Annals of Forest Science (2020) 77: 55
https://doi.org/10.1007/s13595-020-00956-y

RESEARCH PAPER

Which matters more for wood traits in *Pinus halepensis* Mill., provenance or climate?

Andrea Hevia[1,2,3] · Filipe Campelo[4] · Regina Chambel[5] · Joana Vieira[4] · Ricardo Alía[5] · Juan Majada[2] · Raúl Sánchez-Salguero[3]

Received: 20 August 2019 / Accepted: 22 April 2020 / Published online: 9 June 2020

Abstract

· ***Key message*** **Intra-annual wood density fluctuations are valuable indicators of the role of the local climate and provenance origins on tree growth. These intra-ring wood features were the most informative about local adaptation and phenotypic plasticity of *Pinus halepensis* Mill. in a provenance trial. This highlights the importance of taking provenance into account when selecting forest reproductive material to mitigate the effects of climate change.**

· ***Context*** It is essential to disentangle the influence of climate from the effect of provenance on inter- and intra-annual wood traits to identify populations' responses to climate changes. This will be even more relevant in the drought-prone Mediterranean region, where species have high genetic differentiation among populations.

· ***Aims*** We investigated the effects of provenance and climate driving *Pinus halepensis* Mill. wood traits, as imprinted phenotypic adaptations to the Mediterranean climate.

· ***Methods*** Inter- and intra-annual wood trait variation (ring-, early-, and latewood width, wood density) was studied by microdensitometry in 8 provenances from Spain, France, Greece, and Italy in a common-garden experiment. We related wood traits and density fluctuations with inter-annual climate variations at the trial site and the provenance origin.

· ***Results*** Provenances showed distinct responses to climate regarding tree growth, wood density, and intra-annual fluctuations. Density fluctuations in latewood were more frequent than in earlywood. Climate at the provenance origin was a more important force for density fluctuations than climatic variations at the planting site, with different trends between coastal and inland provenances, and higher frequency of latewood fluctuations in provenances from arid and semiarid sites.

· ***Conclusion*** Differences in *P. halepensis* wood density fluctuations confirmed the imprinted origin provenance control in response to climate variations and indicated a relation with local adaptation of these xylem anatomical features. Moreover, the position of these fluctuations in rings reflected the high plasticity of *P. halepensis* to cope with high intra-seasonal variability of climatic conditions. This underlines the importance of considering tree-ring features for the selection of provenances in reforestation material for conservation and silvicultural programs.

Handling Editor: Patrick Fonti

Contribution of the co-authors AH prepared the samples and performed the wood density analysis. RSS and AH proposed the hypothesis. AH, FC, and RSS explored and analyzed the data, prepared figures and tables, and wrote the first draft of the manuscript. All authors read, revised, and approved the final manuscript.

✉ Andrea Hevia
aheviacabal@gmail.com

[1] Departamento de Ciencias Agroforestales, Escuela Técnica Superior de Ingeniería, Universidad de Huelva, 21819 Palos de la Frontera, Spain

[2] Forest and Wood Technology Research Centre (CETEMAS), Pumarabule, Carbayín, s/n, 33936 Siero, Asturias, Spain

[3] Departamento de Sistemas Físicos, Químicos y Naturales. DendrOlavide, Universidad Pablo de Olavide, Crta. Utrera km. 1, 41013 Sevilla, Spain

[4] Department of Life Sciences, Centre for Functional Ecology, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal

[5] Department of Ecology and Forest Genetics, INIA-CIFOR, Ctra. Coruña km. 7.5, 28040 Madrid, Spain

Keywords Dendroecology · ITRAX · Aleppo pine · Intra-annual density fluctuations · Mediterranean · Local adaptation

1 Introduction

The forecasted increase in temperature and higher frequency and intensity of severe dry spells (Christensen et al. 2007) may act as selective forces by accelerating the evolutionary rate of drought-adaptive traits in widely distributed tree species (Kremer et al. 2014; Sánchez-Salguero et al. 2018). In the drought-prone Mediterranean region, water shortage leads to reduce productivity and forest growth, which often translates into dieback and mortality (e.g., Camarero et al. 2015; Giorgi and Lionello 2008). Identifying tree populations more adapted to drought by structure-function or physiological adjustments across different regions is one of the main concerns of tree breeding programs (Rosner et al. 2008, 2014). Therefore, the development of woody tissue, especially the xylem conduits that allow plants to efficiently transport water along the soil-plant-atmosphere continuum, must be explored considering tree provenances (e.g., George et al. 2015, 2019; Klein et al. 2013; Lamy et al. 2014).

The influence of climate change may vary depending on the species phenotypic plasticity and on its ability to adapt to future climate conditions (Nicotra et al. 2010). This is closely related to the provenance (geographic and genetic origin) of tree populations (e.g., Heer et al. 2018; Sánchez-Salguero et al. 2018) but also to ontogenetic factors such as tree size, tree age, or sex (e.g., Bogino and Bravo 2009; Campelo et al. 2007, 2013, 2015; Carrer and Urbinati 2004; Nabais et al. 2014; Olano et al. 2015; Olivar et al. 2012; Rigling et al. 2001; Vieira et al. 2009; Wimmer 2002). However, there is a lack of knowledge for Mediterranean species in the identification of the most sensitive wood traits to climatic stress (e.g., radial-growth plasticity) and the understanding of climate-adaptive genetic variation (e.g., Valladares et al. 2014).

Adaptive phenotypic plasticity has been evaluated through the natural distribution of forest species (e.g., Benito-Garzón et al. 2011; de Luis et al. 2013; Sánchez-Salguero et al. 2018), but common-garden trials (e.g., George et al. 2019; Housset et al. 2018; Klisz et al. 2016, 2019) are also needed to find populations with desirable traits (e.g., Chambel et al. 2013; Nabais et al. 2018). The fact that some traits differ among provenances in the same species, growing in homogeneous environments (common garden), indicate population-level differences (*sensu* Isaac-Renton et al. 2018). Indeed, among-population variation in wood traits is also related to climate in their origin (e.g., Climent et al. 2008; García-Esteban et al. 2010; Vander Mijnsbrugge and Janssens 2019; Voltas et al. 2008), which involve local adaptation to climate (Housset et al. 2018). Under similar environmental conditions (common-garden experiments), the understanding of the plastic response of wood traits to favorable (wet) or unfavorable (dry) years can be expected to show indirect evidence for provenance origin differences in adaptation (Santos-del-Blanco et al. 2013; David-Schwartz et al. 2016). However, genetic differentiation, plasticity (c.f. Chevin et al. 2013), and adaptation will be also necessary to achieve long-term persistence in the context of climate change (Anderson et al. 2012). To this end, common-garden experiments have been conducted for a better understanding of adaptation and maladaptation of trees (Montwé et al. 2018).

Since responses to environmental conditions are recorded in the wood structure (Carrer et al. 2017), the capacity of trees to adjust their cambial activity (Vieira et al. 2015) to climatic variations is of great interest (De Micco et al. 2016a). In particular, the formation of intra-annual density fluctuations (IADFs, c.f. Campelo et al. 2007) in response to intra-seasonal variations of environmental conditions. These structural features could provide a functional understanding of the population's variability in wood traits and phenotypic plasticity (e.g., Balzano et al. 2018; Campelo et al. 2007, 2013; de Luis et al. 2011; Vieira et al. 2010; Zalloni et al. 2018). However, the intra-specific variability of the IADFs' frequency also appears to be genetically determined (Klisz et al. 2016), which leads to an increasing interest in species distribution (e.g., Edmonson 2010; Nabais et al. 2014; Novak et al. 2013b; Rigling et al. 2002) and also among populations within the same species (e.g., George et al. 2015, 2019; Klisz et al. 2019).

The anatomical structures of IADFs are frequently formed in the circum-Mediterranean Aleppo pine (*Pinus halepensis* Mill.; e.g., de Luis et al. 2011; García-Esteban et al. 2010; Olivar et al. 2012; Pacheco et al. 2016). This species shows a wide climate niche, with high phenotypic plasticity and functional adaptations in anatomical, morphological, and physiological traits at the intra-specific level (Voltas et al. 2018). The variability in tree growth response (e.g., de Luis et al. 2013; García-Esteban et al. 2010; Voltas et al. 2008) or intra-ring features (e.g., de Luis et al. 2011; Novak et al. 2013a; Olivar et al. 2012, 2015) in relation to climate in *P. halepensis* has been deeply investigated across the Mediterranean area. Nevertheless, provenance trials of this species to disentangle the effect of environment (site) from the effect of population origin (genetic provenance) on wood traits (e.g., ring width, wood density, IADFs) remain scarce. However, it is crucial for identifying strategies to cope with climate change across its wide distribution (de Luis et al. 2013) and to adjust future forest management programs (Wang et al. 2010).

The relevance of *P. halepensis* as one of the most drought-tolerant pine species (e.g., Chambel et al. 2013; Klein et al. 2011) is therefore of even more remarkable interest in finding the best functional trait from different genetic sources (seeds) of this conifer to use in future afforestation programs (David-Schwartz et al. 2016; Montwé et al. 2018). Most of the previous studies in *P. halepensis* provenances have been limited to anatomical, ecophysiological, and morphometric features (e.g., Chambel et al. 2007; Climent et al. 2008; David-Schwartz et al. 2016; García-Esteban et al. 2010; Tognetti et al. 1997; Voltas et al. 2008, 2018), without considering the variation of IADFs as a genetic provenance imprint in wood plasticity (De Micco et al. 2016b).

Here, we explore the among-provenance variability of wood traits (tree-ring width, wood density, and IADFs) in a provenance trial (16 years), allowing a deeper understanding of specific responses of provenances to climate. It is hypothesized that (1) IADFs could be seen as specific anatomical features, which explains the differentiation of well- or maladapted *P. halepensis* provenances to drought events, limiting the ability to take advantage of short periods of favorable weather conditions under projected climate change (Montwé et al. 2018) and (2) this anatomical adaptation is modulated by the provenance site aridity. The objective of this study was to investigate these hypotheses by (i) identifying relationships between wood traits and climate, (ii) quantifying the presence of different types of IADFs in *P. halepensis* provenances growing under common climate, and (iii) establishing the relationship between IADFs' frequency and climate of the provenance origin. To this end, we used wood trait data comprising most of Aleppo pine's range of distribution, from which we selected 8 Mediterranean regions of provenances (5 Spain, 1 France, 1 Greece, 1 Italy) in a common-garden experiment, based on their environmental similarity and geographical proximity.

2 Material and methods

2.1 Trial site and plant material origin

The trial site was established in 1998 with the explicit objective of understanding how climatic factors modulate the phenotype of different *P. halepensis* genotypes from its Mediterranean range of distribution. It is located in a common-garden experiment in Arganda del Rey (Madrid, Spain) at 40°18′ 39″ N and 3° 29′ 32″ W at 534 m a.s.l., at the west edge of the species natural distribution in Spain, where both climate and soil conditions are moderately limiting (for details, see Climent et al. 2008; Santos-del-Blanco et al. 2013; Voltas et al. 2008) (Fig. 1a). Soil type was a fertile typic xerofluvent of about 1.25 m depth (Voltas et al. 2008). The climate is Mediterranean continental, where annual air temperature is 15.0 °C and the annual precipitation is 385 mm, with 158 mm during the vegetation period (AEMET, Arganda weather station; study period data: 1960–2012). A significant increase in annual mean temperature after 1980s (Fig. 1c) has been found and a significant reduction in summer precipitation alternating wet years (2004, 2008, 2010) with extreme droughts (2005, 2009, 2012) (Fig. 1c).

Seed material from 56 Mediterranean provenances of *P. halepensis* from across its natural distribution area was collected in 1995 (c.f. Climent et al. 2008; Voltas et al. 2008). The study trial was planted in 1998 with 1-year-old seedlings from that seed material (see Cortina et al. (2006) for nursery details and experimental design of provenance trial) and is maintained by the Spanish network of forest genetic trials (GENFORED) (Alía et al. 1996). In the winter of 2012–2013, a subset of 18 representative populations, grouped in 8 regions of provenance (see Table 1, cf. Climent et al. 2008; Gil et al. 1996), was chosen for this study. This included eight ecologically distinct regions (distributed in continental Spain, the Balearic Islands, France, Italy, and Greece) based on common environmental and geographical proximity (see Gil et al. 1996) and five ecotypes (genetic units with divergent adaptive responses triggered by climate; see Voltas et al. 2018) (Fig. 1, Table 1).

Climate of the provenance origin for the period 1979–2013 was obtained from CHELSA database (Climatologies at high resolution for the Earth's land surface areas v. 1.2; Karger et al. 2017) at 30″ resolution from the nearest grid point. We explored the 19 bioclimatic variables (Table 7) and selected variables with recognized influence on phenotypic variation of *P. halepensis* (see Climent et al. 2008; Tapias et al. 2004; Voltas et al. 2008, 2018): Mean January temperature (Tmean1) and March maximum temperature (Tmax3) to characterize each *P. halepensis* population (Fig. 1, Table 1).

2.2 Tree-ring sampling and wood density analysis

In the winter of 2012–2013, at least five representative trees for each region of provenance (8 Reg Prov; Table 1) were randomly chosen (see Table 2). Tree-ring data were collected using a 12 mm diameter increment borer at breast height. The samples were taken to the laboratory, where approximately 1.4 mm thick laths of each core were produced with a double-blade circular saw (AFUME, France). Wooden laths were kept under constant temperature and humidity and X-ray scanned in Itrax Multiscanner (Cox Analytical Systems, Sweden) at the laboratory of CETEMAS (Asturias, Spain) (see Hevia et al. 2018). The samples were exposed to 20 kV, 50 mA and 25 ms in the radial direction (20-μm step size) (Moreno-Fernández et al. 2018). The radiographic images were visually cross-dated and wood density profiles obtained for each sample (i.e., a vector of wood density values measured along the wood sample). Density profiles were extracted from the radiographic images by calibrating the pixel-wise data to gray-scale intensities using a light calibration curve derived from a calibration step-wedge sample (Schweingruber 1996). Tree-ring boundaries were automatically detected on density profiles using the *detectRings* function from

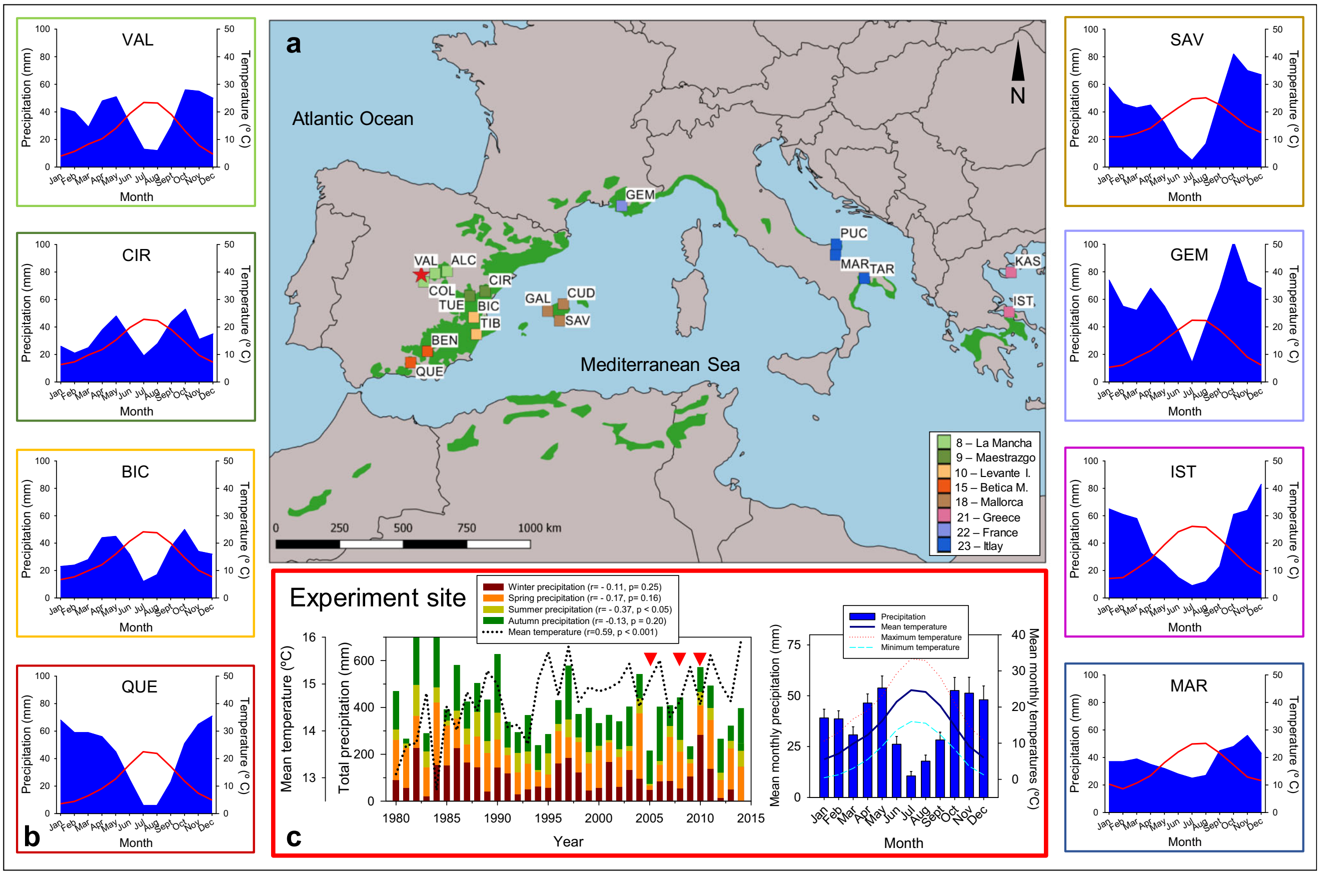

Fig. 1 **a** Location of the *Pinus halepensis* provenance-progeny trial (red star) and the provenances used in the present study (c.f. Climent et al. 2008; Gil et al. 1996) (squares; different colors of squares correspond to the classification of regions of provenances described in Table 1). The green area represents the natural distribution of the species (source EUFORGEN). **b** Climatic diagrams of the studied sites for the period 1979–2013 based on CHELSA global climate database (Karger et al. 2017). **c** Climatic trends (Pearson correlation coefficients; *r*) in mean temperature and seasonal precipitation (left column; red triangles indicate favorable and unfavorable selected years) and climatic diagrams (right column) of the trial site for the period 1979–2014 based on the local climate station (AEMET, Spanish Meteorological Agency). The statistics show the corresponding significance levels (*p*)

the R package *xRing* (Campelo et al. 2019; R Development Core Team 2019) and when necessary manual corrections were made using the *correctRings* function. Then, the function *detectEwLw* in the *xRing* package was used to detect the end of earlywood and the start of latewood automatically (Campelo et al. 2019); we used the 35% (40%) between *Dmin* and *Dmax* values of each ring (see Polge 1978) to define the end of earlywood (start of latewood), which were also visually confirmed (c.f. Mäkinen and Hynynen 2014). Finally, the functions *getDensity* and *getRwls* were used to produce time series for each tree of different ring features: ring width (hereafter *RW*), earlywood width (*EW*), latewood width (*LW*), *EW* to *LW* ratio (*EW/LW*), and wood transition width (*TW*, as the transition from *EW* to *LW*), as well as for mean ring density (hereafter *Dmean*), earlywood (*Dew*), latewood (*Dlw*), and maximum density (*Dmax*). Density parameters were measured in g/cm^3, while ring width parameters were measured to the nearest 0.001 mm.

2.3 Intra-annual density fluctuations

For each ring in each dated core, IADFs were automatically identified on microdensity profiles following the methodology proposed by George et al. (2019) (Fig. 2). Rings without IADFs were identified as the rings with typical early- and latewood and a gradual transition between them, whereas abrupt changes in this pattern were defined as IADFs (de Luis et al. 2011; De Micco et al. 2014). The IADFs were classified according to their positions within the tree-ring (cf. Campelo et al. 2007): type E characterized by latewood-like cells within earlywood, type L formed by earlywood-like cells within latewood, and type L$^+$ showing earlywood-like cells between latewood and earlywood of the next tree-ring (Fig. 2). We excluded IDAFs type E$^+$ based on the low frequency presented in *P. halepensis* (see de Luis et al. 2011; Novak et al. 2013a). The percentage of IADFs was calculated per population and also per region of provenance (Reg Prov; Table 1). Since

Table 1 Description of the provenances of *Pinus halepensis* used in the provenance-progeny trial (Arganda, Madrid)

ID	Prov[1]	Prov ID	Code, Reg Prov	Location	Country	Long	Lat	Alt	Pan	Ta	Ecotype[2]
1	082	VAL	08, La Mancha	Valdeconcha, Guadalajara	Spain, SP	2°52′ W	40°26′ N	800	458	12.7	C
2	083	ALC	08, La Mancha	Alcantud, Cuenca	Spain, SP	2°19′ W	40°34′ N	950	525	11.9	C
3	084	COL	08, La Mancha	Colmenar de Oreja, Madrid	Spain, SP	3°20′ W	40°05′ N	750	414	14.3	C
4	091	CIR	09, Maestrazgo-Los Serranos	Cirat, Castellon	Spain, SP	0°28′ W	40°03′ N	500	401	13.8	C
5	092	TUE	09, Maestrazgo-Los Serranos	Tuéjar, Valencia	Spain, SP	1°09′ W	39°49′ N	600	362	13.7	C
6	101	TIB	10, Levante Interior	Tibi, Alicante	Spain, SP	0°39′ W	38°31′ N	1010	420	12.9	A
7	105	BIC	10, Levante Interior	Bicorp, Valencia	Spain, SP	0°51′ W	39°06′ N	650	378	14.4	C
8	151	QUE	15, Bética Meridional	Quentar, Granada	Spain, SP	3°24′ W	37°13′ N	1250	534	11.6	A
9	152	BEN	15, Bética Meridional	Benamaurel, Granada	Spain, SP	2°44′ W	37°42′ N	920	398	14.6	C
10	183	SAV	18, Mallorca	Ses Salines, Baleares	Spain, SP	3°03′ W	39°17′ N	10	529	17.2	A
11	184	CUD	18, Mallorca	Alcudia, Mallorca	Spain, SP	3°10′ W	39°52′ N	100	740	16.2	E
12	185	GAL	18, Mallorca	Son Marti/Calviá, Mallorca	Spain, SP	2°29′ W	39°35′ N	300	471	16.5	E
13	211	IST	21, Greece	Istiaia-Euboea, Greece	Greece, GR	23°29′ W	38°44′ N	53	509	16.1	D
14	214	KAS	21, Greece	Kassandra, Greece	Greece, GR	23°52′ W	40°05′ N	25	494	14.5	D
15	221	GEM	22, France	Gemenos, France	France, FR	5°40′ W	43°25′ N	391	708	13.2	F
16	231	TAR	23, Italy	Litorale Tarantino, Italy	Italy, IT	17°06′ W	40°37′ N	10	590	15.2	E
17	232	PUC	23, Italy	Gargano Monte Pucci, Italy	Italy, IT	15°56′ W	41°54′ N	100	210	15.6	E
18	233	MAR	23, Italy	Gargano Marzini, Italy	Italy, IT	15°51′ W	41°32′ N	200	452	16.4	F

Climate data for the 18 seed source provenances used in this study for the period 1979–2013 based on CHELSA global climate database (Karger et al. 2017)

[1] Prov, provenance code per site; Prov ID, provenance name; Code, Reg Prov, provenance code of each region of provenance; Location, population, province; Long, longitude; Lat, latitude; Alt, altitude (m); Pan, annual precipitation (mm); Ta, annual mean temperature (°C)

[2] Ecotypes by Voltas et al. (2018): temperate winters and an arid (A); colder areas having cold winters and a semiarid climate (C) or cool winters and a sub-humid climate (D); temperate winters and a semiarid climate (E) or cool winters and a sub-humid climate (F)

Table 2 Dendrochronological statistics of the tree-ring (*RW*), earlywood (*EW*), transition wood (*TW*), latewood width (*LW*), and the *EW* to *LW* ratio (*EW/LW*) chronologies for each provenance during the common period 2004–2012

			RW							*EW*						*TW*	
Code	N° cores	Reg Prov	Length	Mean	SD	Ar1	MS	GLK	rbt	Mean	SD	Ar1	MS	GLK	rbt	Mean	SD
08	12	La Mancha	2002–2013	7.24	3.33	0.12	0.59	0.73	0.63	3.99	2.08	0.10	0.69	0.66	0.50	0.18	0.17
09	6	Maestrazgo	2003–2013	6.79	3.08	0.21	0.52	0.85	0.65	3.75	2.33	0.07	0.70	0.74	0.57	0.18	0.16
10	5	Levante I.	2003–2013	9.12	4.52	0.05	0.65	0.89	0.75	4.58	2.58	0.02	0.76	0.71	0.71	0.14	0.10
15	6	Bética M.	2004–2013	6.11	3.18	0.41	0.60	0.84	0.86	3.81	2.10	0.24	0.77	0.76	0.81	0.14	0.14
18	12	Mallorca	2003–2013	7.39	3.87	0.13	0.60	0.75	0.66	4.13	2.58	0.10	0.81	0.71	0.66	0.22	0.22
21	6	Greece	2000–2013	8.37	3.45	0.04	0.47	0.77	0.69	4.87	2.39	− 0.02	0.66	0.71	0.69	0.13	0.10
22	6	France	2004–2013	4.99	2.45	0.05	0.53	0.74	0.70	3.56	1.87	0.12	0.60	0.64	0.75	0.10	0.07
23	9	Italy	2003–2013	6.06	2.83	− 0.02	0.54	0.72	0.61	3.37	1.66	− 0.07	0.67	0.70	0.56	0.12	0.08

	TW				*LW*						*EW/LW*					
Code	Ar1	MS	GLK	rbt	Mean	SD	Ar1	MS	GLK	rbt	Mean	SD	Ar1	MS	GLK	rbt
08	0.02	0.73	0.66	0.20	3.05	2.02	0.07	0.64	0.70	0.48	1.79	1.22	− 0.04	0.74	0.58	0.28
09	0.02	0.67	0.51	0.24	2.84	1.32	0.12	0.49	0.60	0.17	1.69	1.38	− 0.26	0.81	0.66	0.10
10	− 0.15	0.76	0.59	0.26	4.38	2.74	0.23	0.66	0.78	0.32	1.55	1.07	0.06	0.67	0.75	0.28
15	0.06	0.69	0.71	0.64	2.15	1.48	0.16	0.58	0.65	0.52	2.15	1.39	− 0.32	0.86	0.68	0.46
18	0.00	0.75	0.69	0.34	3.02	1.78	− 0.01	0.59	0.63	0.27	1.80	1.23	−0.11	0.81	0.71	0.38
21	− 0.16	0.63	0.53	− 0.03	3.35	1.28	0.05	0.38	0.65	0.45	1.92	0.96	−0.10	0.61	0.59	0.16
22	0.15	0.51	0.65	0.31	1.31	0.88	− 0.01	0.56	0.61	0.28	3.61	2.01	0.00	0.67	0.67	0.18
23	− 0.14	0.70	0.65	0.26	2.56	1.56	− 0.10	0.57	0.56	0.28	1.98	1.46	−0.14	0.76	0.65	0.38

Mean width in mm; SD, standard deviation; Ar1, first-order autocorrelation; MS, mean sensitivity, Gleichläufigkeit coefficient (GLK, %), calculated to evaluate the synchronicity within each series from the same provenance (see Buras and Wilmking 2015) and rbt, mean between-trees correlation of ring width indices. Code numbers and regions of provenance are given in Table 1

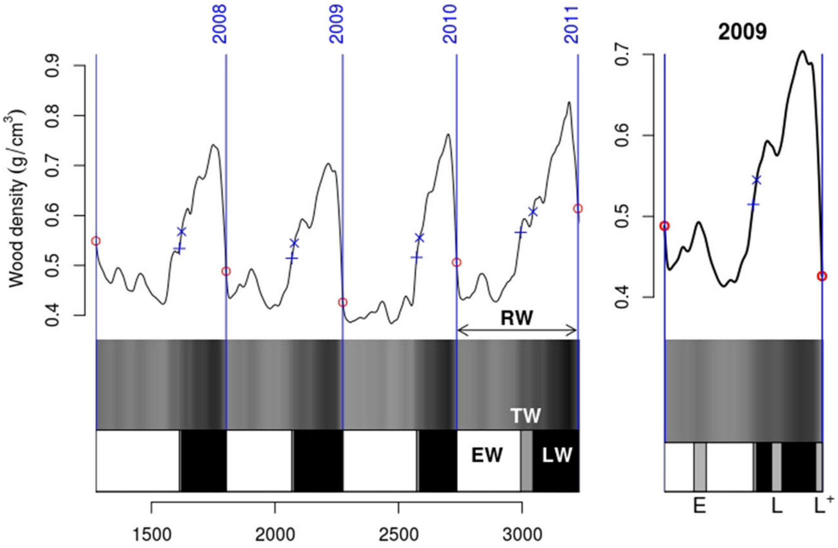

Fig. 2 Example of the output obtained using the *xRing* package for R environment. In the left figure, tree-ring features were shown for the period 2008–2011 (*RW,* tree-ring width; *EW*, earlywood width; *LW,* latewood width; *TW*, wood (earlywood-latewood) transition). In the right plot is depicted the year 2009 to illustrate the three IADF types: E (i.e., with *LW* like-cells in *EW*), L (with earlywood like-cells in latewood), and L$^+$ (between latewood and earlywood of the next tree-ring). The plus sign "+" (in blue) indicates the end of earlywood, and the symbol "×" shows the start of the latewood. Red circles indicate tree-ring borders

the sample depth is almost constant over the common interval for each provenance, we did not stabilize the frequency of IADFs per year.

2.4 Statistical analysis

For each provenance, chronologies for ring widths were developed by fitting a smoothing spline of 20-year wavelength and a response of 0.5 to each tree-ring series. A first autoregressive model was applied to each ring-index series, and the resulting series were used to compute the residual chronology. Chronology building (Table 2) and climate-growth associations were performed using the packages *dplR* (Bunn 2008) and *detrendeR* (Campelo et al. 2012) for R (http://www.cran.r-project.org). The quality of chronologies was assessed by several dendrochronological statistics (Fritts 2001) considering the complete core period (see Tables 2 and 3): mean sensitivity (MS), first-order autocorrelation of raw data (Ar1), and mean correlation between trees (rbt). The coefficient of coherence was also quantified by average *Gleichläufigkeit* (glk; c.f. Buras and Wilmking 2015; Eckstein and Bauch 1969) in all ring width variables (Table 2).

Firstly, we assessed differences of wood properties (ring width and density), calculated as annual average values (inter- and intra-ring) for the common period 2004–2012. For this, we fitted a linear mixed-effect model (LME) to analyze the difference among *RW*, *EW*, *TW*, *LW*, *EW/LW*, *Dmean*, *Dmax*, *Dew*, and *Dlw* using the *lme* function of the *nlme* package (Pinheiro et al. 2020) with provenance as fixed factor and year as a random factor. The difference in fluctuations of wood density (different types of IADFs) among populations and region of provenances was assessed using one-way ANOVA. Principal component analysis (PCA) was also applied to the matrix IADF variables (frequency of IADFs per type of IADF (E, L, L$^+$)). The PCA was performed by singular value decomposition, using the R function *prcomp* (Venables and Ripley 2002) after standardizing variables to have a mean of zero and standard deviation of one.

Lastly, for the 8 grouped provenances, the relationships between the site experiment's monthly climate series (mean, maximum, and minimum temperatures and precipitation) and individual wood traits: ring width (*RW*, *EW*, *LW, TW*), wood density (*Dmean*, *Dew*, *Dlw*, *Dmax*), and IADFs' frequency was assessed by Pearson correlation coefficients for the common period 2004–2012. The temporal window of growth-climate comparisons included the last 4 months of the previous year of the tree-ring and all months of the current year. To assess differences in the IADF types under extreme climatically contrasting years (c.f. Santos-del-Blanco et al. 2013) and define the peak shifting to different ring portion depending on the provenance response, we analyzed unfavorable climatic years (i.e., years with a combination of low precipitation and high temperatures: 2005) and favorable climatic years (i.e., years with a combination of high precipitation and high temperatures under different seasons: 2008 (autumn), 2010 (spring)) (Fig. 1c).

We also assessed the relationship between density fluctuations (IADFs' frequency) and climate conditions (bioclimatic variables, monthly and annual precipitation, and minimum, maximum, and mean temperature) at the population origin. PCA analyses were created with the *FactoMineR* (Husson

Table 3 Dendrochronological statistics for mean ring density (*Dmean*), maximum density (*Dmax*), earlywood density (*Dew*), and latewood density (*Dlw*) during the common period 2004–2012

			Dmean					*Dmax*					*Dew*					*Dlw*				
Code	N° trees	Provenance	Mean	SD	Ar1	MS	rbt	Mean	SD	Ar1	MS	rbt	Mean	SD	Ar1	MS	rbt	Mean	SD	Ar1	MS	rbt
08	12	La Mancha	0.62	0.06	−0.06	0.10	0.28	0.86	0.08	0.09	0.09	0.32	0.56	0.05	0.03	0.09	0.20	0.76	0.07	0.01	0.09	0.18
09	6	Maestrazgo	0.49	0.04	−0.06	0.10	0.46	0.66	0.03	0.23	0.05	0.11	0.44	0.03	−0.13	0.08	0.06	0.60	0.03	0.23	0.04	−0.06
10	5	Levante I.	0.63	0.05	0.14	0.07	0.27	0.82	0.05	0.13	0.06	0.16	0.54	0.05	0.19	0.08	0.22	0.74	0.04	0.21	0.05	0.11
15	6	Bética M.	0.57	0.06	−0.24	0.12	0.80	0.82	0.05	−0.01	0.07	0.31	0.50	0.05	−0.26	0.10	0.63	0.72	0.04	0.07	0.06	0.33
18	12	Mallorca	0.57	0.04	−0.11	0.08	0.64	0.74	0.04	0.17	0.05	0.46	0..51	0.04	−0.01	0.07	0.26	0.67	0.03	0.17	0.04	0.34
21	6	Greece	0.62	0.08	−0.17	0.13	0.60	0.93	0.04	0.04	0.04	0.26	0.52	0.05	−0.15	0.12	0.67	0.84	0.04	−0.08	0.06	0.06
22	6	France	0.60	0.05	0.03	0.08	0.51	0.88	0.07	0.24	0.06	0.40	0.55	0.04	−0.05	0.08	0.45	0.78	0.05	0.11	0.06	0.36
23	9	Italy	0.61	0.05	−0.03	0.09	0.41	0.82	0.06	0.02	0.06	0.04	0.54	0.04	0.04	0.08	0.18	0.74	0.05	0.05	0.06	0.07

Mean density in g/cm^3; SD, standard deviation; Ar1, first-order autocorrelation; MS, mean sensitivity, and rbt, mean between-trees correlation of ring-density indices, and the code numbers and regions of provenance are given in Table 1

et al. 2019) and *factoextra* (Kassambara and Mundt 2019) R packages, and correlation analyses were carried out by using the *cor.test* function in R (R Development Core Team 2019). The relationship between a selection of climatic variables and each type of IADF was also examined by linear regressions.

3 Results

3.1 Intra- and inter-provenance growth and density variations

The mean width values of *EW*, *LW*, and *RW* varied significantly ($p < 0.001$) among provenances (Tables 2 and 5; Figs. 3 and 4b), with wider *RW*, *EW*, and *LW* in 2004, 2009, and 2010 and the narrowest ring in 2007, for most of the study provenances (Figs. 3 and 4b); results were also confirmed by the PCAs which accounted for 51.9% of the variance for all wood traits and 87.8% of *RW* variance in its first principal components (PC1), respectively (Fig. 4a, b). Considering variables independently, we found significant differences among provenances on tree growth (*RW*; $p < 0.001$) with more clear differences in *LW* ($p < 0.001$) than in *EW* ($p = 0.013$) or *TW* ($p = 0.056$) (see Table 5; Fig. 3). Faster growth was observed in Levante I.-10 provenance (mean *RW* = 9.12 mm, Table 2), whereas the slowest was observed in coastal France-22 provenance (mean *RW* = 4.99 mm, *LW* = 0.10 mm; Table 2).

We also found significant ($p < 0.001$) differences among provenances for wood density variables (see Table 5; Figs. 5 and 4c). On average, *Dmean* was higher in Levante I.-10, La Mancha-08, Greece-21, France-22, and Italy-23 (0.60–0.63 g/cm^3) than in Maestrazgo-09 (0.50 g/cm^3), Bética M.-15, and Mallorca-18 provenances (0.55–0.57 g/cm^3) (Table 3 and Fig. 5). The wider variation in wood density and highest values were found for *Dew* in continental Spain (i.e., La Mancha-08) and for *Dlw* in coastal Greece-21 provenance, whereas Maestrazgo-09 showed the lower density values (see Table 3 and Fig. 5). Based on the biplot of the two principal components, a distinct pattern has emerged, namely, *Dmean* was closer related to *Dew* (PC1) and *Dmax* to *Dlw* (PC2; Fig. 4a). Besides, *Dmean* and *Dew* variables are almost orthogonal to *Dmax*.

3.2 IADFs' frequencies and provenances

In all provenances, most rings presented IADFs (59.1–83.3%), and there was even more than one type of

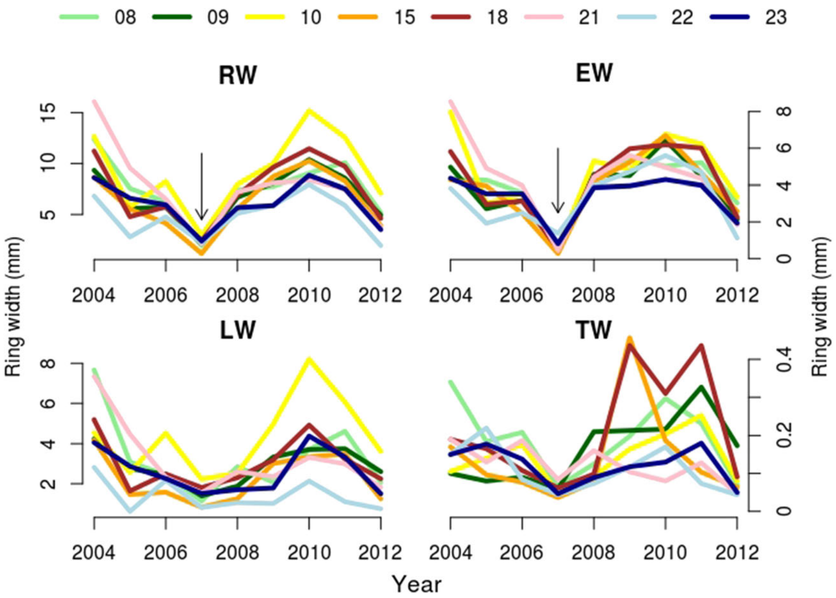

Fig. 3 Tree-ring width chronologies (*RW*, ring width; *EW*, earlywood width; *LW*, latewood width; *TW*, early- to latewood transition) for the common period 2004–2012. Arrows indicate event years in coincidence with low spring precipitation values. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

IADF present in some rings. More IADFs were observed in the latewood (ranged from 42.9 to 65.1%) than in earlywood (Table 4), except for the France-22 provenance (20.5% in latewood and 47.7% in earlywood). In general, IADFs were more frequent in the wider rings (e.g., 2004, 2010) than in the narrower ones (i.e., 2007), and this relation was stronger in IADF type L than in type L^+ (Fig. 6). Across provenances, this relation was only significant for IADF L (Fig. 7). Of the 495 analyzed tree-rings, 362 (73.1%) showed IADFs, 218 (44.0%) IADF type E, 256 type L (51.7%), and 77 type L^+ (15.6%). The frequency of IADF type E reached its maximum in 2008 (62.3%) and 2010 (73.4%) (wet and warm autumn and spring, respectively), whereas IADF type L in 2004 (84.4%) and L and L^+ in 2006 (62.7 and 22.0%) and 2012 (62.5 and 21.4%) (dry growing seasons) (Fig. 6). However, the frequency of IADFs varies among the *P. halepensis* provenances, with the higher differences in rings containing IADF type L and more markedly L^+ than type E (Table 4; Fig. 6). The occurrence of IADF type E was more frequent in Maestrazgo-09, whereas latewood IADFs were more frequent in Levante I.-10 (L) and Italy-23 (L^+) (Fig. 6; Table 4). The colder inland and major drier provenances produced more fluctuations in earlywood (e.g., 49–56% in Levante I.-10, La Mancha-08, and Maestrazgo-09) than coastal provenances (e.g., 30% in Italy-23), whereas IADF type L^+ was more frequent in the coastal and warmest provenances specially Italy-23 (42.5%) (Fig. 6; Table 4). In contrast, in the coldest and wettest provenances of France-22 and Bética M.-15 are formed only fewer latewood IADFs (types L and L^+).

First two (three) principal components account for 78% (91%) of the explained variance (Fig. 4a). The two first principal components separate the chronologies into four groups (*Dmean-Dew*, *RW-EW-LW-* IADF type E, *Dmax-Dlw*, latewood IADFs L and L^+). Variables with high scores on PC1 (e.g., 2004, 2010) correspond to wider rings (Figs. 3 and 4a) and frequent IADF type E (Figs. 6 and 4a), whereas negative scores (e.g., 2007) match up with narrower rings (Figs. 3 and 4a) and an increase of mean ring- and earlywood density variables (*Dmean* and *Dew*; see Figs. 5 and 4a). PC2 is associated to latewood density variables and latewood IADFs. The positive scores on PC2 were associated to years (e.g., 2004, 2006) with the formation of latewood IADFs (L and L^+ type) and, consequently, lower latewood density. The negative scores on PC2 correspond to years (e.g., 2009, 2011) with increased maximum wood density (Figs. 5 and 4a). PC3 is mainly associated to the formation of latewood density variables and IADFs in latewood (Table 6).

3.3 Climate-wood trait relationships

Tree-ring widths (*RW*, *EW*, *LW*) were positively correlated to climatic conditions at the planting site (e.g., wetter winter and warmer summer) in most of the provenances but with some differences (e.g., La Mancha-08, Levante I.-10, Italy-23) (Fig. 8). Previous November precipitation (significantly *RW* and *EW* in most provenances) was associated with lower growth values, whereas higher growth was associated with previous winter precipitation (more significantly in December) and March precipitation and minimum temperature (Fig. 8).

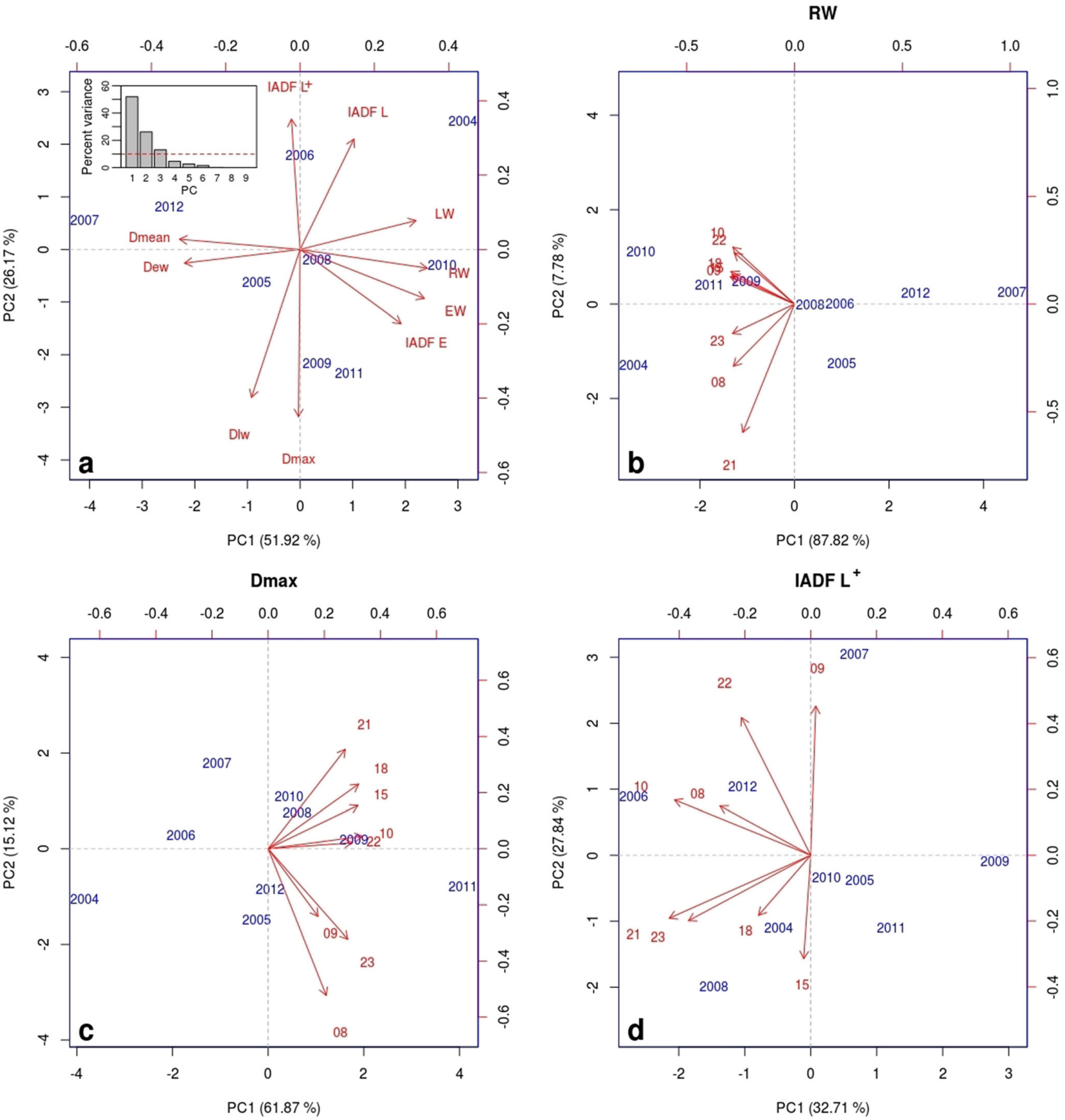

Fig. 4 Aleppo pine sites' loadings plotted on the first two principal components (PC1, PC2) of Principal Component Analyses (PCA). The PCAs were calculated on the matrix of all wood traits (**a**), and matrices for different variables with all provenances (**b**, **c**, and **d**). Chronologies of tree-ring width, *RW* (**b**), maximum density, *Dmax* (**c**), and frequency of intra-annual density fluctuations at the end of latewood, IADF L^+ (**d**) considering the common period (2004–2012). The variances explained by the two first principal components are indicated between parentheses. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

However, contrasting effects in the response of growth (Fig. 8) and wood density (Fig. 9) were also found among provenances, such as precipitation (e.g., growth) among wettest (e.g., France-22) and drier (e.g., La Mancha-08, Levante I.-10) provenances, and temperature (e.g., density) among warmer (e.g., coastal Greece-21 and Italy-23) and coldest (e.g., inland Maestrazgo-09) provenances.

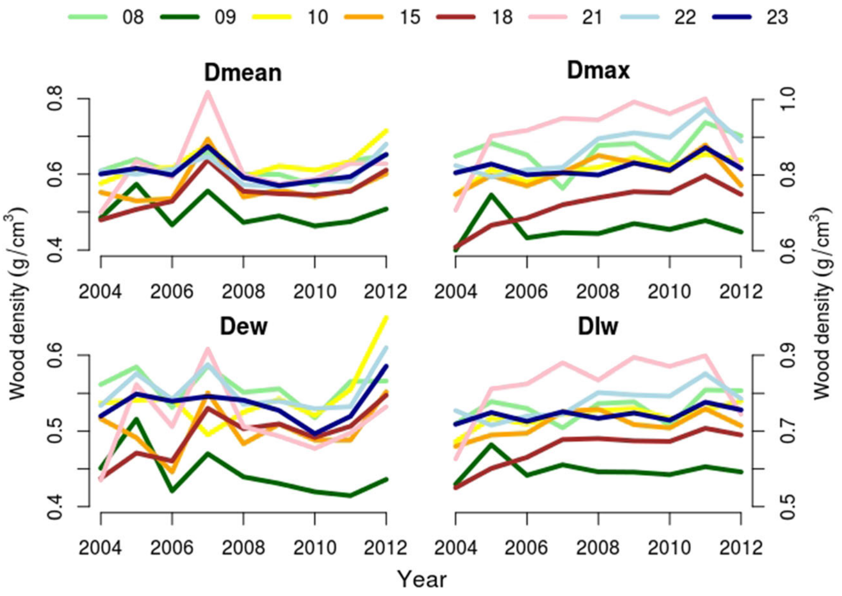

Fig. 5 Time series of wood density (*Dmean*, mean ring density; *Dmax*, maximum wood density; *Dew*, earlywood density; *Dlw*, latewood density) averaged provenances. Provenances are shown in different colors (see Fig. 1). Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

Drier years in the experimental site (e.g., 2005, 2007) were linked to a denser wood in all provenances (Figs. 5 and 4a). Contrary, wet years (e.g., 2008, 2010) were associated to lower density in wood (*Dmean* and *Dew*) (Figs. 5 and 4a), whereas warmer summers (e.g., years 2009, 2011) increased the maximum ring density (*Dmax*) of most of the studied provenances (Figs. 5, 4a, and 9). For most of the provenances, *Dlw* and *Dmax* showed to be sensitive to climatic conditions in March (precipitation and minimum temperature) and August (minimum temperature), respectively (see Fig. 9).

3.4 IADFs as indicator of local adaptation to climate

We found that IADFs' occurrence is also modulated by climate of planting site (Fig. 10). Thus, IADF type E was related to wet and warmer winter-early spring, with a positive relation also to June precipitation in most of the provenances ($r \geq 0.4$; significant at $p < 0.05$ for coastal Greece-21 and France-22 and inland La Mancha-08). In contrast, maximum previous December and current March temperatures decreased the frequency of IADF type E in most of the provenances (see Fig. 10). The formation of IADF type L was influenced by precipitation (positively in March; significant for coastal France-22 and Italy-23 and inland La Mancha-08 at $p < 0.05$ level) and Tmax in spring (negatively in March and May; significant for Italy-23), whereas minimum temperatures showed the higher differences among provenances (e.g., inland vs. coastal provenances) (see Fig. 10). IADF type L$^+$ was negatively

Table 4 Descriptive statistics of the intra-annual density fluctuations (IADFs) for the common period 2004–2012

Code	Provenance	Rings analyzed	Rings with IADFs	%	Rings with IADF E	%	Rings with IADF L	%	Rings with IADF L$^+$	%
08	La Mancha	99	78	78.8	49	49.5	57	57.6	7	7.1
09	Maestrazgo	48	40	83.3	27	56.3	28	58.3	3	6.3
10	Levante I.	43	34	79.1	22	51.2	28	65.1	6	14.0
15	Bética M.	49	35	71.4	21	42.9	21	42.9	2	4.1
18	Mallorca	94	68	72.3	41	43.6	51	54.3	16	17.0
21	Greece	45	36	80.0	15	33.3	29	64.4	8	17.8
22	France	44	26	59.1	21	47.7	9	20.5	4	9.1
23	Italy	73	45	61.6	22	30.1	33	45.2	31	42.5

The IADF type E is located inside the earlywood, and IADF types L and L$^+$ are inside and at the end of the latewood, respectively

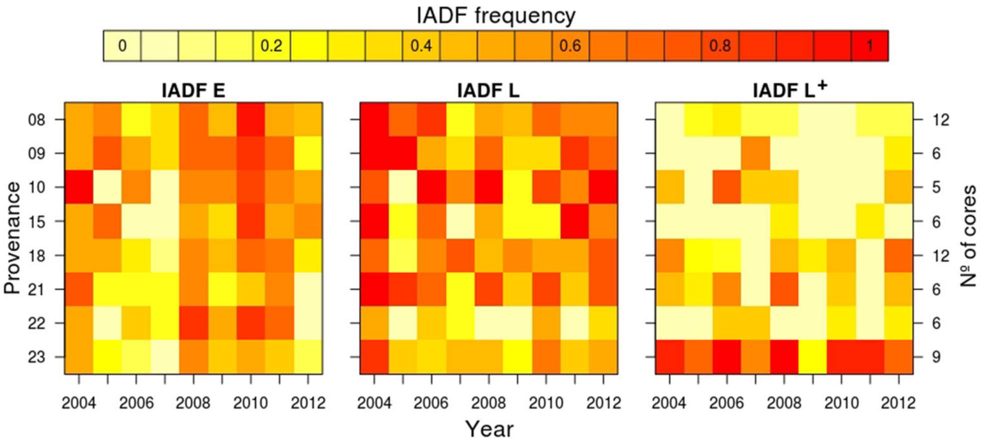

Fig. 6 Heat map showing the frequency of intra-annual density fluctuations (IADFs) in the earlywood (type E) and latewood (type L and L$^+$) for the common period 2004–2012. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

correlated to previous autumn and winter precipitation with differences among provenances, with the highest intra-specific variability for L$^+$, in inland compared to coastal provenances. Thus, higher (and lower) precipitation during previous autumn and winter at the provenance trial seemed to be prominent and stressful climatic conditions promoting IADF type L$^+$ formation in inland Maestrazgo-09 (and coastal Italy-23). Overall, a high variability of IADFs L$^+$ was also observed among provenances in relation to maximum and minimum temperatures (Fig. 10).

The occurrence of IADFs peak over the tree-ring position under contrasted climatically years showed a common initial decrease followed by an increase in density in all provenances (Fig. 11). However, we found differences among provenances regarding the rate of response to short periods (Fig. 11) with favorable climate (e.g., Maestrazgo-09 with lower wood density in 2008 and 2010 and Greece-21 with higher wood density in the LW in 2008 and 2010, types L$^+$ (2008) and E (2010)) and unfavorable climate conditions (e.g., Greece-21 (Mallorca-18) with higher (lower) wood density in the LW during 2005 forming IADF type L).

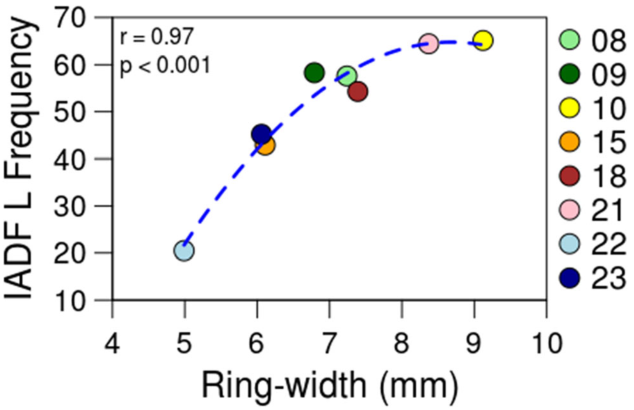

Fig. 7 Variation of the frequency of intra-annual density fluctuations in latewood (IADF L) in function of tree-ring width for the studied provenances. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

The formation of IADFs is also related to the climate of the provenance origin (Fig. 12). The two first principal components contributed to 53.8% of the total variance when the 19 bioclimatic variables at the provenance origin of the 18 populations (Table 1) and climatic variables at the planting site were considered (Fig. 12a), increasing to 68.5% of the variance for the selected variables (Fig. 12b). Interestingly, the occurrence of IADF type E was positively related to March maximum temperature (Tmax3), isothermality (bio03), and temperature annual range (bio07) (Fig. 12 d, e, and c, respectively) and IADF type L to precipitation seasonality (bio15; Fig. 12f), with differences among provenances (Fig. 12). IADF type L$^+$ was positively related to temperatures (e.g., mean temperature of wettest quarter (bio08), mean temperature of coldest quarter (bio11), and January mean temperature (Tmean1)) (Fig. 12g, i, and h, respectively). Moreover, different trends were observed in coastal provenances (e.g., Italy-23 and Mallorca-18, Fig. 12c, h, and i; also Greece-21, Fig. 12e) to those from inland regions (e.g., La Mancha-08, Maestrazgo-09, and Bética M.-15). Lastly, IADF type L$^+$ was more frequent in the coastal provenances, where autumn and winter temperatures are higher in their provenance origin than in the local trial (Fig. 12h, i), suggesting a longer growing season in the coastal than continental provenances.

4 Discussion

Estimating tree responses to climate change has important implications for forest sustainability, but few

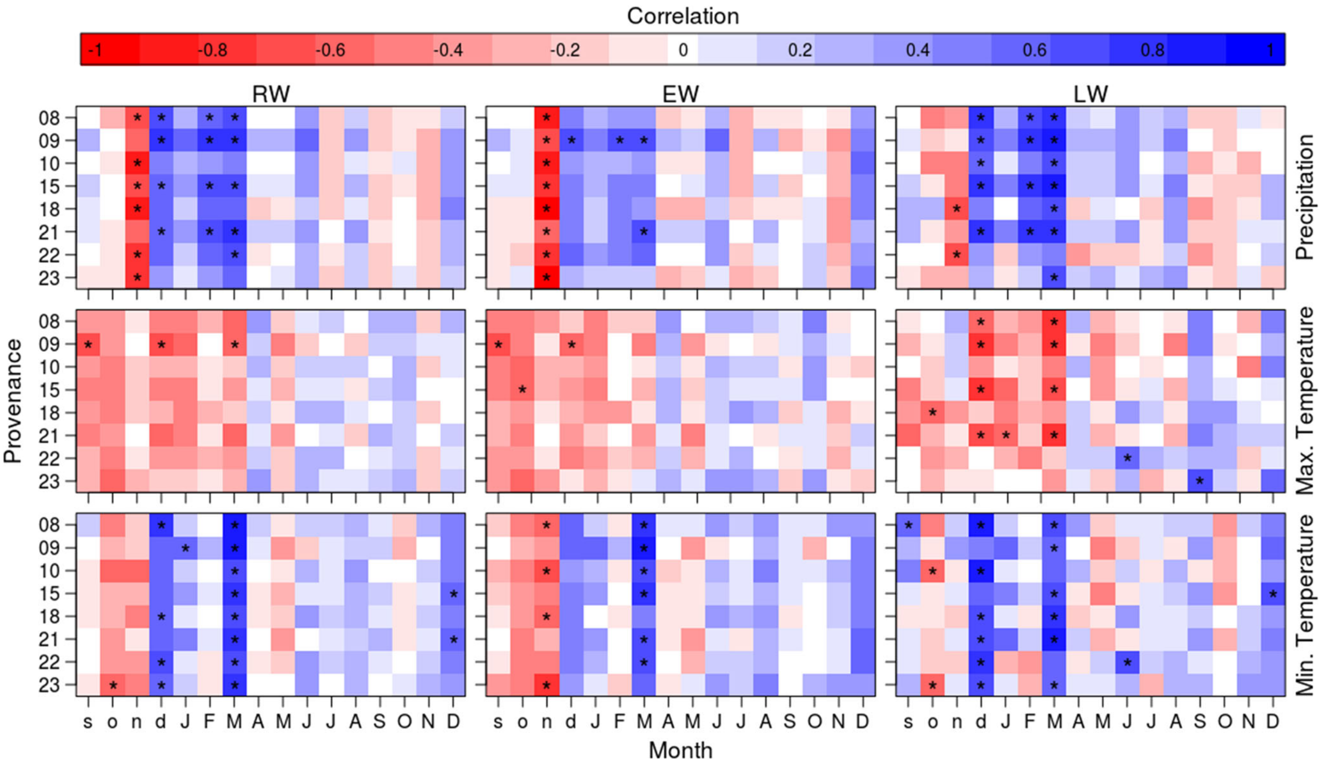

Fig. 8 Pearson correlation coefficients calculated between monthly precipitation and temperatures (outer right *y-axis*) at the planting site and *Pinus halepensis* tree-ring width chronologies (ring, *RW*; earlywood, *EW*; and latewood, *LW*) by provenance (left *y-axis*). The *x-axis* shows the temporal window from the previous September to the current December (prior year months are in lowercase letters and current year months in uppercase letters). Positive correlations are displayed in blue and negative ones in red. Asterisks denote significant correlations at the 95% level. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

studies have assessed them using provenance data in relation to wood trait plasticity in the Mediterranean Region (e.g., García-Esteban et al. 2010; Santos-del-Blanco et al. 2013), which is a major climate change hotspot. Our work shows the importance of taking into account the inter-provenance variability of inter- and intra-ring wood traits (ring width, wood density, and IADFs) in *P. halepensis*, one of the most important Mediterranean pine species, to study and separate provenance and climate (local and origin) effects on these traits in the climate change context. By doing so, it was possible to characterize the intra-specific variation and identify the different provenance responses, being of considerable interest to find the best genetic source to use in future plantations (David-Schwartz et al. 2016). Altogether, our results provide valuable information for future reforestations (David-Schwartz et al. 2016) and adaptive forest management programs in the Mediterranean region (Wang et al. 2010).

4.1 Intra-specific variation in wood traits

Variations among provenances in tree-ring growth variables (*RW*, *EW*, and *LW*; Table 5, Fig. 3) in *P. halepensis* were related to climate at seed origin, indicating local adaptation (George et al. 2019; Isaac-Renton et al. 2018), but also to climate at the planting site (Fig. 8), suggesting that phenotypic plasticity (cf. de Luis et al. 2013) can play a role in acclimation and/or adaptation processes, which ultimately can affect tree responses to climate forecasts (Martinez-Meier et al. 2008a).

Further information on tree growth and wood properties can be gained by analyzing early- and latewood separately (Lebourgeois et al. 2010). For instance, the sub-humid provenance (i.e., France-22) showed the highest *EW* to *LW* ratio (i.e., improved hydraulic efficiency), whereas the semiarid provenance (Levante I.-10) had the lowest value (Table 2), improving resistance to drought (Domec and Gartner 2002; Martinez-Meier et al. 2008a) and mechanical strength (De Micco et al. 2008; Froux et al. 2002; Martinez-Meier et al. 2008a). These findings confirm the existence of trade-offs between hydraulic efficiency, xylem cavitation resistance (Lachenbruch and McCulloh 2014), and mechanical strength (Baas et al. 2004) at intra-specific level in *P. halepensis*, as previously observed in Douglas-fir (George et al. 2019). In fact, the sub-humid provenance (France-22) had low latewood production, variability, and recover capacity after drier years (Fig. 3), indicating maladaptation to drought (Isaac-Renton

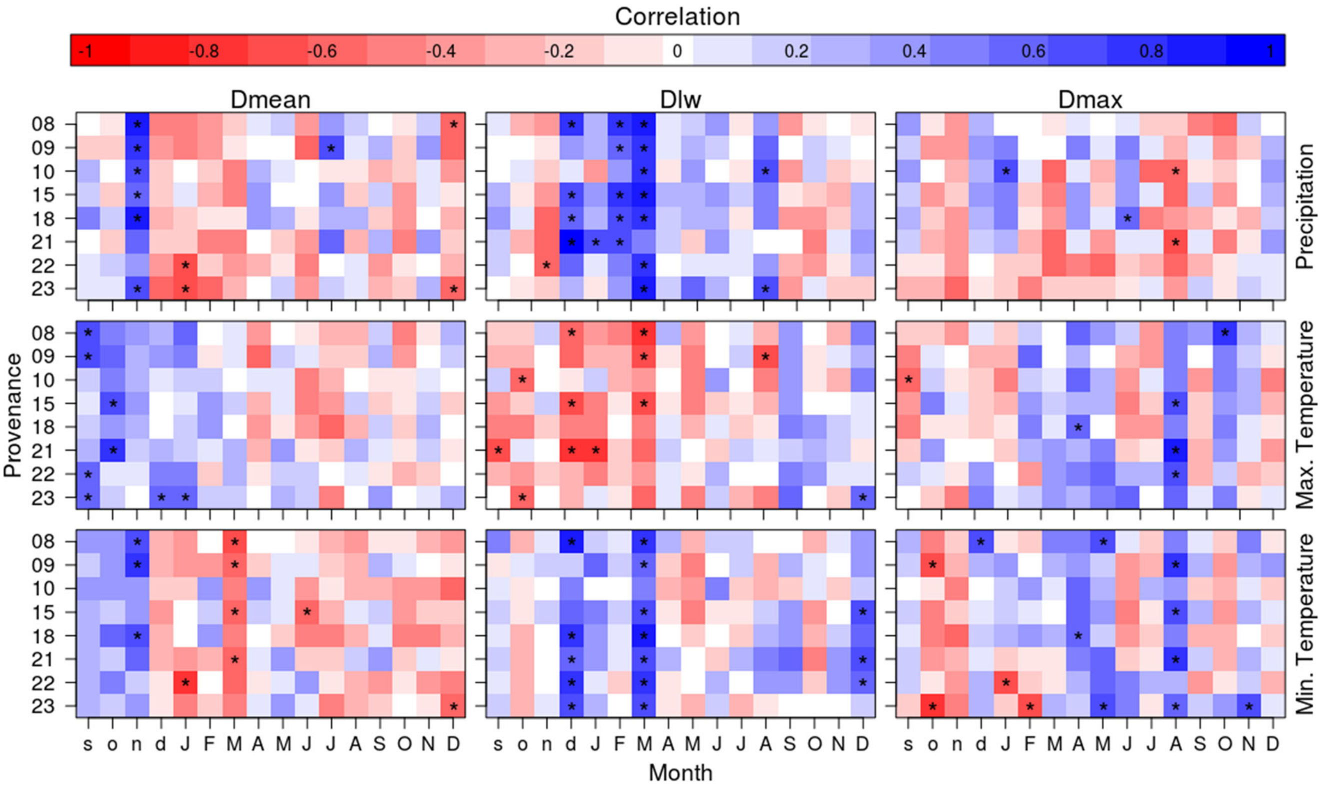

Fig. 9 Pearson correlations calculated by relating monthly precipitation and temperatures at the planting site and *Pinus halepensis* wood densities (*Dmean*, *Dmax*, *Dlw*) by provenance. The *x-axis* shows the temporal window running from September of the previous year (months abbreviated by lowercase letters) up to December of the year of tree-ring formation (months abbreviated by uppercase letters). Positive correlations are displayed in blue and negative ones in red. Asterisks denote significant correlations at the 95% level. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

et al. 2018). Additionally, genetically inherited growth patterns in the long term can result in loss of functionality (e.g., loss of conductivity and increased risk of cavitation; cf. David-Schwartz et al. 2016), if droughts become more frequent. Altogether corroborates the need to analyze tree growth response at different temporal scales to prevent false statements about future responses to climate change (Sánchez-Salguero et al. 2018; George et al. 2019). Additionally, common-garden experiments showed an adaptive genetic variation among provenances in early- to latewood transition dates in conifers (Jayawickrama et al. 1997). Thus, provenances that are still producing earlywood when drought occurs are more drought vulnerable than those already producing latewood (George et al. 2019). This affects water transport and tree survival (e.g., De Micco et al. 2008; Martinez-Meier et al. 2008a; Novak et al. 2013a) and the provenances' ability to withstand climate changes.

In contrast to ring width variables (Fig. 3), wood density variation among provenances was greater (Tables 3 and 5; Figs. 11, 5, and 7; cf. George et al. 2019; Klisz et al. 2016, 2019), being shaped by provenance origin (Nabais et al. 2018) or microclimatic conditions at the growth site (e.g., Klisz et al. 2016). This was expected since growth traits are more regulated by environmental conditions and wood density by genetic factors (e.g., Klisz 2011; Martinez-Meier et al. 2008b; Zobel and Jett 1995). High wood density heritability has been previously reported in several conifer species, such as *Larix decidua* Mill. (Klisz 2011), *Picea abies* L. Karsten (Hylen 1999), and *P. pinaster* (Louzada 2003; Louzada and Fonseca 2002). Besides, higher genetic control has been associated with earlywood rather than latewood density (e.g., Louzada and Fonseca 2002; Hannrup et al. 2004; Hylen 1999; Rozenberg and Cahalan 1997), although conflicting results were discussed in Pâques (2013).

4.2 Inter-provenance variation of climate-wood trait relationships

The role of climate in shaping adaptive patterns of *P. halepensis* has been previously recognized (e.g., Calamassi et al. 2001; Climent et al. 2008; David-Schwartz et al. 2016; Klein et al. 2013; Schiller and

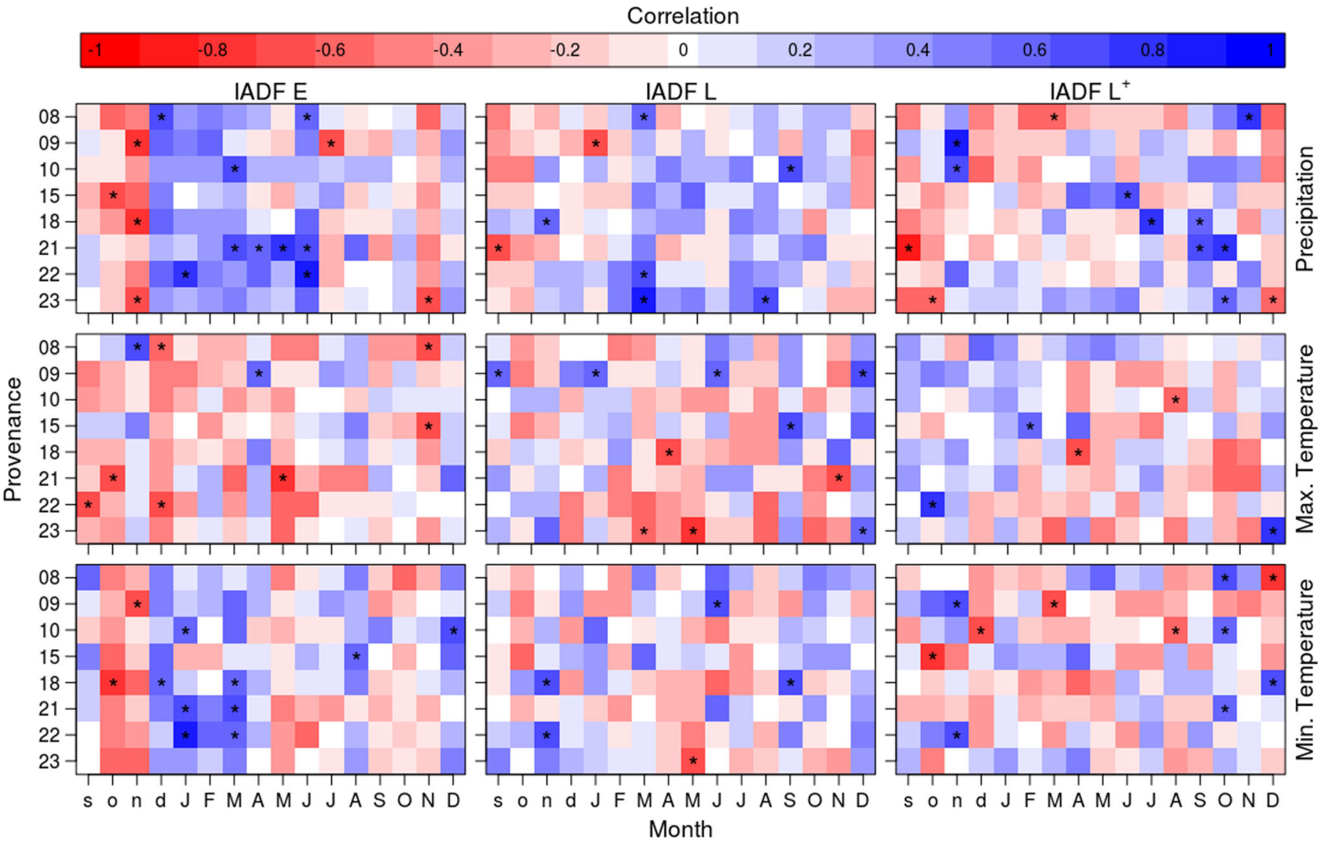

Fig. 10 Pearson correlations between intra-annual density fluctuations (IADFs; type E (inside earlywood), L, and L^+ ((inside and at the end of latewood)) in *Pinus halepensis* and monthly precipitation and temperatures at the planting site (outer right *y*-axis) by provenance (left *y*-axis). The *x-axis* shows the temporal window from the previous September to the current December (prior year months are in lowercase letters and current year months in uppercase letters). The correlation coefficients (positive correlations are displayed in blue and negative in red). Asterisks denote significant correlations at the 95% level. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

Atzmon 2009; Voltas et al. 2015). High phenotypic plasticity in this conifer is important in the Mediterranean climate (e.g., Camarero et al. 2010; de Luis et al. 2011), since it allows trees to cope with water scarcity (Ne'eman and Trabaud 2000). We found that ring width variables were positively controlled by winter and spring precipitation in most provenances, as previously reported for this species (e.g., de Luis et al. 2007, 2013; Novak et al. 2013a; Papadopoulos et al. 2008; Pasho et al. 2012). Wider rings were formed in favorable years (Fig. 3) with rainy winters (de Luis et al. 2013) and warm springs (Fig. 8). However, the expected increase in temperature and changes in precipitation pattern for the Mediterranean region may also cause phenological modifications in tree growth (Peñuelas et al. 2002) and growing season length (de Luis et al. 2011), which can affect differently *P. halepensis* provenances (Figs. 3, 8; Table 5).

Variations in water availability during the growing season can also affect xylogenesis and drive changes in cell anatomical features (e.g., Olano et al. 2012; Pacheco et al. 2016) and consequently on wood density and hydraulic conductivity efficiency which, in turn, could affect tree growth (e.g., Camarero et al. 2017). The water availability in the provenance origin and planting site could also explain the higher wood density traits (i.e., smaller lumen size) in the sub-humid provenances in drier years (e.g., France-22 and Greece-21; Fig. 5), as opposed to drier provenances (e.g., semiarid-cold Maestrazgo-9). Drier conditions were also linked to a denser wood in other conifers (e.g., *Juniperus thurifera*) in the Mediterranean region (Camarero et al. 2014).

Most provenances responded to temperature but showed less significant correlations than precipitation (Fig. 8). Previous studies found the importance of adjusting earlywood growth to temperature under climate change (George et al. 2019; Levesque et al. 2013). Our results showed that only Greece-21 provenance increased *EW* as minimum temperature and precipitation increase in

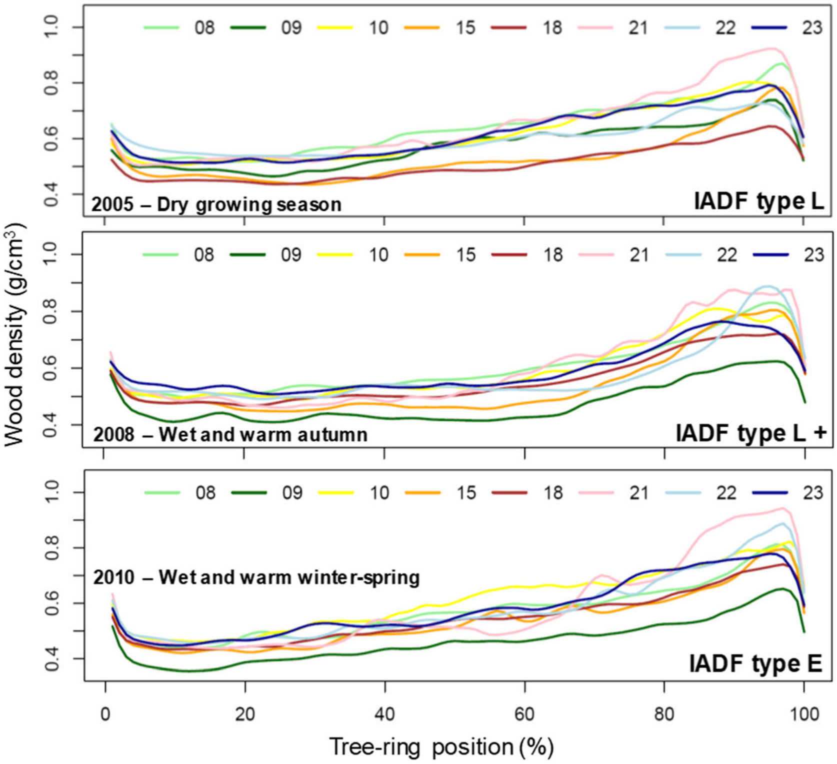

Fig. 11 Wood density profile of each region of provenance for the selected unfavorable (2005) and favorable (2008 and 2010) years. Provenance codes are La Mancha-08, Maestrazgo-09, Levante I.-10, Bética M.-15, Mallorca-18, Greece-21, France-22, and Italy-23. See Table 1 for details

March (Fig. 8), suggesting that this provenance could adjust the length of earlywood formation period. Moreover, Greece-21 provenance showed the highest wood density in latewood (Fig. 5), indicating good acclimation to unfavorable environmental conditions (Chave et al. 2009). In fact, trees with higher latewood density are more likely to survive extreme drought and heat waves, which could be linked to the plasticity of the xylem and drought resistance (Martinez-Meier et al. 2008a). Analogously, *Dmax* was enhanced by warmer conditions (Figs. 5 and 9), which agrees with previous reports on conifer species in boreal environments (Kirdyanov et al. 2007) and Alpine high-elevation forests (Büntgen et al. 2010).

4.3 Functional significance of IADFs

Previous studies in *P. halepensis* from Mediterranean forests found more IADFs on drier sites, where water availability is limited (de Luis et al. 2011). We also detected a higher frequency of IADFs in provenances from arid and semiarid ecotypes (*sensu* Voltas et al. 2018) (i.e., La Mancha-08, Maestrazgo-09, Levante I.-10) in contrast to the sub-humid ecotype (France-22 provenance; Table 4). These findings confirmed our hypotheses that IADF formation differs in well- and maladapted provenances to dry conditions and that the production of these anatomical features is modulated by aridity at the provenance origin.

Formation of IADFs is linked to climatic conditions in the current growing season (Figs. 10 and 11) but also to climate at the provenance origin (Fig. 12; cf. Nabais et al. 2018), with a genetic control of density peak position (Fig. 11) and characteristics (Rozenberg et al. 2002). This can explain the high variability in IADFs' frequency and position observed among provenances (Figs. 6, 11, and 4d), meaning that although all trees faced the climatic conditions that induce IADF formation, not all trees produced them (Klisz et al. 2016).

A high frequency of IADF E has been observed in conifers growing in temperate climates (e.g., *Larix decidua* or *Picea abies* (L.) Karst in Poland; Klisz et al. 2016, 2019) since tree water status is a key driver of IADF E, allowing safer water transport during drought periods (De Micco and Aronne 2012). On the contrary, we found more IADFs in latewood than in earlywood, as previously observed in other pines in coastal Mediterranean areas (e.g., Campelo et al. 2007, 2013; Rozas et al. 2011). This happens because more weather fluctuations occur in the second part of the growing season, when latewood is laid down, and latewood tracheids are more plastic and responsive to these fluctuations (Carvalho et al. 2015) than earlywood tracheids (George et al. 2019). The formation of more

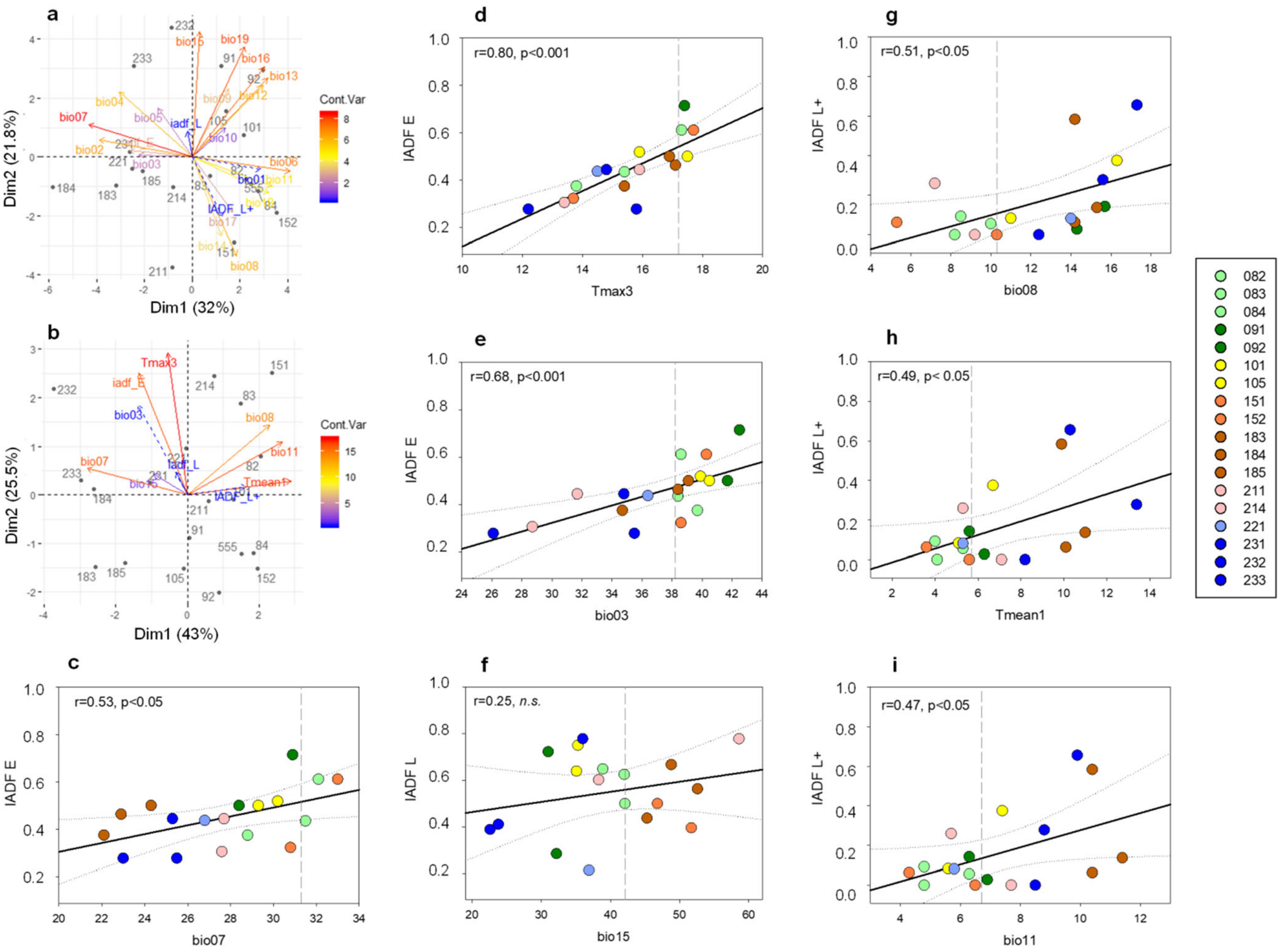

Fig. 12 Principal component analysis (PCA) of the 19 bioclimatic variables (**a**) and selected climatic variables (from CHELSA database) (**b**) with intra-annual density fluctuations (IADFs; type E (inside earlywood), L, and L^+ (inside and at the end of latewood, respectively)) (**a**, **b**). Relationship between frequency of IADFs (*y-axis*) and selected climatic variables (*x-axis*) from each population origin and local experimental site (**c**, **d**, **e**, **f**, **g**, **h**, **i**). Linear regression (solid black line) and 95% confidence interval (dotted black line); correlation coefficients with their significance levels (*p*) are also shown. The vertical dark gray–dashed line indicates the value at the trial experimental site. For bioclimatic variables description, see Table 7, and for provenance codes see Table 1 (The experimental site (Arganda) code is 555; a, b)

IADFs in earlywood than in latewood in France-22 provenance could indicate more sensitivity to water stress during earlywood formation or shorter latewood production period, which reflects the wetter conditions at the provenance origin (Table 1). A lower frequency of IADF type E in Greece-21 and Italy-23 provenances (Table 4) indicates a better adjustment of the earlywood formation period to climate conditions in the experimental study. However, Greece-21 provenance exhibited a general better adaptation (cf. Voltas et al. 2018) because it produced more IADFs and had higher wood density. In Greece-21 provenance, the IADF E was associated with low temperatures in May and high precipitation in June, suggesting that favorable conditions can prolong earlywood formation (Campelo et al. 2007). Previous studies have also found positive relationships between precipitation in June and IADF E frequency in *P. pinea* (Campelo et al. 2007) and in *P. pinaster* (Campelo et al. 2013).

Relative high frequencies of IADF L were found for all provenances (20–65%). A high occurrence of latewood IADFs is related to wider rings (Fig. 7), which has also been observed in other pine species (e.g., Campelo et al. 2007; Nabais et al. 2014; Rozas et al. 2011; Vieira et al. 2009; Zalloni et al. 2016). A high frequency of IADF L was associated with fast-growing provenances (Fig. 7), suggesting that this type of IADF is predisposed by favorable conditions for tree growth and a longer growing season (e.g., Balzano et al. 2018; Campelo et al. 2013; Vieira et al. 2015; Zalloni et al. 2016), which is common in the Mediterranean climate.

In contrast, the formation of IADF L^+ was not related to growth rates, and its formation was more frequent in the coastal than in the inland populations, with warmer conditions at the provenance origin (Tables 1 and 4; Fig. 12h, i). This could be explained by an environmental gradient in the frequency of IADFs across the geographical distribution of *P. halepensis*, with more IADFs' occurrence at coastal sites (Novak et al. 2013b). The higher frequency of IADF type L^+ in the Italian-23 provenance (42.5 vs. 6–18% in the remaining provenances) could be related with the milder conditions in fall or to a longer growing season at its origin. These findings confirm that provenance response also depends on the climatic conditions in the origin (George et al. 2017; Kapeller et al. 2017; Klisz et al. 2019).

The different position of IADFs in rings reflects also the high plasticity of *P. halepensis* to cope with seasonal water deficits (Battipaglia et al. 2010; Novak et al. 2013b), which agrees with previous studies in this species in different environments (e.g., Attolini et al. 1990; Camarero et al. 2010; de Luis et al. 2011; Nicault et al. 2001; Serre 1976a, 1976b) and confirms its ability to maintain cambial activity while favorable conditions last (de Luis et al. 2011).

4.4 How provenance trials can support forest management

Our results show that the ability of *P. halepensis* to take advantage of favorable conditions in autumn is provenance dependent. Therefore, more productive and drought-tolerant provenances (Broadmeadow et al. 2005; Eilmann et al. 2013) should be considered in reforestation programs and adaptive forest management plans although the uncertainties due to a single experimental site imply that cautions should be taken when integrating our results at management plans at large scales.

Traditionally, local seed provenances have been used in habit creation (Wilkinson 2001), since it is assumed that local seeds produce individuals locally adapted. However, this assumption may no longer be valid under ongoing and future climate change scenarios. Under rapid climate changes, it is important to know which provenance should be planted to meet the expected primary forest function (Aitken and Whitlock 2013). For example, reforestations after drought-induced forest dieback or wildfires should consider multiple provenances, by assisted migration, to enhance genetic diversity and thus assure success under different climate scenarios (Gray and Hamann 2011).

We suggest that information gathered in provenances trials should be combined with species distribution models (e.g. Serra-Varela et al. 2017) to define tailored forest management strategies (Sánchez-Salguero et al. 2018) to deal with future climate uncertainty (Bolte et al. 2009). Moreover, our results confirm the great value of intra-specific wood traits to withstand climate change.

5 Conclusions

Our study showed the importance of studying the intra-specific response of wood traits to climate in *P. halepensis*, a widespread Mediterranean conifer, considering climate of the provenance origin and inter-annual variations of microclimate in a provenance trial. Among all wood traits, intra-ring wood features were the most informative about local adaptation and phenotypic plasticity in *P. halepensis*. Differences in latewood IADFs among provenances indicated a high plasticity of this species to cope with Mediterranean conditions and to take advantage of short favorable periods in autumn. Further research should combine ring width variables, wood density analysis, and IADFs' occurrence to obtain information about local adaptation and seasonal phenotypic plasticity. Moreover, genetic associations in long-term experiments and multienvironmental trials will be especially important to determine the influence of genotype by environmental interaction (GxE) on tree-ring features and identify better-adapted provenances to mitigate future climate change effects.

Acknowledgments We acknowledge I. Rodriguez for the information about the study site and CIFOR-INIA staff for field work. This article is based upon work from COST Action FP1106 Studying Tree Responses to Extreme Events: a SynthesiS (STReESS), supported by COST (European Cooperation in Science and Technology). Thanks are also due to the colleagues from DendroLab Cristina Nabais for making possible this visit and Ana Carvalho for ensuring the warmer time in Coimbra. We thank the editors Erwin Dreyer and Patrick Fonti and two anonymous reviewers for improving the manuscript.

Funding information AH is supported by PinCaR project (UHU-1266324, FEDER Funds, Andalusia Regional Government, Consejería de Economía, Conocimiento, Empresas y Universidad 2014–2020); JV (SFRH/BPD/105656/2015) and FC (SFRH/ BPD/ 111307/2015) were supported by postdoctoral research grants from FCT with funds from POPH (Portuguese Operational Human Potential Program), QREN Portugal (Portuguese National Strategic Reference Framework), and FSE (European Social Fund). RSS was supported by the Spanish Ministry of Economy, Industry and Competitiveness by the postdoctoral grant (IJCI-2015-25845, MCIU funds), CoMo-ReAdapt (CGL2013-48843-C2-1-R) project, RTI2018-096884-B-C31 and RTI2018-096884-B-C33 projects (Ministry of Ministry of Science, Innovation and Universities, Spain), and VULBOS project (UPO-1263216, FEDER Funds, Andalusia Regional Government, Consejería de Economía, Conocimiento, Empresas y Universidad 2014–2020).

Data availability The data are available upon reasonable request to the corresponding author.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

Table 5 Results of the linear mixed-effect models (mean value and ANOVA table) testing the wood trait differences among provenances for the period 2004–2012

	Provenances*									
Variable	08	09	10	15	18	21	22	23	*F*	*P*
RW	7.51 bc	6.82 ab	9.15 c	6.24 ab	7.39 bc	7.68 bc	4.82 a	6.10 ab	8.158	< 0.001
EW	4.01 ab	3.73 ab	4.62 b	3.81 ab	4.15 ab	4.34 ab	3.30 a	3.36 a	2.863	0.013
TW	0.19 a	0.16 a	0.14 a	0.14 a	0.21 a	0.12 a	0.11 a	0.12 a	2.125	0.056
LW	3.30 bc	2.90 b	4.36 c	2.27 ab	3.01 b	3.20 bc	1.39 a	2.60 ab	8.243	< 0.001
EW/LW	1.73 a	1.73 a	1.56 a	2.10 a	1.86 a	1.87 a	3.28 b	2.03 a	5.274	< 0.001
Dmean	0.62 d	0.50 a	0.63 d	0.57 bc	0.55 b	0.62 d	0.61 cd	0.61 cd	17.864	< 0.001
Dmax	0.86 cde	0.66 a	0.82 cd	0.81 c	0.72 b	0.91 e	0.87 de	0.82 cd	38.245	< 0.001
Dew	0.56 e	0.44 a	0.55 de	0.50 bc	0.50 b	0.51 bcd	0.55 e	0.54 cde	17.606	< 0.001
Dlw	0.76 cd	0.60 a	0.74 cd	0.72 c	0.65 b	0.82 e	0.78 de	0.74 cd	35.08	< 0.001

Different letters indicate significant differences between provenances means ($p < 0.05$)

*Provenances: 08-La Mancha, 09-Maestrazgo, 10-Levante I., 15-Bética M., 18-Mallorca, 21-Greece, 22-France, and 23-Italy. See Table 1 for details

Table 6 Loadings of the first three principal components PC1, PC2, and PC3

Variable	PC1	PC2	PC3
RW	*0.43*	−0.06	−0.10
EW	*0.42*	−0.16	−0.01
Dmean	*−0.41*	0.03	−0.05
LW	*0.39*	0.10	−0.19
Dew	*−0.39*	−0.05	−0.02
IADF E	*0.34*	−0.25	0.24
Dmax	−0.01	*−0.56*	*0.33*
Dlw	−0.16	*−0.50*	*0.39*
IADF L$^+$	−0.03	*0.44*	*0.59*
IADF L	0.18	*0.37*	*0.53*

The principal component analysis was calculated on the matrix of chronologies of tree-ring width and density variables (*RW*; tree-ring width, *EW* and *LW*; earlywood and latewood width, *Dmean* and *Dmax*; ring and maximum densities, *Dew* and *Dlw*; earlywood and latewood densities) and IADFs' frequency (IADF types E, L, and L$^+$) considering the common period 2004–2012.

Table 7 Meaning of the bioclimatic variables

Code	Bioclimatic variables	Definition
Bio01	Annual mean temperature	The annual mean temperature
Bio02	Mean diurnal range	The mean of the monthly temperature ranges (monthly maximum minus monthly minimum)
Bio03	Isothermality	The ratio of the mean diurnal range (Bio02) to the annual temperature range (Bio07), multiplying by 100
Bio04	Temperature seasonality	The standard deviation of the 12 mean monthly temperature values, multiplying by 100
Bio05	Max temperature of warmest month	The maximum monthly temperature occurrence over a given year
Bio06	Min temperature of coldest month	The minimum monthly temperature occurrence over a given year
Bio07	Temperature annual range	Temperature variation over a given year, difference between maximum and minimum monthly temperature
Bio08	Mean temperature of wettest quarter	The mean temperatures during the wettest 3 months of the year
Bio09	Mean temperature of driest quarter	The mean temperatures during the driest 3 months of the year
Bio10	Mean temperature of warmest quarter	The mean temperatures during the warmest 3 months of the year
Bio11	Mean temperature of coldest quarter	The mean temperatures during the coldest 3 months of the year
Bio12	Annual precipitation	The sum of all total monthly precipitation values
Bio13	Precipitation of wettest month	The total precipitation of the wettest month
Bio14	Precipitation of driest month	The total precipitation of the driest month
Bio15	Precipitation seasonality	The ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation expressed as a percentage
Bio16	Precipitation of wettest quarter	The total precipitation during the wettest 3 months of the year
Bio17	Precipitation of driest quarter	The total precipitation during the driest 3 months of the year
Bio18	Precipitation of warmest quarter	The total precipitation during the warmest 3 months of the year
Bio19	Precipitation of coldest quarter	The total precipitation during the coldest 3 months of the year

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