial growth sensitivity to drought among genetic groups of common yew (*Taxus baccata* L.) in central Italy

Enrico Tonelli [a,*], Camilla Avanzi [b], Elena Bitocchi [a], Alessandro Vitali [a], Andrea Piotti [b], Ilaria Spanu [b], Elena Barocci [a], Carlo Urbinati [a]

[a] Department of Agricultural, Food and Environmental Sciences, Marche Polytechnic University, Ancona, Italy
[b] Institute of Biosciences and Bioresources, Italian National Research Council, Florence, Italy

ARTICLE INFO

Keywords:
Dendroecology
Dendrogenetics
Climate change
Resilience
Tree-rings
Conservation

ABSTRACT

Common yew (*Taxus baccata* L.) is a long-living European species, with significant ecological importance. Climate change and severe droughts threaten its growth, emphasizing the need for preserving genetic diversity. By combining dendroecology and genetics, we aimed to identify groups of trees most resilient to changing climatic conditions. We analysed radial growth trends from 1951 to 2018 in three populations located in two mountain areas of central Italy with different rainfall regimes. From 298 selected yew trees, needles were collected for DNA extraction, and tree-ring cores were obtained for dendrochronological analysis. We assessed the relationship between tree growth and drought using the Standardized Precipitation Evapotranspiration Index (SPEI). The studied populations clustered in two distinct genetic groups, corresponding to the driest and wettest areas. At the rainiest site, in the period 1951–2018 yew growth was less constrained by evapotranspiration rates than at the driest area, but climate-growth analysis on moving windows indicates an increasing impact of drought. Growth recovery time after the 2003 drought was longer in individuals at the rainiest area compared to the more xeric sites. The yew trees of the driest area, which were further subdivided in two genetically distinct but spatially intermingled sub-groups, appeared to be better adapted to drought events and therefore more suitable for future warmer scenarios. This study highlights the climate sensitivity of common yew, showing that summer droughts can limit growth, and suggests the advantages of using a dendrogenetic approach to delve deeper into ecophysiological responses to be exploited for reforestation and conservation efforts.

1. Introduction

Common yew (*Taxus baccata* L., 1753) is a long-living dioecious coniferous species native to most of Europe, including central Italy (Caudullo et al., 2017). Yew has a long history of human use and symbolism. In ancient times its wood was used for making weapons, tools, and ceremonial objects (Uzquiano et al., 2015). Nowadays, it is a popular choice for gardens and landscaping and has a more limited interest in timber use. Yew is an ecologically valuable species, providing shelter and food for various birds, mammals and insects (Thomas and Polwart, 2003). Yew can be found in various habitats, such as woodlands, forests both in mountain and hilly areas, often growing alongside other tree species and more rarely forming pure stands (Benham et al., 2016). It is a highly shade-tolerant species and grow frequently in forests' understory (Perrin and Mitchell, 2013). Common yew has undergone a significant decline, ranking among the most severe ones observed among all European tree species (Benham et al., 2016). For this reason, most of the forests harbouring yew have been designated as a priority habitat for biodiversity conservation within the European Union (Natura 2000 habitats 9580, 9210, 91K0 and 91L0).

Yew is a slow-growing and long-lived species, exceeding sometimes 1000 years (Thomas and Polwart, 2003). Long-term existence of yew in the Italian Apennines depends on maintaining and expanding old-growth beech forests that incorporate yew patches, with a minimum continuous cover of 10–50 ha (Piovesan et al., 2009). Temperature, precipitation, and moisture availability can remarkably affect the tree radial growth in Mediterranean basin (Sarris et al., 2007, Castagneri et al., 2020). Generally, yew prefers mild and humid site conditions, and excessive heat or drought can inhibit its growth (Cedro and Cedro, 2015). In regions with colder temperatures, such as in mountainous areas, the growth rate may be slower due to shorter growing seasons (Cedro, 2023). Moreover, *T. baccata* prefers moist, well-drained soil

* Corresponding author.
E-mail address: e.tonelli@univpm.it (E. Tonelli).

https://doi.org/10.1016/j.dendro.2025.126360
Received 4 February 2025; Received in revised form 23 April 2025; Accepted 16 May 2025
Available online 17 May 2025

conditions (Calvia et. al, 2023). Although yew could be considered both a shade and drought tolerant species, excessive waterlogging or extremely dry conditions can negatively impact its growth (Niinemets and Valladares, 2006, Benham et al., 2016). Research on the radial growth sensitivity of yew suggests a certain level of plasticity in response to changing climate and environmental conditions. Wider tree-ring widths in *T. baccata* are determined by winter-spring temperatures, because they lead to an earlier onset of the growing season (Galvin et al., 2014). In response to warming temperatures, common yew may increase radial growth rates, whereas drought conditions can limit growth, increasing the tree susceptibility to pathogens and pests (Linares, 2013).

Efforts to preserve common yew are nowadays focusing on genetic assessments to guide conservation strategies and silvicultural practices for a species particularly vulnerable to the effects of habitat fragmentation (Litkowiec et al., 2018, Maroso et al., 2021, Casier et al., 2024, Chybicki et al., 2024a). Understanding the distribution of its genetic variation at different spatial scales is crucial for suitably managing remnant populations, as it helps identifying vulnerable ones and designing effective strategies for their preservation under climate change scenarios (Maroso et al., 2021). Understanding its radial growth sensitivity to climate is also fundamental for predicting the species' responses to climate change scenarios, particularly as increased droughts threaten its suitability to the Mediterranean basin, which is considered a climate change hotspot (Thomas and Garcia-Martí 2015, Cos et al., 2022). The integrated analysis of genetic and dendrochronological data, often referred to as dendrogenetics or dendrogenomics in recent literature (Krutovsky, 2022), offers, in this regard, a novel and powerful view to study the adaptive potential of forest tree populations to environmental stressors (e.g. Heer et al., 2018, Housset et al., 2018, Avanzi et al., 2020).

In this study, we analysed the tree-ring sensitivity in three mountainous populations in central Italy. Guided by genetic characterization, we aimed to identify the group of yew trees most resilient to intense drought conditions. This will provide the basis for the informed collection of propagation material for future reforestation programs and help define proposals for the maintenance of yew in central Italy.

2. Material and methods

2.1. Study sites

The three study sites, "Macchia delle Tassinete" (MTA), "Internone" (INT) and "Alpe della Luna" (ADL), are in two distinct mountainous areas of the Marche region, in central Italy (Fig. 1). MTA and INT are located on the calcareous-marly pre-Apennine ridge of Cingoli, approximately 35 km from the Adriatic coast. ADL site is situated further inland, in the central Apennine chain, where the lithology is predominantly characterized by sandstone and marl-sandstone formations. Elevations range from 480 to 760 m (MTA), 570–710 m (INT), and 960–1060 m (ADL). All the study sites consist of broadleaf forests with a diffuse presence of *T. baccata*. MTA consists partly of beech forest (habitat 9210) in the western section and transitions to an ash-hornbeam forest in the eastern part. INT is primarily an ash-hornbeam forest with Turkey oak (*Quercus cerris*) and sporadic beech (*Fagus sylvatica*) occurrence. ADL is a mesophilic sub-montane beech forest with numerous broadleaf species, especially Italian maple (*Acer opalus* subsp. *obtusatum*). These forests have been managed mainly as coppice with standard trees and are now in conversion to high forest. ADL and MTA sites, but not INT, fall within a Special Area of Conservation (SAC) as defined in the European Union's Habitats Directive (92/43/EEC). For the climatic characterization of the sites, we extracted meteorological data from the European grid E-OBS v28.0e (0.1° x 0.1° regular grid) (Cornes and Jones 2018). Due to the proximity of MTA and INT populations, we used the same climatic data for both sites. According to the Rivas-Martinez bioclimatic classification system in the period 1950–2020 all sites have a temperate oceanic bioclimate

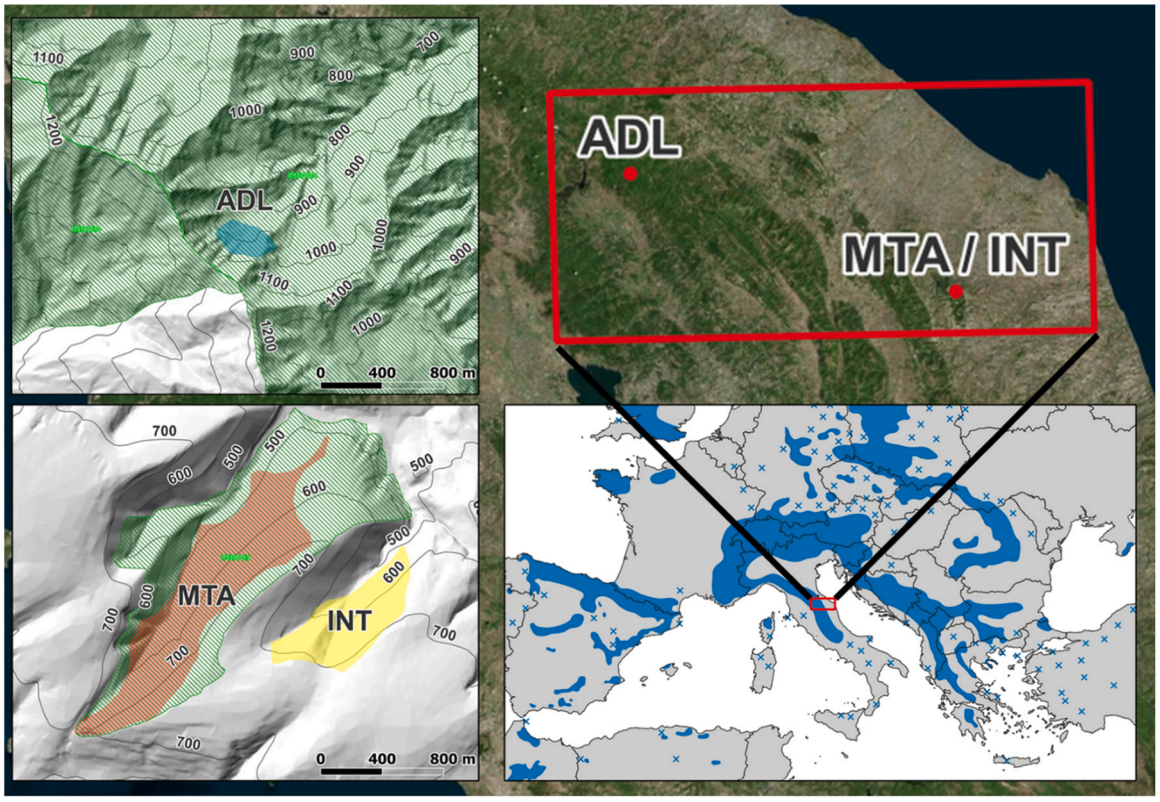

Fig. 1. Location of the study sites in central Italy. The enlarged boxes on the left show the extension of the census populations and the area designated as a Special Area of Conservation (SAC) in green. The bottom right displays the European distribution range of *Taxus baccata* (Caudullo et al. 2017).

(submediterranean variant), whereas the thermotype is low meso-temperate at MTA-INT and low supra-temperate at ADL. The mean annual temperatures are 14.1°C and 11.7°C at MTA-INT and ADL, respectively. Ombrotype is upper subhumid at MTA-INT while low humid at ADL, with mean annual precipitation of 834 mm and 1064 mm in MTA-INT and ADL, respectively. Therefore, MTA and INT sites can be considered more xerothermic than ADL.

2.2. Sampling protocol

In the field, at all sites, we considered only the standing yew trees with a DBH $\geq$ 15 cm. We measured their diameter at breast height (DBH), total tree height and recorded their position respectively with a manual caliper, an ultra-sound hypsometer (Vertex III, Haglöf) and a GNSS RTK receiver (HiPer SR, Topcon). When male cones or female fleshy arils were on trees, we recorded the sex of individuals. The yew populations at MTA, INT and ADL consisted of 1031, 316 and 131 individuals respectively and we selected 95, 107 and 96 evenly distributed yew trees at each site. From these 298 selected individuals, we collected needles of the year for total DNA extraction and wood samples for dendrochronological analysis. We placed the needle samples in tea bags, storing them in silica gel to dehydrate the tissues and prevent DNA degradation. For the dendrochronological analysis, we cored each tree twice at breast height (1.3 m) using a 0.5-mm increment borer (Haglof, Sweden). In multi-stemmed individuals, we took the cores from the largest stem.

2.3. Genetic characterization

We extracted total genomic DNA from 60 mg of silica-dried needles using the GeneAll Exgene Plant SV Mini Kit (GeneAll Biotechnology, Korea) and following the manufacturer's instructions. We genotyped all sampled trees at 10 nuclear microsatellite loci (nSSR) (Me-998–304A, Ma-722–463C, Me-30893–225A, B-20918–231C, Ma-6281–999D: Ueno et al., 2015; Tax92, Tax36, Tax60, Tax86, Tax23: Dubreuil et al., 2008) (Table S1). Except for Tax23 which we amplified alone, we multiplexed the remaining nine loci in two PCR reactions using the Type-it Microsatellite PCR kit (Qiagen, Germany) and optimizing a final volume of 6 µl. The PCR mix for both multiplexes consisted of 3 µl of Type-it Multiple PCR Master Mix, 0.6 µl of primers premix, 1.4 µl of RNase-free water and 1 µl of DNA (~10 ng/µl). The PCR thermal profile was the same for both multiplexes and required an initial step at 95°C for 5 min, followed by 32 cycles at 95°C for 30 s, 57°C for 90 s and 72°C for 30 s, with a final 30 min extension step at 60°C. For Tax23, we performed a single PCR reaction in a total volume of 10 µl, containing 2 µl of Promega 5X green buffer (containing 1.5 mM $MgCl_2$), 0.2 µl of dNTP mix (10 mM each), 0.2 µl of forward and reverse primers (10 mM each) and 1 µl of DNA (~10 ng/µl). The single PCR thermal profile required an initial denaturation at 94°C for 3 min, followed by 10 cycles at 94°C for 30 s, 60°C for 30 s (decreasing 1°C per cycle), and 72°C for 40 s, and further 35 cycles at 94°C for 30 s, 50°C for 30 s, and 72°C for 40 s, with a final 10 min extension at 72°C. We performed all PCRs on a GeneAmp PCR System 9700 thermal cycler (Perkin Elmer, US). We ran PCR products on AB 3500 sequencer (Applied Biosystems, US), using LIZ-500 as internal size standard. We performed allele calling and binning manually using GeneMarker (Softgenetics LC, US).

2.4. Genetic diversity and structure

For each site we calculated standard indexes of genetic diversity, that is the number of alleles, effective number of alleles and private alleles (*Na, Ne* and *Np*, respectively), observed and expected heterozygosity (H_O and H_E, respectively) and inbreeding coefficient (F_{IS}), using the software GenAlEx v6.5 (Peakall and Smouse, 2006). We estimated divergence among populations by computing the F_{ST} pairwise matrices (Weir and Cockerham, 1984), using 1000 permutations in Arlequin version 3.5.1.2 (Excoffier et al., 2005).

We evaluated the genetic structure of yew populations by using the Bayesian clustering approach implemented in the software STRUCTURE v.2.3 (Pritchard et al., 2000). This method infers the most likely number of genetic groups (*K*) in which individuals can be clustered based on genotypic data. We performed ten runs for each value of *K*, ranging from one to ten. Each run consisted of 100,000 burn-in iterations and 100,000 data collection iterations. We averaged multiple runs for the same *K* value by using the online software CLUMPAK (Kopelman et al., 2015). We chose the optimal number of *K,* by calculating both the Evanno et al. (2005)'s ΔK statistic and the Puechmaille (2016)'s coefficients. Diversity estimates and F_{ST} pairwise estimates were also computed for the identified genetic groups.

We complemented the evaluation of the genetic structure of yew populations with a multivariate approach, that is a Principal Coordinate Analysis (PCoA) on the matrix of pairwise among-individual genetic distances by using GenAlEx.

2.5. Tree-ring analysis and climate-growth relationships among genetic groups

We mounted all tree cores on wooden supports after air drying and polished them with progressively finer sandpapers. We visually cross-dated each core and then measured ring widths using a semi-automatic system (LINTAB-TSAP, Rinntech, Germany) at 0.01 mm accuracy. We used the COFECHA software to check the visual cross-dating (Holmes, 1983). Tree-ring widths of most of the samples were dated, measured, and synchronized. However, some samples were rejected because portions of rotten wood made the series too short to be suitably synchronized. Using the "bai.in" function in the dplR package of R software, we transformed tree-ring width series into basal area increment (BAI) series and the 95 % confidence interval of mean BAI series for male and female trees calculated using 1000 bootstrap resampling to detect sex differences. We compared the measurements by calculating descriptive statistics in each population, such as the first-order autocorrelation (AC), the Mean Sensitivity (MS), and the inter-series correlation (Rbar) (Briffa and Jones, 1990). Then, we detrended the tree-ring series by fitting cubic spline functions to remove the age-, size- and disturbance-related trends and to emphasize the high-frequency growth variability (Cook and Kairiukstis, 1990). We set the smoothing spline rigidity at 20 years and its wavelength cut-off value at 50 %. We detrended all measured series dividing observed by fitted values to obtain dimensionless increment indices. We developed the mean chronologies for all genetic groups resulting from the previous analyses (Chapter 2.6). We obtained the mean standard chronologies averaging individual indexed ring width series using a bi-weight robust method. We analysed growth responses to drought by comparing mean standard chronologies with monthly precipitation, temperatures and the SPEI drought index, using Pearson correlations for the common period 1951–2018. Data on precipitation and temperature, essential for calculating the SPEI, were obtained from E-OBS v28.0e 0.1° x 0.1° regular grid (Cornes and Jones 2018). We first computed monthly climate data (precipitation, minimum and maximum temperature) and then we calculated the SPEI using the "SPEI" R package (Vicente-Serrano and Beguería, 2017). The SPEI index was calculated using window lengths of 1, 3, 6, 9, and 12 months. We assessed the stability of climate signals detected in this analysis by calculating moving response coefficients using 40-year moving windows and a 1-year offset. We bootstrapped function parameters to calculate their significance and confidence intervals, using the "treeclim" R package (Zang and Biondi, 2015).

2.6. Growth responses to extreme drought

We detected the potential extreme drought events based on a SPEI threshold of −1.65 (Agnew, 2000). For these years, we calculated the

Lloret resilience components (Lloret et al., 2011) on individual detrended series using the "res.comp" fuction in "pointRes" R package (van der Maaten-Theunissen et al. 2015). For calculating resilience components, we considered 4 years of pre- and post-disturbance and the maximum length of the recovery period equal to 10 years. First, we estimated resistance (*Rt*) on individual series. To determine if Rt values were significantly different from randomly selected sets of years, we used bootstrap resampling to randomly select sets of years from the individual time series and to estimate significances (95 %-confidence) for the departures from the bootstrap mean. Then, we computed the other Lloret indices, i.e. resistance (*Rt*), recovery (*Rc*), resilience (*Rs*) and relative resilience (*RRs*), and the growth recovery time (GRT, Thurm et al., 2016) only on trees showing significant low *Rt* values.

3. Results

3.1. Genetic diversity and structure

Overall, we identified a total of 98 alleles. MTA was the site with the highest mean number of alleles per locus ($Na = 7.2$), while ADL showed the highest number of private alleles ($Np = 18$), i.e. alleles exclusively found in only one site and absent in the others. The inbreeding coefficient (F_{IS}) was positive, even if not significantly larger than zero, in all sites, and it was higher in MTA and INT ($F_{IS} = 0.097$ and 0.071, respectively) with respect to ADL ($F_{IS} = 0.004$). Similar level of genetic diversity was detected for the three populations ($He_{MTA} = 0.60$; $He_{INT} = 0.57$; $He_{ADL} = 0.62$). All estimated indexes of genetic diversity are reported in Supplementary Table 2.

We found a significant ($P < 0.01$) but very low level of genetic differentiation between MTA and INT ($F_{ST} = 0.006$), which means that the two sites showed genetic similarity (Table 1). On the contrary, ADL was more genetically differentiated from the other two sites, with a F_{ST} of 0.138 and 0.174 with MTA and INT, respectively (Table 1).

In agreement with differentiation estimates (Table 1), PCoA showed a clear separation among ADL and the other two sites (MTA and INT), which grouped together (Fig. 2). Similarly, the Bayesian clustering analysis identified $K = 2$ as the best partitioning of the entire sample considering the ΔK value (Fig. 3a), separating MTA and INT from ADL.

The Puechmaille coefficients (MedMedK, MedMeaK, MaxMed K, MaxMeaK) suggest a further level of genetic structuring at $K = 3$ (Fig. S1), with the individuals from MTA and INT splitting in two genetic groups. Sampled individuals in MTA and INT are clearly genetically distinct from the individuals of ADL both considering the subdivision into two (G_1, light blue; G_2, orange) and three ($G_{1.1}$, light blue, $G_{1.2}$, blue and G_2, orange) genetic groups (Fig. 3). For $K = 2$, few individuals show introgression from genetic groups of the other population. At $K = 3$, considering a threshold of $q > 0.7$ to assign individuals to one of the genetic groups, G_2 group was constituted only by ADL trees (94 out of the overall 96 individuals), while $G_{1.1}$ and $G_{1.2}$ groups included both MTA and INT individuals. In particular, $G_{1.1}$ comprised 83 individuals (31 MTA and 52 INT) and $G_{1.2}$ 69 individuals (40 MTA and 29 INT). The remaining 52 trees (24 MTA, 26 INT and 2 ADL) resulted "admixed" ($0.30 < q < 0.70$) among the three genetic groups, mostly between $G_{1.1}$ and $G_{1.2}$. The genetic groups identified in MTA and INT do not show spatial clustering (Fig. S2).

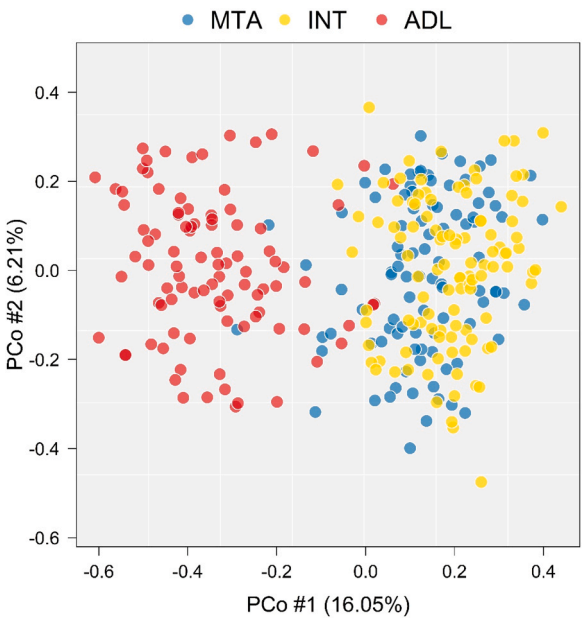

Fig. 2. Results of the Principal Coordinates Analysis (PCoA) on the matrix of pairwise genetic distances. On the axis labels, the percentage of variance explained by the first and second coordinates are shown in brackets. Each circle represents an individual and it is coloured based on its site.

Genetic diversity estimates for the genetic groups identified by STRUCTURE are reported in Supplementary Table 3. No substantial differences were found among genetic groups even if we observed an inbreeding coefficient of $G_{1.1}$ that was lower that of $G_{1.2}$ ($F_{IS} = 0.055$ and 0.091, respectively). Moreover, the two genetic groups $G_{1.1}$ and $G_{1.2}$ showed a significant differentiation ($F_{ST} = 0.061$) supporting the relevance of population sub-structuring.

3.2. Tree-rings statistics

Sampled yews feature a mean age of 105.7, 73.0 and 75.6 years at MTA, INT and ADL, respectively (Table 2, Fig. 4). Mean tree-ring width is similar at all sites, with lower values at MTA where trees are older. Inter series correlation (Rbar) is higher at MTA and INT sites, while ADL has lower mean sensitivity (MS) and higher first order autocorrelation.

We could determine the sex of only 107 individuals (63 females and 44 males), and we did not find any significant differences in BAI between sexes in the period 1981–2020. After 2004, individuals at the INT site experienced a growth release likely due to a silvicultural intervention for converting coppice to high forest (Fig. 4), and there are no significant differences in growth between male and female individuals during the suppressed period or the release phase (Fig. 5).

The G_2 genetic group corresponds almost entirely to the ADL series, except for two trees identified as "admixed". Therefore, we did not set an average ADL "admixed" chronology, while we included the admixed samples of INT and MTA in the same chronology. In the $G_{1.1}$, $G_{1.2}$ and "admixed" genetic groups we found no differences in the average ring

Table 1
Pairwise comparisons of genetic differentiation (F_{ST}) among yew populations (study sites) and genetic groups.

Study sites				Genetic groups				
	MTA	**INT**	**ADL**		**$G_{1.1}$**	**$G_{1.2}$**	**G2**	**Admixed**
MTA	0.000			**$G_{1.1}$**	0.000			
INT	0.006*	0.000		**$G_{1.2}$**	0.061**	0.000		
ADL	0.138**	0.174**	0.000	**G2**	0.189**	0.163**	0.000	
				Admixed	0.016**	0.020**	0.142**	0.000

**, $P < 0.001$; *, $P < 0.01$.

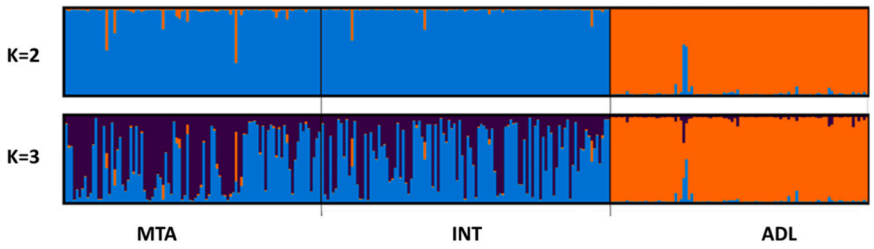

Fig. 3. Percentages of membership (q) for each of the genetic groups identified at $K = 2$ (G_1 in light blue and G_2 in orange) and $K = 3$ ($G_{1.1}$ in light blue, $G_{1.2}$ in dark blue and G_2 in orange). Each individual tree is represented by a bar divided into coloured segments, the lengths of which indicate the proportions of the genome that are attributed to the specific genetic group.

Table 2
Statistics of tree-ring series grouped by site and genetic group. TRW – tree ring width, MS – mean sensitivity, Rbar – interseries correlation, AC – autocorrelation.

		N. trees	Period (years)	Mean Length (years)	Mean TRW (mm) ± σ	MS	Rbar	AC(1)
Site	**MTA**	80	1860–2022	105.7	0.98 ± 0.54	0.304	0.417	0.692
	INT	89	1899–2022	73.0	1.19 ± 0.80	0.321	0.495	0.719
	ADL	80	1883–2018	75.6	1.14 ± 0.69	0.259	0.385	0.803
Genetic group	**$G_{1.1}$**	65	1860–2022	82.3	1.11 ± 0.70	0.313	0.470	0.681
	$G_{1.2}$	53	1869–2022	93.2	1.13 ± 0.71	0.314	0.513	0.693
	G_2	74	1884–2018	74.8	1.16 ± 0.70	0.257	0.393	0.803
	admixed	47	1867–2022	93.3	1.11 ± 0.68	0.307	0.462	0.711

width values, tree cambial age and other tree-ring statistics (Table 2).

3.3. Yew growth response to drought

In the interval 1951–2018, the growth of yew trees was sensitive to temperatures and precipitation (Fig. 6). The average temperatures in February and March have a positive and significant relationship with growth in all sites and genetic groups. However, the temperatures in July and August, as well as low summer precipitation (from June to August), were limiting for radial growth. Regarding the SPEI, which efficiently allows to analyse the combined role of precipitation and temperature, we found significant radial growth responses, especially in genetic groups $G_{1.1}$, $G_{1.2}$ and for the "admixed" trees (Fig. 6). These three groups showed similar response to droughts conditions that were significant in limiting tree growth during the period June-October. In $G_{1.1}$, $G_{1.2}$ and "admixed", the highest and significant correlation coefficients resulted between tree-ring chronologies and 3-month August SPEI. Also, in G_2 there are significant responses to 1-month SPEI in July and 3-month in August. $G_{1.2}$ and "admixed" chronologies were significantly correlated with 3-month March SPEI while 1-month January SPEI resulted significant only for "admixed" chronology. The relationship with long-term droughts (SPEI 9 and SPEI 12 months) is not significant in any genetic group. The moving correlation analyses revealed stability of summer drought sensitivity in $G_{1.1}$, $G_{1.2}$ and "admixed" while a progressive increase of significance of 3-month August SPEI in G_2 (Fig. 7).

3.4. Impact of extreme droughts

The analysis of climate records revealed only one extreme drought occurred in year 2003. We detected this drought event at all study sites, and we quantified it with an August 3-month SPEI value equal to −2.12 in MTA and INT, and a value of −2.18 in INT. In terms of resistance, the 2003 drought affected severely the studied yew trees, causing abrupt radial growth reductions in most of them (Fig. 8). The percentage of trees showing a significant growth decline ranged from 65 % in G1.1 group to 87 % in G1.2. Generally, yews affected by the intense drought event had high recovery rates (Rc>1). Consequently, four years after the drought, the radial increments were equal to pre-disturbance levels in all the genetic groups (Rs=1), except for G2 which showed a lower median value (Rs=0.89). Growth recovery time occurred in around one year for G1.1, G.1.2 and "admixed" groups, while G2 yews needed more than three years to recover (Table 3). Relative resilience indices showed distribution patterns similarly to recovery indices, and they were inversely proportional to Rt, e.g. G1.2 group showed the least Rs and the highest RRs values.

4. Discussions

4.1. Genetic variability and structure

The genetic characterization of forest tree species is crucial from both evolutionary and applied perspectives. It underpins the genetic monitoring needed to track changes in the adaptive potential of specific forests through time (Aravanopoulos, 2016). For endangered species and populations with a complex genetic structure, it could also significantly help selecting the propagation material with ad-hoc genetic features for conservation purposes (Maroso et al., 2021, Vajana et al., 2024). The common yew is a typical case of endangered species, and despite its broad natural range spanning from North Africa to central Europe, its local distribution shrank and became more fragmented over the past centuries (Benham et al., 2016). The most likely drivers of increasing fragmentation are climate change and anthropogenic disturbances, including intensive land use, livestock grazing and wildfires (Paule et al., 1993). Our data, although limited to three stands, were not only functional for the main aim of the work but also revealed population-specific features and a rather peculiar genetic structure which have conservation implications. All three populations, especially ADL, harboured a substantial number of private alleles, most of them at very low allelic frequencies, indicating a high risk of losing this component of diversity.

Intriguing results come from the analysis of the genetic structure of the three populations. As expected, given their spatial contiguity, the MTA and INT populations are genetically similar (F_{ST} close to zero), whereas both are markedly different from ADL, suggesting disrupted genetic connectivity. The genetic divergence featured by the ADL population is also due to the presence of several private alleles, some even at high allelic frequencies. Genetic surveys of fragmented yew populations at the regional scale often found rather high genetic differentiation at short spatial distance [e.g. 13 % and 16 % of the total molecular variance due to differences among populations in Poland and Belgium found by Chybicki et al. (2024a) and Casier et al. (2024), respectively]. These studies also revealed a complex genetic structure in terms of the number

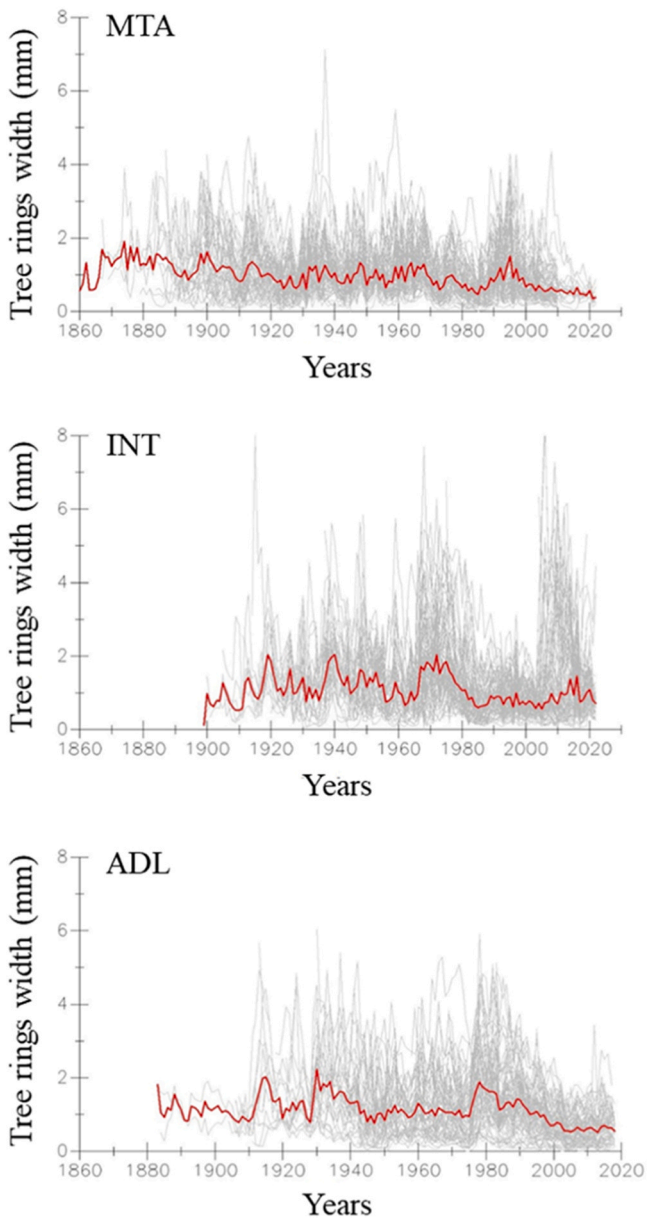

Fig. 4. Raw tree-ring measured series at the three study sites. Red line refers to the mean chronology.

of differentiated genetic groups detected, which often approached the number of characterized populations. A similar scenario was detected, for instance, in the critically endangered, highly fragmented conifer *Picea omorika* (Mataruga et al., 2020) due to strong limitations to gene flow during the pollen release season (Aleksić et al. 2022). The almost complete absence of long-distance pollen flow is indeed the main driver of disrupted connectivity also in yew (Chybicki et al., 2024a), highlighting the impact of spatial isolation on increasing the risk of genetic depauperation in this species. Furthermore, all studied populations showed a positive average fixation index (F_{IS}), with particularly large values in MTA and INT, indicating high inbreeding. Studying the genetic consequences of fragmentation in yew, Chybicki et al. (2011) found similarly high values in a population characterized by high density, exactly as in MTA and INT, thus hypothesising that local density may exacerbate the effect of isolation on gene flow dynamics.

Altogether, our results highlighted signals of negative genetic consequences in the marginal MTA and INT populations and disrupted genetic connectivity with ADL. In addition, the presence of two well-differentiated genetic groups within MTA-INT reveals a further level of complexity in the genetic structure at the local scale. However, the absence of yew populations between MTA-INT and ADL and near MTA-INT, together with the similar age distribution of the two genetic groups observed at MTA-INT, prevented us from developing solid hypotheses about the genesis of such a particularly complex genetic substructure. Such complexity is sometimes detected in wind-pollinated forest trees and might be due to factors, unaccounted in our study, such as flowering phenology or historical management (e.g. Piotti et al., 2013, Danusevičius et al., 2024). Since northern and central Apennines belong to a longitudinal belt considered as a long-lasting admixture zone between genetic groups which started differentiating at the beginning of the Quaternary (Mayol et al., 2015), genetic characterization of other yew populations in the surrounding area could also help to understand the presence of two intermingled genetic groups in MTA and INT.

4.2. *Yew cambial age and tree-ring growth*

The common yew is a very long-lived tree, reaching ages of over 2000 years (Thomas and Polwart, 2003). In our populations, individuals were much younger, primarily due to previous land use and forest coppicing. The oldest individuals were found at MTA with a maximum cambial age of approximately 160 years, even though it could be underestimated since some specimens had a hollow trunk. Tree-ring series exhibited growth release after a recent thinning. In our study sites the yew trees generally grow understory, and their radial growth was often largely limited by the dominant canopy of broadleaved species, both spatially and over time with inter-individual differences. For this reason, tree-ring chronologies exhibited relatively low inter-series correlations ranging between 0.46 and 0.51, but in line with similar studies (Galvin et al., 2014, Tayyab et al., 2023, Bebchuk et al., 2024). This could limit the strength of the climate signal present in the mean chronologies (population level) and their reliability for climate reconstructions (Bebchuk et al., 2024, Bebchuk et al., 2025). For dendroecological purposes, investigating the individual responses to specific extreme climatic events (such as droughts) may provide better comprehension of climate-growth relationships. It is generally accepted that yew trees showed divergent growth trends between male and female trees because the latter's higher reproduction costs cause lower annual increments (Obeso, 2002, Bañuelos and Obeso, 2005, Iszkuło et al., 2009, Cedro and Iszkuło 2011). At our sites we were unable to determine the sex due to the absence of arils or cones on numerous trees. Although female trees on average grew lower than male trees, we did not find a significant influence of dioecy on radial growth, consistent with findings from previous studies in the MTA population (Garbarino et al., 2015). In addition, we found low site fertility at the three sites which may have hidden radial growth inter-gender differences. The low seed production in the studied forests may be associated with water stress conditions, high forest densities, competition with other species, and elevated levels of forest canopy closure (Chybicki et al., 2024b). The reliability of these results is limited by challenges in sex determination during dendrochronological sampling, which could be improved by multi-year data collection beyond the single year of observation.

4.3. *Yew sensitivity to droughts*

Common yew is considered a shade and drought-tolerant species (Ahmadi et al., 2022) and Brzeziecki and Kienast (1994) assigned the species the value 2 in a 1–5 scale where 1 is very tolerant to drought. A recent study revealed that in the Caucasus region average wintertime temperature is the most important factor influencing annual tree-ring growth in common yew (Kvaratskhelia and Gavashelishvili, 2025). Dendroclimatological analyses in Poland reported that winter and early spring air temperature are the main factors affecting the annual ring widths, with summer drought as an additional limiting factor, especially in the northwestern regions (Cedro and Cedro, 2015, Cedro, 2023).

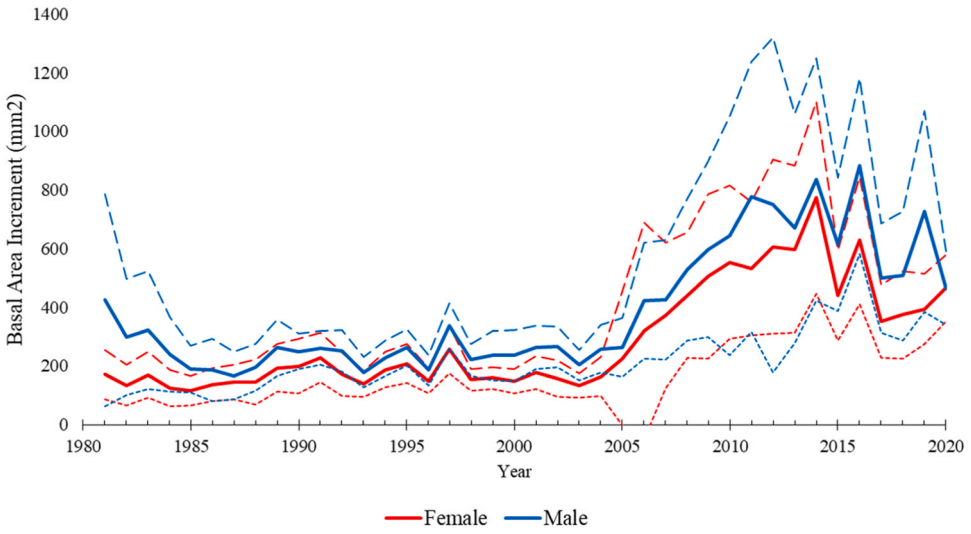

Fig. 5. Female and male yews BAI mean chronologies at INT site. The solid lines correspond to the bootstrapped mean, the dashed lines to the upper limit, and the dotted line to the lower limit (95 % confidence interval).

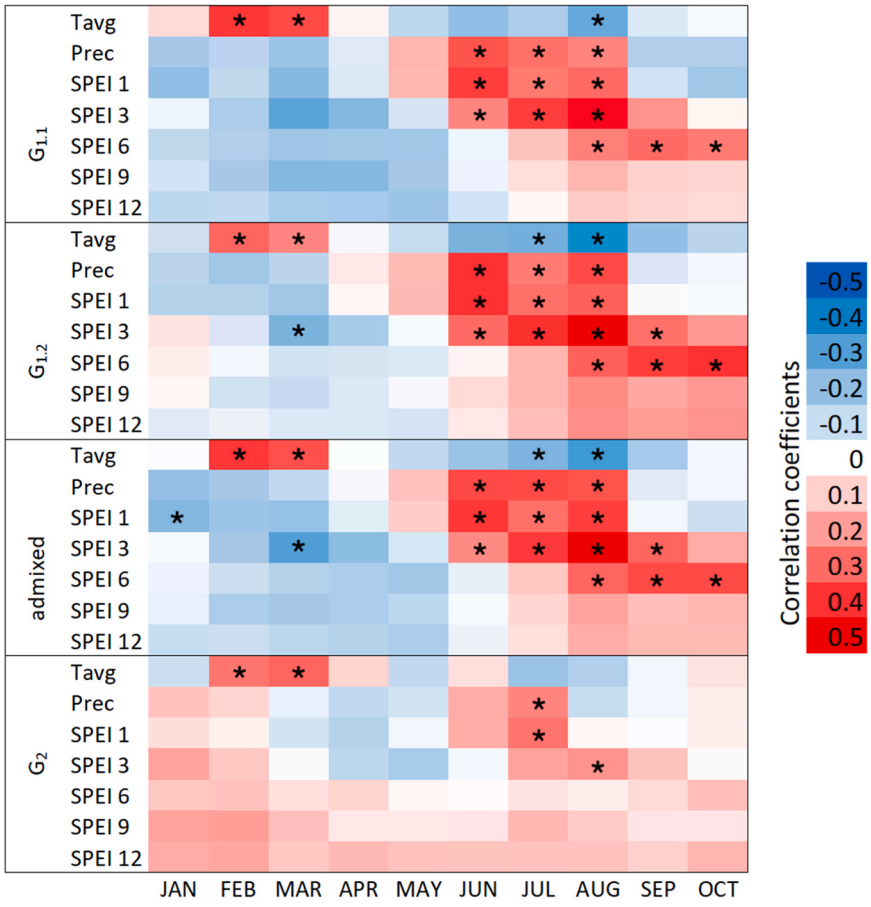

Fig. 6. Correlation coefficients between standard chronologies, average temperature (Tavg), Precipitation (Prec) and 1-, 3-, 6-, 9- and 12-month SPEI index, for the period 1951–2018. Asterisks indicate 95 % significant bootstrap confidence interval.

These findings are also supported by the populations included in our study, which consistently show positive correlations with February and March temperatures. Nonetheless, populations near the southern edge of the species distribution range may be more sensitive to periods of drier conditions (Linares, 2013). In our populations, especially individuals in the G1.1 and G1.2 (growing in MTA and INT sites with lower rainfalls), appeared to be particularly sensitive to the 3-month Standardized Precipitation-Evapotranspiration Index (SPEI) in August. Studies on the sensitivity to drought indices (such as SPEI or PDSI) are lacking because generally these relationships are assessed only in terms of temperatures or precipitation. In Starohorské Mountains (Slovakia), the growth of yew trees was positively affected by higher precipitation during the

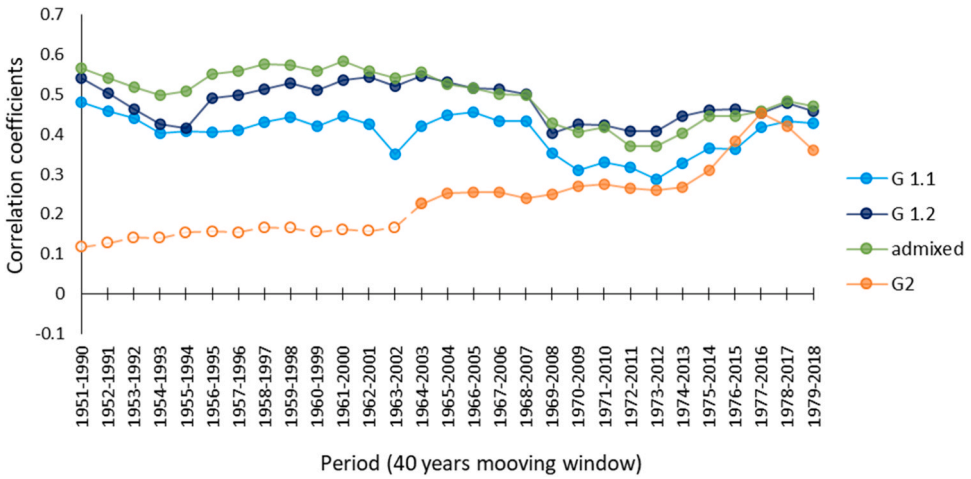

Fig. 7. Pearson's correlation coefficients computed using 40-year moving windows between standard chronologies and August 3-month SPEI index (period of analysis: 1951–2018). Filled dots point to significant 95 % bootstrap confidence interval.

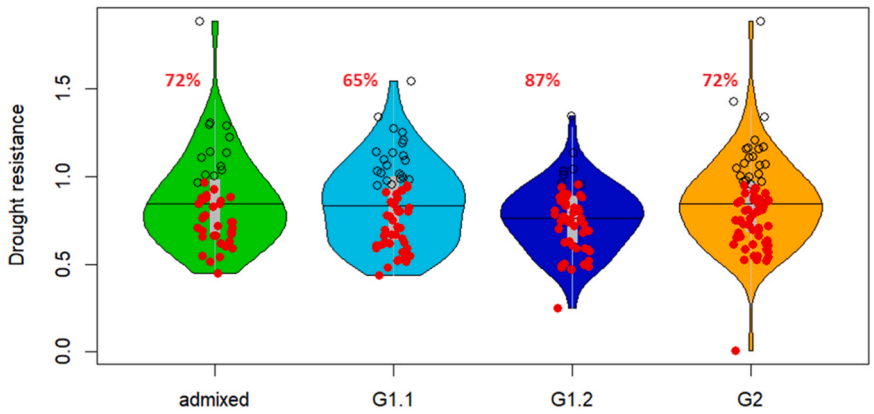

Fig. 8. Individual resistance (Rt) of yew trees during the 2003 severe drought event. Horizontal black line indicates the median. Percentage reported in red indicates the frequency of trees (red points) showing a significant growth decrease (95 % confidence).

Table 3
Median values of Lloret indices grouped by site genetic group. Interquartile ranges are in parentheses. Statistics rely only to drought affected trees (see Fig. 8).

	G1.1	G1.2	G2	admixed
Rc- recovery	1.22 (1.08–1.54)	1.34 (1.16–1.61)	1.19 (0.01–1.35)	1.24 (1.12–1.38)
Rs-resilience	0.97 (0.80–1.14)	0.94 (0.85–1.16)	0.89 (0.77–1.01)	0.95 (0.76–1.03)
RRs-relative resilience	0.18 (0.05–0.42)	0.27 (0.11–0.43)	0.14 (0.01–0.26)	0.19 (0.08–0.28)
GRT- growth recovery time	1.24 (0.53–4.76)	1.02 (0.52–3.66)	3.35 (1.90–7.00)	0.89 (0.60–2.67)

summer (June–August) and September, while higher temperatures in the spring and early summer (May–June) caused radial growth reduction (Sedmáková et al. 2017). In our study, we explored the effect of the extreme drought in 2003 on individual trees. This event was one of the most severe in Europe, and its effects on forest tree species were described by several authors (e.g. Ciais et al., 2005, Rebetez et al., 2006). In our study, most of the genetic groups had relatively low percentages of individuals affected by the drought event. In dendrochronology, usually the 75 % threshold on the percentage of trees showing a negative (or positive) event year are considered negative (or positive) pointer years (Cropper, 1979, Schweingruber et al., 1990). Only in the G1.2 group, more than 75 % of individuals exhibited a significant ring width reduction. In terms of growth recovery time, the G1.1, G1.2 and "admixed" groups showed a similar average period of about one year. The recovery period, on the other hand, appeared to be much longer for individuals at the ADL site, belonging to the G2 genetic group. In this case, the average recovery period was of 3 years, with some individuals raising to seven years the time needed to regain the pre-disturbance growth rates. These results are consistent with those of Peñuelas et al. (2000), where Mediterranean sclerophyllous tree species were negatively physiologically affected for more than 3 years after a drought event in 1994. Altogether, the peculiar responses to drought registered in differentiated genetic groups, particularly those sharing the same environmental conditions, emphasize the urgency of moving to functional genomic studies in natural conditions to understand how specific genes, or gene networks, regulate individual growth. However, studying phenotype-genotype associations in species/populations characterized by strong genetic structure can be particularly challenging due to difficulties in clearly separating the effect of site/microsite conditions from that of genetics (Santure and Garant, 2018). First attempts to disentangle the effect of microsite conditions and genetics on dendrochronological responses in the wild pointed towards the prevalence of the former even in markedly outcrossing species, characterized by low genetic structure (Avanzi et al., 2019; Zacharias et al., 2021). Besides that, the presence of genetic sub-structuring within the MTA and INT populations, associated to different ecophysiological responses, highlighted the need for taking such hierarchy in the genetic layout of populations

into account for conservation initiatives based on seed collection. An accurate spatial survey of genetic diversity represents the basis of seed collections not introducing genetic bottlenecks in reafforestation material (Gömöry et al., 2021).

4.4. Mitigating yew drought stress

Although yew trees in the G2 group showed lower sensitivity to droughts in the period 1950–2018, the analysis on moving windows revealed that the drought influence increased in recent years. This trend is likely due to the overall temperatures rise, a phenomenon affecting particularly the Mediterranean area, which is considered a climate change hotspot (Cos et al., 2022). At the ADL site, drought events may increase both in frequency and severity in the future (Spinoni et al., 2017). G2 group trees were the least resilient to the 2003 drought event, whereas yews at INT and MTA (genetic groups G1.1, G1.2, and admixed) recovered pre-disturbance growth rates in just one year. Additionally, trees belonging to the G1.1 group also exhibited the highest levels of drought resistance. Therefore, we hypothesized that trees of this group were the fittest to withstand periods of drought and could be favoured for future reforestation programs. We never found within the same site a relevant frequency of G1 and G2 individuals, precluding the assessment of these two genetic groups under identical water stress conditions. Nonetheless, the 2003 drought event was more intense at MTA and INT sites than at ADL. Drought stress can also be mitigated by silvicultural treatments in existing populations. Yew conservation actions should focus on selective thinning to reduce the basal area of competing neighbour trees, around the retention yew tree, but also avoid to excessively reduce the canopy cover for maintaining a suitable soil moisture, and a regular radial growth (Piovesan et al., 2009). Furthermore, especially for juvenile trees, the presence of a sheltering layer of shrubs could be necessary for their survival, particularly against summer drought and animal browsing (Calvia et al., 2023).

5. Conclusions

We investigated the climate sensitivity of different genetic groups of common yew at three populations in central Italy. Although yew trees generally exhibit drought tolerance, particularly extreme events like the one in 2003, can limit their radial growth. The genetic characterization revealed medium/low levels of genetic diversity, with significant numbers of private alleles, indicating a high risk of losing genetic diversity. By combining genetic and dendrochronological analyses, we obtained valuable information for planning reforestation programs and implementing species conservation strategies at a local scale. The study suggested that yew trees from certain genetic groups (G1.1 and G1.2) are more resilient to drought and could be prioritized for future reforestation programs, particularly at xeric sites. In future studies it is recommended to characterize regeneration (seedlings and saplings) to better understand reproductive dynamics under changing climatic conditions. Furthermore, including these populations into broader geographical genetic surveys will help reconstruct their origin and evolutionary dynamics. Lastly, when ad-hoc genomic resources will be available for common yew, conducting genetic association studies in natural settings would provide deeper insights into the genetic basis of the species' phenotypic variation.

CRediT authorship contribution statement

Enrico Tonelli: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation. **Camilla Avanzi:** Writing – review & editing, Visualization, Software, Methodology, Formal analysis, Data curation. **Elena Bitocchi:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Alessandro Vitali:** Writing – review & editing, Methodology, Investigation. **Andrea Piotti:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization. **Ilaria Spanu:** Writing – review & editing, Software, Methodology, Data curation. **Elena Barocci:** Writing – review & editing, Data curation. **Carlo Urbinati:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Funding and acknowledgements

This research project was funded by the EU Rural Development Program of the Marche Region (PSR Marche, Measure 15.2, Action a). We wish to thank: Dr. Lorella Brandoni of the Marche Region for administrative support during the different steps of the project; the Volpi family for authorization to conduct the analysis in their forest property (ADL); Dr. Valeria Gallucci of the Forest National Guard (Carabinieri forestali) for sampling authorization; Francesco Malandra, Massimo Prosdocimi, Francesco Belli, Danny Pietroni, and Federica Tartaglia for their contributions during field and laboratory work.

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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2025.126360.

Data availability

Data will be made available on request.

References

Agnew, C., 2000. Using the SPI to identify drought. Drought Netw. N. 12.
Ahmadi, K., Alavi, S.J., Hosseini, S.M., 2022. Modeling response curves of European yew (Taxus baccata L.) using HOF models along the environmental gradient in north of Iran. Acta Ecol. Sin. 42. https://doi.org/10.1016/j.chnaes.2022.04.001.
Aleksić, J.M., Mataruga, M., Daničić, V., Cvjetković, B., Milanović, Đ., Giuseppe Vendramin, G., Avanzi, C., Piotti, A., 2022. High pollen immigration but no gene flow via-seed into a Genetic Conservation Unit of the endangered Picea omorika after disturbance. For. Ecol. Manag. 510. https://doi.org/10.1016/j.foreco.2022.120115.
Aravanopoulos, F.A., 2016. Conservation and Monitoring of Tree Genetic Resources in Temperate Forests (Phil. Curr. For. Rep. https://doi.org/10.1007/s40725-016-0038-8.
Avanzi, C., Piermattei, A., Piotti, A., Büntgen, U., Heer, K., Opgenoorth, L., Spanu, I., Urbinati, C., Vendramin, G.G., Leonardi, S., 2019. Disentangling the effects of spatial proximity and genetic similarity on individual growth performances in Norway spruce natural populations. Sci. Total Environ. 650, 493–504. https://doi.org/10.1016/j.scitotenv.2018.08.348.
Avanzi, C., Heer, K., Büntgen, U., Labriola, M., Leonardi, S., Opgenoorth, L., Piermattei, A., Urbinati, C., Vendramin, G.G., Piotti, A., 2020. Individual reproductive success in Norway spruce natural populations depends on growth rate, age and sensitivity to temperature. Hered. (Edinb.) 124. https://doi.org/10.1038/s41437-020-0305-0.
Bañuelos, M.J., Obeso, J.R., 2005. How is fruit production regulated in the dioecious fleshy-fruited shrub Rhamnus alpinus? Basic Appl. Ecol. 6. https://doi.org/10.1016/j.baae.2004.12.004.
Bebchuk, T., Krusic, P.J., Pike, J.H., Piermattei, A., Friedrich, R., Wacker, L., Crivellaro, A., Arosio, T., Kirdyanov, A.V., Gibbard, P., Brown, D., Esper, J., Reinig, F., Büntgen, U., 2024. Sudden disappearance of yew (Taxus baccata) woodlands from eastern England coincides with a possible climate event around 4.2 ka ago. Quat. Sci. Rev. 323. https://doi.org/10.1016/j.quascirev.2023.108414.
Bebchuk, T., Moir, A.K., Arosio, T., Kirdyanov, A.V., Torbenson, M.C.A., Krusic, P.J., Hindson, T.R., Howard, H., Buchwal, A., Norman, C.A.P., Büntgen, U., 2025. Taxus tree-ring chronologies from southern England reveal western European hydroclimate changes over the past three centuries. Clim. Dyn. 63. https://doi.org/10.1007/s00382-025-07601-2.
Benham, S.E., Houston Durrant, T., Caudullo, G., de Rigo, D., 2016. Taxus baccata in Europe: distribution, habitat, usage and threats. Eur. Atlas For. Tree Species.
Briffa, K.R., Jones, D., 1990. Basic chronology statistics and assessment. Pages in E., editors. Methods of Dendrochronology, pp. 137–153.

Brzeziecki, B., Kienast, F., 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. For. Ecol. Manag. 69. https://doi.org/10.1016/0378-1127(94)90227-5.
Calvia, G., Casula, P., Farris, E., Fenu, G., Fantini, S., Bacchetta, G., 2023. Shrub Cover and Soil Moisture Affect Taxus baccata L. Regeneration at Its Southern Range. Plants 12. https://doi.org/10.3390/plants12091819.
Casier, M., Van Diest, A., Aerts, R., Peeters, G., Van Acker, K., Hellemans, B., Honnay, O., Muys, B., 2024. Genetic diversity and structure of endangered native yew Taxus baccata in remnant populations in Belgium. For. Ecol. Manag. 553. https://doi.org/10.1016/j.foreco.2023.121633.
Castagneri, D., Carrer, M., Regev, L., Boaretto, E., 2020. Precipitation variability differently affects radial growth, xylem traits and ring porosity of three Mediterranean oak species at xeric and mesic sites. Sci. Total Environ. 699. https://doi.org/10.1016/j.scitotenv.2019.134285.
Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data Br. 12, 662–666. https://doi.org/10.1016/j.dib.2017.05.007.
Cedro, A., 2023. Dendrochronology and dendroclimatology of yew in Poland. Dendrochronologia 78. https://doi.org/10.1016/j.dendro.2023.126068.
Cedro, A., Cedro, B., 2015. Growth-climate relationships at yew and wild service trees on the eastern edge of their range in Europe. For. Syst. 24. https://doi.org/10.5424/fs/2015243-07480.
Cedro, A., Iszkuło, G., 2011. Do females differ from males of European yew (Taxus baccata L.) in dendrochronological analysis? Tree-Ring Res 67. https://doi.org/10.3959/2009-9.1.
Chybicki, I.J., Oleksa, A., Burczyk, J., 2011. Increased inbreeding and strong kinship structure in Taxus baccata estimated from both AFLP and SSR data. Hered. (Edinb.) 107. https://doi.org/10.1038/hdy.2011.51.
Chybicki, I.J., Robledo-Arnuncio, J.J., Bodziarczyk, J., Widlak, M., Meyza, K., Oleksa, A., Ulaszewski, B., 2024a. Disrupted connectivity within a metapopulation of a wind-pollinated declining conifer, Taxus baccata L. For. Ecosyst. 11. https://doi.org/10.1016/j.fecs.2024.100240.
Chybicki, Igor J., Bodziarczyk, Jan, Meyza, Katarzyna, Oleksa, Andrzej, 2024b. Seed production in a dioecious subcanopy conifer tree taxus baccata: the positive effect of neighboring males and female heterozygosity. Scand. J. For. Res. 39 (5), 277–286. https://doi.org/10.1080/02827581.2024.2398248.
Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533. https://doi.org/10.1038/nature03972.
Cook, E., Kairiukstis, L.A., 1990. Tree-ring standardization and growth-trend estimation. Methods Dendrochronology.
Cos, J., Doblas-Reyes, F., Jury, M., Marcos, R., Bretonnière, P.A., Samsó, M., 2022. The Mediterranean climate change hotspot in the CMIP5 and CMIP6 projections. Earth Syst. Dyn. 13. https://doi.org/10.5194/esd-13-321-2022.
Cropper, J.P., 1979. Tree-ring skeleton plotting by computer. Tree Ring Bull. 39, 47–59.
Danusevičius, D., Rajora, O.P., Kavaliauskas, D., Baliuckas, V., Augustaitis, A., 2024. Stronger genetic differentiation among within-population genetic groups than among populations in Scots pine provides new insights into within-population genetic structuring. Sci. Rep. 14. https://doi.org/10.1038/s41598-024-52769-y.
van der Maaten-Theunissen, M., van der Maaten, E., Bouriaud, O., 2015. PointRes: an R package to analyze pointer years and components of resilience. Dendrochronologia 35, 34–38. https://doi.org/10.1016/j.dendro.2015.05.006.
Dubreuil, M., Sebastiani, F., Mayol, M., González-Martínez, S.C., Riba, M., Vendramin, G. G., 2008. Isolation and characterization of polymorphic nuclear microsatellite loci in Taxus baccata L. Conserv. Genet 9. https://doi.org/10.1007/s10592-008-9515-3.
Evanno, G., Regnaut, S., Goudet, J., 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. 14. https://doi.org/10.1111/j.1365-294X.2005.02553.x.
Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evol. Bioinforma. 1. https://doi.org/10.1177/117693430500100003.
Galvin, S., Potito, A., Hickey, K., 2014. Evaluating the dendroclimatological potential of Taxus baccata (yew) in southwest Ireland. Dendrochronologia 32. https://doi.org/10.1016/j.dendro.2014.03.004.
Garbarino, M., Weisberg, P.J., Bagnara, L., Urbinati, C., 2015. Sex-related spatial segregation along environmental gradients in the dioecious conifer, Taxus baccata. For. Ecol. Manag. 358. https://doi.org/10.1016/j.foreco.2015.09.009.
Gömöry, D., Himanen, K., Tollefsrud, M.M., Uggla, C., Kraigher, H., Bordács, S., Alizoti, P., A'Hara, S., Frank, A., Proschowsky, Gunnar, Friis, Frýdl, J., Geburek, T., Guibert, M., Ivankovic, M., Jurše, A., Kennedy, S., Kowalczyk, J., Liesebach, H., Maaten, T., Pilipovič, A., Proietti, R., Schneck, V., Servais, A., Skúlason, B., Sperisen, C., Wolter, F., Yükse, T., Bozzano, M., 2021. Genetic aspects in production and use of forest reproductive material: collecting scientific evidence to support the development of guidelines and decision support tools. European Forest Genetic Resources Programme (EUFORGEN). Eur. For. Inst.
Heer, K., Behringer, D., Piermattei, A., Bässler, C., Brandl, R., Fady, B., Jehl, H., Liepelt, S., Lorch, S., Piotti, A., Vendramin, G.G., Weller, M., Ziegenhagen, B., Büntgen, U., Opgenoorth, L., 2018. Linking dendroecology and association genetics in natural populations: stress responses archived in tree rings associate with SNP genotypes in silver fir (Abies alba Mill. Mol. Ecol. 27. https://doi.org/10.1111/mec.14538.
Holmes, R., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull.
Housset, J.M., Nadeau, S., Isabel, N., Depardieu, C., Duchesne, I., Lenz, P., Girardin, M. P., 2018. Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. N. Phytol. 218. https://doi.org/10.1111/nph.14968.
Iszkuło, G., Jasińska, A.K., Giertych, M.J., Boratyński, A., 2009. Do secondary sexual dimorphism and female intolerance to drought influence the sex ratio and extinction risk of Taxus baccata? Plant Ecol. 200. https://doi.org/10.1007/s11258-008-9447-5.
Kopelman, N.M., Mayzel, J., Jakobsson, M., Rosenberg, N.A., Mayrose, I., 2015. Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Mol. Ecol. Resour. 15. https://doi.org/10.1111/1755-0998.12387.
Krutovsky, K.V., 2022. Dendrogenomics Is a New Interdisciplinary Field of Research of the Adaptive Genetic Potential of Forest Tree Populations Integrating Dendrochronology, Dendroecology, Dendroclimatology, and Genomics. Russ. J. Genet 58. https://doi.org/10.1134/S1022795422110059.
Kvaratskhelia, R., Gavashelishvili, A., 2025. Common Yew (Taxus baccata) as a climate archive: Reconstructing 200 years of temperature change in Georgia (Caucasus). Dendrochronologia 89. https://doi.org/10.1016/j.dendro.2024.126285.
Linares, J.C., 2013. Shifting limiting factors for population dynamics and conservation status of the endangered English yew (Taxus baccata L., Taxaceae). For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2012.11.009.
Litkowiec, M., Lewandowski, A., Wachowiak, W., 2018. Genetic variation in Taxus baccata L.: A case study supporting Poland's protection and restoration program. For. Ecol. Manag. 409. https://doi.org/10.1016/j.foreco.2017.11.026.
Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.
Maroso, F., Vera, M., Ferreiro, J., Mayol, M., Riba, M., Ramil-Rego, P., Martínez, P., Bouza, C., 2021. Genetic diversity and structure of Taxus baccata from the Cantabrian-Atlantic area in northern Spain: A guide for conservation and management actions. For. Ecol. Manag. 482. https://doi.org/10.1016/j.foreco.2020.118844.
Mataruga, M., Piotti, A., Daničić, V., Cvjetković, B., Fussi, B., Konnert, M., Vendramin, G. G., Aleksić, J.M., 2020. Towards the dynamic conservation of Serbian spruce (Picea omorika) western populations. Ann. For. Sci. 77. https://doi.org/10.1007/s13595-019-0892-1.
Mayol, M., Riba, M., González-Martínez, S.C., Bagnoli, F., de Beaulieu, J.L., Berganzo, E., Burgarella, C., Dubreuil, M., Krajmerová, D., Paule, L., Romšáková, I., Vettori, C., Vincenot, L., Vendramin, G.G., 2015. Adapting through glacial cycles: insights from a long-lived tree (Taxus baccata). N. Phytol. 208. https://doi.org/10.1111/nph.13496.
Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.
Obeso, J.R., 2002. The costs of reproduction in plants. New phytol. 155 (3), 321–348.
Paule, L., Gömöry, D., Longauer, R., 1993. Present distribution and ecological conditions of the English yew (Taxus baccata L.) in Europe. Yew (Taxus) Conserv. Biol. Interact.
Peakall, R., Smouse, P.E., 2006. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Mol. Ecol. Notes 6. https://doi.org/10.1111/j.1471-8286.2005.01155.x.
Peñuelas, J., Filella, I., Lloret, F., Piñol, J., Siscart, D., 2000. Effects of a severe drought on water and nitrogen use by Quercus ilex and Phillyrea latifolia. Biol. Plant 43. https://doi.org/10.1023/A:1026546828466.
Perrin, P.M., Mitchell, F.J.G., 2013. Effects of shade on growth, biomass allocation and leaf morphology in European yew (Taxus baccata L.). Eur. J. For. Res. 132. https://doi.org/10.1007/s10342-012-0668-8.
Piotti, A., Leonardi, S., Heuertz, M., Buiteveld, J., Geburek, T., Gerber, S., Kramer, K., Vettori, C., Vendramin, G.G., 2013. Within-Population Genetic Structure in Beech (Fagus sylvatica L.) Stands Characterized by Different Disturbance Histories: Does Forest Management Simplify Population Substructure? PLoS One 8. https://doi.org/10.1371/journal.pone.0073391.
Piovesan, G., Saba, E.P., Biondi, F., Alessandrini, A., Di Filippo, A., Schirone, B., 2009. Population ecology of yew (Taxus baccata L.) in the central Apennines: Spatial patterns and their relevance for conservation strategies. Plant Ecol. 205. https://doi.org/10.1007/s11258-009-9596-1.
Pritchard, J.K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155. https://doi.org/10.1093/genetics/155.2.945.
Puechmaille, S.J., 2016. The program structure does not reliably recover the correct population structure when sampling is uneven: Subsampling and new estimators alleviate the problem. Mol. Ecol. Resour. 16. https://doi.org/10.1111/1755-0998.12512.
Rebetez, M., Mayer, H., Dupont, O., Schindler, D., Gartner, K., Kropp, J.P., Menzel, A., 2006. Heat and drought 2003 in Europe: A climate synthesis. Ann. For. Sci. https://doi.org/10.1051/forest:2006043.
Santure, A.W., Garant, D., 2018. Wild GWAS—association mapping in natural populations. Mol. Ecol. Resour. 18, 729–738. https://doi.org/10.1111/1755-0998.12901.
Sarris, D., Christodoulakis, D., Körner, C., 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. Glob. Chang. Biol. 13. https://doi.org/10.1111/j.1365-2486.2007.01348.x.

Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., 1990. Identification, Presentation and Interpretation of Event Years and Pointer Years in Dendrochronology. Dendrochronologia 8, 9–38.
Sedmáková, D., Saniga, M., Kucbel, S., Pittner, J., Kỳpetová, M., Jaloviar, P., Bugala, M., Vencurik, J., Lukácik, I., 2017. Irregular shelterwood cuttings promote viability of european yew population growing in a managed forest: A case study from the Starohorské Mountains, Slovakia. Forests 8. https://doi.org/10.3390/f8080289.
Spinoni, J., Naumann, G., Vogt, J.V., 2017. Pan-European seasonal trends and recent changes of drought frequency and severity. Glob. Planet. Change 148. https://doi.org/10.1016/j.gloplacha.2016.11.013.
Tayyab, M., Muhammad, S., Nawaz, H., Ali, A., Malik, S.M., Waheed, M., Rasool, K., Khan, M.J.T., Khan, Z.U.D., Zahid, M., 2023. Climatically induced anomalies in tree-ring structure of Abies pindrow (Royal ex D. Don) and Taxus baccata (L.) growing in Hindu-Kush mountainous region of Pakistan. Environ. Res. Commun. 5. https://doi.org/10.1088/2515-7620/acd7c8.
Thomas, P.A., Garcia-Martí, X., 2015. Response of European yews to climate change: A review. For. Syst. https://doi.org/10.5424/fs/2015243-07465.
Thomas, P.A., Polwart, A., 2003. Taxus baccata L. Biol. Flora Br. Isles 229. J. Ecol. 91.
Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglasfir stem growth. For. Ecol. Manag. 376, 205–220. https://doi.org/10.1016/j.foreco.2016.06.020.
Ueno, S., Wen, Y., Tsumura, Y., 2015. Development of EST-SSR markers for Taxus cuspidata from publicly available transcriptome sequences. Biochem. Syst. Ecol. 63. https://doi.org/10.1016/j.bse.2015.09.016.
Uzquiano, P., Allué, E., Antolín, F., Burjachs, F., Picornel, L., Piqué, R., Zapata, L., 2015. All about yew: on the trail of Taxus baccata in southwest Europe by means of integrated palaeobotanical and archaeobotanical studies. Veg. Hist. Archaeobot. https://doi.org/10.1007/s00334-014-0475-x.
Vajana, E., Andrello, M., Avanzi, C., Bagnoli, F., Vendramin, G.G., Piotti, A., 2024. Spatial conservation planning of forest genetic resources in a Mediterranean multi-refugial area. Biol. Conserv 293. https://doi.org/10.1016/j.biocon.2024.110599.
Vicente-Serrano, S.M., Beguería, S., 2017. Calc. Stand. Precip. -Evapotranspiration Index. R. -Package.
Weir, B.S., Cockerham, C.C., 1984. Estimating F-statistics for the analysis of population structure. Evol. (N. Y). 38. https://doi.org/10.1111/j.1558-5646.1984.tb05657.x.
Zacharias, M., Pampuch, T., Heer, K., Avanzi, C., Würth, D.G., Trouillier, M., Bog, M., Wilmking, M., Schnittler, M., 2021. Population structure and the influence of microenvironment and genetic similarity on individual growth at Alaskan white spruce treelines. Sci. Total Environ. 798, 149267. ⟨https://doi.org/10.1016/j.scitotenv.2021.149267⟩.
Zang, C., Biondi, F., 2015. Treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography (Cop.) 38, 431–436. https://doi.org/10.1111/ecog.01335.