



## Silver fir (*Abies alba* Mill.) is able to thrive and prosper under meso-Mediterranean conditions

Diego Walder<sup>a,b</sup>, Patrik Krebs<sup>a</sup>, Harald Bugmann<sup>b</sup>, Maria Chiara Manetti<sup>c</sup>, Martina Pollastrini<sup>d</sup>, Solaria Anzillotti<sup>e</sup>, Marco Conedera<sup>a,\*</sup>

<sup>a</sup> Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, a Ramél 18, CH-6953 Cadenazzo, Switzerland

<sup>b</sup> Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zürich, CH-8092 Zürich, Switzerland

<sup>c</sup> Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria, Centro di ricerca Foresta e Legno CREA-FL, Viale S. Margherita, 80 I-52100 Arezzo, Italy

<sup>d</sup> University of Florence, Department of Agriculture, Food, Environment and Forestry, Piazzale delle Cascine, 28, I-50144 Florence, Italy

<sup>e</sup> Università di Bologna, CdL magistrale in Progettazione e gestione degli ecosistemi agro-territoriali, forestali e del paesaggio, Viale Giuseppe, Fanin, 40, I-40127 Bologna, Italy

### ARTICLE INFO

#### Keywords:

Silver fir  
Adaptive forest management  
Drought  
Tree rings  
Global change

### ABSTRACT

The potential ecological envelope of silver fir (*Abies alba* Mill.) based on its present distribution suggests a high suitability for moist rather than warm and dry environments. This contrasts with paleoecological evidence reporting its former presence at low elevations under meso-Mediterranean conditions. In this study, we evaluated the growth performance of silver fir at low elevation (20–60 m a.s.l.) under meso-Mediterranean climatic conditions in Tuscany (central Italy). We conducted a dendroecological analysis on *Abies alba* trees along a geomorphological gradient (from depression to upper slope conditions). Climate-growth relationships were assessed by means of correlations, response functions, pointer years, and superposed epoch analysis.

Silver fir was found to grow and regenerate well in these stands mixed with evergreen (e.g., *Quercus ilex* L.) and thermophilous deciduous Mediterranean tree species (e.g., *Q. cerris* L.). Summer drought was the most growth-influencing factor, with immediate (i.e., current season) negative impacts on tree-ring widths (TRW). No significant impacts were observed in the four years following extreme summer droughts, but the TRW series (which started between the 1930s and 1950s) showed a growth decline since the mid-1990s that is likely drought-related.

Our results show that, provided there is a sufficiently large soil water holding capacity, silver fir provenances exist which are able to withstand Mediterranean summer droughts, can naturally and regularly regenerate in these systems, and may even dominate over typical meso-Mediterranean species. As long as annual precipitation is not too low (i.e., >850 mm) and summer drought conditions not too extreme (i.e., less than three months), silver fir has thus the potential to thrive under warm Mediterranean conditions.

### 1. Introduction

European climate is getting warmer and drier (IPCC 2013) and the frequency and intensity of extreme climatic events and related disturbance regimes are changing (Bowman et al. 2014; Seidl et al. 2014; Seidl et al. 2017). This has a potentially large impact on forest dynamics, tree species distributions and the survival probability of trees in particular (Allen et al. 2010; van Mantgem et al. 2009), eventually affecting ecosystem services (Scheffers et al. 2016).

In a climate change context, adaptive management strategies are thus needed to increase forest resistance and resilience and to mitigate

possible negative impacts (Thurm et al. 2018; Vilà-Cabrera et al. 2018). Different strategies to adapt to climate change exist (Hagerman and Pelai 2018; Madrigal-González et al. 2017), such as increasing the resistance and/or resilience of current forests (i.e. shortening rotation periods and reducing mortality risk or decreasing forest stand density; Rais et al. 2014; Seidl et al. 2011), regulating tree species mixtures by favoring the most suitable ones (Lebourgeois et al. 2013; Pretzsch et al. 2013), or fostering and introducing more drought-tolerant species (Buras and Menzel 2018; Dyderski et al. 2018; Scherrer et al. 2017). Developing adaptive strategies based on the selection of suitable tree species requires an in-depth understanding of their behavior under the

\* Corresponding author.

E-mail address: [marco.conedera@wsl.ch](mailto:marco.conedera@wsl.ch) (M. Conedera).

<https://doi.org/10.1016/j.foreco.2021.119537>

Received 27 May 2021; Received in revised form 12 July 2021; Accepted 14 July 2021

Available online 24 July 2021

0378-1127/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

expected climatic and other environmental conditions (Keenan 2015).

The debate on the potential role of silver fir (*Abies alba* Mill.) under a future European climate is very emblematic in this respect (Vitasse et al. 2019). The current distribution of silver fir ranges from the Pyrenees to the Carpathians and from southern Italy to Poland, mainly following mountain ranges (Mauri et al. 2016; Fig. 1). In such ecosystems, it represents an important keystone species significantly contributing to biodiversity conservation, stand resistance to disturbances such as wind and insects in mixtures with Norway spruce (Ott et al. 1997; Rüegg 2015), as well as to forest ecosystem services, such as timber production and protection from gravitative natural hazards (Tinner et al. 2013; Wolf 2003).

Yet, there is contrasting evidence regarding its suitability to cope with future climate change (Vitasse et al. 2019). Based on its current distribution, silver fir is traditionally considered well adapted to moist conditions (Bucher 2014) and rather poorly adapted to warm and summer drought conditions (Macias et al. 2006; Rigling and Stähli 2020). As a consequence, the modelled potential ecological envelope based on its present distribution suggests a future contraction of its range due to climate change, describing the species as widely unsuited in a climate-adapted European forestry context (Maiorano et al. 2013; Zimmermann et al. 2016). On the contrary, studies based on paleoecological evidence report its former presence at low elevations from southern Switzerland to southern Italy, reaching the Mediterranean coast of central Italy, featuring summer and annual mean temperatures up to 7 °C higher than in its actual distribution range (Tinner et al. 2013). According to this view, the current absence of silver fir under such warm conditions is mainly due to the long-lasting human pressure since 5000–7000 years ago, which caused the decline of this late-successional and strongly fire- and browsing-sensitive species (Carcaillet and Muller 2005; Di Pasquale et al. 2014; Tinner et al. 1999). Combining this paleoecological evidence with process-based modelling, some authors postulated a greater-than-expected climatic tolerance of silver fir, especially in terms of higher temperatures (Henne et al. 2013; Henne et al. 2015; Ruosch et al. 2016).

Dendroecological studies highlighting an increase in the average annual ring width of silver fir during the warming period from 1990 to 2010 confirmed the adaptation of the species to higher temperatures (Büntgen et al. 2014; Bošela et al. 2018), suggesting a higher than expected drought tolerance (e.g., Vitali et al. 2017). Other studies, in contrast, suggested sensitivity to Mediterranean summer droughts (Gazol et al. 2015). Unfortunately, only few and partially outdated studies described growth and regeneration dynamics of silver fir stands growing under low-elevation Mediterranean conditions (Cesarini 1940; Cortini Pedrotti 1967).

In this paper, we aim to fill this gap by conducting a dendroecological study in a meso-Mediterranean low-elevation silver fir forest that is characterized by a steep geomorphological gradient. We particularly address the following research questions:

- Does silver fir develop and regenerate under meso-Mediterranean climatic conditions?
- What are the main climatic factors influencing silver fir radial growth?
- How may the species respond to a climate getting warmer and drier?

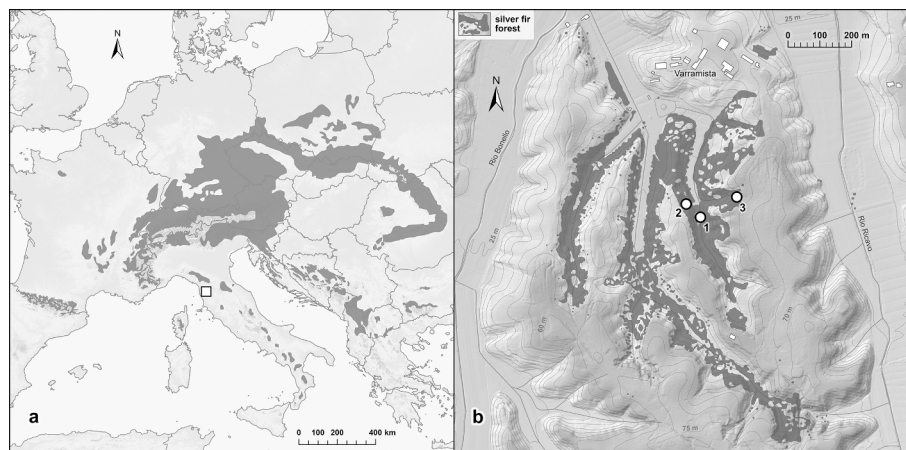
## 2. Methods

### 2.1. Study area and sampling design

The study area features ca. 12 ha of silver fir-dominated stands located at an elevation from 20 to 60 m a.s.l. along the lower part of three small valleys extending in the north–south direction in Varramista (Tuscany, Central Italy; 43°39'45"N, 10°42'55"E; Fig. 1) that were probably reclaimed at the end of the 18th century (Baroni 1810; Giorgi 2009). The forests originate from a plantation dating back to the beginning of the 19th century or even earlier (Capponi 1882; Cesarini 1940; Cortini Pedrotti 1967). Although the provenance of the planted stock is unknown, the historical and botanical descriptions allow us to assume that the trees are *Abies alba* very likely originating from the Apennines (Susmel 1957; Cortini Pedrotti 1967). No originally planted trees survived to date and current stands originate from natural regeneration (Cesarini 1940), presently representing the lowest fir occurrence in Tuscany (Municipality of Montopoli in Val d'Arno 2008). In the last few decades, silvicultural interventions were limited to the phytosanitary clearing of fallen and damaged trees after a storm in March 2015, which mainly affected the valley bottoms (A. Casarosa 2018, personal communication).

At present, in these stands silver fir grows in mixture with typical broadleaved and coniferous Mediterranean species, such as manna ash (*Fraxinus ornus* L.), holm oak (*Quercus ilex* L.), and the strawberry tree (*Arbutus unedo* L.). Towards the top of the hills, silver fir is increasingly substituted by Turkey oak (*Quercus cerris* L.), sessile oak (*Q. petraea* (Matt.) Lieb.), holm oak, Italian stone pine (*Pinus pinea* L.), maritime pine (*P. pinaster* Ait.), and other minor species.

The shrubs and herbaceous layers are heterogeneous and characterized by taxa typical of the *Abies alba* and evergreen and thermophilous oak vegetation types, respectively. The list of phanerogamic flora in Varramista includes 140 taxa, 65% of them belonging to the geoclimatic boreal element, while the Mediterranean species make up only 26%



**Fig. 1.** Study area. a) Location of the Varramista study area (white square) with respect to the current distribution of silver fir (grey). Sources: adapted from EUFORGEN (2003). b) Silver fir forest stands in Varramista (dark grey area) and location of the assessed macroplots (white dots): (1) Depression, (2) Lower slope, (3) Upper slope.

(Cortini Pedrotti 1967). A few eastern species (Illyria, Pontus and Eurasia) are present, summing up to about 5%. The biological spectrum of Raunkiaer life form types (Raunkiaer 1934) shows a prevalence of hemipterophytes (H), phanerophytes (P) and geophytes (G) and a low percentage of therophytes (Th) due to the unsuited temperature and humidity conditions of the understory, while chamaephytes (Ch) are in general not frequent in forests (P 30%, Ch 6%, H 38%, G 19%, Th 7%; Cortini Pedrotti 1967).

According to the Tuscan Regional Hydrologic Service (SIR 2019a, 2019b), annual mean temperature in the study area is 15.3 °C, with a mean temperature of 6.9 °C in the coldest month (January) and 24.5 °C and 24.4 °C in the warmest months (July and August, respectively). Annual precipitation amounts to 867 mm, mainly occurring from late autumn to early winter. The driest month is July (31.5 mm in average) while the wettest is November (114.4 mm). Temperatures are rarely below 0 °C and it hardly ever snows. These conditions were classified by Fratianni and Acquaotta (2017) as hot temperate (Csa after the Köppen-Geiger classification), pointing out the importance of summer arid periods, which usually occur between June and August.

The geology is characterized by sand layers of Pliocene origin and younger continental deposits, with sparsely emerging clay formations (Cortini Pedrotti 1967; SGR 2006). Soils are acidic Luvisols and have different properties within the investigated area, ranging from the presence of an albic horizon in the slopes and stagnic horizon in the depressions, indicating water flow from the hilltops towards the mesic valley bottoms (Fig. S1; Corongiu et al. 2016; Regione Toscana 2018).

The study design followed the existing geomorphological gradient by selecting three macroplots, going from the depression to the lower and the upper part of the slopes, respectively (Fig. 1). The valley is quite open and all macroplots, including the one in the depression, are rich in woody and herbaceous vegetation of meso-Mediterranean character. This allows us to exclude any significant micro-climatic effect due to the terrain morphology. The east-facing lower slope macroplot is steeper than the west-facing upper slope, with an average slope of 25–30° and 10–15°, respectively (Table 1). Within each macroplot, at least 34 adult, dominant and visibly healthy fir trees were selected for coring. In addition, three circular plots of 12 m in radius (corresponding to 452 m<sup>2</sup> in area) were placed in each macroplot (i.e., 9 circular plots in all) for assessing stand structure, including tree regeneration.

**Table 1**  
Characteristics of macroplots, forest stands, sampled trees and related tree ring-width series and chronologies.

Macroplot position	Upper slope	Lower slope	Depression
Area [ha]	0.38	0.42	0.38
Aspect	W	E	N
Elevation [m a.s.l.]	35–60	30–50	25–30
Mean slope [°]	10–15	25–30	0–5
Basal area [m <sup>2</sup> ha <sup>-1</sup> , ±SD]	36.7 ± 5.0	28.6 ± 7.3	35.1 ± 2.7
Light transmittance [%, ±SD]	3.2 ± 3.9	3.0 ± 4.8	8.9 ± 10.8
Number of cored trees	38	35	34
Average DBH of cored trees [cm, ±SD]	34.4 ± 9.1	39.3 ± 7.9	49.9 ± 6.8
Maximum DBH [cm]	55.4	51.8	66.0
Minimum DBH [cm]	19.3	20.0	37.7
Average height of cored trees [m, ±SD]	23.1 ± 4.8	26.3 ± 4.8	30.5 ± 3.0
Number of trees used in chronologies	32	30	29
Average ring width [mm, ±SD]	2.5 ± 1.0	2.7 ± 1.2	3.3 ± 1.5
Average series length [years, ±SD]	54.3 ± 9.7	61.6 ± 13.1	59.1 ± 12.6
Oldest measured ring	1943	1931	1930
Oldest ring used in chronologies	1947	1931	1930
First year of chronologies	1955	1945	1948
Average series intercorrelation	0.62	0.64	0.62

SD = Standard Deviation.

## 2.2. Field work

From each selected dominant silver fir tree, two opposite cores at 1.3 m height were taken perpendicular to the slope direction using an increment borer (3-threaded, 40 cm long with a diameter of 5 mm, Haglöl Co.). Each cored tree was georeferenced (x, y coordinate) and characterized by measuring diameter at breast height (DBH), height, height of the crown base, and crown width (average of the four cardinal directions).

In each circular plot, species, DBH, social position, height, and height of the crown base of all trees with DBH > 5 cm were measured. In this study we considered as established regeneration (saplings) individuals with height > 1.3 m and DBH < 5 cm. Their location, species, stem diameter at the ground, and height were recorded. In each plot, the number of seedlings (H < 1.3 m) was assessed for each species using a square frame (1 × 1 m<sup>2</sup>) placed at distances of 2, 6 and 10 m from the plot center and along the eight cardinal directions, for a total assessed area of 24 m<sup>2</sup> per circular plot. Species diversity was calculated using the Shannon diversity index (Shannon 1948). A selected number (i.e., 49 individuals for the whole study area) of seedlings and established regeneration of silver fir were cut or cored in order to determine the germination year. Finally, light transmittance (ratio of photosynthetically active radiation – PAR – reaching the forest floor) through the canopy was estimated using a radiation sensor. The measurements were carried out in each macroplot, along 8 cardinal directions, at 12:00 a.m. during a sunny summer day. Field work took place between October 2018 and January 2019, except for PAR measurements which were carried out between July and August 2019.

## 2.3. Dendrochronological analyses

The tree cores were glued on wood supports, dried and sanded with a belt sander using progressively finer grit sizes (150, 320, 600 and 800) in order to increase the visibility of the tree rings. Tree-ring widths (TRWs) were measured at the WSL research campus in Cadenazzo (Switzerland) with a precision of 0.005 mm on a measuring table (DENDROTAB 2003) connected to the software T-Tools Win Pro, both produced by WALESCH Electronic GmbH.

The measured tree-ring sequences were imported in the TSAP Win Professional software v4.5 (RINNTECH, Heidelberg). The matching of the two sequences belonging to the same tree was first visually assessed to identify possible measurement errors. The pairs were then averaged to get a single TRW series for each tree. The TRW series were cross-dated within each macroplot. The quality of this process was evaluated with the average inter-series intercorrelation (Cerrato et al. 2018). The TRW series were then detrended with a spline function and standardized by dividing their values by the corresponding estimates of the spline, creating unitless ring-width index (RWI) series that were pre-whitened using standard procedures to remove autocorrelation (Cook and Kairiukstis 1990).

Next, residual chronologies were calculated for every macroplot by averaging the RWI series belonging to the same macroplot. To enhance the robustness of the signal, sampling depth for the chronologies was set to a minimum of five RWI series. The similarity between chronologies was quantified by calculating their Gleichläufigkeit (Buras and Wilkming 2015; Eckstein and Bauch 1969).

## 2.4. Climatic data

Daily precipitation and daily maximum and minimum temperature data were retrieved from the San Miniato Cimitero meteorological station (102 m a.s.l., 43.68403°N, 10.83152°E) of the Tuscan Regional Hydrologic Service (SIR 2019a, 2019b). This station was chosen as reference because it is the closest weather station to Varramista (9.8 km away) with long data series for both temperature (since 1951) and precipitation (since 1958). The suitability of San Miniato Cimitero as

reference station was additionally confirmed by the high mean Pearson correlation coefficient ( $r = 0.88$ ) with the data of a rain gauge in Varramista, which is operated since 2012 (see Fig. S2 for details).

Missing precipitation data between 1997 and 1999 and missing temperature data in 1955, 1956, 1969, between 1996 and 1999 as well as single monthly gaps in precipitation (2000, 2004, and 2010) and temperature (2000, 2004, and 2013) were filled by estimates from a linear regression with precipitation data from Fattoria Scaletta (22 m a.s.l., 43.70739°N, 10.83063°E) and temperature data from Orto Botanico Lucca (16 m a.s.l., 43.84144°N, 10.51126°E). Moreover, precipitation data were extended back to 1951 (i.e., by 7 years) using data from Pontedera (14 m a.s.l., 43.66522°N, 10.63120°E). These weather stations were chosen considering their distance from Varramista and the availability of data during the measurement gaps for San Miniato Cimitero meteorological station.

The three-month Standardised Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010) was used as a proxy for drought conditions because it considers the role of evapotranspiration and temperature and is sensitive to short-term events (Abramopoulos et al. 1988; WMO and GWP 2016). Longer periods than three months have been shown not to be suitable in the analysis of drought effects on silver fir (Toromani et al. 2011), whereas shorter periods would not take into account the influence of precipitation and temperature of previous months. Estimates of potential evapotranspiration (PET) were calculated with a modified version of the Hargreaves equation (Beguería et al. 2014; Droogers and Allen 2002; Hargreaves and Samani 1985).

## 2.5. Climate-growth relationships

### 2.5.1. Correlation and response functions analysis

For the correlation and response function analysis of the RWI, we first detrended the climate series by means of a local regression (Baker 1990; Cleveland et al. 1992). Monthly precipitation, maximum temperature and SPEI data were then related to annual tree growth data with a correlation and response function analysis. Maximum temperature was preferred over minimum temperature because of its higher correlation with tree growth in other Italian silver fir populations (Gentilesca and Todaro 2008; Santini and Martinelli 1991) and the ecological assumption that maximum temperatures should be more important at this site than the mellow (typically above-zero) minimum temperatures.

Since the growth of the current year may be affected by the previous year's climatic conditions and related carbon and nutrients reserves, the time span for the analysis was set from March of the previous year to October of the current growing season. The growing season was assumed to start in March and end in October. This resulted in a total of 60 potential predictor variables (i.e., 20 independent parameters for three climatic variables). Pearson correlation and response function coefficients between variables and chronologies were calculated as described by Fritts et al. (1971) and Fritts (1976), differentiating from the correlation analysis by taking into account the possible multicollinearity of climatic variables. This analysis firstly runs a Principal Components Analysis and then estimates response coefficients using multiple regression (Rozas 2005).

Significance was tested at the level of  $p < 0.05$  for both correlation and response functions, applying a bootstrap technique with 1000 resampling runs.

### 2.5.2. Superposed epoch analysis (SEA)

The reaction of tree growth to summer droughts was assessed using a SEA. Summer drought was quantified by averaging SPEI values between June and September, thus expressing summer drought intensity (Tan et al. 2015). Years with a value  $< -1$ , indicating moderate to extreme drought conditions (McKee et al. 1993), were selected as drought years, and the behavior of growth during these drought years and up to four years after the drought year was analyzed. Significance was tested using

the four previous years as well. The growth reaction was quantified from scaled values: firstly, the mean chronology value was subtracted from the RWIs, and secondly RWIs were divided by their standard deviation. Therefore, growth differences are expressed as standard deviation difference. Significance at  $p < 0.05$  of the growth reactions was tested with a bootstrap technique with 5000 simulations over the whole site chronologies.

### 2.5.3. Pointer year analysis

For the analysis of the relation between extreme growth and climate, years with growth extremes (pointer years) were selected from the raw tree-ring series. Pointer years were defined at the macroplot level as years where at least 75% of the cored trees showed a relative growth increase or decrease of at least 20% compared to the average of the previous four years. Since similarities in the selected years were high, we decided to unify them all in a single dataset. Climatic conditions during positive and negative pointer years were analyzed qualitatively and compared to mean climatic conditions.

## 2.6. Statistical analyses

Crossdating was carried out using the software COFECHA (Holmes 1983). The R package *dplR* v1.7.1 (Bunn 2008, 2010; Bunn et al. 2020) was used to calculate detrended series and site chronologies and to conduct the SEA. SPEI and potential evapotranspiration (PET) were calculated with the R package *SPEI* v1.7 (Beguería et al. 2014; Vicente-Serrano et al. 2010). Correlation and response function analysis was made with the R package *treeclim* v2.0.5.1 (Zang and Biondi 2015); pointer years were selected with the R package *pointRes* v1.1.3 (van der Maaten-Theunissen et al. 2015). All analyses except for crossdating were performed using R v4.0.3 (R Core Team 2020).

## 3. Results

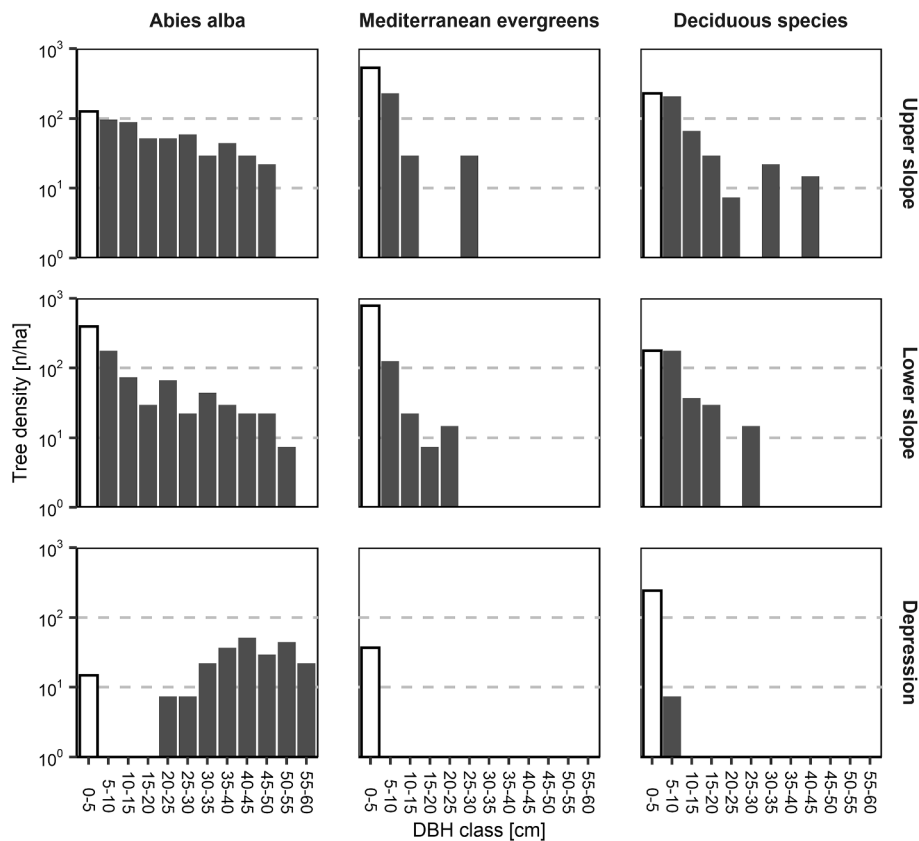
### 3.1. Stand structure

The average length of the TRW series ranges from 54.3 ( $\pm 9.7$ , upper slope macroplot) to 61.6 ( $\pm 13.1$ ) years (lower slope macroplot), with a maximum value of 89 years (Table 1). The average height of dominant trees in the macroplots confirms the existence of a gradient in growing conditions (Figure S3).

The three macroplots feature distinctly different basal area, with the lower slope macroplot having the lowest value of 28.6 ( $\pm 7.3$ )  $\text{m}^2 \text{ha}^{-1}$ , the depression 35.1 ( $\pm 2.7$ )  $\text{m}^2 \text{ha}^{-1}$ , and the upper slope the highest with 36.7 ( $\pm 5.0$ )  $\text{m}^2 \text{ha}^{-1}$ . Silver fir accounts for 99.7% of the basal area in the depression, 82.0% in the lower slope and 71.4% on the upper slope. Deciduous species contribute with a relative basal area of 10.9% in the lower slope, despite their absence from DBH classes  $> 30$  cm (Fig. 2), and 18.7% in the upper slope (58.0% of which were  $> 30$  cm DBH), respectively.

In every macroplot, the highest tree density is found in the lowest DBH class, i.e. below 5 cm, where shrubs and small trees are present. Silver fir regularly regenerates in all macroplots (Fig. S4). Species diversity is lower in the depression macroplot and in high DBH classes (Table 2), while the relative amount of silver fir increases with DBH, becoming the most frequent species starting from a DBH of 10 cm.

The macroplot in the depression has an overall lower tree density (Fig. S5), is characterized by a one-layered structure of silver fir only and no trees between 10 and 20 cm DBH, and displays with 8.9% the highest fraction of photosynthetically active radiation reaching the forest floor, which is more than twice as much as in the upper (3.2%) and lower slope (3.0%) macroplot, respectively (Table 1). At the established regeneration class (individuals below 5 cm DBH), the Shannon index is highest in the depression (Table 2), where deciduous species such as manna ash (*Fraxinus ornus* L.) prevail over evergreens. The two slope macroplots show a very similar species structure, with the relative amount of silver



**Fig. 2.** Tree density distribution per macroplot, species group and DBH class. The white column refers to the established regeneration (height > 1.3 m and DBH < 5 cm). Note that the y-axis has a logarithmic scale.

**Table 2**  
Shannon index values ( $\pm$ SD) in the different macroplots and stand layers.

	Established regeneration	Lower main layer	Upper main layer
Upper slope	1.32 ( $\pm$ 0.38)	1.52 ( $\pm$ 0.15)	0.55 ( $\pm$ 0.51)
Lower slope	1.33 ( $\pm$ 0.05)	1.36 ( $\pm$ 0.33)	0.52 ( $\pm$ 0.14)
Depression	1.53 ( $\pm$ 0.35)	0.00	0.00 ( $\pm$ 0.00)

Established regeneration = DBH < 5.0 cm and height > 1.3 m.

Lower main layer = DBH > 5.0 cm and < 15.0 cm.

Upper main layer = DBH > 15.0 cm.

Please note that the Shannon index of the lower main layer in the depression has no standard deviation due to the presence of only one tree.

fir increasing monotonically with DBH, and Mediterranean evergreens and English holly (*Ilex aquifolium* L.) in particular dominating the established regeneration stage. This pattern changes to a higher amount of deciduous species, such as sweet chestnut (*Castanea sativa* Mill.) and Turkey oak (*Quercus cerris* L.) for larger DBH values (Fig. S4).

In terms of seedlings (i.e., trees < 1.3 m in height) in the depression macroplot, the density of silver fir is twice as high compared to the slope macroplots (Fig. 3). Along the macroplot gradient, seedlings of deciduous species are highly significantly more frequent in the two slope macroplots, whereas Mediterranean evergreens are significantly denser in the upper slope macroplot only, compared to the depression.

### 3.2. Climate and dendroecological analyses

#### 3.2.1. Recent climate evolution in the study area

The 1951–1990 time series of annual precipitation and temperature shows no clear increasing or decreasing trends in inter- and intra-annual variability (Fig. 4). Starting in 1990, temperatures tend to increase, in the 2010s reaching a mean decadal value more than 1 °C higher

compared to the 1970s, whereas precipitation tends to be lower. As a consequence, SPEI has been decreasing since ca. 1990.

#### 3.2.2. Tree-ring width series

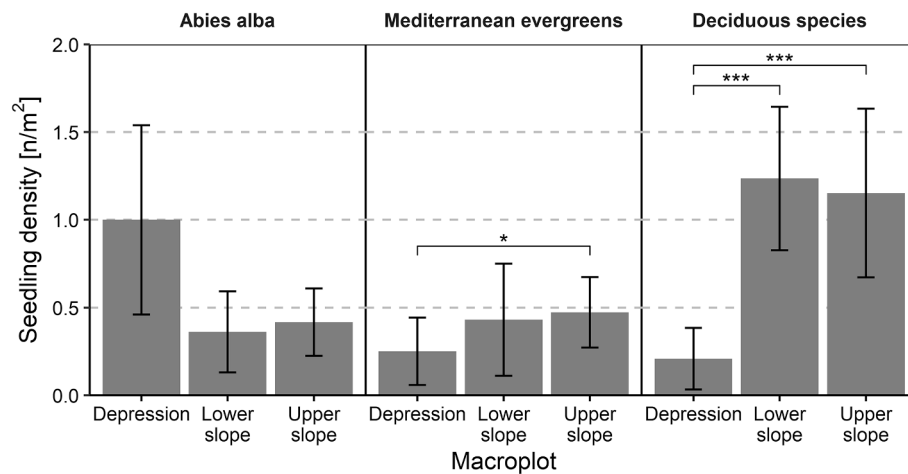
The overall average annual ring width is 2.8 ( $\pm$ 1.5) mm, ranging from 2.5 ( $\pm$ 1.0) mm in the upper slope macroplot, across 2.7 ( $\pm$ 1.2) mm on the lower slope macroplot, to 3.3 ( $\pm$ 1.5) mm in the depression macroplot (Table 1). At the macroplot level, the tree-ring series show very similar patterns (Fig. 5), with a first phase until about 1980 that is characterized by a slightly decreasing growth trend. Between 1980 and 2000, TRWs experienced an increase in all three macroplots, before decreasing again.

Average series intercorrelations range from 0.62 to 0.64, whereas Gleichläufigkeit values are 79.4% between upper slope and lower slope chronologies, 81.0% between upper slope and depression, and 81.4% between lower slope and depression, respectively. Similarly, the site chronologies show synchronous peaks, although at different magnitudes (Figure S7).

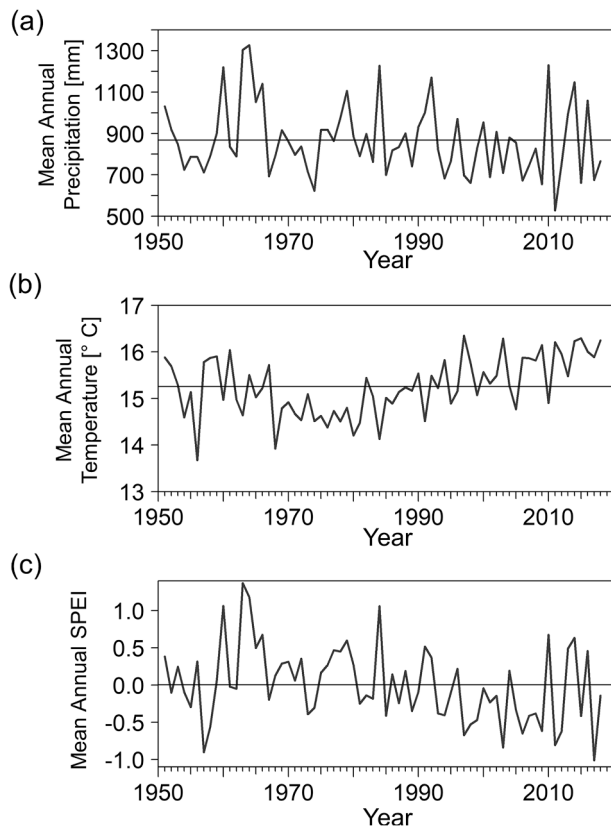
#### 3.2.3. Climatic response functions

Significant correlation coefficients are mostly found in the period between May and September of the current growing season (Fig. 6), even though the previous year’s conditions yield significant correlations as well, with differences between the climate variables, as follows.

Temperature features significant negative correlations with TRW for at least three months during the growing season of the current year in all macroplots and for November of the previous year. Previous summer precipitation has a somewhat negative influence on TRW, contrary to current summer, whose influence is distinctly positive for at least two months across all macroplots. This is also highlighted by the highest response function coefficient in the upper slope macroplot for current June.



**Fig. 3.** Seedling density per macroplot and species group. Vertical bars represent the 95% confidence interval; \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . For details on tree species grouping, please refer to Table S6.



**Fig. 4.** Meteorological time series (1951–2018) for Varramista. (a) mean annual precipitation (SIR 2019b), (b) mean annual temperature (SIR 2019a), (c) mean annual three-month SPEI. The horizontal lines represent the average values of the entire series.

Three-month SPEI shows positive and very high correlation coefficients during three to five months of the current summer. In contrast, previous summer SPEI is negatively correlated with growth, although a moving response analysis reveals that this influence was higher between 1970 and 2000 than at present (Fig. 7). The SPEI correlation and response coefficients reflect the patterns of the precipitation values, while they tend to be opposite to the coefficients calculated for temperature.

As a general trend, the upper slope macroplot shows a higher number

of large coefficients and significant values than the other macroplots, whereas the lower slope is least sensitive to the climate of the current summer season (Fig. S8).

The years selected as drought years (i.e., with summer SPEI values  $< -1$ ) are 1957, 1958, 2003, 2006, 2009, 2011, and 2017. The Superposed Epoch Analysis (SEA) indicates a significant growth decrease ( $p < 0.01$ ) during the drought years, but no significant consequences in the following years, irrespective of the macroplot (Fig. 7). The average ring-width index (RWI) in these drought years is 0.82 in the depression, 0.84 along the lower slope and 0.86 on the upper slope, respectively (Fig. S7).

Selected negative pointer years based on growth deviations are 1946, 1948, 1955, 1958, 2009, 2011, 2015, and 2017, while positive pointer years are 1953, 1956, 1963, 1984, 1991, 1996, and 2014. In general, the negative pointer years have below-average yearly mean SPEI values (-0.62). In particular, monthly values between May and November are lower than 0.75 in negative pointer years, reaching a minimum of -1.32 and -1.31 in June and July, respectively. In positive pointer years, the average SPEI is 0.62, with a maximum in February (1.13) and values from 0.66 to 0.79 between June and November.

In negative pointer years, climate is characterized by a mean temperature of 15.9 °C and a mean precipitation sum of 683 mm. Pointer-year temperature is thus comparable with the overall mean temperature in Varramista, but annual precipitation is more than 20% lower than the average. In negative pointer years, monthly precipitation exceeded the threshold of 100 mm in December only, i.e. outside the vegetation period, and reached the lowest value in July, with less than 20 mm. February and March were wetter than average, while summer and autumn were drier. In these years, the dry period starts almost two months earlier with respect to a standard season (when it usually spans from late June to August) and extends from May to August, which is more than twice as long as the average duration of a usual dry season.

Positive pointer years featured a mean annual precipitation of 1041 mm (i.e., 20% higher than the average) and a number of very moist months with rainfall exceeding 100 mm (i.e., January, September, October, and November). In these years, spring was wet and the dry period was only half as long with respect to the overall mean (e.g., dry July only). In addition, mean temperature amounted to 14.8 °C, i.e. 1.1 °C lower than during negative pointer years.

#### 4. Discussion

##### 4.1. Stand structure and regeneration dynamics

In Varramista, silver fir grows and regenerates together with Mediterranean species such as holm oak (*Q. ilex* L.) as well as thermophilous

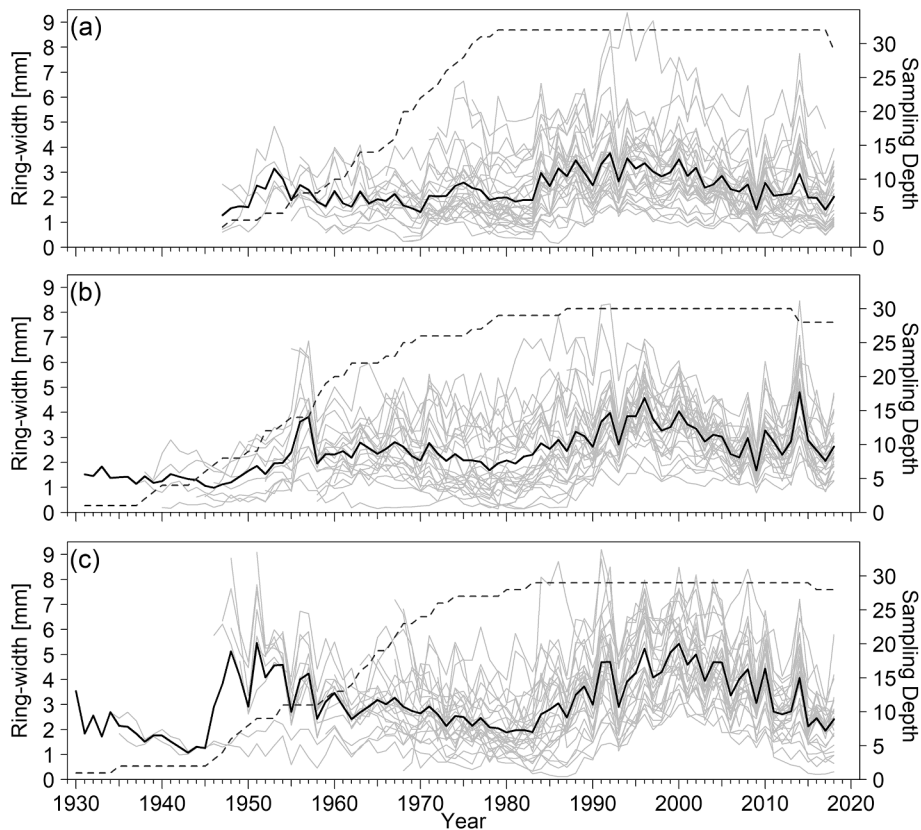


Fig. 5. Tree-ring-width (TRW) series of the cored trees in each macroplot. (a) upper slope, (b) lower slope, (c) depression. The black lines represent the TRW average series of the macroplot, whereas the dashed grey lines report the sampling depth.

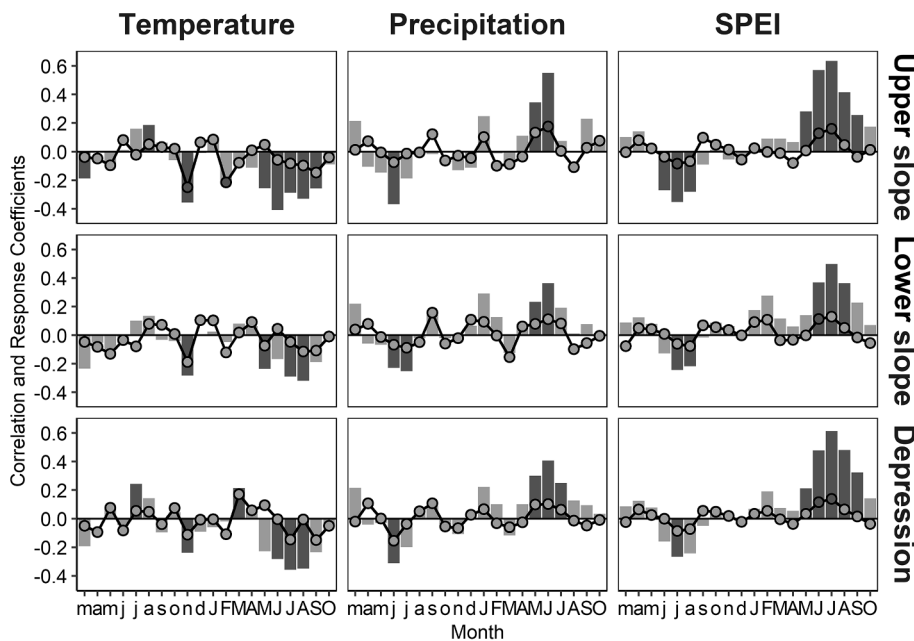


Fig. 6. Correlation and response functions coefficients for temperature, precipitation, and three-months SPEI monthly data for each macroplot. Bars show correlation coefficients and dots represent response coefficients. Dark grey bars refer to significant values, light grey bars to non-significant ones. Months of the current year are in capital letters, months of the previous year in lowercase. The analysis covers the period 1953–2018 for the upper and lower slope macroplots and 1955–2018 for the depression macroplot.

deciduous species such as Turkey oak (*Q. cerris* L.). This confirms the suitability of the species for such environmental conditions as reported by several palynological studies and models (Bellini et al. 2009; Di Pasquale et al. 2014; Tinner et al. 2013).

Nevertheless, regeneration capacity and growth performance of silver fir clearly follow a geomorphological gradient. In comparison to the slope macroplots, in the depression the stand structure is nearly single-

layered and features a higher silver fir density in the seedling class (Fig. 3) and at DBH values above 40 cm (Fig. 2). Although no detailed information exists on the effective impact of the 2015 windstorm, which was concentrated on the stands of the valley bottom, we can assume that the event highly influenced the stand structure of the depression macroplot, which was open enough to allow for the development of rather light-demanding deciduous species, such as manna ash (*Fraxinus ornus*

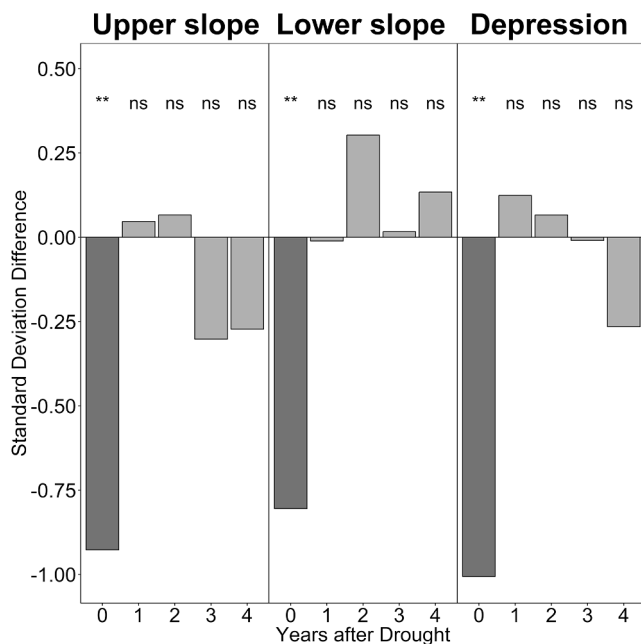


Fig. 7. Deviation from the mean growth in years with extreme summer droughts (0) and in the four following years (1–4). Dark grey bars refer to significant values (i.e.,  $**p < 0.01$ ), light grey bars to non-significant ones (i.e.,  $p > 0.05$ ).

L.).

For the highest DBH classes, silver fir densities tend to decrease (Fig. 2) and species diversity increases (Table 2) from the depression towards the slope macroplots, in particular the macroplot on the upper slope, which has a multi-layered structure and includes deciduous tree species that have a DBH larger than 30 cm, such as sweet chestnut and Turkey oak. The differences between the upper and lower slope macroplots may be due not only to their position on the slope but also to their aspect. In fact, west-facing slopes have been shown to usually host more dry-adapted vegetation communities than east-facing ones (Bennie et al. 2008). In the established regeneration stage, the dominance of Mediterranean evergreens in the slope macroplots mostly refers to the high densities of the shade-tolerant English holly (*Ilex aquifolium* L.), which was favored by the lower light transmittance of these stands.

The observed differences in stand structure and tree growth as a function of geomorphology are in line with previous studies on the susceptibility of the species when growing at low elevations under Mediterranean climate conditions (Henne et al. 2013; Henne et al. 2015; Tinner et al. 2013). In our case, however, Turkey oak played a much more prominent role than holm oak, which may be related to the broad use of *Q. cerris* for coppice management in this climatic zone (Fabbio and Cutini 2017).

#### 4.2. Trends in tree-ring growth

The long-term mean tree-ring widths in Varramista are comparable for similar time spans with the growth rates of silver fir in sub-Mediterranean and Mediterranean thermophilous mixed oak forests (e. g., Battipaglia et al. 2009; Lebourgeois et al. 2010; Mazza et al. 2014) as well as in the range of European beech and beech-fir forests of western, central and southeastern Europe, where annual precipitation rates are almost twice as high as in Varramista (i.e., 1500 mm/year; Fig. 8 and Fig. S9; Bijak 2010; Lebourgeois et al. 2010; Toromani et al. 2011; van der Maaten-Theunissen et al. 2013). In Varramista, mean TRWs in the depression macroplot and in the upper slope macroplot, which can be assumed to be most exposed to drought, do not substantially differ from the growth performance of silver fir in the Black Forest (van der Maaten-

Theunissen et al. 2013), which is considered to represent a well-suited mesic environment for the species.

Furthermore, the observed multi-annual (e.g., decadal) TRW trends in Varramista are in line with corresponding data at the continental level (Gazol et al. 2015; Vitasse et al. 2019), although with different magnitudes along the geomorphological gradient. In particular and rather unexpectedly, silver fir growing on the upper slope responds less sensitively to dry years.

The Varramista stands feature a decrease in TRWs from the early 1950s until the middle of the 1980s. Similar trends are reported from Central Europe (Germany and Poland in particular; Bošela et al. 2014; Büntgen et al. 2014; Elling et al. 2009; Łuszczynska et al. 2018; Uhl et al. 2013) to the Apennines in the Italian Peninsula (Clauser 1981; Clauser and Gellini 1986) and are usually ascribed to air pollution-induced stress due to high atmospheric  $SO_2$  and  $NO_x$  concentrations.

Starting from the 1980s, the TRW trends in Varramista followed again the general European pattern, i.e. the reduction in  $SO_2$  and nitrogen oxides ( $NO_x$ ) emissions (Bošela et al. 2014; Łuszczynska et al. 2018) combined with climate warming (Büntgen et al. 2014) allowed silver fir to recover and to considerably increase its growth rate until the end of the 1990s. A partial exception to this general growth release after 1980 is represented by silver fir stands in southern Italy and in the Pyrenees, where drier local climates combined with frequent drought events counterbalanced the positive effects of increased air quality (Büntgen et al. 2014).

A generalized increase in summer drought frequency and intensity as revealed by the SPEI values of the last 20 years in Varramista caused a TRW reduction starting at the beginning of the present century. This is in line with what is reported at the European scale (Bošela et al. 2018; EEA 2017; Gazol et al. 2016). In this context, Lebourgeois et al. (2010) emphasized the importance of soil water holding capacity for buffering the negative consequences of increasing summer drought intensities and frequencies for silver fir stands at low elevation.

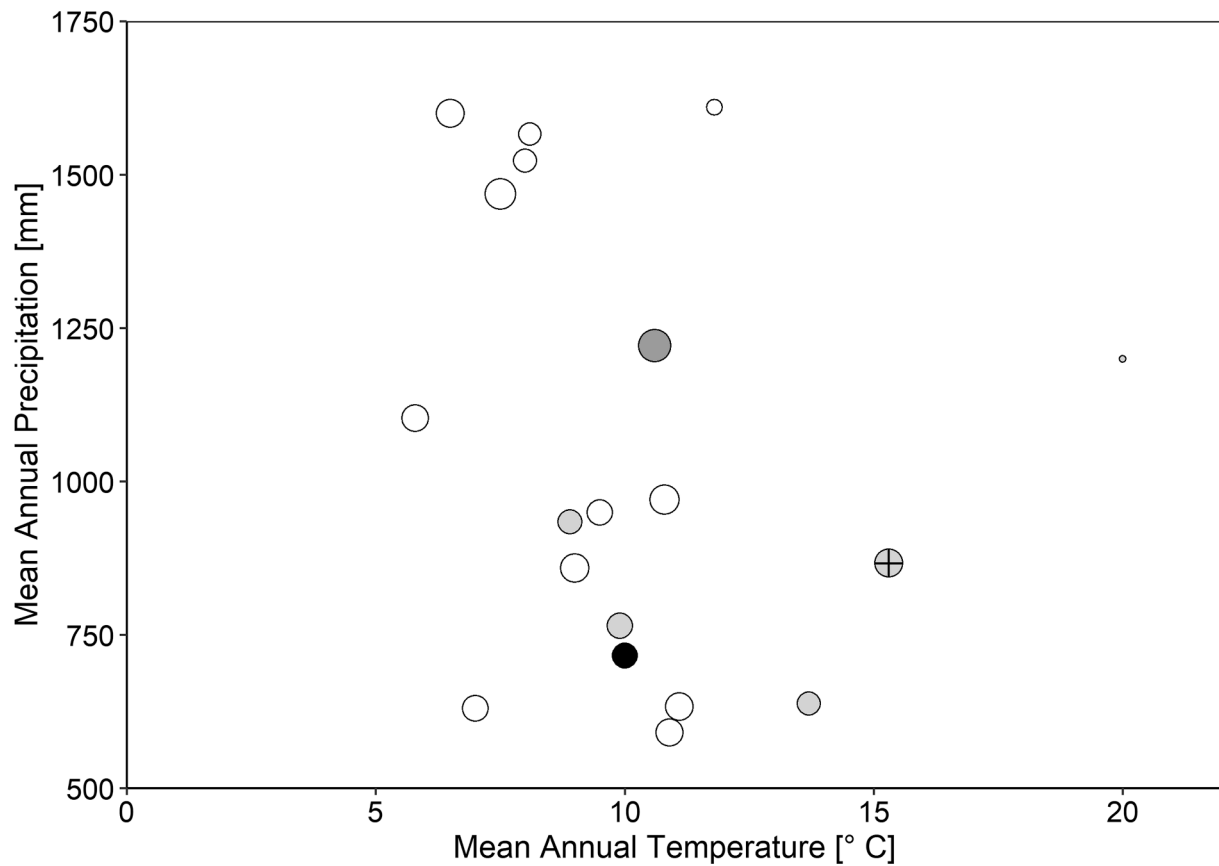
#### 4.3. Climate-growth relationships

The correlation and response functions analysis confirmed the high sensitivity in terms of annual ring width of lowland silver fir to water shortage and summer drought in particular. Therefore, longer-than-usual season aridity starting in May usually results in negative pointer years. A severe and early-starting water shortage period may in fact significantly restrict the available time for sustained growth, which in silver fir mostly occurs in early summer (Aussenac 2002; Lebourgeois 2007; Santini and Martinelli 1991). For the same reason, wet spring years allow silver fir to continuously foster the growth rates, which eventually results in positive pointer years (Cailleret et al. 2013).

The key limiting factor for tree-ring growth in silver fir at low elevation is thus summer drought, whereas with increasing elevation the main growth-regulating factors are winter and spring temperatures (Lebourgeois et al. 2013; Rolland et al. 1999; van der Maaten-Theunissen et al. 2013; Vitali et al. 2018).

Surprisingly, no negative impact or even a slight positive impact of previous-year drought conditions on TRWs has been observed in Varramista, especially during the growth release phase in the 1980s (Vitali et al. 2017). This lack of negative influence of dry summers on the growth in the next season contrasts with the immediate and mid-term negative post-drought growth reactions reported by other authors (Battipaglia et al. 2009; Macias et al. 2006; van der Maaten-Theunissen and Bouriaud 2012). According to Guicherd (1994), such mid-term negative reactions are due to the trait of silver fir to suspend drought-induced stomatal closure even during short and weak rainfall events, which possibly leads to water stress and lack of reserves for the next growing period (Toromani et al. 2011). In some cases, severe droughts and related decreases in water availability are even reported to have caused silver fir dieback, e.g. in the Pyrenees (Camarero et al. 2011; Hernández et al. 2019), in southern France (Cailleret et al. 2013) and in





Mean TRW [mm]	Vegetation Type
○ 1	● Montane and subalpine mountain coniferous forests and Krummholz bushes (Lebourgeois et al. 2010)
○ 2	● Central and Eastern European mixed oak forests (Lebourgeois et al. 2010)
○ 3	● Submediterranean and southern Mediterranean thermophilous mixed oak forests (Battipaglia et al. 2009; Lebourgeois et al. 2010; Mazza et al. 2014)
○ 4	○ Western, Central and Southeastern European beech and beech fir forests (Bijak 2010; Lebourgeois et al. 2010; Toromani et al. 2011; van der Maaten-Theunissen et al. 2013)

**Fig. 8.** Mean tree-ring widths of Silver fir for the period after 1900 AD and under different climate conditions (mean annual precipitation and temperature) and in different forest types. Point size represents the mean TRW of the series, the grey-scale color refers to the vegetation type following Lang (1994). The crossed point represents the depression macroplot of Varramista.

Switzerland (Rigling and Stähli 2020). There is no information on past dieback events in Varramista, however. Nevertheless, large diebacks following drought periods cannot be excluded, even if today the stands do not seem to have experienced any. Furthermore, the analyzed silver fir individuals are relatively young (ca. 60 years) and their response to climatic stress may feature an age-dependent component, as found for other coniferous tree species (e.g., Carrer and Urbinati 2004; Carrer 2011, Wu et al. 2018).

Clearly, the provenance of silver fir influences its response to drought (Matias et al. 2016; Mihai et al. 2021), as well as local adaptations of trees growing under frequent drought stress, which may to some extent buffer the negative consequences of water shortage (Csillery et al.

2020a; Csillery et al. 2020b; Nourtier et al. 2012). The study case of Varramista provides however the opportunity to further analyze this issue.

Lastly, the question remains open whether the high winter temperatures in Varramista may allow silver fir to restore part of the summer drought-induced missing reserves through a reactivation of the photosynthetic activity and the accumulation of carbon before the start of the next growing season (Carrer et al. 2010; Guehl et al. 1985; Kozłowski et al. 1991), as recently highlighted in different evergreen species of Mediterranean and temperate environments (Saarinen et al. 2011; Zhang et al. 2017). To elucidate this, ecophysiological measurements for several years would need to be made.

## 5. Conclusions

Our dendroecological investigation on *meso*-Mediterranean silver fir stands in Varramista confirms the potential of the species to thrive at the warm edge of its distribution, reaching similar growth performance as in Central Europe, in spite of substantially higher temperatures and much lower summer precipitation sums. The silver fir stands in Varramista follow the general long-term (decadal) growth trends of most European silver fir populations, including a continuous reduction of tree-ring width over the last ca. 25 years as a consequence of increasing water stress.

The most limiting factor for silver fir growth under these conditions is summer water shortage, but not temperature. We propose that in Varramista soils have a sufficient water holding capacity, allowing the local population of silver fir to not only overcome the typical and strong Mediterranean summer drought lasting at least two months, but also to regularly regenerate naturally and to successfully compete with *meso*-Mediterranean species such as *Quercus ilex* and *Q. cerris*.

The potential climatic envelope of silver fir should be extended to warm Mediterranean conditions, provided a sufficient annual precipitation (i.e., 850 mm) and the absence of extreme (i.e., three and more months lasting) summer droughts. In the face of ongoing climate change, future research should focus on the genetics and the provenances of existing *meso*-Mediterranean silver fir occurrences, such as the Varramista stands, and on their physiological adaptation mechanisms to summer drought in particular (e.g., growth performance, cambial activity and reserve use capacity under drought-stress during the growing season). Our study suggests that silver fir may have a bright future also under warmer and partially drier conditions in central Europe.

## CRedit authorship contribution statement

**Diego Walder:** Conceptualization, Methodology, Data curation, Formal analysis, Writing - review & editing, Software. **Patrik Krebs:** Methodology, Data curation, Visualization. **Harald Bugmann:** Conceptualization, Methodology, Supervision, Writing - review & editing. **Maria Chiara Manetti:** Conceptualization, Methodology, Data curation, Validation. **Martina Pollastrini:** Methodology, Data curation, Validation. **Solaria Anzillotti:** Methodology, Data curation. **Marco Conedera:** Project administration, Conceptualization, Methodology, Supervision, Writing - review & editing.

## Declaration of Competing Interest

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

## Acknowledgments

We would like to thank the ownership and the management of Varramista site and Dr. Carlo Maria Rebay, Dr. Michela Bulleri, Geom. Andrea Casarosa, and Rag. Giancarlo Carleschi for making this research possible and providing us with important historical information. Special thanks also go to the CREA FL technicians Leonardo Tonveronachi, Eligio Bucchioni, Walter Cresti, and Claudio Bidini for the support and help during the field survey.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119537>.

## References

- Abramopoulos, F., Rosenzweig, C., Choudhury, B., 1988. Improved ground hydrology calculations for global climate models (GCMs): soil water movement and evapotranspiration. *J. Clim.* 1 (9), 921–941.
- Allen, C.D., Macalady, A.K., Chenchoumi, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259 (4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- Aussenac, G., 2002. Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. *Ann. For. Sci.* 59 (8), 823–832. <https://doi.org/10.1051/forest:2002080>.
- Baker, W.L., 1990. Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *J. Biogeogr.* 17 (1), 59–73.
- Baroni, L., 1810. Modo di render fertili i terreni di pianura messo in pratica da Gio. Batt. Piccardi Agente alla Fattoria di Valramista del Sig. Ruberto Capponi. *Atti della Imp. Società economica di Firenze, ossia de' Georgofili* 6, 411–417.
- Battipaglia, G., Saurer, M., Cherubini, P., Siegwolf, R.T.W., Cotrufo, M.F., 2009. Tree rings indicate different drought resistance of a native (*Abies alba* Mill.) and a nonnative (*Picea abies* (L.) Karst.) species co-occurring at a dry site in Southern Italy. *For. Ecol. Manage.* 257 (3), 820–828. <https://doi.org/10.1016/j.foreco.2008.10.015>.
- Beguieria, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *Int. J. Climatol.* 34 (10), 3001–3023. <https://doi.org/10.1002/joc.3887>.
- Bellini, C., Mariotti-Lippi, M., Montanari, C., 2009. The Holocene landscape history of the NW Italian coasts. *The Holocene* 19 (8), 1161–1172. <https://doi.org/10.1177/0959683609345077>.
- Bennie, J., Huntley, B., Wiltshire, A., Hill, M.O., Baxter, R., 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecol. Model.* 216 (1), 47–59. <https://doi.org/10.1016/j.ecolmodel.2008.04.010>.
- Bijak, S., 2010. Tree-ring chronology of silver fir and its dependence on climate of the Kaszubskie Lakeland (Northern Poland). *Geochronometria* 35 (1), 91–94. <https://doi.org/10.2478/v10003-010-0001-9>.
- Bošela, M., Petráš, R., Sitková, Z., Priwitzer, T., Pajtlík, J., Hlavatá, H., Sedmák, R., Tobin, B., 2014. Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. *Environ. Pollut.* 184, 211–221. <https://doi.org/10.1016/j.envpol.2013.08.036>.
- Bošela, M., Lukac, M., Castagneri, D., Sedmák, R., Biber, P., Carrer, M., Konopka, B., Nola, P., Nagel, T.A., Popa, I., Roibu, C.C., Svoboda, M., Trotsiuk, V., Büntgen, U., 2018. Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Sci. Total Environ.* 615, 1460–1469. <https://doi.org/10.1016/j.scitotenv.2017.09.092>.
- Bowman, D.M.J.S., Murphy, B.P., Neyland, D.L.J., Williamson, G.J., Prior, L.D., 2014. Abrupt fire regime change may cause landscape-wide loss of mature obligate seedling forests. *Glob. Chang. Biol.* 20 (3), 1008–1015. <https://doi.org/10.1111/gcb.12433>.
- Bucher, H.U., 2014. *Abies alba*. In: Stimm, B., Roloff, A., Lang, U.M., Weisgerber, H. (Eds.), *Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie*.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26 (2), 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28 (4), 251–258. <https://doi.org/10.1016/j.dendro.2009.12.001>.
- Bunn, A.G., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2020. dplR: Dendrochronology Program Library in R.
- Büntgen, U., Tegel, W., Kaplan, J.O., Schaub, M., Hagedorn, F., Bürgi, M., Bräzdil, R., Helle, G., Carrer, M., Heussner, K.-U., Hofmann, J., Kontic, R., Kyncl, T., Kyncl, J., Camarero, J.J., Tinner, W., Esper, J., Liebhold, A., 2014. Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Front. Ecol. Environ.* 12 (2), 100–106. <https://doi.org/10.1890/130089>.
- Buras, A., Wilmking, M., 2015. Correcting the calculation of Gleichläufigkeit. *Dendrochronologia* 34, 29–30. <https://doi.org/10.1016/j.dendro.2015.03.003>.
- Buras, A., Menzel, A., 2018. Projecting tree species composition changes of European forests for 2061–2090 under RCP 4.5 and RCP 8.5 scenarios. *Front. Plant Sci.* 9, 1986. <https://doi.org/10.3389/fpls.2018.01986>.
- Caillieret, M., Nourtit, M., Amm, A., Durand-Gillmann, M., Davi, H., 2013. Drought-induced decline and mortality of silver fir differ among three sites in Southern France. *Ann. For. Sci.* 71 (6), 643–657. <https://doi.org/10.1007/s13595-013-0265-0>.
- Camarero, J.J., Bigler, C., Linares, J.C., Gil-Pelegrín, E., 2011. Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *For. Ecol. Manage.* 262 (5), 759–769.
- Capponi, G., 1882. *Lettere di Gino Capponi e di altri a lui. Successors Le Monnier*, Florence.
- Carcaillet, C., Muller, S.D., 2005. Holocene tree-limit and distribution of *Abies alba* in the inner French Alps: anthropogenic or climatic changes? *Boreas* 34 (4), 468–476. <https://doi.org/10.1080/03009480500231377>.
- Carrer, M., 2011. Individualistic and time-varying tree-ring growth to climate sensitivity. *PLoS ONE* 6.
- Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85, 730–740.

- Carrer, M., Nola, P., Motta, R., Urbinati, C., 2010. Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. *Oikos* 119 (9), 1515–1525. <https://doi.org/10.1111/j.1600-0706.2010.18293.x>.
- Cerrato, R., Salvatore, M.C., Brunetti, M., Coppola, A., Baroni, C., 2018. Dendroclimatic relevance of “Bosco Antico”, the most ancient living European larch wood in the Southern Rhaetian Alps (Italy). *Geografia Fisica e Dinamica Quaternaria* 41 (1), 35–49. <https://doi.org/10.4461/GFDQ.2018.41.3>.
- Cesarini, P., 1940. Un'abetina nelle basse colline pisane. *Rivista Forestale Italiana* 2 (4), 177–181.
- Clauser, F., 1981. Una nuova moria dell'abete bianco a Vallombrosa. *Il Montanaro d'Italia - Monti e Boschi* 6, 51–55.
- Clauser, F., Gellini, R., 1986. Moria del bosco: osservazioni sulle latifoglie nel triennio '82-84 in Toscana. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie B* 93, 11–25.
- Cleveland, W.S., Grosse, E., Shyu, W.M., 1992. Local regression models. In: Chambers, J. M., Hastie, T.J. (Eds.), *Statistical Models in S*. Wadsworth and Brooks/Cole, New York, pp. 309–376.
- Cook, E.R., Kairiukstis, L.A., 1990. *Methods of Dendrochronology: Applications in the Environmental Sciences*. Springer Science & Business Media.
- Corongiu, M., Gardin, L., Romanelli, S., Bottai, L., Gozzini, B., and Trevisani, M., 2016. La banca dati pedologica di Regione Toscana ed il tema SOIL di INSPIRE. In: ASITA. Cagliari.
- Cortini Pedrotti, C., 1967. L'abetina Di Varramista (Pisa). *Webbia* 22 (1), 39–65. <https://doi.org/10.1080/00837792.1967.10669860>.
- Csillery, K., Buchmann, N., Fady, B., 2020a. Adaptation to drought is coupled with slow growth, but independent from phenology in marginal silver fir (*Abies alba* Mill.) populations. *Evol. Appl.* 13 (9), 2357–2376. <https://doi.org/10.1111/eva.13029>.
- Csillery, K., Ovaskainen, O., Sperisen, C., Buchmann, N., Widmer, A., Gugerli, F., 2020b. Adaptation to local climate in multi-trait space: evidence from silver fir (*Abies alba* Mill.) populations across a heterogeneous environment. *Heredity* (Edinb) 124 (1), 77–92. <https://doi.org/10.1038/s41437-019-0240-0>.
- Di Pasquale, G., Allevalo, E., Cocchiara, A., Moser, D., Pacciarelli, M., Saracino, A., Woods, S., 2014. Late Holocene persistence of *Abies alba* in low-mid altitude deciduous forests of central and southern Italy: new perspectives from charcoal data. *J. Veg. Sci.* 25 (5), 1299–1310. <https://doi.org/10.1111/jvs.12196>.
- Droogers, P., Allen, R.G., 2002. Estimating reference evapotranspiration under inaccurate data conditions [journal article]. *Irrig. Drain. Syst.* 16 (1), 33–45. <https://doi.org/10.1023/a:1015508322413>.
- Dyderski, M.K., Paź, S., Frelich, L.E., Jagodziński, A.M., 2018. How much does climate change threaten European forest tree species distributions? *Glob Chang Biol.* 24 (3), 1150–1163. <https://doi.org/10.1111/gcb.13925>.
- Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagegüte. *Forstwissenschaftliches Zentralblatt* 88 (1), 230–250. <https://doi.org/10.1007/bf02741777>.
- Elling, W., Dittmar, C., Pfaffelmoser, K., Rötzer, T., 2009. Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. *For. Ecol. Manage.* 257 (4), 1175–1187. <https://doi.org/10.1016/j.foreco.2008.10.014>.
- European Environment Agency (EEA), 2017. *Climate change, impacts and vulnerability in Europe 2016. An indicator-based report*. Office for Official Publications of the European Union, Luxembourg.
- Fabbio, G., Cutini, A., 2017. Coppice today: which management beyond definitions? *Forest@ - Rivista di Selvicoltura ed Ecologia Forestale* 14 (5), 56–73. <https://doi.org/10.3832/efor2562-014>.
- Fratini, S., Acquavita, F., 2017. The Climate of Italy. In: Soldati, M., Marchetti, M. (Eds.), *Landscapes and Landforms of Italy*. Springer International Publishing, Cham, pp. 29–38.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, London.
- Fritts, H.C., Blasing, T.J., Hayden, B.P., Kutzbach, J.E., 1971. Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. *J. Appl. Meteorol.* 10 (5), 845–864.
- Gazol, A., Camarero, J.J., Gomez-Aparicio, L., 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. *J. Ecol.* 104 (4), 1063–1075. <https://doi.org/10.1111/1365-2745.12575>.
- Gazol, A., Camarero, J.J., Gutiérrez, E., Popa, I., Andreu-Hayles, L., Motta, R., Nola, P., Ribas, M., Sangüesa-Barreda, G., Urbinati, C., Carrer, M., Vetaas, O., 2015. Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J. Biogeogr.* 42 (6), 1150–1162. <https://doi.org/10.1111/jbi.12512>.
- Gentilesca, T., Todaro, L., 2008. Crescita radiale e risposte climatiche dell'abete bianco (*Abies alba* Mill.) in Basilicata. *For. J. Silvicult. For. Ecol.* 5 (1), 47. <https://doi.org/10.3832/efor0505-0050047>.
- Giorgi, C., 2009. *Il paesaggio della fattoria di Varramista*. Faculty of Architecture, University of Florence, Florence.
- Guehl, J.-M., Clerc, B., Desjeunes, J.-M., 1985. Étude comparée des potentialités hivernales d'assimilation carbonée de trois conifères de la zone tempérée (*Pseudotsuga menziesii* Mirb., *Abies alba* Mill. et *Picea excelsa* Link.). In: *Annales des sciences forestières*. EDP Sciences, pp. 23–38.
- Guicherd, P., 1994. Water relations of European silver fir (*Abies alba* Mill.) in 2 natural stands in the French Alps subject to contrasting climatic conditions. *Ann. For. Sci.* 51 (6), 599–611. <https://doi.org/10.1051/forest:19940606>.
- Hagerman, S.M., Pelai, R., 2018. Responding to climate change in forest management: two decades of recommendations. *Front. Ecol. Environ.* 16 (10), 579–587. <https://doi.org/10.1002/fee.1974>.
- Hargreaves, G.H., Samani, Z.A., 1985. Reference crop evapotranspiration from temperature. *Appl. Eng. Agric.* 1 (2), 96–99. <https://doi.org/10.13031/2013.26773>.
- Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O., Tinner, W., 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landscape Ecol.* 28 (5), 819–833. <https://doi.org/10.1007/s10980-012-9782-8>.
- Henne, P.D., Elkin, C., Franke, J., Colombaroli, D., Calò, C., La Mantia, T., Pasta, S., Conedera, M., Dermody, O., Tinner, W., 2015. Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Front. Ecol. Environ.* 13 (7), 356–362. <https://doi.org/10.1890/150027>.
- Hernández, L., Camarero, J.J., Gil-Peregrín, E., Saz Sánchez, M.Á., Cañellas, I., Montes, F., 2019. Biotic factors and increasing aridity shape the altitudinal shifts of marginal Pyrenean silver fir populations in Europe. *For. Ecol. Manage.* 432, 558–567. <https://doi.org/10.1016/j.foreco.2018.09.037>.
- Holmes, R., 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 44, 69–78.
- Intergovernmental Panel on Climate Change (IPCC), 2013. *Climate Change 2013: The Physical Science Basis*. In: T. F. Stocker et al. (Eds.) Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 1535.
- Keenan, R.J., 2015. Climate change impacts and adaptation in forest management: a review. *Ann. For. Sci.* 72 (2), 145–167. <https://doi.org/10.1007/s13595-014-0446-5>.
- Kozłowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. *The Physiological Ecology of Woody Plants*. Academic Press, New York.
- Lebourgeois, F., 2007. Climatic signal in annual growth variation of silver fir (*Abies alba* Mill.) and spruce (*Picea abies* Karst.) from the French Permanent Plot Network (RENECOFOR). *Ann. For. Sci.* 64 (3), 333–343. <https://doi.org/10.1051/forest:2007010>.
- Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). *J. Veg. Sci.* 21 (2), 364–376. <https://doi.org/10.1111/j.1654-1103.2009.01148.x>.
- Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manage.* 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>.
- Łuszczynska, K., Wistuba, M., Malik, I., 2018. Reductions in tree-ring widths of silver fir (*Abies alba* Mill.) as an indicator of air pollution in southern Poland. *Environ. Socio-Econ. Stud.* 6 (3), 44–51. <https://doi.org/10.2478/environ-2018-0022>.
- Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir (*Abies alba* (Mill.) water stress in its South-Western distribution limit. *Clim. Change* 79 (3–4), 289–313. <https://doi.org/10.1007/s10584-006-9071-0>.
- Madrigal-González, J., Herrero, A., Ruiz-Benito, P., Zavala, M.A., 2017. Resilience to drought in a dry forest: Insights from demographic rates. *For. Ecol. Manage.* 389, 167–175. <https://doi.org/10.1016/j.foreco.2016.12.012>.
- Maiorano, L., Cheddadi, R., Zimmermann, N.E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B.L., Pearman, P.B., Psomas, A., Singarayer, J.S., Broennimann, O., Vittoz, P., Dubuis, A., Edwards, M.E., Binney, H.A., Guisan, A., 2013. Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Glob. Ecol. Biogeogr.* 22 (3), 302–317. <https://doi.org/10.1111/j.1466-8238.2012.00767.x>.
- Matias, L., Gonzalez-Diaz, P., Quero, J.L., Camarero, J.J., Lloret, F., Jump, A.S., 2016. Role of geographical provenance in the response of silver fir seedlings to experimental warming and drought. *Tree Physiol.* 36 (10), 1236–1246. <https://doi.org/10.1093/treephys/tpw049>.
- Mauri, A., de Rigo, D., and Caudullo, G., 2016. *Abies alba* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. e01493b+.
- Mazza, G., Gallucci, V., Manetti, M.C., Urbinati, C., 2014. Climate-growth relationships of silver fir (*Abies alba* Mill.) in marginal populations of Central Italy. *Dendrochronologia* 32 (3), 181–190. <https://doi.org/10.1016/j.dendro.2014.04.004>.
- McKee, T.B., Doesken, N.J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. In: *Proceedings of the 8th Conference on Applied Climatology*. American Meteorological Society Boston, MA, pp. 179–183.
- Mihai, G., Alexandru, A.M., Stoica, E., Birsan, M.V., 2021. Intraspecific growth response to drought of *Abies alba* in the Southeastern Carpathians. *Forests* 12 (4). <https://doi.org/10.3390/f12040387>.
- Municipality of Montopoli in Val d'Arno, 2008. *Il piano strutturale di Montopoli in Val d'Arno - Relazione generale - Sintesi quadro conoscitivo*.
- Nourtier, M., Chanzy, A., Cailleret, M., Yingge, X., Huc, R., Davi, H., 2012. Transpiration of silver fir (*Abies alba* Mill.) during and after drought in relation to soil properties in a Mediterranean mountain area. *Ann. For. Sci.* 71 (6), 683–695. <https://doi.org/10.1007/s13595-012-0229-9>.
- Ott, E., Fehner, M., Frey, H.-U., Lüscher, P., 1997. *Gebirgsnadelwälder: Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung*. Haupt, Bern.
- Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* 15 (3), 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rais, A., Poschenrieder, W., Pretzsch, H., van de Kuilen, J.-W.G., 2014. Influence of initial plant density on sawn timber properties for Douglas-fir (*Pseudotsuga menziesii*

- (Mirb.) Franco). *Ann. For. Sci.* 71 (5), 617–626. <https://doi.org/10.1007/s13595-014-0362-8>.
- Raunkjær, C., 1934. The life forms of plants and statistical plant geography, trans. Gilbert-Carter, H.; Fausbøll, A.; Tansley, A.G., Oxford: Clarendon Press, OCLC 4300750; reprinted (1977) in History of ecology series, New York: Arno Press, ISBN 978-0-405-10418-3.
- Regione Toscana. 2018. DataBase Pedologico in scala 1:10.000 della Regione Toscana. Regione Toscana (Ed.).
- Rigling, A., Stähli, M., 2020. Erkenntnisse aus der Trockenheit 2018 für die zukünftige Waldentwicklung. *Schweizerische Zeitschrift für Forstwesen* 171 (5), 242–248.
- Rolland, C., Michalet, R., Desplanque, C., Petetin, A., Aimé, S., 1999. Ecological requirements of *Abies alba* in the French Alps derived from dendro-ecological analysis. *J. Veg. Sci.* 10 (3), 297–306.
- Rozas, V., 2005. Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: tree-ring growth responses to climate. *Ann. For. Sci.* 62 (3), 209–218. <https://doi.org/10.1051/forest:2005012>.
- Rüegg, D., 2015. Im Glarner Schutzwald alle 60 m eine Weissstanne. *Schweizerische Zeitschrift für Forstwesen* 166 (1), 40–41. <https://doi.org/10.3188/szf.2015.0040>.
- Ruosch, M., Spahni, R., Joos, F., Henne, P.D., van der Knaap, W.O., Tinner, W., 2016. Past and future evolution of *Abies alba* forests in Europe - comparison of a dynamic vegetation model with palaeo data and observations. *Glob. Chang. Biol.* 22 (2), 727–740. <https://doi.org/10.1111/gcb.13075>.
- Saariinen, T., Lundell, R., Hänninen, H., 2011. Recovery of photosynthetic capacity in *Vaccinium vitis-idaea* during mild spells in winter. *Plant Ecol.* 212 (9), 1429–1440. <https://doi.org/10.1007/s11258-011-9918-y>.
- Santini, A., Martinelli, N., 1991. *Indagine dendroecologica sull'abete bianco (Abies alba Mill.) di Serra San Bruno (CZ)*. *Giornale botanico italiano* 125, 895–906.
- Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R. T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., Watson, J.E.M., 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354 (6313). <https://doi.org/10.1126/science.aaf7671>.
- Scherrer, D., Massy, S., Meier, S., Vittoz, P., Guisan, A., Serra-Diaz, J., 2017. Assessing and predicting shifts in mountain forest composition across 25 years of climate change. *Divers. Distrib.* 23 (5), 517–528. <https://doi.org/10.1111/ddi.12548>.
- Seidl, R., Rammer, W., Lexer, M.J., 2011. Adaptation options to reduce climate change vulnerability of sustainable forest management in the Austrian Alps. *Can. J. For. Res.* 41 (4), 694–706. <https://doi.org/10.1139/x10-235>.
- Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Chang.* 4 (9), 806–810. <https://doi.org/10.1038/nclimate2318>.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyser, C.P.O., 2017. Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402. <https://doi.org/10.1038/nclimate3303>.
- Servizio Geologico Regionale (SGR), 2006. Carta geologica della Toscana.
- Servizio Idrologico Regionale (SIR), 2019a. Precipitazioni giornaliere - Sez. B, Tab. 1. Servizio Idrologico Regionale.
- Servizio Idrologico Regionale (SIR), 2019b. Temperature giornaliere - Sez. A, Tab. 1. Servizio Idrologico Regionale.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27 (3), 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>.
- Susmel, L., 1957. Premesse storico-climatiche e bio-ecologiche alla selvicoltura della foresta montana appenninica. *Accad. Econ. Agr. Geografici* 4, 1–42.
- Tan, C., Yang, J., Li, M., 2015. Temporal-spatial variation of drought indicated by SPI and SPEI in Ningxia Hui Autonomous Region, China. *Atmosphere* 6 (10), 1399–1421. <https://doi.org/10.3390/atmos6101399>.
- Thurm, E.A., Hernandez, L., Baltensweiler, A., Ayan, S., Rasztovits, E., Bielak, K., Zlatanov, T.M., Hladnik, D., Balic, B., Freudenschuss, A., Büchsenmeister, R., Falk, W., 2018. Alternative tree species under climate warming in managed European forests. *For. Ecol. Manage.* 430, 485–497. <https://doi.org/10.1016/j.foreco.2018.08.028>.
- Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B., Conedera, M., 1999. Long-term forest fire ecology and dynamics in southern Switzerland. *J. Ecol.* 87 (2), 273–289. <https://doi.org/10.1046/j.1365-2745.1999.00346.x>.
- Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G., Conedera, M., Joos, F., Lotter, A.F., Luterbacher, J., Samartin, S., Valsecchi, V., 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecol. Monogr.* 83 (4), 419–439. <https://doi.org/10.1890/12-2231.1>.
- Toromani, E., Sanxhaku, M., Pasho, E., 2011. Growth responses to climate and drought in silver fir (*Abies alba*) along an altitudinal gradient in southern Kosovo. *Can. J. For. Res.* 41 (9), 1795–1807. <https://doi.org/10.1139/x11-096>.
- Uhl, E., Ammer, C., Spellmann, H., Schölich, M., Pretzsch, H., 2013. Zuwachstrend und Stressresilienz von Tanne und Fichte im Vergleich. *Allgemeine Forst- und Jagdzeitung* 184 (11–12), 278–292.
- van der Maaten-Theunissen, M., Bouriaud, O., 2012. Climate–growth relationships at different stem heights in silver fir and Norway spruce. *Can. J. For. Res.* 42 (5), 958–969. <https://doi.org/10.1139/x2012-046>.
- van der Maaten-Theunissen, M., Kahle, H.-P., van der Maaten, E., 2013. Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. *Ann. For. Sci.* 70 (2), 185–193. <https://doi.org/10.1007/s13595-012-0241-0>.
- 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>.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323 (5913), 521–524. <https://doi.org/10.1126/science.1165000>.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscale drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index. *J. Clim.* 23 (7), 1696–1718. <https://doi.org/10.1175/2009jcli2909.1>.
- Vilà-Cabrera, A., Coll, L., Martínez-Vilalta, J., Retana, J., 2018. Forest management for adaptation to climate change in the Mediterranean basin: a synthesis of evidence. *For. Ecol. Manage.* 407, 16–22. <https://doi.org/10.1016/j.foreco.2017.10.021>.
- Vitali, V., Büntgen, U., Bauhus, J., 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. *Glob. Chang. Biol.* 23 (12), 5108–5119. <https://doi.org/10.1111/gcb.13774>.
- Vitali, V., Büntgen, U., Bauhus, J., 2018. Seasonality matters—The effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe. *Dendrochronologia* 48, 1–9. <https://doi.org/10.1016/j.dendro.2018.01.001>.
- Vitasse, Y., Bottero, A., Rebetez, M., Conedera, M., Augustin, S., Brang, P., Tinner, W., 2019. What is the potential of silver fir to thrive under warmer and drier climate? *Eur. J. Forest Res.* 138 (4), 547–560.
- Wolf, H., 2003. EUFORGEN Technical Guidelines for genetic conservation and use for silver fir (*Abies alba*). International Plant Genetic Resources Institute, Rome.
- World Meteorological Organization (WMO) and Global Water Partnership (GWP), 2016. Handbook of Drought Indicators and Indices. Integrated Drought Management Tools and Guidelines Series 2, Geneva.
- Wu, G.J., Liu, X.H., Kang, S.C., Chen, T., Xu, G.B., Zeng, X.M., Wang, W.Z., Wang, B., Zhang, X.W., Kang, H.H., 2018. Age-dependent impacts of climate change and intrinsic water-use efficiency on the growth of Schrenk spruce (*Picea schrenkiana*) in the western Tianshan Mountains, China. *For. Ecol. Manage.* 414, 1–14.
- Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography* 38 (4), 431–436. <https://doi.org/10.1111/ecog.01335>.
- Zhang, C., Filella, I., Liu, D., Ogaya, R., Llusà, J., Asensio, D., Peñuelas, J., 2017. Photochemical Reflectance Index (PRI) for detecting responses of diurnal and seasonal photosynthetic activity to experimental drought and warming in a Mediterranean Shrubland. *Remote Sensing* 9 (11). <https://doi.org/10.3390/rs9111189>.
- Zimmermann, N.E., Schmatz, D.R., Gallien, L., Körner, C., Huber, B., Frehner, M., Küchler, M., Psomas, A., 2016. Baumartenverbreitung und Standorteignung. In: Pluess, A.R.; Augustin, S.; Brang, P. (Red.), Wald im Klimawandel. Grundlagen für Adaptionsstrategien. Bundesamt für Umwelt BAFU, Bern; Eidg. Forschungsanstalt WSL, Birmensdorf; Haupt, Bern, Stuttgart, Wien. 199–221.