



Drought responses of Italian silver fir provenances in a climate change perspective

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ABSTRACT

In a climate change perspective, the resilience of Mediterranean forest ecosystems is closely linked to their ability to cope with drought and rising temperatures. This ability can be influenced by genetic differences between and within species or provenances. In a changing environment, management guidelines should weight the risks associated both to local and/or non-local provenances, to promote the effective conservation and sustainable management of resilient forest genetic resources. In this study, we analysed the growth responses to drought of silver fir (*Abies alba*) in the Tuscan-Emilian Apennine National Park in natural and planted forests, comparing the growth performance of three provenances of this species in Italy: (a) Western Alpine - (b) Northern Apennine (local) - (c) Southern Apennine. Drought severity was defined by the Standardised Precipitation-Evapotranspiration Index (SPEI). We carried out dendrochronological analyses by assessing climate-growth relationships and applying drought 'resilience indices' (RRR) based on tree ring width. Planted forests showed faster mean growth than highly fragmented natural forests, higher resilience to severe drought and significantly higher recovery to severe drought. Fir provenances do not differ in mean growth rate, while the Southern Apennine provenance showed significantly better recovery (rec) and resilience (resl) especially compared to the Western Alpine provenance during moderate (rec +5–15%, resl +13–15%) and extreme (rec +20% %, resl +22%) drought years. The local provenance showed an intermediate behaviour. Southern and local provenances showed higher resilience to drought compared to the Western Alpine one, proving to be very important forest genetic resources in the context of climate change response strategies. Finally, the RRR indices trends calculated on the years identified by SPEI6 generally showed greater differences between provenances and regeneration modes than on the years identified by SPEI12, possibly due to the increase in recurrent short-duration droughts in mountainous contexts during the growing season. These results provide important information on the drought response of different silver fir provenances under climate change, highlighting the importance of taking into account the genetic background of forest reproductive materials in forest management and planning. Thanks to the close collaboration with the National Park and local forest managers, these results may find concrete application, e.g., by properly evaluating the usefulness of provenance assisted migration in the National Park forests and providing better management of remnant silver fir natural forests.

1. Introduction

The increasing impacts of climate change are severely affecting European forest ecosystems, which have shown signs of drought stress in recent years (Gazol and Camarero, 2022). Recent heat waves have triggered unprecedented mortality episodes in many forest tree species (Schuldt et al., 2020), leading to the loss of ecosystem services (Linder et al., 2010). A comprehensive understanding of the adaptive strategies

that forest tree species can adopt to cope with climate change is therefore required in order to mitigate its effects and inform forest management and planning (Keenan, 2015).

To boost forest resilience against the stressful conditions caused by climatic extreme events, planting new trees is considered a useful tool to increase the specific (Nadrowski et al., 2010) and genetic (Thompson et al., 2009) diversity. Indeed, the study of forest genetic resources (FGR) is an important aspect of forest management in a context of

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climate change (Knoke et al., 2008; Vinceti et al., 2020), and increasing intra-specific genetic diversity can have positive effects on the adaptive potential of a population (Dorado-Liñán et al., 2020). To increase the adaptive potential and resilience of forests to drought, ‘assisted migration’ is in the portfolio of silvicultural tools (Aitken and Bemmels, 2016), resulting in the use of forest reproductive material (FRM) from non-local provenances that can be better adapted to future climatic conditions (Breed et al., 2013; Mihai et al., 2021; Millar et al., 2007). Indeed, there is solid evidence that different forest provenances can show different eco-physiological and growth-dependent responses to environmental conditions (Correia et al., 2018; Fierravanti et al., 2020) and that some may perform better than others in the face of extreme drought events (Zas et al., 2020).

Planting non-local provenances is nonetheless a challenging task. Possible risks are the use of maladapted FRM or the introduction of new pests and diseases (Alfaro et al., 2014). Another barrier is the restrictions imposed by forest policies, which often limit the transfer of FRM across borders (Gömöry et al., 2021; Konnert et al., 2015). However, increasing scientific knowledge on the current and future species response to climate change may lead to more sensitive policies on these issues and raise awareness among forest managers, reducing the limitations and risks associated with the use of non-local FRM (Vinceti et al., 2020). The European Forest Genetic Resources Programme (EUFORGEN) has highlighted the importance of studies that address the performances of different forest species provenances and facilitate the sustainable use of FGRs and FRMs (Gömöry et al., 2021). These practices could greatly increase the resilience, stability and genetic diversity of forest ecosystems, and provide new insights into when and where assisted migration processes can help to effectively increase the adaptive potential of forests towards climate change (Konnert et al., 2015).

Silver fir (*Abies alba* Mill.) is among the most important forest tree species in Europe (Wolf, 2003). It is distributed in mountainous areas throughout Europe and contribute significantly to maintain biodiversity in forested areas (Dobrowolska et al., 2017), playing a key role in several habitats of conservation importance in the EU, including priority habitats (e.g., 9510*; European Union, 1992). Furthermore, its wood is widely used in construction (Dobrowolska et al., 2017; Mauri et al., 2016). In Italy, it is mainly distributed throughout the Alps while, in the Apennines, it has a highly fragmented distribution (Piotti et al., 2017; Rovelli, 1995). There is evidence that this species is suffering a decline due to climate warming mainly at its southern limits (Robson et al., 2018). Spring and midsummer droughts in both previous and current year significantly impact *A. alba* growth and mortality (George et al., 2015; Lebourgeois et al., 2013; Mazza et al., 2014; Mikulenska et al., 2020). However, the susceptibility of this species to climate change is still debated, as better drought tolerance has been observed in central Europe with respect to other forest species (Latreille et al., 2017; Tinner et al., 2013; Vitasse et al., 2019b).

Little is known about the range-wide levels of local responses of silver fir to climate. However, different silver fir provenances revealed very heterogeneous growth responses to drought, showing different recovery and resilience behaviours after a drought event (Dobrowolska et al., 2017; Lloret et al., 2011; Mihai et al., 2021; Wolf, 2003). Different silver fir provenances have also shown a diverse ecophysiological response to drought, in terms of photosynthetic rates and water and nutrient utilisation (Konôpková et al., 2020; Matfás et al., 2016). Such pieces of evidence reveal that genetically differentiated provenances could impact metabolic and developing ecosystem processes as well as forest growth and health. Differences among silver fir provenances facing drought years suggest the importance of using diverse FRM in reforestation, management, and conservation programmes. Given the lack of local scale data regarding growth responses to drought of genetically differentiated silver fir provenances, it is a priority to deepen our knowledge in order to adopt correct silvicultural measures, especially in a context of climate change. The main factors controlling tree growth are climate, competition and site conditions, which act through

close interactions (Calama et al., 2019) and must be taken into account to unravel the genetic component of tree growth.

The main objective of this study is to analyse the growth responses to drought of different provenance of silver fir during drought years. The study area is the National Park of the Tuscan-Emilian Apennines (Northern Apennines) where both natural and planted forests of silver fir occur. By investigating the genetic background of the planted forests, we found that they were established with material of mixed provenance (Southern Apennines, Northern Apennines (local) and Western Alps). This provided us with an ideal experimental setting to test the existence of differences in growth performances among silver fir provenances growing under similar environmental and climatic conditions. The specific objectives are to evaluate the growth responses to climate as a function of (i) the regeneration method of the forest (natural vs planted) and (ii) the silver fir provenances under investigation, while assessing (iii) the effect of competition and environmental factors on the growth response. In order to assess the growth response to changing climatic conditions, three levels of drought were assessed based on the SPEI drought index value (moderate, severe and extreme). The results can provide insights into the relationships between climate and growth, and can be actively useful for local forest management and planning, e.g., in the selection of the most suitable provenance for reforestation or assisted migration programs, and will contribute to study the effect of climate change on silver fir in Italy.

2. Materials and methods

2.1. *Abies alba* autochthonous and planted stands in the study area

The study area is within the Tuscan-Emilian Apennine National Park in the northern part of the Apennines, a Mediterranean mountain range in the Italian Peninsula. In this area, silver fir has a highly fragmented distribution, with few small and isolated natural populations (Piovani et al., 2010; Avanzi et al., submitted). These stands are the remnants of previously larger populations which were progressively eroded over the last thousand years by a still debated combination of climatic and anthropogenic factors (Di Pasquale et al., 2014; Magri et al., 2015; Morales-Molino et al., 2021). Several silver fir planted forests are present nearby natural populations. Such plantations were established during the 20th century, but no documentation is available about the origin of the planted material. The planted stands ranged from an elevation of 1000–1650 a.s.l. while natural populations from 1400 to 1650 a.s.l. From visual assessment, natural populations generally grow on more rocky and difficult terrain with respect to planted stands. Overall, the area is characterised by a Mediterranean Apennine climate, with dry summers and rainy autumns (Fig. S.4). The average annual rainfall is of 2100 mm, the average annual temperature of 7.5°C and the average daily temperature range of 6°C. The historical climate data of the study area was derived through the methodology described in (Brunetti et al., 2012) and refers to the period 1957–2017, considered as the study period based on the dominant age of the trees under study.

2.2. Reconstruction of the planted individual's provenance by genetic markers

In July-October 2019, sampling for genetic analysis was carried out. Approximately 24 trees at least 20 m apart were sampled from ten planted forests, selected to be the nearest and/or the largest stands in the reach of gene flow with natural populations (Fig. 1, Table S.1). Each individual was tagged and georeferenced with a metric handheld GNSS device (Garmin Ltd., USA). Fresh needles were collected from each individual for genetic analyses aimed at determining the genetic provenance of the planted trees. To this purpose, we took advantage of a genetic dataset collected through an extensive characterization of silver fir natural populations (Piotti et al., 2017; Santini et al., 2018 Avanzi et al., submitted). The available dataset was enriched by adding further

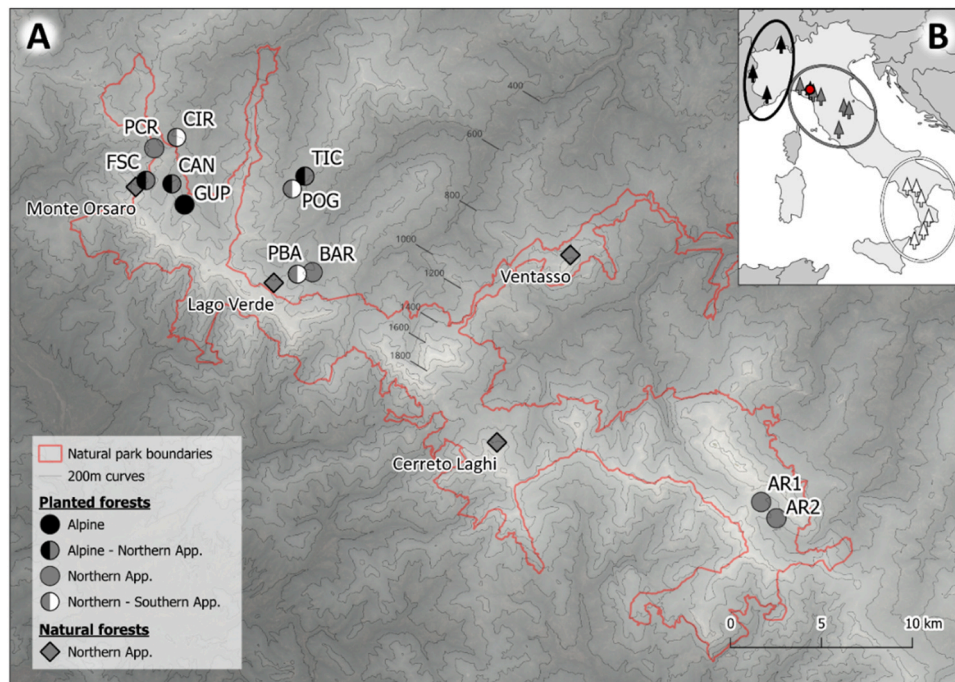


Fig. 1. A) Map of the 15 stands sampled in the National Park of the Tuscan-Emilian Apennine. Diamonds and circles represent natural and planted stands, respectively. Colours represent the provenance of each stand, as reconstructed by means of molecular markers (black: 'Western Alps'; dark grey: 'Northern Apennine' (local); white: 'Southern Apennine'). B) Map of the natural populations used as a reference dataset to reconstruct the provenance of the planted trees.

three natural populations from areas that represent potential seed sources for plantations (i.e., CLR, GOU and SUM in [Supplementary Materials 1](#), Fig. S.2).

All sampled trees from planted stands were genotyped at 16 unlinked and null allele free microsatellite markers (SSRs) (Aag01, Aat01, Aat02, Aat03, Aat04, Aat05, Aat06, Aat08, Aat09, Aat10, Aat11, Aat13, Aat14, Aat15 and Aat16: ([Postolache et al., 2014](#), NFF7: [Hansen et al., 2005](#)). The multiplexing and amplification procedures are described in [Postolache et al. \(2014\)](#).

A preliminary Bayesian clustering analysis was performed on 1907 silver fir individuals from 39 natural populations by using STRUCTURE v2.3 ([Pritchard et al., 2000](#)) to identify the most likely number of genetic clusters (K). STRUCTURE was run varying K from one to 15 and replicating each K ten times. Each run was made up of 1×10^5 burn-in iterations and 2×10^5 data collection iterations. Different runs for the same K were averaged by using CLUMPAK ([Kopelman et al., 2015](#)). The most likely K was selected based on the empirical statistic ΔK ([Evanno et al., 2005](#)) (Fig. S.1). An assignment test was then performed to compute the probability of silver fir individuals from planted stands to belong to each of the genetic clusters identified by the preliminary Bayesian clustering analysis (Fig. S.2). The assignment test was carried out by running STRUCTURE with the option USEPOPINFO, i.e., using individuals from natural populations as a reference dataset to which individuals from planted stands were to be assigned to. The reference dataset was assembled by selecting only the individuals which were assigned to a genetic cluster with a probability $>80\%$ in the previous analysis (Fig. S.3).

2.3. Data collection

During July-October 2020, the field survey sampling was carried out. Dendrometric, edaphic, and topographic data were collected in the field from 155 trees in 11 stands (2 natural and 9 planted). Data collection was completed, with an additional sampling of 45 trees in four stands, in June-September 2021 (2 natural and 2 planted, AR1 and AR2, whose local origin was demonstrated by genetic evidence in a previous study,

[Piotti and Avanzi, 2022](#)). In planted stands, only individuals which had been genetically characterized, and so for which provenance was known, were sampled for subsequent analysis. Each planted individual was assigned to a specific provenance based on two criteria applied on the assignment test results from genetic analyses (Fig. S.3): a probability of belonging $\geq 60\%$ to the first likely provenance, and $\leq 30\%$ probability of belonging to a second likely provenance. Approximately ten trees were sampled from each of the provenances included in that planted stand (Tab S.1). Trees were identified in the forest through the previously affixed tags. Approximately ten trees were sampled also in natural stands, and they were all considered as belonging to the local provenance. The following morphological data were collected for each tree: diameter, height, crown diameter, crown insertion height. Average topographic characteristics of the stand (elevation, exposure and slope) were measured by sampling the data for each of the 10 sampled trees and then averaging the values at stand level. At five points per stand, collected at one meter from the base of some of the measured trees, soil samples were collected to measure some edaphic parameters in the laboratory. Soil texture was obtained by means of the "Pipette Method" ([Paturno et al., 1997](#)). Soil samples were sieved at 2 mm, grinded $<200 \mu\text{m}$, and organic carbon I and percentage nitrogen (N) content was estimated using an elemental analyser (Carlo-Erba NA-1500 Elemental Analyzer). C/N ratio has been used as soil fertility proxy. For each sampled tree (i), the neighbourhood competition index (NCI) was calculated, which is a distance-dependent competition index that considers the competition experienced by each tree based on the diameter and distance of competing trees within a 10 m radius to a subject tree according to the following formula ([Canham et al., 2004](#))

$$\text{NCI} = \sum_{i=1}^n \frac{DBH_i}{dist_i} \quad (1)$$

Where DBH_i and $dist_i$ are the diameter and the distance of each competitor tree i to the subject tree, respectively. Finally, two wood cores corresponding to the trunk radius were collected at breast height (i.e., 1.30 m) from each of the surveyed trees using a Pressler's increment borer to perform dendrochronological analyses. When the trees

grow on a slope, the woody cores were taken perpendicularly to the slope to avoid wood compression or expansion (Martínez-Sancho et al., 2020).

2.4. Dendrochronological analysis

Tree cores were processed manually and analysed by scanning with an EPSON Perfection v850 Pro scanner at 2400 dpi resolution. Core samples were read using CooRecorder and CDendro software (v. 9.3.1 – Cybis, 2022; Maxwell and Larsson, 2021). The CDendro software was also used for crossdating the samples. Crossdating was carried out at two levels: at tree level, comparing the two cores collected on the same individual, and among trees. Different trees were crossdated by comparing, at the stand level, the two individual mean chronologies with the highest correlation coefficient and then proceeding with the comparison on the remaining trees. A final check was made by comparing the mean chronologies of the different stands. Growth rate of trees from different provenances and forest regeneration mode (natural vs. planted) was compared using generalised linear models (GLMs), climate-growth relationships and the application of RRR indices (Lloret et al., 2011).

We built two GLMs with a Gamma distribution including, respectively, tree provenance or forest regeneration mode as explanatory factor (fixed effect), and several environmental and edaphic parameters as continuous predictors: elevation, slope, exposition, NCI (competition), tree age, and edaphic C/N ratio. Exposition was included in the model after a transformation by the cosine of the exposition angle, to have a continuous variable ranging from -1 to 1 , whereby 1 means a northern exposure and -1 a southern exposure. Annual Tree Ring Width (TRW, mm) was transformed into Basal Area Increment (BAI, cm^2) to be used as the main response variable in GLMs. In the GLM, BAI is intended as the mean BAI of each i -th tree. The models have the following formulation:

$$\text{BAI}_i = \alpha + \beta_1 * (\text{Provenance} \mid \text{Regeneration mode})_i + \beta_2 * (\text{Elevation})_i + \beta_3 * (\text{Slope})_i + \beta_4 * (\text{Exposition})_i + \beta_5 * (\text{NCI})_i + \beta_6 * (\text{Age})_i + \beta_7 * (\text{C/N})_i + \epsilon_i$$

Depending on the explanatory factor used, tree provenance or forest regeneration mode, we refer in the text to the specific GLM with the expressions of 'provenance GLM' and 'regeneration mode GLM', respectively. All statistical analyses were performed using the R software (version 4.2.3) (R Core Team, 2022). GLMs were run through the *stats* package. To estimate the model fit, McFadden's R-squared was used. The contribution of individual predictors in explaining BAI variation was quantified by the F-test through the Anova function of the *car* R package and their importance has been assessed by importance plots through the *vip* R package (Greenwell, 2023), quantifying the relative impact of each variable on the model fit. The Variance Inflation Factor (VIF) has been used to evaluate collinearity among predictors, implementing the *vif* function of the *car* R package (Fox et al., 2023): $\text{VIF} < 5$ indicates no or low collinearity, $5 < \text{VIF} < 10$ indicates moderate collinearity and VIF values > 10 indicate high collinearity among variables (Dormann et al., 2013). Significant differences among provenances and forest regeneration mode were quantified by Tukey post-hoc tests using the *multcomp* R package (Hothorn et al., 2023).

The climate-growth relationships were conducted over the period 1957–2017 using Ring Width Index (RWI) as the response variable, i.e., TRW data detrended and standardised to a unitless variable to correct for age trend and temporal autocorrelation. Detrending of the growth data from TRW to RWI was performed via the *dplr* R package using the modified negative exponential function method ('ModNegExp') and the 'Spline' methods (Bunn et al., 2023). The 'ModNegExp' method is used to remove the biological growth effect (increased growth in juvenile stages) from growth series, leaving signals that could be associated with environmental or climatic factors. The further application of the 'Spline' method helps to remove long-term variations, helping to highlight

annual or seasonal variations related to climate (Bunn et al., 2023). RWI was correlated with monthly temperature and precipitation for a biological year extending from April of the previous year to September of the current year. Response coefficients from bootstrap correlations were used to analyse the response to climate, taking 1000 bootstrap samples from the original dataset of tree rings and climate data (Zang and Biondi, 2015a). To analyse climate-growth relationships over time, moving plots were produced with a window size of 30 years every year. Climate-growth relationships were carried out using the *treeclim* R package (Zang and Biondi, 2015b) and partial autocorrelation (PACF) was assessed through the *forecast* R package (Hyndman et al., 2023). PACF is considered as a reference variable to analyse possible growth relationships among rings, helping to understand how much previous years' conditions influence current year plant growth, for each of the years analysed and for an increasing number of lag years between the reference year and previous ones (Dorado Liñán et al., 2011; Monserud, 1986). The presence of a significant autocorrelation suggests that growth may be the result of processes occurring in the growth year and determined by the previous year conditions. This could be due to climate, forest dynamics (e.g., disturbances, cuttings, pest outbreaks) or to the influence of individual genetic background, so subsequent analyses of RRR indices will help to analyse this relationship more specifically.

The sensitivity of silver fir to drought was analysed in specific drought years. The Standardised Precipitation-Evapotranspiration Index (SPEI) was used to identify drought years of interest (Beguería et al., 2014). Drought years were identified using the SPEI6 and SPEI12 indices, which refer to drought events that occur in the spring-summer period (SPEI6 of September) or that affect the whole year (SPEI12 of December), respectively. A year is defined as droughty when the SPEI value is ≤ -1 (Liu et al., 2021; Mckee et al., 1993). Based on SPEI6 and SPEI12 values, years were classified as moderate drought (-1.5 to -1), severe drought (-1.5 to -2) and extreme drought years (≤ -2) (Fig. S.8, Tab. S.4) (Li et al., 2021; Mckee et al., 1993; Tirivarombo et al., 2018'). The RRR indices proposed by (Lloret et al., 2011) were used to analyse the sensitivity to drought years. These indices estimate the recovery, resilience, and resistance to a disturbance, in this case drought. They are calculated based on the ratios between growth during the drought year and pre- and post-drought growth, according to the following formulas:

$$\text{Resistance} = \text{Dr}/\text{PreDr}$$

$$\text{Recovery} = \text{PostDr}/\text{Dr}$$

$$\text{Resilience} = \text{PostDr}/\text{PreDr}$$

$$\text{Relative Resilience} = ((\text{PostDr}-\text{Dr})/(\text{PreDr}-\text{Dr})) (1-(\text{Dr}/\text{PreDr}))$$

Where *Dr* referred to the growth during the drought year, while *PreDr* and *PostDr* indicate the average growth in the years before and after the drought, respectively. To calculate *PreDr* and *PostDr*, an average increment of the three years before and three years after the drought year is considered (Gazol and Camarero, 2016). The 'Relative Resilience' index is estimated as the resilience to disturbance weighted by the growth during the disturbance. RRR indices among tree provenance and forest regeneration mode were compared via ANOVA and subsequent Tukey post-hoc test. When comparing provenances in the 'provenance GLM' and in the RRR indices analysis we only refer to the trees grown in the planted stands, to be able to compare the performances of trees grown in similar conditions. When comparing forest regeneration methods in the 'regeneration mode GLM' and in the RRR indices analysis we only refer to the trees from the local provenance (Northern Apennines), to be able to compare the performances of trees with the same genetic background but grown in different environmental and management conditions.

3. Results

3.1. Mean BAI

The results from the Generalized Linear Models did not show significant differences among provenances or forest regeneration mode (Figs. 2,3). In the 'provenance GLM', the most significant and important variable was the elevation, with a significant and negative effect on growth and accounting for the 35.2% of the BAI variance explained. The NCI competition index had also a significant and negative effect on growth (p-value = 0.035) and counting as 18.2% of the BAI explained variance. The Southern Apennine provenance showed higher mean BAI (22.8 mm²/year), followed by the Northern Apennine provenance (19 mm²/year) and the Western Alps one (17.5 mm²/year), even if there was no statistical support for these differences (Southern Apennine – Western Alps differed with a p-value of 0.09, while other differences show higher p-values). VIF values did not show any signs of collinearity among model predictors. When comparing provenances, we only refer to the trees grown in planted stands. The 'regeneration mode GLM' showed the tree age as mode as the most important variable that affect tree BAI (29.2% of the variance explained) followed again by the NCI competition index (23.8%) as significant variables (Fig. 3b; Tab. S_3). Planted forests showed higher mean predicted BAI (16.4 mm²/year) than natural forests (13.2 mm²/year) even if the difference was not significant (p-value = 0.16). VIF values showed moderate collinearity between CN and elevation. When comparing the regeneration mode of the forest, we only used trees of local provenance.

3.2. Tree ring chronologies and climate-growth relationships

Tree ring chronologies were quite similar among provenances and between forest regeneration mode (Fig. S_5) and showed no signal of autocorrelation among rings. Partial autocorrelation analysis showed no significant autocorrelation at one year lag among rings, except for the local provenance in planted stands. No significant partial autocorrelation emerged for lags of up to eight years for the Western Alps provenance and up to 15 years for the Southern Apennines provenance (Fig. S_6).

Climate-growth relationships were generally similar among provenances and between forest regeneration mode, although they showed a few differences between the examined trees. In these analyses, positive response coefficients indicate a positive relationship between growth and climate variable (i.e., high temperature -> high growth, but also low temperature -> low growth) while negative response coefficients indicate an inverse correlation (i.e., high temperature -> low growth, and vice versa). The growth of the local provenance (Northern Apennine)

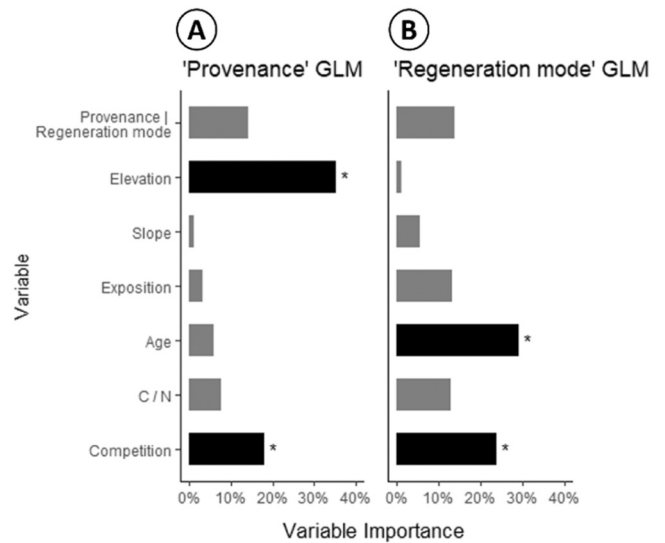


Fig. 3. Importance plots of the predictors of the (A) 'provenance GLM' and (B) 'regeneration mode GLM'. The asterisk (*) indicates the significant predictors in the respective model.

and the Southern Apennine provenance was significantly positively influenced by summer precipitation (June and July) of the current year, a trend that was also observed in the trees of the Western Alps provenance and in natural forests, although it was not significant. The Southern Apennine provenance was not significantly limited by any other climatic factor, while the growth of the local provenance (Northern Apennine) in planted forests was also significantly and negatively influenced by the temperatures in June of the current year. This relationship was observed also in the other provenances, but it was not significant. The growth of the Western Alps provenance was significantly and positively correlated with winter temperatures in February and March, as it was for the local provenance in natural forests. This relationship was observed also in the trees of the Southern Apennine provenance and the local provenance in planted forests, but it was not significant. Finally, natural forests showed a positive and significant correlation between growth and June precipitation of the previous year, a trend that was only slightly noticeable in the other levels of analysis (Fig. 4).

Moving plots analysis revealed some additional differences. The Southern Apennine provenance showed a significant and positive correlation with the June temperatures of the current year (Fig. S_7c), which was also confirmed by the other provenances, albeit to a lesser

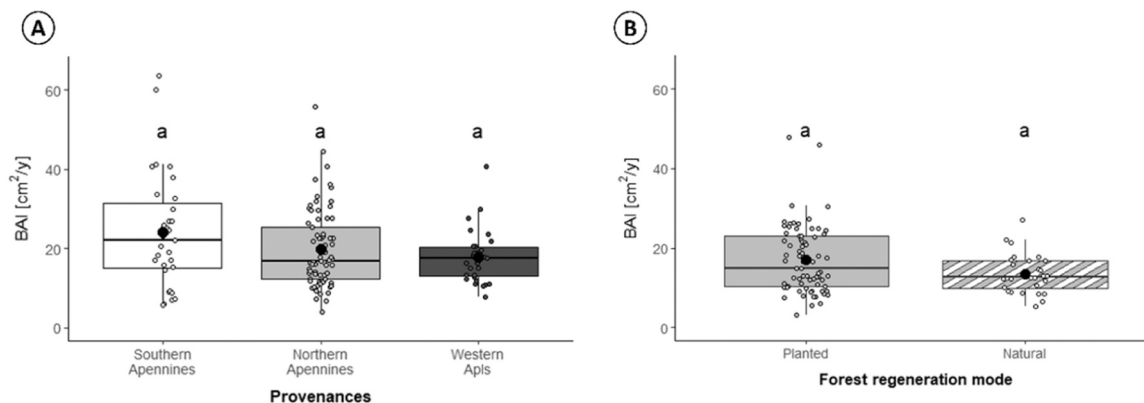


Fig. 2. Distribution of BAI values across A) provenances and B) forest regeneration mode. The black dots represent mean BAI values. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicate no significant differences (e.g., a-a; a-ab; b-ab), according to the results of the GLMs.

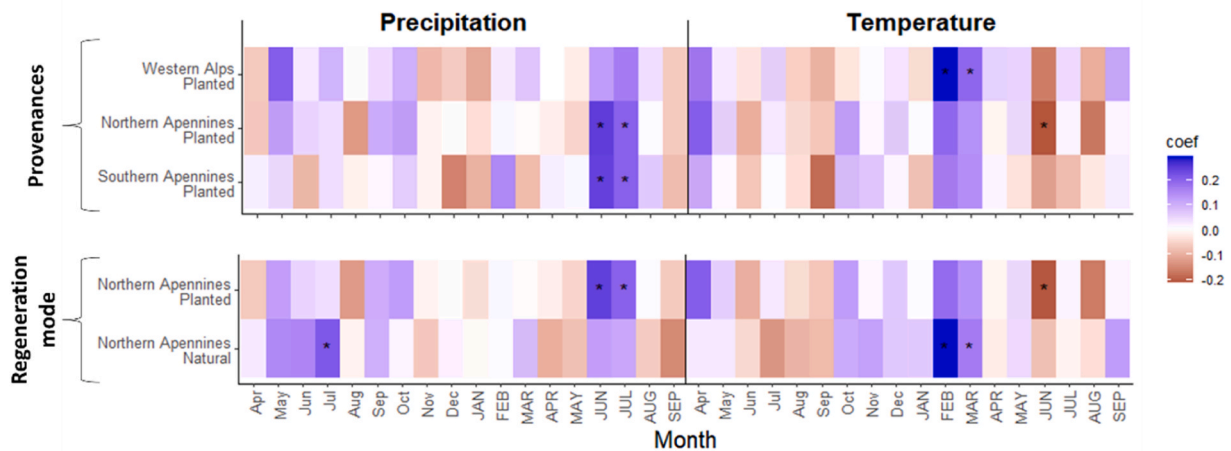


Fig. 4. Response coefficients showing the climate-growth relationships of silver fir in the period 1957–2017. * Indicate significant response correlations between RWI and climate data.

degree. July temperatures of the current year, on the other hand, showed a negative correlation with the growth of both the Western Alps and the local provenance in planted forests (Fig. S.7a,b), a trend that was reversed in the most recent time windows and it showed slightly positive correlation values. A positive correlation between growth and winter temperatures was observed for all provenances, with less evidence for the Southern Apennine provenance (Fig. S.7c). The positive correlation between growth of the Southern Apennine provenance and the local provenance in natural forests with the temperatures of the previous autumn was notable (Fig. S.7c,d). The positive correlation with summer precipitation (June and July) of the current year was significant and/or continuous especially for the local provenance (Northern Apennine) in planted forests (Fig. S.7b), while it was significant for the other provenances and forest regeneration mode only in the most recent time windows. The sensitivity to the precipitation regime during the whole year was then significant and positive only for the natural forests of local provenance, with emphasis on the summer of the previous year and the spring of the current year (Fig. S.7d). The Southern Apennine provenance was the only one to show negative, though not significant, correlations with precipitation in the summer of the previous year (Fig. S.7c).

3.3. Drought years and RRR indices

Using SPEI6, ten drought years were identified, of which seven were of moderate, two severe and one extreme intensity (Fig. S.8a, Tab. S.6).

SPEI12 identified ten drought years as well, of which six were moderate and four were severe (Fig. S.8b, Tab. S.6). Five years coincided between SPEI6 and SPEI12: 1983, 1988, 2003, 2007 and 2011.

Analyses of RRR indices showed more significant differences both among provenances and in drought years identified by SPEI6 than by SPEI12. It should be emphasised that, when comparing the performance of the three provenances, only trees growing in planted forests were compared. For the years identified by SPEI6, the Southern Apennine provenance showed greater recovery, resilience, and relative resilience with respect to the Western Alps provenance in almost all drought intensity classes (except for resilience during severe drought years and relative resilience in moderate drought years) (Fig. S.9). The behaviour of the local provenance (Northern Apennine) was generally intermediate. The resistance index showed no significant differences among provenances, while lower resilience for all provenances during the extreme drought year was found (Fig. 5, Fig. S.9a), with average values < 1 (Tab. S.7). Drought resilience was also lower in the extreme drought year for all provenances (Fig. 5, Fig. S.9c), although the Southern Apennine provenance was the only one that showed mean values > 1 (Fig. 8, Tab. S.7). In the years identified by SPEI12, the Southern Apennine provenance showed statistically higher values of resistance and resilience in moderate drought years and higher recovery in severe drought years than the Western Alps provenance (Fig. S.10). The local provenance (Northern Apennine) showed no significant differences compared to the other provenances, except for higher resilience in moderate droughts with respect to the Western Alps provenance

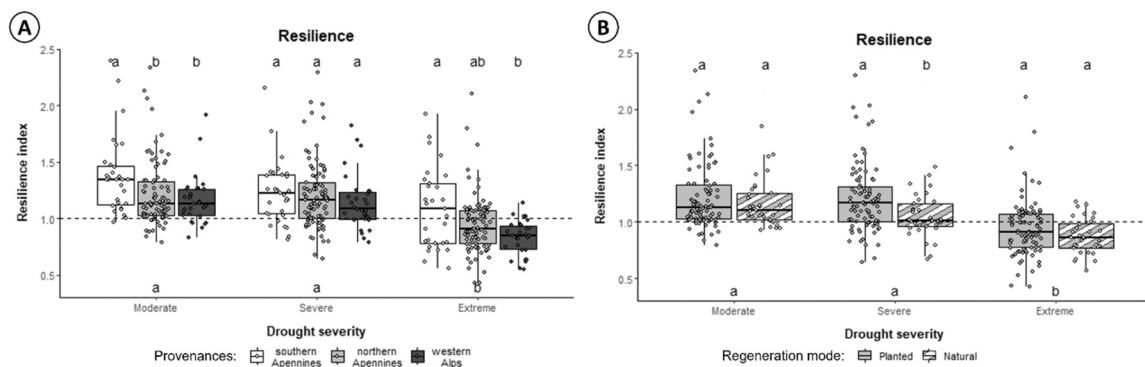


Fig. 5. Distribution of the resilience index calculated for drought years identified by SPEI6 across (A) provenance and (B) forest regeneration mode. Different letters above the boxes indicate significant differences (e.g., a-b), while including one common letter indicate no significant differences (e.g., a-a; a-ab; b-ab) according to post-hoc tests. The upper line of letters refers to the comparison of (A) provenances and (B) forest regeneration mode within the same drought intensity level; the lower line of letters compares the reference mean index (all provenances together) between drought intensity levels.

(Fig. S_10a).

Forest regeneration mode has a significant effect on RRR indices, with planted forests showing an overall greater capacity to react to drought episodes than natural stands. It should be emphasised that these analyses compared the growth performance of the same provenance (Northern Apennine) between natural and planted conditions. In the years identified by SPEI6, planted forests showed greater recovery, resilience and relative resilience in severe drought years and greater recovery and relative resilience in extreme drought years (Fig. 8, Fig. S_11b,c,d). Resistance and resilience in extreme drought years were significantly lower than in other drought years (Fig. 5, Fig. S_11a,c), also with average values < 1 (Tab. S_5). Resistance in extreme drought years was the only index where natural forests performed significantly better than planted forests (Fig. S_11a). In the years identified by SPEI12, planted forests performed better in terms of drought resistance and resilience in severe drought years (Fig. S_12a,c).

4. Discussion

Our work aims to investigate responses of silver fir to drought in a mountain environment in Italy. By taking advantage of the ideal experimental setting represented by *Abies alba* plantations established during the 20th century in the Northern Apennines, we tested the existence of differences in growth rates, growth-climate relationships, and growth responses to drought among different silver fir provenances (originated from Southern Italy to the Alps) growing under similar climatic and environmental conditions. The results obtained from this study show an influence of the provenance and forest regeneration mode in the growth response of silver fir to climate and drought, although this response may appear more or less clearly depending on environmental conditions. Our results highlight the importance of taking into account the genetic background of forest reproductive materials to valorise forest genetic resources available in the Italian territory and their response to drought.

4.1. BAI and environmental drivers of tree growth

4.1.1. Effect of provenance

Analysing the average growth of the three provenances, we observe that silver fir from the Southern Apennines has a slightly higher growth rate compared to the Western Alps provenance, although the difference is only marginally significant in statistical terms. The absence of a statistically significant difference allows us to proceed with the subsequent analyses with greater confidence, marking the results of the climate-growth relationships and RRR indices as related to climate trends. The constructed model explains only one third of the variance in the data (Tab S_3), emphasising the existence of multiple unconsidered factors affecting growth. The BAI data predicted by the GLM were corrected for the effect of multiple environmental parameters, revealing which predictors have a more pronounced effect on growth. Elevation reveals to be the most limiting factor for growth, confirming previous results from other authors on its negative effect on growth of silver fir (Dinca et al., 2022; Gazol and Camarero, 2016; Jevšenak and Skudnik, 2021). Elevation has also been recognized as one of the main factors shaping recent adaptive and neutral evolutionary dynamics in silver fir (Brousseau et al., 2016; Major et al., 2021). Altogether, our results indicate that the average growth rate is rather uniform among Italian silver fir genetic provenances. The lack of difference in average growth rate, however, does not imply the same physiological response to drought. Therefore, the results calls for a more in-depth analysis to study the differences in drought response among provenance found by other authors (Bosela et al., 2016; Dobrowolska et al., 2017; Martínez-Sancho et al., 2021; Mihai et al., 2021; Vitasse et al., 2019b; Walder et al., 2021). NCI index, as a proxy for the competition level experienced by each individual, has a significant effect. The NCI index is widely used to measure competition intensity (Canham et al., 2004; Opgenoorth et al., 2021) and our results

confirm its negative relationship with growth and the importance of including competition as a factor in forest growth analysis (Burkhardt and Tomé, 2012; Canham et al., 2004).

4.1.2. Effect of regeneration mode

Similarly, the 'regeneration mode GLM' (planted vs. natural) showed age and competition as significant predictors. Even if there are no significant differences in BAI between regeneration modes for this species, the regeneration mode of the forest has been identified as the third most important predictor from the GLM, explaining almost 14% of model variance. Therefore, although not explaining the differences in BAI in our study, regeneration mode needs to be considered when building models to analyse forest data, as suggested by other studies on the Italian territory (Manetti and Cutini, 2006).

NCI competition index has a significant effect, underlying the importance of including it as a predictor in forest data analysis. The inversely proportional relationship between plant age and BAI has already been observed in many tree species (Anning and McCarthy, 2013; Cienciala et al., 2016; Jögiste, 2000) even though conflicting results can be found in literature (see Johnson and Abrams, 2008). In this study, the negative relationship is mainly driven by a small number of plants that reach 200–300 years in natural forests. Old individuals are slow-growing and possibly disadvantaged by the difficult micro-environmental conditions, explaining the decreased BAI in this age extreme.

4.2. Climate growth relationships

4.2.1. Effect of provenance

The chronology analysis shows partial autocorrelation (PACF) values between tree rings at the first lag level only for the Northern Apennines provenance in planted forests, revealing a possible link between the growth of successive years. The correlation coefficient of the first lag level (PAC1) is often considered as a reference value to analyse possible growth relationships between tree rings (Dorado Liñán et al., 2011; Monserud, 1986). Significant PACF values at lag levels nine and 16, on the other hand, are not considered problematic in the analysis of the results due to the distance from the target tree ring and, thus, not related to climate (Liutsko and Monleon-Getino, 2009; Monserud, 1986). The relationships between climate and growth show common trends among the studied provenances that are positively correlated with summer precipitation and winter temperatures in the current year. These results reflect the sensitivity of silver fir to climate found by other authors, revealing the vulnerability of this species to summer drought and winter frost (Latreille et al., 2017; Lebourgeois et al., 2013). Our results highlight some differences between provenances and regeneration modes of the forest in the response coefficients between climate and growth, further corroborated by previously published work (Carrer et al., 2010; Gazol et al., 2015; Mazza et al., 2014). Silver fir stands from the south-western distribution limit express high correlation coefficients with summer precipitation, while stands from a more continental climate are more limited by winter temperatures (Gazol et al., 2015). Mazza et al. (2014) analysed some silver fir stands in the Tuscan-Emilian Apennines and found correlation values with precipitation and temperature very similar to those of the Southern and Northern Apennines in planted pure stands shown in the present study. Similarly, Carrer et al. (2010) analysed natural populations of silver fir from all the Italian Peninsula, classifying them into three geographical macro categories based on growth response. In Carrer classification, populations from a Mediterranean climate have a high correlation with current summer precipitation. Our results show the same results for the Southern Apennine provenances. The results of our study show high correlation also between the Northern Apennines provenance growth response and summer precipitation. This is in contrast to the classification from Carrer et al. (2010), where no correlation was found. Local adaptations and microclimatic conditions can play a significant role in growth

responses, potentially overriding broader climatic patterns (Gazol et al., 2015). Mazza et al. (2014) also noted similar responses in varying geographical locations, suggesting a complex interplay of local and regional climate influences. The Western Alps provenance showed a positive relationship between growth and current winter temperatures in Carrer et al., (2010), again in line with our results. It is also interesting to note the effect of the previous year's summer precipitation, which tended to be negative for the Southern Apennines provenance in June and for the local provenance in August, showing signs of positive response to the summer drought in relation to the previous year's rainfall regime. The local provenance, at the same time, seems to suffer more from high temperature of the current year.

4.2.2. Effect of regeneration mode

Natural forests are particularly sensitive to winter temperatures, possibly being penalised by very cold winters, probably due to local conditions in high mountain environments (Carrer et al., 2010; Gazol and Camarero, 2016; Mihai et al., 2021). Climate susceptibility may not only be related to the climatic regime at higher altitudes, but also to environmental differences. In our case, natural forests grow on more impervious soils, with higher rockiness and reduced depth. This may affect the ability to effectively absorb water and nutrients, and thus the ability to respond effectively to climate stresses in certain contexts. Furthermore, these forests showed a positive growth response in relation to the previous year's summer precipitation, showing a possible vulnerability to summer drought. Natural forests appear to be less constrained by the climatic conditions of the current year than planted forests of the same provenance, which may be due to the lower climatic sensitivity of high-elevation marginal silver fir forests found by other authors (Mazza et al., 2014).

4.3. RRR indices

4.3.1. Effect of provenance

Analyses of RRR indices show a high drought tolerance of silver fir, with average values of resistance, recovery and resilience indices tending to be higher than 1. This suggests that silver fir tends not to be impacted by drought in the first place but, when it is, it has the ability to recover from such stressful episodes (Tab S.5). This trend, already observed by other authors in silver fir, suggests a high resilience of the species to the climatic threats imposed by climate change (Bottero et al., 2021). However, our results show a general sensitivity of silver fir to extreme drought, identified with SPEI6 in the year 2003, then to moderate or severe drought events. Extreme droughts affect both the resistance and resilience of silver fir to drought, always resulting in average values below 1. This result is in line with current literature on silver fir (Lloret et al., 2011; Serra-Maluquer et al., 2018), emphasising that extreme drought events can negatively affect growth and the ability of silver fir trees to respond to it. Anyway, when considering specific provenances, the picture shows interesting differences. For instance, Western Alps provenance shows RRR indices around 1 or lower, with a particularly low recovery ability. On the other hand, the Southern Apennines provenance is the only one with average resilience index values above 1 during extreme drought, even indicating slightly improved growth. The main trend that can be observed in the RRR indices analyses is a generally better response, in almost all its components, of the Southern Apennines provenance than the Western Alps provenance, confirming diversified drought responses among provenances (Dobrowolska et al., 2017; Mihai et al., 2021). This trend is respected in both SPEI6 and SPEI12 analyses, especially for the recovery and resilience components. The non-significant effect between provenances in the resistance index may be related to the results of the climate-growth relationships, which show a high sensitivity of the Southern Apennines and local provenances in planted stands to summer precipitation. This may denote a limitation of growth during drought years, however, it is compensated by a generally high resilience. Silver

fir provenances from southern Italy (Calabria and Molise regions) have demonstrated high production yields in provenance trials in Europe in recent decades, both in terms of growth and adaptation to climate change (Hansen and Larsen, 2004; Kerr et al., 2015), besides high genetic diversity (Piotti et al., 2017), underlining the importance they can play in forestation or assisted migration programmes to increase forest resilience. However, this is not the case in all locations or climates, as demonstrated in continental climate sites in the Czech Republic (Fulín et al., 2023). However, the differences between provenances found in the results based on SPEI6 drought years are sometimes not confirmed by those based on SPEI12 years, such as differences in growth recovery during moderate droughts or in relative resilience during severe droughts. This may be due to the ability of the SPEI index to identify the intensity and duration of droughts according to the time scale at which it is calculated. SPEI 6, in fact, is better able to identify droughts of short duration and variations in water availability, while SPEI 12 is generally used to study droughts over longer periods and long-term impacts on vegetation (Eris et al., 2020; Pei et al., 2020). This is further supported by the occurrence of a drought year of extreme intensity in SPEI6 analyses (SPEI62003 = -2.4), whereas in SPEI12 years the maximum drought intensity is 'severe' (SPEI12 > -1.9). Our results suggest that the different provenances may respond similarly to long-term climatic variations, while showing higher differences when subjected to sudden climatic stress. Other authors have found a diversified response of forest provenances when varying the scale at which climate vulnerability is analysed, indicating the importance of analysing the appropriate scale for the specific case study (George et al., 2019; Stefanidis et al., 2023).

4.3.2. Effect of regeneration mode

When discussing the effect of the genetic background on growth performance, also the regeneration mode should be taken into account. In the study area, both natural regenerated forests and planted forests of local provenance can be found. Average growth of local natural forests was not different from the same provenance in planted forests, but their ability to respond to water shortage can vary with drought intensity. Natural forests, in fact, suffer from extreme drought levels, showing values below the threshold of 1 in all indices, exhibiting susceptibility to drought similar to that of the Western Alps provenance in this study. The only index where the natural forests show better performance than the planted ones is the resistance with SPEI6. However, due to the lower recovery to drought years (considering SPEI6) the natural forests have a resilience index lower than the threshold value 1 and no significant differences than planted forests. When considering SPEI12, the natural forests show consistently lower RRR indexes compared to planted ones (Carrer et al., 2010). The poorer resistance to drought of natural population might be related to the difficult environmental conditions in which the natural populations grow (assessed in the field using a visual approach): Higher elevation characterized by rocky substrate, resulting in reduced water availability in the soil and a very thin edaphic organic layer. In a climate change perspective, planted Northern Apennines populations outperform natural ones when considering drought resistance, probably due to the more favourable conditions of the stands and the historical management, avoiding high competition among individuals. Similarly to the provenance analysis, the differences between the regeneration modes are more abundant in the analyses of the RRR indices of the years identified by SPEI6, not confirmed by the SPEI12 results as in the case of recovery and resistance. This could be due to the general high adaptability of silver fir to the surrounding environmental conditions. Silver fir is considered to be a conifer with high climate plasticity when translocated to different climates, allowing for good long-term adaptation, but possibly susceptible to sudden changes (Dobrowolska et al., 2017; George et al., 2019). The differences between natural and planted forests could also follow this trend, both generally responding well to drought in the long term (mean RRR > 1 in SPEI12 analysis), while showing a negative response of natural forests to severe or extreme droughts. These differences, in addition to the management

methods of the two forest types, can be related once again to the difficult soil conditions in which the trees grow, marking the role of the environment in climate adaptability. Droughts of high intensity over short periods can have a marked effect on the ability of trees to respond to climate, highlighting the importance of proper forest management in natural forests. These nucleus of natural forests in the Apennines needs to be protected as they represent a very important genetic heritage, both historically and for the future adaptation of the species. Northern Apennines are proven to be one of the glacial refugia from which silver fir recolonised parts of Central Europe, revealing natural forests as a reservoir of potentially distinctive and diverse forest genetic material (Konnert and Bergmann, 1995; Piotti et al., 2017; Piovani et al., 2010). The conservation of these natural stands is therefore of paramount importance, both for the functioning of local forest ecosystems and for the conservation of the forest genetic heritage. For these reasons, active management to maintain and improve health and growth status of natural silver fir stands is suggested (Gentilesca and Todaro, 2008; Piovani et al., 2010).

4.4. Future for *Abies alba* under climate change pressure and possible management perspectives

From these results we can generalize a positive ability of silver fir to respond to drought, showing a marked ability to recover its growth and being resilient, at least for its Northern and Southern Apennine provenances. Indeed, the literature about silver fir shows that the species is particularly plastic in its response to drought (Mihai et al., 2021) and possibly well adaptable to future climatic conditions (Vitasse et al., 2019b; Walder et al., 2021). The resilience of silver fir to drought is usually higher as compared to other forest tree species, such as spruce or beech (Gillerot et al., 2021; Mikulenska et al., 2020; Vitasse et al., 2019a). Our results show a decline in silver fir growth responses to drought under extreme drought conditions, showing that, beyond certain climatic thresholds, the ability of the species to functionally respond to drought is limited by physiological processes (Larysch et al., 2021). In addition, the effect of genetic provenance on drought responses is clear, highlighting how material from southern Italy and of local provenance can perform in terms of production and drought resilience in mountainous territories of Tuscan-Emilian Apennines. These results also confirm that silver fir stands in the Tuscan-Emilian Apennines include trees that are highly adaptable to drought, that may be linked to high neutral genetic diversity of this species in this area despite the extreme fragmentation of natural stands (Piotti et al., 2017). Forest planning should value and maintain the genetic diversity of forest stands, increasing their functional traits and resilience in the face of environmental and climatic stresses (Mihai et al., 2021).

One of the tools of sustainable silviculture is the translocation of forest reproductive material that is more adaptable to future climates through assisted migration, adopting forest provenances that can be more resilient to drought. Assisted migration is a silvicultural option to improve the climate performance of forest species (Aitken and Bemmels, 2016; Breed et al., 2013; Millar et al., 2007), not only at the scientific level but also by forest owners and managers (Gömöry et al., 2021; Vinceti et al., 2020). The assisted migration accidentally put in place in the postwar period to reforest the Tuscan-Emilian Apennines has resulted in some provenances (i.e., Southern Apennines) showing similar drought responses with respect to the local genotypes, and others (i.e., Western Alps provenance) showing a different behaviour. This evidence can be employed by local forest management to adopt sustainable silvicultural management in a climate change context, with respect to both the management of existing forests and the future planting of new forest stands by translocating more adaptable material for the future. Thus, the use of tested provenances to mitigate the effects of climate change is recommended, as long as specific local conditions are taken into account (Dobrowolska et al., 2017). However, future assisted migration projects will need both further evidence about the

performance of regeneration from external provenances in the current climate and to be accompanied by sound sustainable forest management plans, as there is already evidence that assisted migration under extreme climate scenarios can only partially improve widespread adaptation to climate change (Gustafson et al., 2023). The loss of ecosystem services related to climate crisis could be only partially mitigated by planting provenances more adapted to future climate, especially in Mediterranean settings, enhancing the role of local sustainable forest management (Mauri et al., 2023).

5. Conclusions

This work analyses the ability of silver fir trees of different genetic provenance (Southern Apennines, Northern Apennines, Western Alps) and regeneration mode (natural populations and planted forests) to respond to drought, a topic of pivotal importance given the relevance of the species at the European level and the threat of climate change. We thus attempt to define some guidelines for local silvicultural management that can foster the provision of ecosystem services linked to silver fir and mitigate the effects of climate change on local forests. An analysis of growth according to tree provenance shows that silver fir trees from local provenance and from Southern Apennines result in greater resilience to drought and greater ability to take advantage of summer rains when compared to the Western Alps provenance. Similarly, local material in planted stands is found to have greater drought resilience than trees from natural stands, and a possible explanation is related to the difficult soil conditions in which natural silver fir forests grow. This evidence reveals the potential of using non-local forest reproductive material to maintain or improve the response of forests to climate change, as long as the origin and the performances of the FRM is thoroughly tested (e.g. through genetic tests and common garden experiments). Future silver fir assisted migration programmes should consider the use of local material accompanied by material from the southern distribution limit of the species, in particular after assessing possible issues related to outbreeding depression and maladaptive gene flow. In addition, in order to functionally employ local genetic resources, timely silvicultural management is necessary to effectively conserve the local genetic heritage in the original natural stands, so as to be able to benefit from them in the future. These results add to a growing body of information on the growth response mechanisms of silver fir to climate change, and it is hoped that local silvicultural management will benefit directly from them.

CRedit authorship contribution statement

S.D.Oggioni: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M.Marchetti:** Supervision, Project administration, Funding acquisition, Conceptualization. **A.Piotti:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L.M.W.Rossi:** Writing – review & editing, Writing – original draft, Resources, Investigation, Formal analysis, Data curation. **C.Avanzi:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis. **G.Vacchiano:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dendro.2024.126184](https://doi.org/10.1016/j.dendro.2024.126184).

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