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Adaptive effects of geographic origin on ring-width and radial growth—climate relationships in *Pinus nigra* Arnold, the European black pine

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Abstract

Key message Radial growth is a fitness related trait that is expected to vary among forest tree populations when habitat conditions change. Yet, the genetic variability of ring-width and radial growth–climate relationships among geographic origins within species is rarely investigated. This is what we analyzed in the European black pine, *Pinus nigra* J.F. Arnold (1785), a forest tree species widely but patchily distributed. Using four partially replicated common gardens in France, we show that late spring minimum temperatures affect radial growth negatively and early summer precipitations positively across all provenances. In contrast, there was a strong provenance effect on mean ring-widths, as well as high phenotypic plasticity and significant genotype by environment interactions in most provenances and all subspecies. Provenances of the subspecies *P.n.* subsp. *salzmannii* often displayed the smallest mean ring widths except in the least fertile common garden. A few provenances of *P.n.* subsp. *pallasiana*, *P.n.* subsp. *laricio* and *P.n.* subsp. *nigra* performed equally well in all common gardens. Climate smart forestry should consider provenance and not just subspecies recommendations for plantations where black pine is not native, either for ecological restoration or timber production.

Context *Pinus nigra* J.F. Arnold (1785), the European black pine, is a forest tree species widely but patchily distributed throughout southern Europe, from isolated locations in North Africa to the Black Sea and Western Asia. While it has been widely used as a plantation species since the mid-nineteenth century because of its rapid growth even on rather poor soils, the effect of geographic origin within genetic lineage on radial growth and climate sensitivity has not yet been assessed.

Aims We analyze the effects of geographic origin on radial growth variability and radial growth–climate relationships within four subspecies of the European black pine.

Methods Using a tree-ring to climate relationship approach and a 40-year-long chronology, we first estimated how variable the effect of monthly climate was on radial growth, among 16 provenances within four subspecies, in four bioclimatically contrasted common gardens in France. We then used the tree-ring data to estimate genetic and plasticity effects and to test for the existence of genotype by environment interactions. Lastly, we ranked the growth performance of the different subspecies and provenances measured in each common garden.

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Results There were few differences in climate effects among provenances and subspecies. Late spring minimum temperatures affect radial growth negatively and early summer precipitations positively. The provenance effect on ring-widths was stronger than the subspecies effect. Radial growth phenotypic plasticity was high across the four common gardens and so were genotype by environment interactions in most subspecies. Provenances of the subspecies *P.n. subsp. salzmannii* often displayed the smallest mean ring widths except in the least fertile test site.

Conclusion Provenance, in addition to subspecies variability should be considered in climate-smart forestry practice, whether for ecological restoration and timber production.

Keywords Common garden, Genetic diversity, Phenotypic plasticity, Climate change, Dendroecology

1 Introduction

Radial (or secondary) growth is an adaptive, fitness-related trait in forest trees and is expected to vary among populations in response to varying habitat conditions (Eilmann et al. 2014, Gárate-Escamilla et al. 2019, Latreille et al. 2017). Radial growth is frequently measured using ring-width in relation to age as it usually correlates with biomass production, a trait of high interest in forestry (Campbell et al. 2004; Graumlich et al. 1989). It is also measured to decipher past climate variations and, conversely, analyze the effects of climate on growth patterns across time (Fritts 1971; Rathgeber et al. 2000). Understanding how radial growth of species, populations and geographic origins, reacts to climate is particularly important in a context of rapidly changing climate. So-called climate-smart forestry (Cooper and MacFarlane 2023) requires such knowledge, particularly assisted migration, the translocation of potentially pre-adapted material to future, warmer climates (Chakraborty et al. 2024; Gray et al. 2011; Housset et al. 2018; Klisz et al. 2019; Palik et al. 2022; Wang et al. 2022).

Common garden tests are a widely employed experimental tool for assessing genetic variability, genotype by environment interaction and phenotypic plasticity of fitness-related traits (Schwinning et al. 2022; Taïbi et al. 2014; Vitasse et al. 2010). Provenance tests, a particular type of common garden, are composed of plant material (often seed lots) of known geographic origin collected from (reputedly) unrelated seed trees.

Provenances that have evolved local adaptations express diverging phenotypes in a common garden. Replicated in common gardens under different environmental conditions, diverging provenance performances indicate phenotypic plasticity and genotype $\times$ environment interaction (Langlet 1971; de Villemereuil et al. 2016; Fady and Rihm 2022). Provenance tests thus provide key genetic and phenotypic information about the performance of populations from diverse origins while minimizing confounding environmental effects (Varelides et al. 2001). This is essential for the conservation of genetic resources and the deployment of adapted reproductive material for

reforestation programs (Koskela et al. 2014; Vinceti et al. 2020; Woolridge et al. 2023).

Pinus nigra J.F. Arnold (1785), the European black pine, belongs to the family *Pinaceae*, genus *Pinus* and subgenus *Pinus* (Mirov 1967; Price et al. 1998). Its current distribution extends from isolated locations in North Africa eastwards to larger populations across southern and central Europe and to Türkiye and Crimea, covering a wide range of soil types, topographic conditions and climates (Isajev et al. 2004; Zaghi 2008). Its currently large but highly fragmented geographic distribution contrasts with a relatively limited genetic differentiation and high levels of admixture which result from incomplete lineage sorting during the Pleistocene glacial cycles and recent divergence during the Holocene (Bogunic et al. 2007; Scotti-Saintagne et al. 2019). Plantations using material of unknown origin during the nineteenth and twentieth centuries may have further admixed populations (Scotti-Saintagne et al. 2023). As a result, morphological, anatomical and physiological traits are highly variable within geographic origins (Isajev et al. 2004; Naydenov et al. 2006).

In addition, the taxonomy of *P. nigra* is complex, with nomenclatures recognizing two to seven subspecies (Fukarek 1958; Enescu et al. 2016). International taxonomic authorities such as The Catalogue of Life (<http://www.catalogueoflife.org/>), Plants of the World Online (<https://powo.science.kew.org/>) or Euro+Med Plant-Base (<https://europlusmed.org/>), recognize five subspecies based on the morphological and biogeographic work of Gaussen et al. (1964). These are, from west to east: *P. nigra* subsp. *salzmannii* (Dunal) Franco in North Africa, Spain and continental France, *P. nigra* subsp. *lario* (Poir.) Maire in Corsica (France), Calabria and Sicily (Italy), *P. nigra* subsp. *dalmatica* (Vis.) Franco on the coast of Croatia, *P. nigra* subsp. *nigra* in northern Italy, Austria and most of Central Europe and the western Balkans, and *P. nigra* subsp. *pallasiana* (Lamb.) Holmboe in parts of Greece and the eastern Balkans, Cyprus, Türkiye and Crimea. The most recent phylogenetic analysis of the species (Scotti-Saintagne et al. 2019) identified six lineages, splitting *P.n. subsp. pallasiana* into two distinct genetic groups, one homogeneous in Cyprus and one

relatively admixed encompassing all other eastern Mediterranean and Black Sea populations, confirming results obtained from common gardens (Wheeler et al. 1976) and isozyme analyses (Nikolić and Tucić 1983).

Several dendroclimatic studies have shown that black pine is sensitive to high summer temperatures and to water deficit during spring and summer (Amodei et al. 2013; Lebourgeois 2000; Martín-Benito et al. 2008). This sensitivity is critical in areas where drought is frequent, such as the Mediterranean region (Génova and Fernández 1999, Lebourgeois 2000, Linares and Tíscar 2011, Martín-Benito et al. 2010, Richter et al. 1991). An increase in mean temperature and a decrease in precipitation are likely to occur in a foreseeable future (Sumner et al. 2003; Giorgi and Lionello 2008; MedECC 2020). Camarero et al. (2013) showed that, in relict rear-edge *P. nigra* populations in southern Spain and Morocco, growth responses to drought changed along an aridity gradient, and that dry conditions during the months preceding tree-ring formation constituted the major constraint for growth. Earlier studies also highlighted that *P. nigra* growth in Iberian forests was enhanced by wet and cold conditions during the previous autumn and by warm late winters (Andreu et al. 2007; Martín-Benito et al. 2010). Finally, soil texture and its ability to store water were identified as major drivers for radial growth (Génova and Martínez-Morillas 2002; Camarero et al. 2013), even at very short spatial scales (Amodei et al. 2013).

Yet, little data and few analyses exist about the genetic diversity of the correlation between radial growth and climate in trees. When such tree-ring studies exist, they demonstrate the existence of intra-specific diversity (Oleksyn et al. 1998; Savva et al. 2008; Sang et al. 2019). They also provide predictions for the risks associated with seed transfer (e.g. Savva et al. 2007). In black pine, as in other forest tree species (Park and Rogers 2023), most multi-site common gardens were established with the aim of providing information on the best seed sources for plantation forestry and as a basis for breeding. They focused on traits such as mortality, height and diameter growth, and resistance to insects and pathogens. Variation in growth traits was large among subspecies and provenances. They also tended to demonstrate a stronger general hardiness in *P. nigra* subsp. *nigra*, and fast growth, slender branches and higher volume in *P.n.* subsp. *laricio* in high fertility sites under milder climate (Kreyling et al. 2012; Seho et al. 2010; Wheeler et al. 1976; Wilcox and Miller 1975). Most of these experiments poorly sampled the easternmost and westernmost *P. nigra* lineages (but see Varelides et al. 2001) and led to breeding programs focused on Corsican black pine (Lee and Connolly 2004; Portefaix et al. 1987; Portefaix 1989), while Austrian

black pine was mostly used in erosion control and restoration projects (Vallauri et al. 2002).

The objective of our experiment was to describe and understand how variable the effects of monthly climate are on the radial growth of the European black pine, depending on subspecies or provenance, and on location of the common gardens used for tests. Using annual tree-ring data and subspecies/provenances replicated in four common gardens, we assessed provenance and subspecies effects on ring-width and tested for the occurrence of phenotypic plasticity and genotype $\times$ environment interactions. Lastly, having in mind a typology for forest management, we discussed whether recommendations for planting should be made at provenance rather than at subspecies level, as currently done in practice.

2 Material and methods

2.1 Common gardens and provenances

Radial growth data were collected from trees in four common gardens located in different locations covering the main bioclimatic zones of France (Table 1, Fig. 1): Cestas in southwestern France (oceanic climate), Levens in southeastern France (Mediterranean mountain climate), Pomet in southeastern France (peri-Mediterranean climate with a slight water deficit during the summer) and Verdun in northeastern France (semi-continental climate).

The common gardens were planted between 1968 and 1974 with the purpose of comparing the performance of provenances and subspecies for tree breeding and selection of high-quality forest reproductive material in environmental conditions where black pine plantation forests were a target of management, both for wood production and erosion control. Cestas and Pomet are part of a series (same provenances planted during the same campaign) while Levens and Verdun are part of another one. It is unclear whether the provenances that are common between the two series originate from a single or from two different seed lots collected at different times.

Sixteen provenances covering the European geographic range of *P. nigra* were selected (Table 2). Most provenances were present in at least three of the four sites and seven were present in all sites. The sixteen provenances belonged to four subspecies (Table 2). Together, they covered all genetic lineages described for *P. nigra*, either as pure or admixed provenances, the admixture being likely the result of ancient, natural contact between genetic groups, although plantations using mixed origins cannot be excluded (Scotti-Saintagne et al. 2019).

Provenance and site metadata are provided in Fady et al. (2024). Please note that the code names GASGUL, TZKU and YIMU are not found in Fady et al. (2024).

Table 1 Common garden locations selected for the experiment and their main characteristics

Location	Cestas	Levens	Pomet	Verdun
Common garden code in Fady et al (2024)	01–4200-09-02	01–4200-02-01	01–4200-09-03 (latt/mono)	01–4200-02–03/01–4200-06-03
Bioclimate	Oceanic	Mountain	Supra-Mediterranean	Semi-Continental
Latitude (degree decimal)	44.7388	43.8775	44.2926	49.2111
Longitude (degree decimal)	– 0.7623	6.2939	5.7952	5.4496
Elevation (m)	58	1332	838	335
Aspect	Flat	North-West	South-West	Flat
Substrate	Sedimentary silica	Sedimentary limestone	Sedimentary limestone	Sedimentary limestone
Site status	Private (INRAE)	State forest	State forest	State forest
Plantation date (year-month-day)	1974-03–06	1968-Spring	1973-Fall	1968-03–08/1971-05–28
Trial design*	CB	BICA	BICA/CB	BICA
Seedlings age at plantation time	2 + 0	1 + 2	1 + 1	1 + 2
Mean annual precipitation (mm)	980	840	763	882
Mean annual temperature (°C)	12.3	7.4	10.2	9
Mean monthly minimum temperature (°C)	5.7	– 1	1.1	1.3
Mean monthly maximum temperature (°C)	19.6	16.8	19.9	17.2
Initial spacing (m)	4×1.1	2×2	2×2	2×2
Total area (ha)	2.21	4.83	0.96/0.53	3.2/3.46
Number of provenances	105	31	25/19	31/25
Number of blocks	7	30	30/70	36/30
Number of plots per block	105	6	5/19	6/5
Number of trees per plot	6	56	16/1	25/36
Number of trees per test	4716	10,109	2400/1330	5400/5410
Mortality in % in 2014	75	60	6/6	28/34

*Trial design: *BICA*, incomplete blocks with random composition; *BC*, complete blocks. Common garden characteristics are described in detail in Fady et al. (2024).

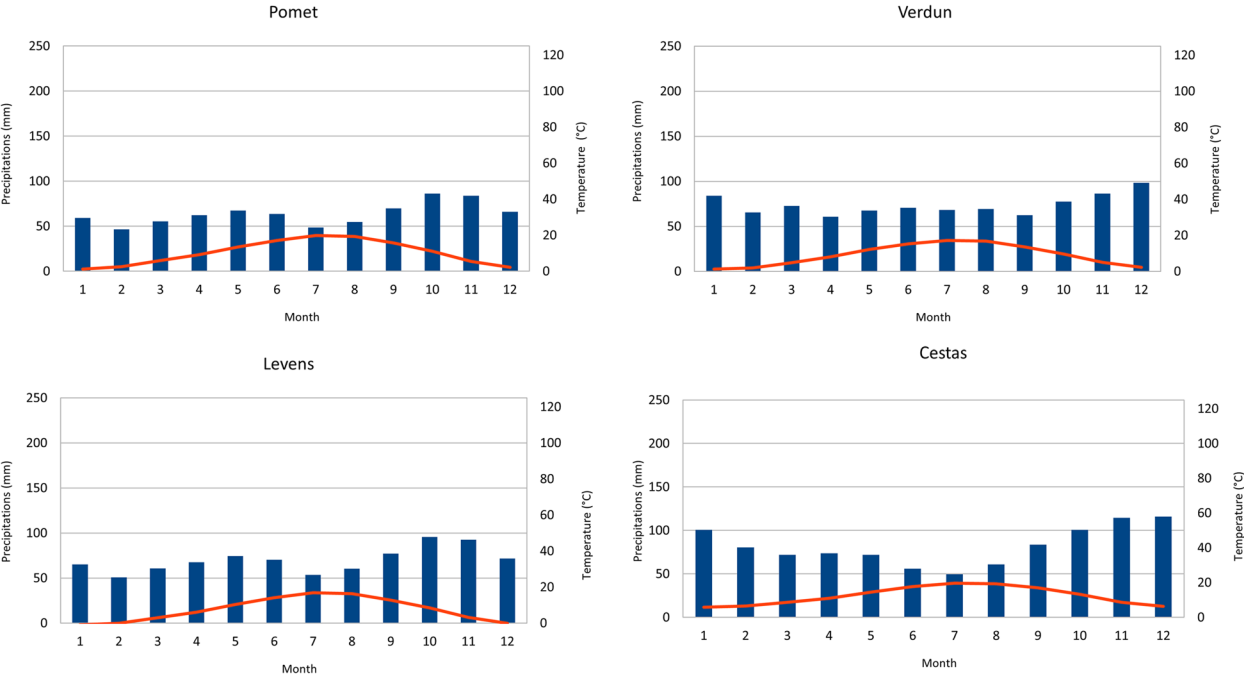


Fig. 1 Ombrothermic diagrams of the four *Pinus nigra* common gardens. The temperature scale is twice that of the precipitation scale. Precipitations are featured as blue bars, temperatures as red curves. Months are numbered from January onward

Table 2 *Pinus nigra* provenances selected for the experiment and their main characteristics. Genetic group is according to Fig. 3 of Scotti-Saintagne et al. (2019) where six different genetic groups were identified range-wide. Sample size indicates the number of trees for which there were usable tree ring data in the dataset in Fady et al. (2024)

Provenance name	Provenance code	Subspecies	Country	Genetic group	Geographic coordinates			Sample size in each common garden			
					Latitude	Longitude	Altitude (m)	Cestas	Levens	Pomet	Verdun
Aspromonte	ASPR	<i>P.n. laricio</i>	Italy	2	38°05'N	16°00'E	1300	11	13	17	18
Cosenza	COSE	<i>P.n. laricio</i>	Italy	2 + 3	39°15'N	16°17'E	1300	11	15	22	16
Valdoniello	VALD	<i>P.n. laricio</i>	France	2	41°51'N	9°06'E	1100	8	16	17	19
Doblhoff	DOBL	<i>P.n. nigra</i>	Austria	3	48°00'N	16°13'E	280	5	na	20	na
Perithorion	PERT	<i>P.n. nigra</i>	Greece	3	38°05'N	22°15'E	1300	5	na	21	na
Studenica	STUD	<i>P.n. nigra</i>	Serbia	3 + 4	43°30'N	20°33'E	930	9	na	18	16
Thasos	THAS	<i>P.n. nigra</i>	Greece	4 + 5	40°40'N	24°40'E	850	12	na	22	18
Tzarvaritza/ Kustendil	TZKU	<i>P.n. nigra</i>	Bulgaria	3	42°01'N	22°50'E	1050	10	15	16	37
Aluchtin	CRIM	<i>P.n. pallasiana</i>	Crimea	5	44°33'N	34°17'E	500	6	16	20	29
Ayanick	AYAN	<i>P.n. pallasiana</i>	Türkiye	5	41°43'N	34°31'E	1400	6	16	17	19
Popova-Livada	POLV	<i>P.n. pallasiana</i>	North Macedonia	3 + 4	41°10'N	21°55'E	1450	8	na	17	17
Yilanli/Mugla	YIMU	<i>P.n. pallasiana</i>	Türkiye	4 + 5 + 6	37°20'N	28°24'E	975	10	na	19	17
Cazorla	CAZO	<i>P.n. salzmannii</i>	Spain	1	37°50'N	3°00'W	1500	na	15	na	15
Fresneda	FRES	<i>P.n. salzmannii</i>	Spain	1	40°23'N	2°08'W	1025	9	na	21	19
Priego	PRIE	<i>P.n. salzmannii</i>	Spain	1	40°27'N	2°18'W	850	9	na	21	na
St.Guilhem/ Gagnières	GASGUL	<i>P.n. salzmannii</i>	France	2	44°07'N	4°17'E	350	16	31	22	28

They indicate that provenances originally named differently (St.Guilhem/Gagnières, Tzarvaritza/Kustendil, and Yilanli/Mugla, respectively) were grouped into a single provenance as they have the same geographic origin.

2.2 Sampling of tree rings

Annual ring-widths were measured on wood cores collected during 2014 on a subset of 16 individuals per provenance in each common garden on average (Table 2), using a Swedish increment borer mounted on a combustion engine (Grissino-Mayer 2003). We sampled two radii per individual at breast height. As radial growth is sensitive to competition and social status (Lebourgeois et al. 2014; Martín-Benito et al. 2008), we selected healthy, dominant and cylindrical trees without forking defects, surrounded by an equal number of four codominant neighbors. Mortality (excluding thinned trees) was very high in 2014 at Cestas (Table 1) because of two successive wind storms (1999 and 2009), leading to fewer available trees than in the other three common gardens. In Levens, mortality was high but affected only some of the blocks due to local water logging.

The collected cores were dried at room temperature for one month and then sanded. Once cross dated under a binocular, ring-width was measured with a precision of 1/100 mm using a LinTabTM measuring table (Rinn 1996), a robust and precise station for the measurement

of ring-width series from increment cores in association with a Leica stereo microscope and the TSAP-WIN software (Frank Rinn®). Individual annual ring-widths (rw) were calculated as the mean of the two annual ring-widths obtained from each of the two wood cores collected on each tree. Ring-width data and their associated metadata are available in Fady et al. (2024).

2.3 Climate data

Climate data were collected from SAFRAN® (Système d'Analyse Fournissant des Renseignements Adaptés à la Nivologie), a reanalysis dataset initially designed to provide atmospheric forcing data in mountain areas for avalanche forecasting (Durand et al. 1993). It has been extended to feed macroscale soil–vegetation–atmosphere transfer models over France (Le Moigne 2002). SAFRAN provides hourly climatic data with a resolution of 8 km using the Lambert-II projection (Pagé 2008). Climate data were collected, for each common garden, from 1959 to 2013. The period is characterized by some exceptional years, such as 1976 (summer drought except in southern France) and 2003 (summer heat wave).

To estimate relationships between ring-width and climate and account for black pine's known sensitivity to high summer temperatures and water deficit during spring and summer (Amodei et al. 2013; Lebourgeois

2000, Martin-Benito et al. 2008), we selected monthly variables potentially able to limit radial growth: mean minimal and maximal temperature and monthly precipitation.

Climate data and their associated metadata are available in Fady et al. (2024).

2.4 Data analysis

We used the datasets containing all provenances, thus replicated two to four times across common gardens, to analyze climate-growth trends and genetic diversity at subspecies and provenance levels. To assess phenotypic plasticity and genotype $\times$ environment interactions, we used the dataset restricted to the seven provenances present in all common gardens (Table 2).

2.4.1 Effect of climate on ring-width

To identify the relationships between climate variables and radial growth, individual ring-width series were standardized using the “*detrend.series*” function of the R package “*dplR*” (Bunn et al. 2016). The detrending removed the low and intermediate frequency variability due, for example, to ontogenic effects (Fig. 2). This was done by dividing each series by the growth trend to produce dimensionless ring-width indices (rwi) with constant mean and standard deviation over time. In this study, ring-width series were standardized with the autoregressive method which removes all but the high frequency variation in the series, a procedure well adapted to short chronologies such as ours. The detrended ring-width series were then used to build mean individual, provenance and subspecies chronologies using the “*chron*” function of the R package “*dplR*” (Bunn et al. 2016). Pearson’s correlation coefficients were then calculated between each mean chronology and their corresponding monthly climatic variables over a twelve-month period, from October of the previous year to September of the current year, using the “*dcc*” function of the R package “*bootRes*” (Zang and Biondi 2012) which adjusts results for multiple testing.

2.4.2 Effects of subspecies and provenance on ring-width

We estimated provenance and subspecies effects using a simple analysis of variance (ANOVA) model and the “*lmer*” function in R (R Core Team 2015), as follows:

$$Y = \mu + P + B + \epsilon$$

where Y is the individual (not detrended) ring-width, μ is the general mean, P is the provenance (or subspecies) random effect, B is the random block effect in each common garden and ϵ is the error term. We did not nest provenances within subspecies as many provenances

are often admixed between at least two genetic clusters corresponding to subspecies (Table 2, Scotti-Saintagne et al. 2019). As recommendations for forest reproductive material are often done at the subspecies level, we wanted to measure variance components for provenances and subspecies independently to analyze if recommendations were preferable at the provenance level than at the subspecies level.

Due to the experimental constraint of using individuals surrounded by four neighbors, provenance sample replication within blocks was uneven in the different common gardens. However, provenances were always replicated at least once in at least two different blocks. Block design was treated as incomplete in all sites. To avoid biases linked to normal distribution assumptions, we compared provenance means using a Kruskal–Wallis test and the post-hoc Wilcoxon Mann–Whitney procedure.

To test for the existence of provenance level phenotypic plasticity, we compared provenance variance across common gardens, with the assumption that similar provenance effects would indicate an absence of between-provenance phenotypic plasticity. We tested for genotype $\times$ environment (GxE) interactions using reaction norms, where ring-width mean values per provenance were ranked within common gardens, with the assumption that rank changes across common gardens would indicate GxE interactions.

3 Results

3.1 Climate-growth relationships

We obtained high quality annual ring-width data with a precision to ± 0.01 mm spanning the period 1970 to 2013 from 867 individuals sampled from all common gardens (Table 3). Mean ring-width (rw) was 3.02 mm. Common garden values ranged from 2.51 mm in Pomet to 3.31 in Levens, while subspecies values ranged from 2.76 mm in Salzmann’s pine to 3.12 mm in Austrian black pine, and provenance values ranged from 2.26 mm in provenance PERT to 3.24 mm in provenance AYAN.

At species level, aggregated data showed significant negative correlations between growth and late spring maximum temperatures at all sites except Levens, the coldest, highest elevation site where growth-climate correlations were rarely significant. Growth was negatively correlated to winter maximum temperatures at the warmest sites (Cestas, Pomet) and positively (February) at Verdun, the semi-continental common garden. Growth was negatively correlated to late spring minimum temperatures at all common gardens. The warmest common garden of Cestas showed a positive correlation with September minimum temperatures; the semi-continental common garden of Verdun revealed a positive correlation with February minimum temperatures. Finally, there

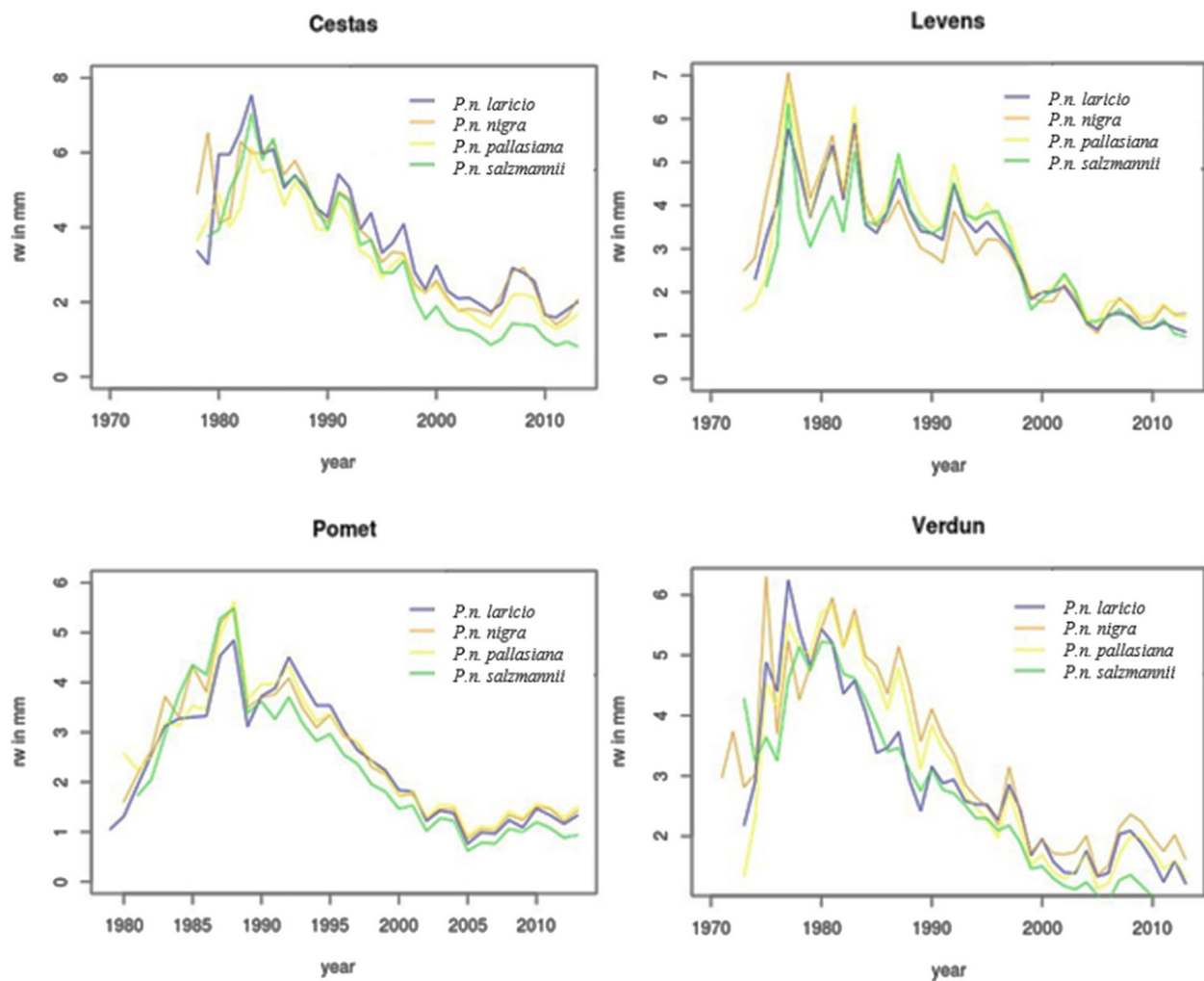


Fig. 2 Mean tree ring width over four decades for the 4 tested *P. nigra* subspecies within the 4 common gardens

was a positive correlation between June precipitation and radial growth at all common gardens except Levens, the Mediterranean mountain site.

Correlations at subspecies level were similar to those aggregated at species level, with some variation depending on common garden conditions (Fig. 3). While negative correlations between growth and late spring maximum temperatures remained significant at all common gardens except Levens, *Pn. subsp. nigra* exhibited less sensitivity overall to maximum temperatures at the wettest (Verdun and Cestas) than at the driest common gardens (Pomet). At Verdun, *Pn. subsp. nigra* exhibited fewer negative correlations with minimum temperatures while at Pomet and Levens, it was *Pn. subsp. laricio*. As for precipitations, *Pn. subsp. salzmannii* diverged slightly from the general pattern with a negative effect in August and no effect in June at Verdun, and a positive effect of October at Cestas.

Similar correlations at provenance level showed some differences with those aggregated at subspecies level (Fig. 3). For example, the *Pn. subsp. laricio* provenances ASPR from Italy and VALD from France (belonging to the same genetic group) were less sensitive to minimum and maximum temperatures than the admixed *Pn. subsp. laricio* provenance COSE from Italy, while in Cestas it was the opposite for minimum temperatures. The three *Pn. subsp. laricio* provenances diverged in their reaction to precipitations irrespectively of their genetic group at all sites except Levens where precipitation anomalies did not affect growth. Some divergence between the two *Pn. subsp. pallasiana* provenances tested at Levens was found for sensitivity to minimum temperatures during fall. The Bulgarian *Pn. subsp. nigra* provenance TZKU was less negatively influenced by winter maximum temperatures at Pomet and by summer minimum temperatures at Cestas, than the overall *Pn. subsp. nigra*

Table 3 Ring-width mean, minimum and maximum values (mm, 1970 to 2013) obtained for the four subspecies and the sixteen provenances of *P. nigra* within each common garden. The seven provenances found in all common gardens are in bold and the significance of the differences of their mean ring-widths are indicated by different letters (Kruskal–Wallis test, letters "a" to "e" in bold, "a" denoting the significantly highest value group)

	Sites	CESTAS	LEVENS	POMET	VERDUN	Mean
Subspecies	Mean	3.21	3.31	2.51	3.04	3.02
	(min/max)	(1.25/5.16)	(2.02/4.82)	(1.55/4.00)	(1.58/4.84)	
	<i>P.n. laricio</i>	3.59	3.26	2.48	3.07	3.1
	<i>P.n. nigra</i>	3.31	3.28	2.55	3.33	3.12
	<i>P.n. pallasiana</i>	3.02	3.49	2.58	3.09	3.05
Provenances	<i>P.n. salzmannii</i>	2.89	3.14	2.34	2.65	2.76
	ASPR	3.48 a	3.18 d	2.38 b	2.94 d	2.99
	COSE	3.71 a	3.4 b	2.63 a	3.19 abc	3.23
	VALD	3.59 a	3.19 d	2.36 b	3.09 cd	3.06
	TZKU	3.29 ab	3.28 c	2.74 a	3.27 a	3.15
	AYAN	3.6 ab	3.5 a	2.72 a	3.12 bcd	3.24
	CRIM	3.05 bc	3.81 a	2.45 b	3.24 ab	3.14
	GASGUL	2.81 c	3.14 d	2.18 c	2.45 e	2.65
	DOBL	2.86	na	2.25	na	2.56
	PERT	2.18	na	2.33	na	2.26
	STUD	3.89	na	2.57	3.23	3.23
	THAS	3.45	na	2.7	3.54	3.23
	POLV	2.76	na	2.55	2.8	2.70
	YIMU	2.95	na	2.59	3.13	2.89
	CAZO	na	3.11	na	2.82	2.97
	FRES	2.83	na	2.73	2.8	2.79
	PRIE	3.1	na	2.51	na	2.81

provenance mean. Finally, the French *P.n.* subsp. *salzmannii* provenance GASGUL diverged from the *P.n.* subsp. *salzmannii* overall mean for sensitivity to maximum temperatures during cold months at all sites.

3.2 Environmental, provenance and subspecies effects on phenotypic trait variation

Block effects on ring-widths were only significant at Pomet (Table 4), and provenance and subspecies means were adjusted to block effects there.

Subspecies effects were significant in half the sites and explained between 6.3% (Pomet) and 24.7% (Verdun) of ring-width variance in the sixteen-provenance dataset. Provenance effects were significant at all sites and explained between 13.5% (Pomet) and 23.2% (Verdun) of ring-width variance. Provenance effects were higher than subspecies effects in all sites except Verdun. (Table 4).

Subspecies and provenance rankings varied across sites (Table 3 and Fig. 4) and provenance differences were often larger than mean subspecies differences in most sites. For example, although *P.n.* subsp. *laricio* rarely ranked last, provenances attributed to *P.n.* subsp. *laricio* were often

outperformed by at least one provenance attributed to one other subspecies. Within subspecies, rankings were also variable except for COSE and GASGUL which always ranked first and last within the provenances of *P.n.* subsp. *laricio* and *P.n.* subsp. *salzmannii*, respectively.

Provenance effects remained significant when concentrating on the seven provenances present in all common gardens (except at Cestas) and were variable among sites, explaining 16.9% to 22.4% of total provenance variance when significant (Table 4). Subspecies effects were significant at Cestas and Pomet only and explained 11.0% to 22.0% of total provenance variance when significant (Table 4). Overall, provenance and subspecies effects varied from non-significant to over 22%, suggesting stronger phenotypic plasticity across sites for provenances than subspecies.

Overall mean rw increased by 32% from Pomet to Levens and Cestas (Table 3). Considering provenances that were present in all common gardens, rw increased by 46% for ASPR between Pomet and Cestas, and from 44% for GASGUL to 55% for CRIM between Pomet and Levens, for example. Mean rw variation was

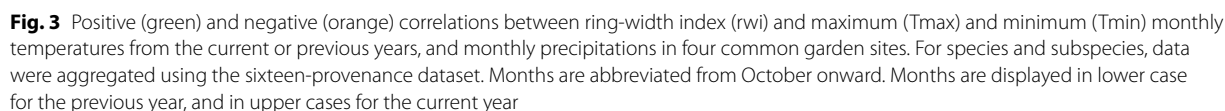


Table 4 Percentages of total phenotypic variance of ring-width (rw) explained by the subspecies, provenance and respective block effects at the four study sites, using the sixteen-provenance (rw 16 prov) or the balanced seven-provenance (rw 7 prov) datasets

		rw 16 prov	rw 7 prov
Cestas	Prov	20.3*	8.6
	Block (prov)	2.7	3.9
	Subsp	11.3	11.0*
	Block (subsp)	1.4	3.2
Levens	Prov	15.9*	16.9*
	Block (prov)	9.9	10.9
	Subsp	13.1	11.7
	Block (subsp)	12.9	129.9
Pomet	Prov	13.5*	19.7*
	Block (prov)	12.1*	8.97*
	Subsp	6.3*	22.0*
	Block (subsp)	17.3*	10.2
Verdun	Prov	23.2*	22.4*
	Block (prov)	0	0
	Subsp	24.7*	33.7
	Block (subsp)	3.1	0

*Effects statistically significant at the 5% level

mostly irrespective of plantation date, and decreased from the wettest sites to the driest and hottest site (Pomet) (Figs. 4 and 5).

The provenances with the highest mean rw over all sites were from different phylogenetic backgrounds: AYAN (*P.n.* subsp. *pallasiana*, Türkiye), COSE (*P.n.* subsp. *laricio*, Italy), TZKU (*P.n.* subsp. *nigra*, Bulgaria). However, they did not rank first at all sites (Table 3). Except for GASGUL (*P.n.* subsp. *salzmannii*, France) which ranked last at all sites, substantial provenance × site interactions occurred everywhere (Fig. 5).

4 Discussion

4.1 Climate and radial growth

Radial growth is the result of cambium activity which depends mainly on water and carbon availability (Savidge 2003), both strongly determined by local microclimate (Linares and Tíscar 2010). Radial growth of the European black pine was positively correlated with early summer precipitations (June or July) and negatively correlated with spring (March and May) and summer temperatures (June and July) across experimental sites and genotypes, as previously shown by Leal et al. (2008) and Lebourgeois (2000). Older studies have also identified a significant positive influence of lower spring temperatures and higher early summer precipitations on ring-width

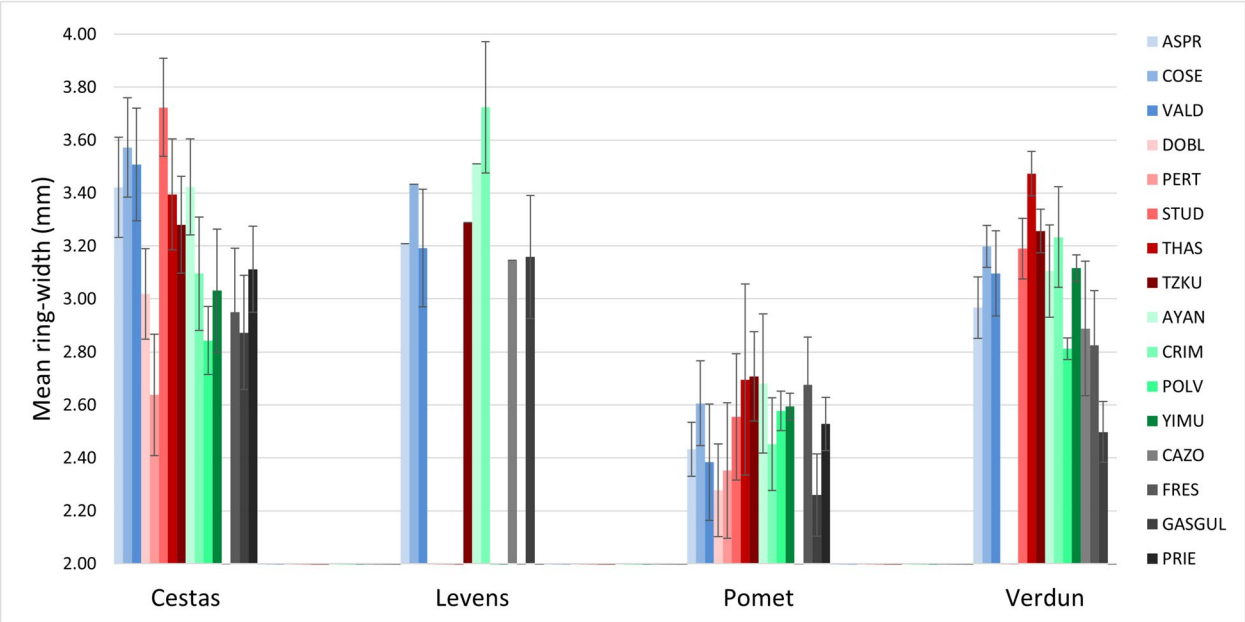


Fig. 4 Mean ring width (rw, in mm) over 40 years of growth at all sites for all 16 provenances. Colors indicate the subspecies (blue for *Pinus nigra* ssp. *laricio*, red for *P.n.* ssp. *nigra*, green for *P.n.* ssp. *pallasiana* and grey for *P.n.* ssp. *salzmannii*, see Table 2). Vertical bars are standard deviations of the mean

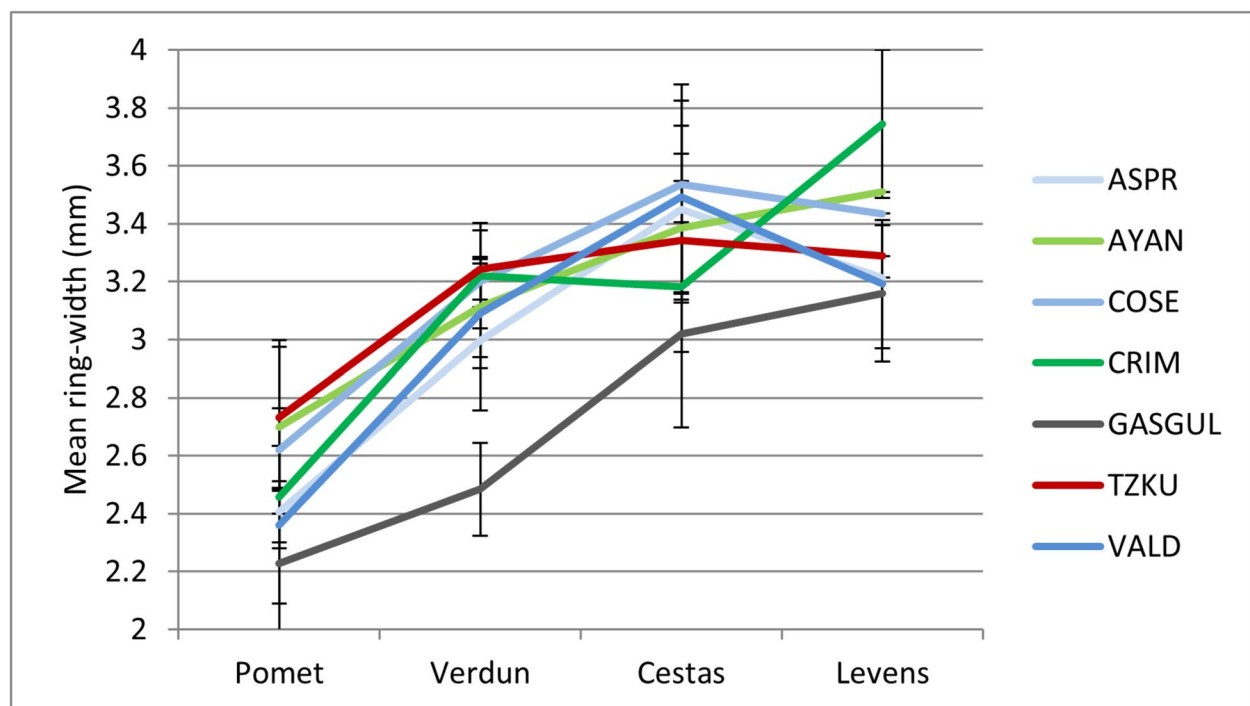


Fig. 5 Reaction norms for mean ring width (rw) for each of the 7 provenances that were present in all common gardens. Sites are ordered by increasing mean rw. Colors indicate the subspecies (blue for *Pinus nigra* ssp. *laricio*, red for *P.n.* ssp. *nigra*, green for *P.n.* ssp. *pallasiana* and grey for *P.n.* ssp. *salzmannii*, see Table 2). Vertical bars are standard deviations of the mean

of black pine in Mediterranean sites (Izmir et al. 2024; Jevšenak and Saražin 2023, Martin-Benito et al. 2010). In Tunisia, at the dry end of the ecological spectrum of *Pinus nigra*, April precipitations had a significant positive effect on radial growth (Fkiri et al. 2018). These results highlight the fundamental and beneficial role of precipitations during early wood formation when temperatures are starting to reach their maximum, and the negative effects of summer heat and drought (Andreu et al. 2007; Camarero et al. 2013; Lebourgeois 2000).

Common garden differences for climate effects on radial growth were small. The most visible difference was the opposite positive correlations with winter temperatures at Verdun, the most continental common garden, and negative correlations elsewhere, particularly at Cestas under a wet oceanic climate. This may suggest that under a continental climate, warmer than average winters will increase growth in *P. nigra* as observed in previous studies (Amodei et al. 2013; Andreu et al. 2007). Conversely, too warm winters under mild and wet climates such as at Cestas limit growth, perhaps because of delayed xylem formation or premature dormancy breaking which can expose first cambial cell divisions to late spring frost (Begum et al. 2013; Ladwig et al. 2019).

As observed by Fkiri et al. (2018), we found only few differences among subspecies and provenances in their

sensitivity to monthly precipitations and temperatures. Within the species, a notable difference was the positive correlation between growth and October precipitations at Cestas and the negative correlation between growth and August precipitations at Verdun in *P.n.* subsp. *salzmannii*. This could indicate that in wet sites, an excess of precipitations during fall may be beneficial to growth of *P.n.* subsp. *salzmannii* while late summer precipitations are not. In the dry calcareous conditions at Pomet, two *P.n.* subsp. *pallasiana* provenances benefited from late spring precipitations, which potentially indicates an increased drought tolerance in comparison to other black pine subspecies.

4.2 Genetic diversity, differentiation, and plasticity

Provenance differences accounted for up to 24% of the observed variance in mean ring-width. To our knowledge, there are few studies that used common gardens to analyze provenance effects on ring-width (possibly because old-enough common gardens are rare). These studies have generally observed that large site effects rendered provenance effects very small (George et al. 2019; Matisons et al. 2019; Savva et al. 2007; Unterholzner et al. 2024). Despite substantial differences among common gardens, we detected significant differences among provenances with biologically plausible causes. Provenance

effects on ring-width variance were generally higher than subspecies effects (except at Verdun). Pomet displayed the lowest provenance effect as well as the lowest performance, indicating that among provenance variation decreases when ecological constraints increase.

Although our design does not make it possible to measure additive genetic variance and thus formally compare phenotypic trait differentiation due to selection from that due to genetic drift (Leinonen et al. 2013), the differentiation measured in Scotti-Saintagne et al. (2019) on a slightly geographically wider set of provenances ($F_{ST}=0.09$) was lower than the within-site provenance effects we measured for ring-width (from 13.5 to 23.2%), suggesting a potential effect of natural selection on provenance ring-width differences.

Our design, also, cannot formally test for local adaptation as it is not a reciprocal transplant experiment including local and foreign genotypes and sites (Kawecki and Ebert 2004). Yet, the fact that we observed significant genotype by environment interaction may be an indication of local adaptation. The provenances from continental France and Spain (*P.n. subsp. salzmannii*) had higher growth during their first 15 years of life at Pomet, the harshest site which resembles most the ecological conditions of their place of origin. Despite the fact that growth later on becomes average or lower than average, this early growth advantage could reveal some level of local adaptation in *P.n. subsp. salzmannii* (Taïbi et al. 2016). Differences in early growth among *P. nigra* provenances have also been observed in other studies of common gardens (Wheeler et al. 1976; Wilcox and Miller 1975) and Varélides et al. (2001) hypothesized the existence of local adaptation at least for some provenances, such as the Greek provenance Thasos (*P.n. subsp. nigra*) in a Greek common garden.

Not only were provenance effects significant, their magnitude was also different in the different common gardens, suggesting a marked variation of the phenotypic plasticity for radial growth among provenances. A 4.9 °C temperature difference between the coldest (Levens) and warmest (Cestas) common garden and a 217 mm average precipitation difference between the driest (Pomet) and the wettest (Cestas) one led to up to a 55% increase in provenance mean ring-width. Although such variations are not uncommon in pines (e.g. Savva et al. 2008), they are quite substantial for *P. nigra*. This indicates that significant growth gains may be reached by carefully selecting provenances at sites where ecological conditions are optimal.

5 Conclusion and limits of the study

Taken together, our results suggest a limited adaptive divergence to temperature and precipitation differences among the subspecies of the European black pine

and a shared sensitivity to water deficit and early summer drought across subspecies and provenances, confirming early reports on different traits, from common gardens (Santini et al. 2019) or growth chambers (Thiel et al. 2012). This limited differentiation of provenances and subspecies for a key fitness-related trait also fits well with demographic inferences using molecular markers that show a recent divergence of populations at continental scale in this species during the Holocene (Scotti-Saintagne et al. 2019). Yet, there were large provenance effects on radial growth which could indicate provenance differences in resource acquisition or defense strategies (Esteban et al. 2012; Santini et al. 2019).

Although they are solely based on radial growth in trees free of defects, our results can provide a typology for the subspecies and provenances of the European black pine. Whereas *P.n. subsp. salzmannii* never ranked first in any common garden, at least one of its provenances (not always the same) performed well in most common gardens, particularly in the driest one where most other provenances suffered a much larger growth reduction than *P.n. subsp. salzmannii* compared to the other common gardens.

At the other end of the growth spectrum, *P.n. subsp. laricio* provenances never ranked last except in the driest, most Mediterranean site, while they were outperformed or equaled by *P.n. subsp. pallasiana* and *P.n. subsp. nigra* provenances in all other sites. As genotype $\times$ environment interactions are significant within subspecies, we suggest that provenance profiling rather than just subspecies profiling would probably be beneficial for identifying the best-suited material for plantation.

With its strong phenotypic plasticity, this species of pine (like others, see Richter et al. 2012) is well adapted to a wide range of environments, both for timber production and ecological restoration. Subspecies *P.n. subsp. laricio* and *P.n. subsp. nigra* have been a popular plantation material in Europe, but our results demonstrate that some provenances of the lesser-known and used (at least outside of its distribution range) *P.n. subsp. pallasiana* should be considered as well, both on acidic and calcareous soils. As *P. nigra* subspecies and provenances express different insect and disease susceptibilities (Perret et al. 2021; Watt et al. 2009), using a mixture of provenances from these subspecies in the highest fertility sites would probably be the safest plantation method both for timber production and ecological restoration outside the natural range of the species (Candido-Ribeiro and Aitken 2024), including in an assisted migration context (St Clair and Howe 2007). Our study also suggests to not disregard *P.n. subsp. salzmannii* provenances for dry site reforestation, and where drought is expected to increase due to climate change during the next decades (MedECC 2020).

Finally, our results demonstrate the importance of common gardens for forest trees (Fady and Rihm 2022). Difficult to manage, expensive and requiring a long-term investment and maintenance, they are the only experimental tools able to validate phenotypic trait adaptation and plasticity, in the era of genomics and climate change. As they age, they become a precious resource for studying growth variations retrospectively while controlling for environmental effects. Common gardens also constitute precious *ex situ* biodiversity reserves of high patrimonial value. The generation of common gardens used here was designed to select the best material for plantation forestry before global climate change was identified as a major issue. We suggest that a new generation of common gardens is now needed given the high phenotypic plasticity in forest tree species, with wide-ranging testing of new genotypes across contrasted environments, including at the early seedling stage, as suggested for other Mediterranean forest tree species (Ramírez-Valiente et al. 2022). We also suggest, in view of the strong genotype $\times$ environment interaction found here, that countries protect their native local resources both in *in situ* and as *ex situ* conservation plantations (Scotti Saintagne et al. 2023).

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Authors' contributions

GG, BF and FG participated to the production of the data. GG, CT, CSS and HD performed data analyses. GG wrote the first draft of the manuscript. BF wrote the later drafts of the manuscript. BF and FG coordinated the research. All authors reviewed the manuscript and approved the final version of the text.

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Data availability

Data and their metadata are available open access at the following address: <https://doi.org/10.57745/SKPSYI>. They can be cited as: Fady et al. (2024) Phenotypic trait and dendrometric data (1971–2023) for *Pinus nigra* Arn., the European black pine, from French common gardens. Recherche Data Gouv V2. <https://doi.org/10.57745/SKPSYI>.

Declarations

Competing interests

The authors declare no competing interests.

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References

- Amodiei T, Guibal F, Fady B (2013) Relationships between climate and radial growth in black pine (*Pinus nigra* Arnold ssp. *salzmannii* (Dunal) Franco) from the south of France. *Ann for Sci* 70:41–47. <https://doi.org/10.1007/s13595-012-0237-9>
- Andreu L, Gutiérrez E, Macías M, Ribas M, Bosch Camarero JJ (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Glob Chang Biol* 13:804–815. <https://doi.org/10.1111/j.1365-2486.2007.01322.x>
- Begum S, Nakaba S, Yamagishi Y, Oribe Y, Funada R (2013) Regulation of cambial activity in relation to environmental conditions: understanding the role of temperature in wood formation of trees. *Physiologia Plantarum* 147:46–54. <https://doi.org/10.1111/j.1399-3054.2012.01663.x>
- Bogunic F, Muratovic E, Ballian D, Siljak-Yakovlev S, Brown S (2007) Genome size stability among five subspecies of *Pinus nigra* Arnold s.l. *Environmental and Experimental Botany* 59:354–360. <https://doi.org/10.1016/j.jenvexpbot.2006.04.006>
- Bouffier, L. (2026) Common gardens are essential tools to study forest tree adaptation: a case study with the European black pine. *Peer Community in Forest and Wood Sciences*, 100188. <https://doi.org/10.24072/pci.forestwoodsci.100188>
- Bunn A, Korpela M, Biondi F, Campelo F, Mérian P, Qeadan F, Zang C (2016) dplR: Dendrochronology Program Library in R. R package version 1.6.4. <http://CRAN.R-project.org/package=dplR>
- Camarero JJ, Manzanedo RD, Sanchez-Salguero R, Navarro-Cerrillo RM (2013) Growth response to climate and drought change along an aridity gradient in the southernmost *Pinus nigra* relict forests. *Annals of Forest Science* 70(8):769–780. <https://doi.org/10.1007/s13595-013-0321-9>
- Campbell J, Sun O, Law BE (2004) Disturbance and net ecosystem production across three climatically distinct forest landscapes. *Global Biogeochemical Cycles* 18:1–11. <https://doi.org/10.1029/2004GB002236>
- Candido-Ribeiro R, Aitken SN (2024) Weak local adaptation to drought in seedlings of a widespread conifer. *New Phytol* 241:2395–2409. <https://doi.org/10.1111/nph.19543>
- Chakraborty D, Ciceu A, Ballian D, Benito Garzón M, Bolte A, Bozic G et al (2024) Assisted tree migration can preserve the European forest carbon sink under climate change. *Nature Climate Change* 14:845–852. <https://doi.org/10.1038/s41558-024-02080-5>
- Cooper L, MacFarlane D (2023) Climate-smart forestry: promise and risks for forests, society, and climate. *PLoS Clim* 2(6):e0000212. <https://doi.org/10.1371/journal.pclm.0000212>
- de Villemereuil P, Gaggiotti OE, Mouterde M, Till-Bottraud I (2016) Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity* 116(3):249–254. <https://doi.org/10.1038/hdy.2015.93>
- Durand Y, Brun E, Merindol L, Guyomarc'h G, Lesaffre B, Martin E (1993) A meteorological estimation of relevant parameters for snow models. *Ann Glaciol* 18:65–71. <https://doi.org/10.3189/S0260305500011277>
- Eilmann B, Sterck F, Wegner L, de Vries SMG, von Arx G, Mohren GMJ, den Ouden J, Sass-Klaassen U (2014) Wood structural differences between northern and southern beech provenances growing at a moderate site. *Tree Physiol* 34:882–893. <https://doi.org/10.1093/treephys/tpu069>
- Enescu CM, de Rigo D, Caudullo G, Mauri A, Houston Durrant T (2016) *Pinus nigra* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayaz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, e015138+. https://ies-ows.jrc.ec.europa.eu/efdac/download/Atlas/pdf/Pinus_nigra.pdf

- Esteban LG, Martín JA, de Palacios P, García Fernández F (2012) Influence of region of provenance and climate factors on wood anatomical traits of *Pinus nigra* Arn. subsp. *salzmannii*. *Eur J For Res* 131:633–645. <https://doi.org/10.1007/s10342-011-0537-x>
- Fady B, Rihm G (2022) Arboretums, common gardens and forest tree resilience. *New For* 53:603–606. <https://doi.org/10.1007/s11056-022-09908-y>
- Fady B, Vauthier D, Rei F, Scotti-Saintagne C, Veisse D, Bernier F, Severin L (2024) Phenotypic trait and dendrometric data (1971–2023) for *Pinus nigra* Arn., the European black pine, from French common gardens. *Recherche Data Govv V2* [dataset]. <https://doi.org/10.57745/SKPSYI>
- Fkiri S, Guibal F, Fady B, El Khorchani A, Khaldi A, Khouja ML, Nasr Z (2018) Tree-rings to climate relationships in nineteen provenances of four black pines sub-species (*Pinus nigra* Arn.) growing in a common garden from Northwest Tunisia. *Dendrochronologia* 50:44–51. <https://doi.org/10.1016/j.dendro.2018.05.001>
- Fritts HC (1971) Dendroclimatology and dendroecology. *Quat Res* 1(4):419–449. [https://doi.org/10.1016/0033-5894\(71\)90057-3](https://doi.org/10.1016/0033-5894(71)90057-3)
- Fukarek P (1958) Prilog poznavanju crnoga bora (*Pinus nigra* Arn.) / A contribution to the knowledge of black pine (*Pinus nigra* Arn.) / . Rad Poljopr-Šumarsk Fak Univ u Sarajevu 3:3–92. <https://doi.org/10.54652/rsf.1958.v6.i3.398>
- Gárate-Escamilla H, Hampe A, Vizcaíno-Palomar N, Robson TM, Benito Garzón M (2019) Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change. *Glob Ecol Biogeogr* 28(9):1336–1350. <https://doi.org/10.1111/geb.12936>
- Gausсен H, Haywood VH, Chater AO (1964) *Pinus*. In: Tutin TG (ed) *Flora Europaea*, Vol. 1. Cambridge University Press, Cambridge, UK, pp 32–35
- Génova M, Fernández A (1999) Tree rings and climate of *Pinus nigra* subsp. *salzmannii* in central Spain. *Dendrochronologia* 16:17–75–85
- Génova M, Martínez-Morillas D (2002) Estudio dendroecológico de *Pinus nigra* en Checa (Guadalajara). *Ecologia* 16:83–95
- George J-P, Grabner M, Campelo F, Karanitsch-Ackerl S, Mayer K, Klumpp RT, Schüler S (2019) Intra-specific variation in growth and wood density traits under water-limited conditions: long-term-, short-term-, and sudden responses of four conifer tree species. *Sci Total Environ* 660:631–643. <https://doi.org/10.1016/j.scitotenv.2018.12.478>
- Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. *Glob Planet Change* 63:90–104. <https://doi.org/10.1016/j.gloplacha.2007.09.005>
- Graumlich LJ, Brubaker LB, Grier CC (1989) Long-term trends in forest net primary productivity: Cascade Mountains, Washington. *Ecology* 70:405–410. <https://doi.org/10.2307/1937545>
- Gray LK, Gylander T, Mbogga MS, Chen PY, Hamann A (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecol Appl* 21(5):1591–1603. <https://doi.org/10.1890/10-1054.1>
- Grissino-Mayer HD (2003) A manual and tutorial for the proper use of an increment borer. *Tree-Ring Res* 59(2):63–79
- Housset JM, Nadeau S, Isabel N, Depardieu C, Duchesne I, Lenz P, Girardin MP (2018) Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. *New Phytol* 218:630–645. <https://doi.org/10.1111/nph.14968>
- Isajev V, Fady B, Semerci H, Andonovski V (2004) EUFORGEN Technical Guidelines for genetic conservation and use for European black pine (*Pinus nigra*). International Plant Genetic Resources Institute, Rome, Italy. ISBN 92–9043–659-X
- Izmir SC, Jevšenak J, Krajnc L, Hafner P, Köse N (2024) Distinct spatial patterns in climate–growth relationships, vegetation and resilience indices of black pine (*Pinus nigra* J.F. Arnold) from its northern and southern distribution range. *Dendrochronologia* 88:126236. <https://doi.org/10.1016/j.dendro.2024.126236>
- Jevšenak J, Saražin J (2023) *Pinus halepensis* is more drought tolerant and more resistant to extreme events than *Pinus nigra* at a sub-Mediterranean flysch site. *Trees* 37:1281–1286. <https://doi.org/10.1007/s00468-023-02413-5>
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecol Lett* 7(12):1225–1241. <https://doi.org/10.1111/j.1461-0248.2004.00684.x>
- Klisz M, Ukalska J, Koprowski M, Tereba A, Puchalka R, Przybylski P, Jastrzebowski S, Nabais C (2019) Effect of provenance and climate on intra-annual density fluctuations of Norway spruce *Picea abies* (L.) Karst. in Poland. *Agric For Meteorol* 269–270:pine145–156. <https://doi.org/10.1016/j.agrformet.2019.02.013>
- Koskela J, Vinceti B, Dvorak W, Bush D, Dawson IK, Loo J, Kjaer ED, Navarro C, Padolina C, Bordacs S, Jamnadass R, Graudal L, Ramamonjisoa L (2014) Utilization and transfer of forest genetic resources: a global review. *For Ecol Manage* 333:22–34. <https://doi.org/10.1016/j.foreco.2014.07.017>
- Kreyling J, Wiesenberger GLB, Thiel D, Wohlfart C, Huber G, Walter J, Jentsch A, Konner M, Beierkuhnlein C (2012) Cold hardiness of *Pinus nigra* Arnold as influenced by geographic origin, warming, and extreme summer drought. *Environ Exp Bot* 78:99–108. <https://doi.org/10.1016/j.envexpbot.2011.12.026>
- Ladwig L, Chandler JL, Guiden PW, Henn JJ (2019) Extreme winter warm event causes exceptionally early bud break for many woody species. *Ecosphere* 10(1):e02542. <https://doi.org/10.1002/ecs2.2542>
- Langlet O (1971) Two hundred years genealogy. *Taxon* 20:653–721
- Latreille A, Davi H, Huard F, Pichot C (2012) Variability of the climate–radial growth relationship among *Abies alba* trees and populations along altitudinal gradients. *For Ecol Manage* 396:150–159. <https://doi.org/10.1016/j.foreco.2017.04.012>
- Le Moigne P (2002) Description de l'analyse des champs de surface sur la France par le système SAFRAN. Technical report, Centre national de recherches météorologiques, Météo-France
- Leal S, Eamus D, Grabner M, Wimmer R, Cherubini P (2008) Tree rings of *Pinus nigra* from the Vienna basin region (Austria) show evidence of change in climatic sensitivity in the late 20th century. *Can J For Res* 38:744–759. <https://doi.org/10.1139/X07-189>
- Lebourgeois F (2000) Climatic signals in earlywood, latewood and total ring-width of Corsican pine from Western France. *Ann For Sci* 57(2):155–164. <https://doi.org/10.1051/forest:2000166>
- Lebourgeois F, Eberlé P, Mérian P, Seynave I (2014) Social status-mediated tree-ring responses to climate of *Abies alba* and *Fagus sylvatica* shift in importance with increasing stand basal area. *For Ecol Manage* 328:209–218. <https://doi.org/10.1016/j.foreco.2014.05.038>
- Lee SJ, Connolly T (2004) Selection of parents for the Corsican pine breeding population in Britain. *Forestry* 77(3):205–212. <https://doi.org/10.1093/forestry/77.3.205>
- Leinonen T, McCairns RJS, O'Hara RB, Merilä J (2013) QST–FST comparisons: evolutionary and ecological insights from genomic heterogeneity. *Nat Rev Genet* 14:179–190. <https://doi.org/10.1038/nrg3395>
- Linares JC, Tiscar PA (2010) Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. *Tree Physiol* 30:795–806. <https://doi.org/10.1093/treephys/tpq052>
- Linares JC, Tiscar PA (2011) Buffered climate change effects in a Mediterranean pine species: range limit implications from a tree-ring study. *Oecologia* 167:847–859. <https://doi.org/10.1007/s00442-011-2012-2>
- Martín-Benito D, Cherubini P, del Río M, Cañellas I (2008) Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees* 22:363–373. <https://doi.org/10.1007/s00468-007-0191-6>
- Martín-Benito D, Del Río M, Cañellas I (2010) Black pine (*Pinus nigra* Arn.) growth divergence along a latitudinal gradient in Western Mediterranean Mountains. *Ann For Sci* 67:401. <https://doi.org/10.1051/forest/2009121>
- Matisons R, Jansone D, Elferts D, Adamovičs A, Schneck V, Jansons Ā (2019) Plasticity of response of tree-ring width of Scots pine provenances to weather extremes in Latvia. *Dendrochronologia* 54:1–10. <https://doi.org/10.1016/j.dendro.2019.01.002>
- MedECC (2020) Climate and Environmental Change in the Mediterranean Basin – Current Situation and Risks for the Future. First Mediterranean Assessment Report. In: Cramer W, Guiot J, Marini K (eds). Union for the Mediterranean, Plan Bleu, UNEP/MAP, Marseille, France. <https://doi.org/10.5281/zenodo.4768833>
- Mirov NT (1967) The genus *Pinus*. Ronald Press, New York
- Naydenov KD, Tremblay FM, Fenton NJ, Alexandrov A (2006) Structure of *Pinus nigra* Arn. populations in Bulgaria revealed by chloroplast microsatellites and terpenes analysis: provenance tests. *Biochem Syst Ecol* 34:562–574. <https://doi.org/10.1016/j.bse.2006.01.011>
- Nikolić D, Tucić N (1983) Isoenzyme variation within and among populations of European black pine (*Pinus nigra* Arnold). *Silvae Genet* 32(3/4):80–89
- Oleksyn J, Tjoelker MG, Reich PB (1998) Adaptation to changing environment in Scots pine populations across a latitudinal gradient. *Silva Fenn* 32(2):691. <https://doi.org/10.14214/sf.691>

- Pagé C (2008) Format des données SAFRAN et scénarios climatiques désagrégés au CERFACS. Technical Report TR/CMGC/08/27, Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique (CERFACS)
- Palik BJ, Clark PW, D'Amato AW, Swanston C, Nagel L (2022) Operationalizing forest-assisted migration in the context of climate change adaptation: examples from the eastern USA. *Ecosphere* 13(10):e4260. <https://doi.org/10.1002/ecs2.4260>
- Park A, Rodgers JL (2023) Provenance trials in the service of forestry assisted migration: a review of North American field trials and experiments. *For Ecol Manage* 537:120854. <https://doi.org/10.1016/j.foreco.2023.120854>
- Perret S, Fady B, Ginisty C, Giovannelli G, Matz S, Philippe G, Roig A, Scotti-Saintagne C (2021) Les pins laricio sont-ils tous égaux face à la maladie des bandes rouges ? *Forêt Entrepre* 259:33–41
- Portefaix C (1989) Exploration de la variabilité génétique présente dans cinq peuplements naturels de pin Laricio de Corse (*Pinus nigra* ssp. *laricio* var. *corsicana* Loud.). *Ann Sci For* (Paris) 46(3):217–232. <https://doi.org/10.1051/forest:19890302>
- Portefaix C, Faucher M, Veisse D (1987) Défaut de fourchaison chez le Pin laricio de Corse (*Pinus nigra* Arn. ssp. *laricio* var. *corsicana* Loud.): décomposition du phénomène en vue de l'amélioration génétique. *Ann Sci For* (Paris) 44(4):435–454. <https://doi.org/10.1051/forest:19870404>
- Price RA, Liston A, Strauss SH (1998) Phylogeny and systematics of *Pinus*. In: Richardson DM (ed) *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge, pp 49–68. ISBN: 9780521789103
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Ramírez-Valiente JA, del Santos Blanco L, Alía R, Robledo-Arnuncio JJ, Climent J (2022) Adaptation of Mediterranean forest species to climate: Lessons from common garden experiments. *J Ecol* 110:1022–1042. <https://doi.org/10.1111/1365-2745.13730>
- Rathgeber C, Nicault A, Guiot J, Keller T, Guibal F, Roche P (2000) Simulated responses of *Pinus halepensis* forest productivity to climatic change and CO₂ increase using a statistical model. *Glob Planet Change* 26:405–421. [https://doi.org/10.1016/S0921-8181\(00\)00053-9](https://doi.org/10.1016/S0921-8181(00)00053-9)
- Richter K, Eckstein D, Holmes RL (1991) The dendrochronological signal of pine trees (*Pinus* spp.) in Spain. *Tree-Ring Bull* 51:1–13
- Richter S, Kipfer T, Wohlgemuth T, Calderón Guerrero C, Ghazoul J, Moser B (2012) Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia* 169:269–279. <https://doi.org/10.1007/s00442-011-2191-x>
- Rinn F (1996) TSAP V3.6 Reference Manual: Computer program for tree-ring analysis and presentation. Heidelberg, p 263
- Sang Z, Sebastian-Azcona J, Hamann A, Menzel A, Hacke U (2019) Adaptive limitations of white spruce populations to drought imply vulnerability to climate change in its western range. *Evol Appl* 12(9):1850–1860. <https://doi.org/10.1111/eva.12845>
- Santini F, Serrano L, Kefauver SC, Abdullah-Al M, Aguilera M, Sin E, Voltas J (2019) Morpho-physiological variability of *Pinus nigra* populations reveals climate-driven local adaptation but weak water use differentiation. *Environ Exp Bot* 166:103828. <https://doi.org/10.1016/j.jenvexpbot.2019.103828>
- Savidge RA (2003) Tree growth and wood quality. In: Wood quality and its biological basis, J.R. Barnett and G. Jeronimidis (eds.), Blackwell Scientific, Oxford. Chapter 1, 1–29
- Savva Y, Denneler B, Koubaa A, Tremblay F, Bergeron Y, Tjoelker MG (2007) Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada. *For Ecol Manage* 242(2–3):636–647. <https://doi.org/10.1016/j.foreco.2007.01.073>
- Savva Y, Bergeron Y, Denneler B, Koubaa A, Tremblay F (2008) Effect of interannual climate variations on radial growth of jack pine provenances in Petawawa, Ontario. *Can J For Res* 38(3):619–630. <https://doi.org/10.1139/X07-178>
- Schwinning S, Lortie CJ, Esque TC, DeFalco LA (2022) What common-garden experiments tell us about climate responses in plants. *J Ecol* 110:986–996. <https://doi.org/10.1111/1365-2745.13887>
- Scotti-Saintagne C, Giovannelli G, Scotti I, Roig A, Spanu I, Vendramin GG, Guibal F, Fady B, et al (2019) Recent, late-Pleistocene fragmentation shaped the phylogeographic structure of the European black pine (*Pinus nigra* Arnold). *Tree Genet Genomes* 15:76. <https://doi.org/10.1007/s11295-019-1381-2>
- Scotti-Saintagne C, de Sousa Rodrigues A, Roig A, Fady B (2023) A comprehensive strategy for the conservation of forest tree genetic diversity: an example with the protected *Pinus nigra* subsp. *salzmannii* (Dunal) Franco in France. *Conserv Genet* 25:469–480. <https://doi.org/10.1007/s10592-023-01581-8>
- Seho M, Kohnle U, Albrecht A, Lenk E (2010) Growth analyses of four provenances of European Black Pine (*Pinus nigra*) growing on dry sites in south-west Germany (Baden-Wuerttemberg). *Allg Forst- Jagdztg* 181:104–116
- St Clair BJ, Howe GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Glob Change Biol* 13:1441–1454. <https://doi.org/10.1111/j.1365-2486.2007.01385.x>
- Sumner G, Romero R, Homar V, Ramis C, Alonso S, Zorita E (2003) An estimate of the effects of climate change on the rainfall of Mediterranean Spain by the late twenty first century. *Clim Dyn* 20:789–805. <https://doi.org/10.1007/s00382-003-0307-7>
- Taïbi K, del Campo AD, Mulet JM, Flors J, Aguado A (2014) Testing Aleppo pine seed sources response to climate change by using trial sites reflecting future conditions. *New For* 45(5):603–624. <https://doi.org/10.1007/s11056-014-9423-y>
- Taïbi K, del Campo AD, Aguado A, Mulet JM (2016) Early establishment response of different *Pinus nigra* ssp. *salzmannii* seed sources on contrasting environments: implications for future reforestation programs and assisted population migration. *J Environ Manage* 171:184–194. <https://doi.org/10.1016/j.jenvman.2016.02.014>
- Thiel D, Nagy L, Beierkuhnlein C, Huber G, Jentsch A, Konnerth M, Kreyling J (2012) Uniform drought and warming responses in *Pinus nigra* provenances despite specific overall performances. *For Ecol Manage* 270:200–208. <https://doi.org/10.1016/j.foreco.2012.01.034>
- Unterholzner L, Stolz J, van der Maaten-Theunissen M, Liepe K, van der Maaten E (2024) Site conditions rather than provenance drive tree growth, climate sensitivity and drought responses in European beech in Germany. *For Ecol Manage* 572:122308. <https://doi.org/10.1016/j.foreco.2024.122308>
- Vallauri DR, Aronson J, Barbero M (2002) An analysis of forest restoration 120 years after reforestation on badlands in the Southwestern Alps. *Restor Ecol* 10(1):16–26. <https://doi.org/10.1046/j.1526-100X.2002.10102.x>
- Varelides C, Brofas G, Varelides Y (2001) Provenance variation in *Pinus nigra* at three sites in Northern Greece. *Ann For Sci* 58:893–900. <https://doi.org/10.1051/forest:2001103>
- Vinceti B, Manica M, Lauridsen N, Verkerk PJ, Lindner M, Fady B (2020) Managing forest genetic resources as a strategy to adapt forests to climate change: perceptions of European forest owners and managers. *Eur J for Res* 139:1107–1119. <https://doi.org/10.1007/s10342-020-01311-6>
- Vitasse Y, Bresson CC, Kremer A, Michalet R, Delzon S (2010) Quantifying phenological plasticity to temperature in two temperate tree species. *Funct Ecol* 24:1211–1218. <https://doi.org/10.1111/j.1365-2435.2010.01748.x>
- Wang H, Zhu A, Duan A, Wu H, Zhang J (2022) Responses to subtropical climate in radial growth and wood density of Chinese fir provenances, southern China. *For Ecol Manage* 521:120428. <https://doi.org/10.1016/j.foreco.2022.120428>
- Watt MS, Kriticos DJ, Alcaraz S, Brown AV, Leriche A (2009) The hosts and potential geographic range of Dothistroma needle blight. *For Ecol Manage* 257(6):1505–1519. <https://doi.org/10.1016/j.foreco.2008.12.026>
- Wheeler NC, Kriebel HB, Lee CH, Read RA, Wright JW (1976) 15-year performance of European black pine in provenance tests in north-central United States. *Silvae Genet* 25:1–6
- Wilcox MD, Miller JT (1975) *Pinus nigra* variation and selection in New Zealand. *Silvae Genet* 24:132–140
- Woolridge CB, Fant JB, Flores AI, Schultz K, Kramer AT (2023) Variation in overall fitness due to seed source: projections for predictive provenancing. *Restor Ecol* 31(1):e13717. <https://doi.org/10.1111/rec.13717>
- Zaghi D (2008) Management of Natura 2000 habitats. 9530 *(Sub)-Mediterranean pine forests with endemic black pines. European Commission
- Zang C, Biondi F (2012) Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologia* 31(1):68–74. <https://doi.org/10.1016/j.dendro.2012.08.001>

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