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Tree rings, wood density and climate-growth relationships of four Douglas-fir provenances in sub-Mediterranean Slovenia

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Abstract

Tree rings, wood density and the climate-growth relationship of four Douglas-fir provenances were analysed separately for the juvenile and adult phases. Four provenances were selected from an existing IUFRO provenance trial planted in 1971 based on their diameter at breast height and vitality. Increment cores were extracted from individual trees, on which we measured tree-ring widths (RW), earlywood widths (EWW) and latewood widths (LWW). Wood density was assessed in standing trees using resistance drilling. The climate-growth correlations were calculated between provenance chronologies of RW, EWW, LWW and latewood share, and the day-wise aggregated Standardised Precipitation-Evapotranspiration Index (SPEI). The analysis was done separately for the juvenile and mature phases of growth. Provenances 1064 (Jefferson) and 1080 (Yelm) exhibited larger annual radial increments than provenances 1028 (Merrit) and 1089 (Cathlamet). The two provenances with the highest annual radial increment in the juvenile phase did not exhibit the same trend in the adult phase. In all provenances, RW, and consequently EWW and LWW, were wider in the juvenile than in adult phase. The share of latewood was in all cases higher in juvenile wood than in mature wood. All four provenances had similar wood densities in both analyzed growth phases. Our analysis showed that when selecting the most promising provenance for planting, possible changes in relative growth rate from the juvenile to adult phase need to be considered.

Key message: The relationships between growth rates of examined provenances in the sub-Mediterranean change between juvenile and adult growth phase, while wood density is approximately similar in all four examined provenances.

Keywords: *Pseudotsuga menziesii*, SPEI, juvenile phase, adult phase, latewood share, resistance drilling

1 Introduction

Due to climate change and associated severe events, the tree-species composition in European forests is expected to change in the coming decades, which will influence forest management practices and the global forest sector in terms of timber supply, demand and production (Bolte et al. 2009; Keenan 2015; Dyderski et al. 2018; Buras and Menzel 2019). The abundance of the currently most economically important European tree species is thus expected either to decrease (e.g., Norway spruce and Scots pine) or remain unchanged (common beech and pedunculate oak). Several currently less represented and relatively less economically important native (e.g., black pine, maritime pine, pubescent oak) and/or non-native tree species (e.g., Douglas-fir) are projected partly to fill these gaps (Buras and Menzel 2019). Despite a variety of opinions among experts on non-native tree species, there is general agreement that non-native tree species may become more economically important - but only in a supporting role and not as a replacement for natural succession processes (Jandl et al. 2019). Careful integration of a range of tested non-native tree species into forests thus seems to be one of the solutions for climate change adaptation and mitigation (Bindewald et al. 2020).

In terms of wood properties and improved resilience to climate change, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has already been considered a possible suitable species, whose timber could be used to augment or replace timber from the currently most widespread species (*e.g.* Norway spruce) (Spiecker et al. 2019). Although Douglas-fir is grown on 0.83 million ha in Europe (Brus et al. 2019) and is nowadays one of the most important commercial non-native timber species in West and Central Europe (Eilmann et al. 2013), its yearly harvest in Slovenia is representing only ca. 2.4 % of the total harvested timber volume (Skudnik et al. 2021). Its currently negligible share may change in the coming years for the reasons mentioned above.

The ability of trees to withstand environmental changes depends on phenotypic plasticity, genetic diversity within and between populations, and gene flow (Kramer et al. 2010). Tree species that are more resistant to drought or wind-related damages may thus have better chances of survival in such unpredictable circumstances. Douglas-fir is native to the western United States and Canada, where it grows in a wide range of site conditions and therefore displays high adaptive genetic variability. It is a highly productive tree species that generally copes well with frequent droughts (Eilmann and Rigling 2012); however, the drought tolerance and productivity of Douglas-fir trees depend on their geographical origin. The coastal Douglas-fir variety (*P. menziesii* var. *menziesii*) is less drought-tolerant but more productive than the interior variety (*P. menziesii* var. *glauca*), the latter is also less resistant to needle cast (*Rhabdocline pseudotsugae* Syd., (1922)) when planted in Europe; thus, variety *glauca* has rarely been planted in Europe (Eilmann et al. 2013). Since differences also exist in productivity and drought tolerance among coastal

Douglas-fir populations, the suitability of provenances for different site conditions in Europe has been extensively investigated (e.g. Spiecker et al. 2019; Isaac-Renton et al. 2014).

Thus, for appropriate provenance selection that also considers changing climate conditions, information on the long-term performance of different provenances under current and future European climate conditions is needed. Provenance trials, such as the IUFRO seed collection program established in 1966/1967, in which seeds from the natural range of coastal Douglas-fir were collected and distributed to 20 European countries (Montwé et al. 2015), are ideal for identifying the best performing provenance for selected sites. The Slovene provenance trial was established in 1971 when 15 coastal Douglas-fir provenances were planted in Brkini, characterised by an inland sub-Mediterranean climatic regime (Smolnikar et al. 2021). However, in addition to high productivity and drought-tolerance, wood quality is also an important factor for provenance selection by forest owners and forest managers. Wood density is one of the wood characteristics that has usually been used as a measure of wood quality, whereby higher density generally improves mechanical wood properties resulting in higher-quality wood (Rais et al. 2014).

In this study, we analysed climate-growth relationships and wood density of four coastal Douglas-fir provenances, separately for juvenile and adult phases. This was done because radial growth trend and climate-growth relationships may change from juvenile to adult phases. Juvenile wood is generally considered inferior to adult wood in terms of mechanical and physical properties, which are crucial in determining the suitability of wood for specific end uses (Blohm et al. 2016). Juvenile wood of Douglas-fir will probably become more economically important because of the shortening of rotation periods on commercial plantations, which leads to a higher proportion of juvenile wood

(Blohm et al. 2016). The provenance selection was based on the recent data of Smolnikar et al. (2021), who investigated the survival rate, diameter at breast height growth and branchiness of 1061 surviving trees of 15 different provenances in a Slovene provenance trial. Two of the best-performing (P-1080 and P-1089) and two of the worst-performing (P-1028 and P-1064) provenances in terms of vitality and diameter at breast height (DBH) were selected for the tree-ring and wood density analyses presented in the current study. Since areas with a sub-Mediterranean climate in Europe and worldwide are expected to increase with global warming (Buras and Menzel 2019), the results can provide valuable insight into the future growth of Douglas-fir trees in drier and warmer climates.

2 Material and Methods

2.1 Study site, origin and characteristics of provenances

The studied Douglas-fir trees are growing in a provenance trial designated Padež I. The study site is located in the forest district of Sežana, Slovenia (N 45°36′13″; E 14°3′21″) at 530–580 m above sea level. The relief at the site is smooth with 5% outcrops, and the soil is a distric brown soil on non-carbonate flysch and decalcified marl. The climate is inland sub-Mediterranean (Ogrin 1996), the average annual temperature for the period 1980–2010 is 10.4 °C, the average January temperature is 1.3 °C and the average July temperature is 20.1 °C. The average annual precipitation for this period is 1306 mm and the precipitation is quite favorably distributed within the growing season. The wettest month is October with 152 mm average precipitation, while the driest months are February, January and July, with 76, 81 and 82 mm precipitation, respectively. During the period from 1961 to 2011, there were several dry years with less than 1000 mm rainfall (1983, 2003 and 2011), while 1976, 1979, 1984, 2000 and 2010 were wet years with more than 1600 mm rainfall. Climate data were obtained from the nearest meteorological station, in Ilirska Bistrica (424 m a.s.l.), 16 km from the study area, reference period 1980–2010 (Agencija Republike za Okolje 2014).

The provenance trial is part of an extensive IUFRO program in which seeds from the natural range of Douglas-fir were collected and distributed to several European countries (Kleinschmit and Bastien 1992). The provenance trial in Slovenia was established in 1971 with the planting of 15 coastal Douglas-fir (*P. menziesii* var. *menziesii*) provenances. The experimental plot was rectangular, with an area of 1.56 ha, on which 2460 trees of 15 provenances were planted. Provenances were planted in a systematic distribution to exclude environmental influences such as small differences in soil and slope. Rows with 2.5 m spacing consisted of several series of 10 trees per provenance, again with 2.5 m spacing in a row. Depending on the number of seedlings available, there were 11–20 replicates per provenance. In the establishment phase, the trial was fenced, planting success was over 90% (Mlinšek 1977) and the trial plantation has never been thinned. Prior to this study, data were collected and analyzed for the period from 1975 to 1985 (Breznikar 1991) and again in 2017 (Smolnikar et al. 2021). The latter study showed that the best provenances, based on vitality and current diameter at breast height were Yelm and Cathlamet, while the worst provenances based on these two criteria were Merrit and Jefferson (however, the latter was the provenance with the best log quality, as evaluated by branching (Table 1 and Table 2, Smolnikar et al. (2021)). In the present investigation, these four provenances were used in an in-depth study with regard to their growth performance and wood density.

Table 1: Provenances studied in the experimental plot Padež I: IUFRO code - international provenance IUFRO code; name - provenance name (nearby city); state - state; N (°) and W (°) - geographical coordinates; altitude (m) - elevation in meters above sea level; num. of seedlings - total number of planted seedlings per provenance; num. of series - number of replicates (Eilmann et al. 2013; Breznikar 1991; Isaac-Renton et al. 2014).

IUFRO	Name	State or Province	N (°)	W (°)	Elevation	Number of seedlings	Number of series
1028	Merrit	British Columbia	50.07	120.85	870–950	180	18
1064	Jefferson	Washington	47.80	123.97	240–245	166	17
1080	Yelm	Washington	47.02	122.73	60	170	17
1089	Cathlamet	Washington	46.30	123.27	195–200	160	16

Table 2: Performance of the studied 4 Douglas-fir provenances originating from the west coast of North America and planted in the Slovenian provenance trial. Measurements of height, survival, vitality (vitality classes 3: good vitality, 2: medium vitality, 1: low vitality) and DBH were made on all trees per provenance (Breznikar 1991; Smolnikar et al. 2021).

	Year	1975	1976	1977	1978	1985	2017	2017	2017	2017
IUFRO	Name	Avg. height (cm)					Survival (%)	Vitality	DBH (cm)	SD DBH (cm)
1028	Merrit	106.3	133.3	165.3	208.9	513.4	35.0	1.87	27.0	9.3
1064	Jefferson	124.3	152.0	188.9	234.3	595.8	44.6	2.16	28.6	9.8
1080	Yelm	128.7	157.6	191.4	241.1	591.3	40.6	2.49	36.1	10.5
1089	Cathlamet	135.7	167.2	208.3	262.5	651.9	47.5	2.37	34.1	10.6

2.2 Climate data

Climate data for climate-growth correlations were extracted from E-OBS daily climate datasets, available since 1950 with a 0.1 grid of spatial resolution (Cornes et al. 2018). Precipitation totals and mean, maximum and minimum temperatures were extracted for 25 nearest grid points and interpolated for the exact site coordinates using cokriging with elevation included as an auxiliary variable (Feki et al. 2012). The data for the climate diagrams in Figures 1 and 2 were obtained using the WorldClim 2.1 global climate dataset (Fick and Hijmans 2017) with a spatial resolution of 2.5 minutes, and the climate diagrams were plotted using R library *climatol* (Guijarro 2019).

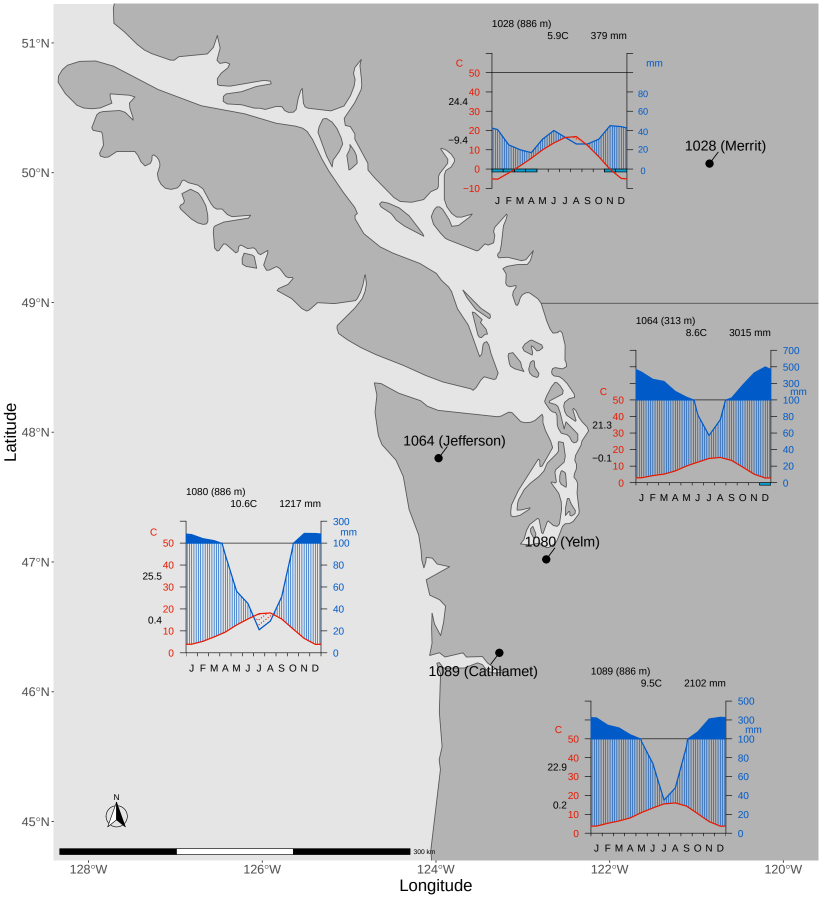

Fig. 1: Provenance origin location map with climate diagrams for each provenance origin location (Walter and Lieth 1960). The provenance code is followed by elevation in m above sea level (in parentheses), displaying the analyzed period, average temperature and precipitation in the second line and average maximum temperature of the warmest month with average minimum temperature of the coldest month on the left side of the diagrams (data from period of 1970-2000). The Merrit site is in the state of Washington and the others are in Oregon.

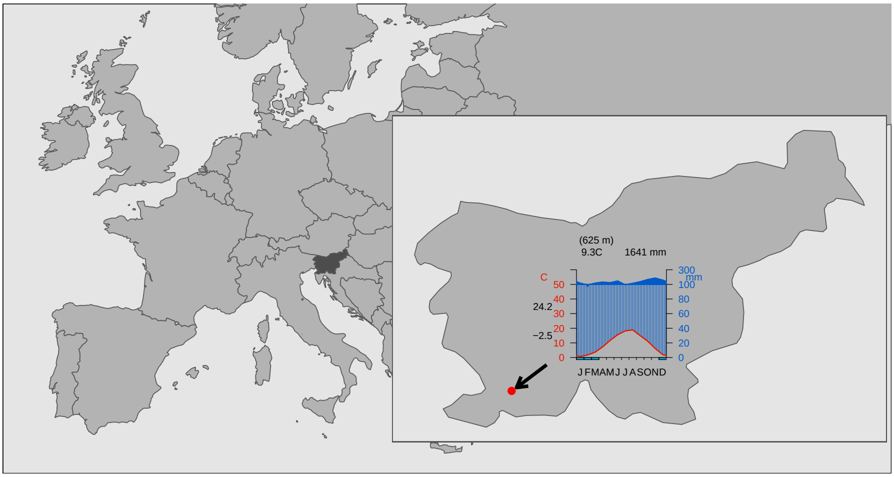

Fig. 2: Provenance trial macro- and micro-location (marked wih red dot) within Europe and Slovenia along with a Walter-Lieth climate diagram for the period 1970-2000.

2.3 Dendrochronological analysis

Twelve to 18 individual trees from each provenance were sampled at random in June of 2020 using a 5.15-mm increment borer (Haglöf, Sweden), taking one core per tree. Increment cores were saved in paper straws, dried at the laboratory and glued into wooden holders. The tree cores were then sanded to obtain a clear surface with distinct tree rings, and high-resolution images were taken and stitched with the ATRICS system (Levanič 2007). Total tree-ring widths (RW), earlywood widths (EWW) and latewood widths (LWW) were measured with CooRecorder (Cybis Elektronik & Data AB), and the final crossdating was performed using PAST-5 software (SCIEM, Brunn, Austria). Latewood share was calculated as LWW divided by RW.

2.4 Climate-growth correlations

All chronologies used in the climate-growth analysis were first standardized using a fixed spline with 32 years of length and 0.5 frequency response. To build provenance chronologies, RW, EW and LW were pre-whitened and averaged using a robust biweight mean. We calculated the climate-growth correlations between provenance chronologies of RW, EWW, LWW and LW shares, and the day-wise aggregated Standardised Precipitation-Evapotranspiration Index (SPEI) (Jevšenak and Levanič 2018; Jevšenak 2020), while correlations with daily temperature and precipitation are shown in Supplementary Material. SPEI accounts for both actual precipitation and potential evapotranspiration (PET) to determine drought (Beguería and Vicente-Serrano 2017). PET was estimated with the Hargreaves-Samani method (Hargreaves and Samani 1985) and the climatic water deficit was calculated for each day as the difference between the daily sum of precipitation and daily PET. We calculated the accumulated drought effects by aggregating climatic water deficits into a log-logistic probability distribution to obtain the SPEI index series of different seasons (Vicente-Serrano et al. 2010), from three weeks to nine months, including the effect of the previous growing season. Finally, we also assessed the effect of age on the temporal stability of SPEI correlations by using a subset window of 25 years and sliding it from the juvenile to adult phase.

2.5 Wood density assessment using resistance drilling

Wood density was assessed in standing trees of the selected four provenances using resistance drilling. For the sake of speed, less damage to the stem, and ease of resistance drilling measurements, a larger number of trees were used here than in extracting increment cores. Thirty trees were measured in each provenance (trees used for increment coring plus additional randomly sampled trees) and the device used was a Resistograph SC-650 (Rinntech, Heidelberg, Germany) with 500-mm long drilling needles, calibrated by the manufacturer for absolute wood density assessment. The measurements were done bark-to-bark through the pith of the tree and the drilling data were saved by the device and then manually imported into the computer. The resistance drilling density measurements (in kg/m^3) were imported into the R statistical environment (R Core Team 2021) with the R package *densitr* (Krajnc 2020). The bark portion (where the drilling needle has not yet entered wood) of each measurement was trimmed away, after which the measurements were detrended automatically using a linear regression fit provided by the R package *densitr*. The presented values of resistance drilling density profiles are median values for each individual tree. As noted in other species (Krajnc et al. 2020), the resistance-drilling density values are generally lower than basic wood density due to the effect of the moisture content in fresh wood. No corrections in this regard were applied, since relative values of wood density are still comparable within the same species.

2.6 Distinguishing between juvenile wood and adult wood

Depending on genetic and external influences, the transition from juvenile to adult phase in Douglas-fir occurs between 17 and 30 years (Abdel-Gadir and Krahmer 1993; Giagli et al. 2017). The exact age at which a tree stops producing juvenile wood and begins producing adult wood cannot be defined because of the gradual change in properties with age. At some point, the properties stabilize, however, and the boundary between juvenile and adult wood depends on tree species and analysed wood traits (i.e., wood density, RW, latewood percentage, cell wall thickness and microfibril angle) (Bendtsen and Senft 1986). Blohm et al. (2016) reported that the age of demarcation between juvenile and adult wood can differ by more than 7 years when identified by different wood characteristics. Information on the methodology used is therefore important for data comparison between different laboratories. Based on previous research (Abdel-Gadir and Krahmer 1993; Giagli et al. 2017) the limit between juvenile and adult phases in our study was set at 20 years, counting outwards from the pith (*i.e.* the year 1991). Using a subset of trees for which both increment cores and resistance drilling were collected and measured, the proportion of juvenile vs. adult wood in the radial direction was calculated (50% juvenile : 50% adult) using the sum of RW of the first 20 years and the overall sum of RW. This ratio was then used to distinguish the first half (bark-to-pith) of the resistance-drilling measurements into juvenile and adult phases.

3 Results

3.1 Tree-ring patterns

RW chronologies for the four analysed provenances are shown in Figure 3. The two provenances with the highest annual radial increment in the juvenile phase do not exhibit the same pattern in the adult phase. Interestingly, the relationship between the two pairs of faster-growing provenances in either phase is not reflected in their current DBH values. Provenances 1080 and 1089 have the largest diameters, while this is not reflected in their annual radial increments in the adult phase. Instead, the largest annual increments in the adult phase were found in 1064 and 1080, the former being second to last in terms of current DBH across the whole trial, while the latter had the largest DBH overall.

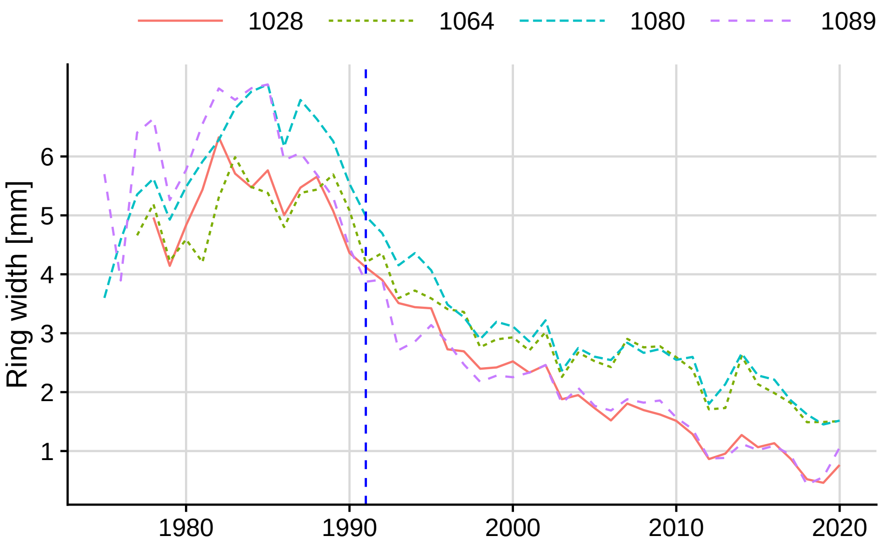

Fig. 3: Robust RW chronologies, blue vertical line marks the transition between juvenile and adult phase in 1991.

In all provenances, RW, and consequently EWW and LWW, were 41% (P-1064) - 65% (P-1089) wider in the juvenile than in the adult phase (Figure 4 and Table A2). In the juvenile phase, the narrowest RWs were found in P-1064 and the widest in P-1080. In the adult period, the narrowest RWs were found in P-1028 and the widest in P-1080. Significantly more variation was observed in the widths of adult wood across all provenances. Some of the differences between provenances were found to be statistically significant, confirming what was already observed in Figure 3: provenances 1064 and 1080 have larger annual radial increments than provenances 1028 and 1089. These relationships persist in both earlywood and latewood. The differences in all tree-ring parameters between juvenile and adult phase were also statistically significant (Figure A2).

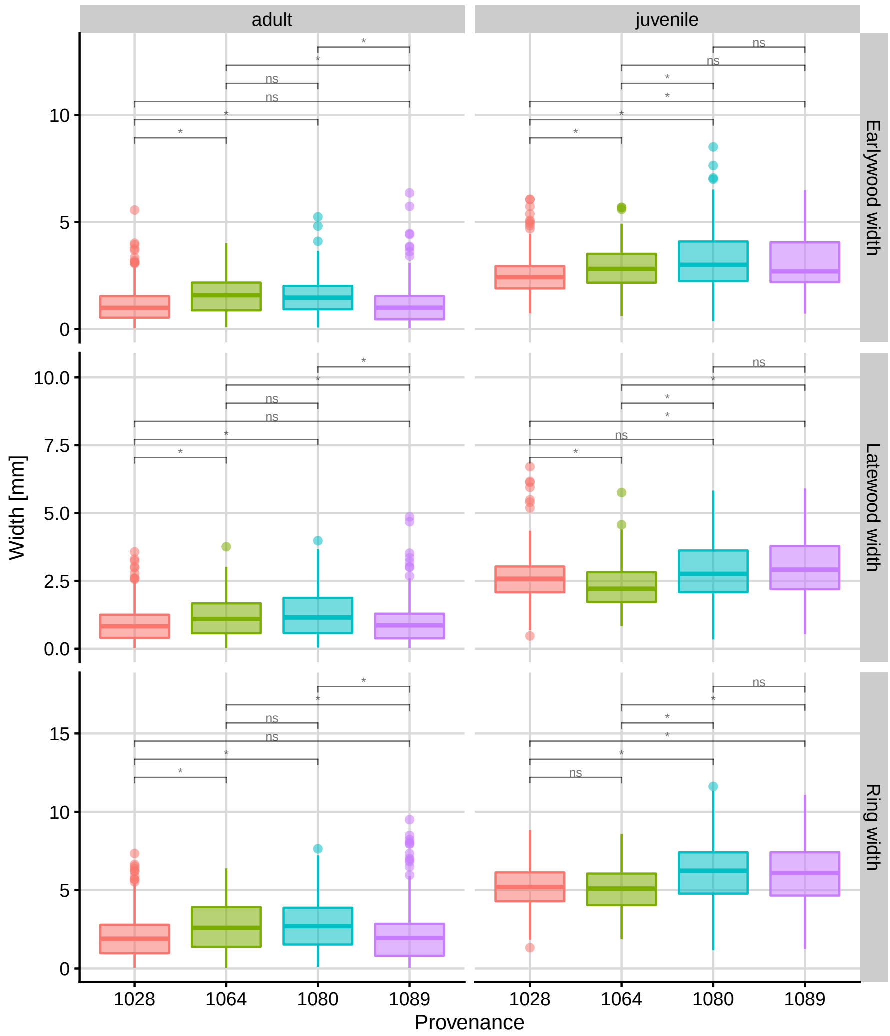

Fig. 4: RW, LWW and EWW by provenance and growth phase, The comparison of means between growth phases was done using a Kruskal-Wallis test and statistical significance is marked with a * symbol ($p < 0.05$).

The share of latewood was in all cases higher in juvenile wood than in adult wood, between 2% (P-1080) and 6% (P-1028) higher on average. Latewood accounted for about half of the annual radial increment (Figure 5). Similar levels of variation in the share of latewood were observed in both analyzed phases and across provenances. While some of the differences between provenances in the juvenile phase were statistically significant, this was not observed in the adult phase.

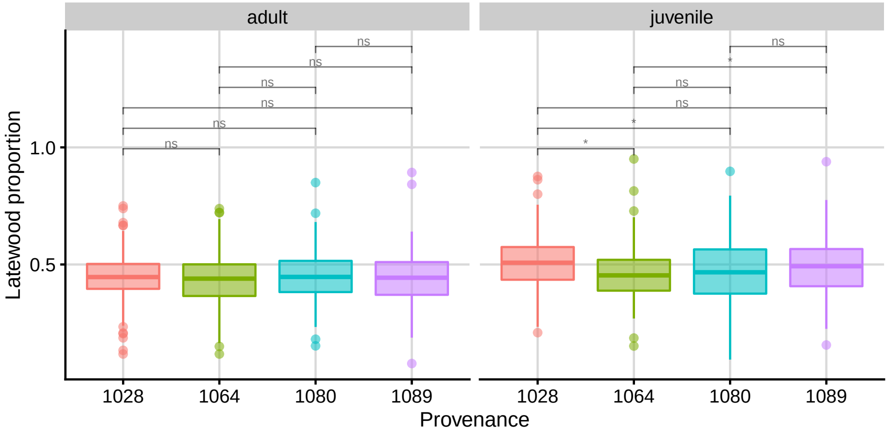

Fig. 5: Latewood share by provenance and growth phase. The comparison of means between growth phases was done using a Kruskal-Wallis test and statistical significance is marked with a * symbol ($p < 0.05$).

3.2 Wood density

The values of resistance-drilling wood density are shown in Figure 6. The overall mean resistance drilling density was 338 kg/m^3 with a standard deviation of 27 kg/m^3. All four provenances had similar wood density in both analyzed growth phases and none of the differences were statistically significant.

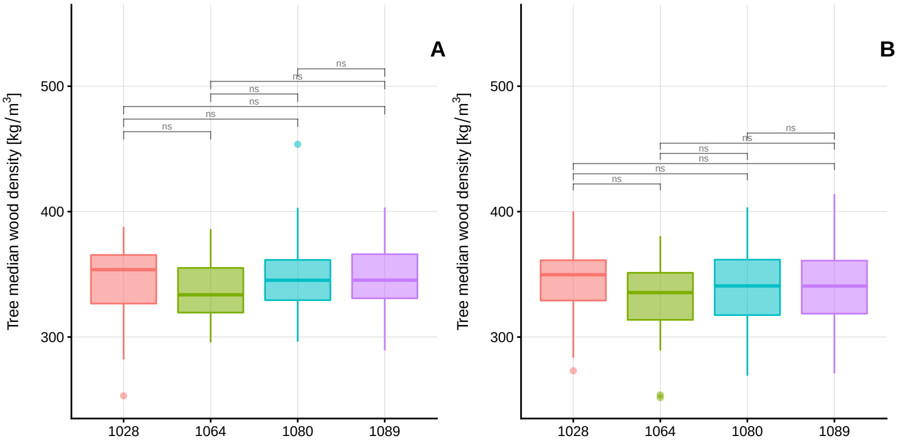

Fig. 6: Comparison of wood density between provenances and growth phases: A) juvenile B) adult. The comparison of means between growth phases was done using a Kruskal-Wallis test and statistical significance is marked with a * symbol ($p < 0.05$).

3.3 Climate-growth relationships

The general effect of wet conditions in the current growing season was positive, indicating that Douglas-fir's radial growth was favoured in moist years, and reduced in dry years. A significant positive effect of SPEI on LW was also observed at the beginning of the previous growing season. The opposite effect was associated with the previous growing season's SPEI, whereby dry summers resulted in wider tree-ring widths in the following year (Figure 7A). This negative correlation pattern was more significant at the juvenile stage, especially the negative SPEI correlations of the previous late summer on LWW and RW, while in the adult phase, these correlations became insignificant (Figure 7B). The opposite pattern was observed for the positive correlations of current-year wet conditions on RW and LWW, which became more significant in recent, adult years. In comparison to LWW and RW, climate-growth correlations with EWW were more stable and varied less with cambial age. The LW share generally correlated positively with current and previous year SPEI.

Generally, all provenances showed synchronous correlations with SPEI, but there were differences in the strength of this signal. Considering both negative correlations with the previous year's SPEI, and positive correlations with the current year's SPEI, the most significant correlations were calculated for provenances P-1028 and P-1064, while the lowest correlations were observed for P-1089. The last provenance also exhibited two exceptions, i.e., 1) the positive correlations with previous year's spring and LWW were not significant, and 2) there was a significant pattern of negative SPEI effect on RW at the end of the current growing season. Of all the proxies, the proportion of latewood was most sensitive for provenances P-1028 and P-1064, for which correlations exceeded 0.50. Strong correlations were also found between radial growth and temperature. The correlations of radial growth with precipitation and temperature are shown in Supplemental Material, Figures A4 and A5.

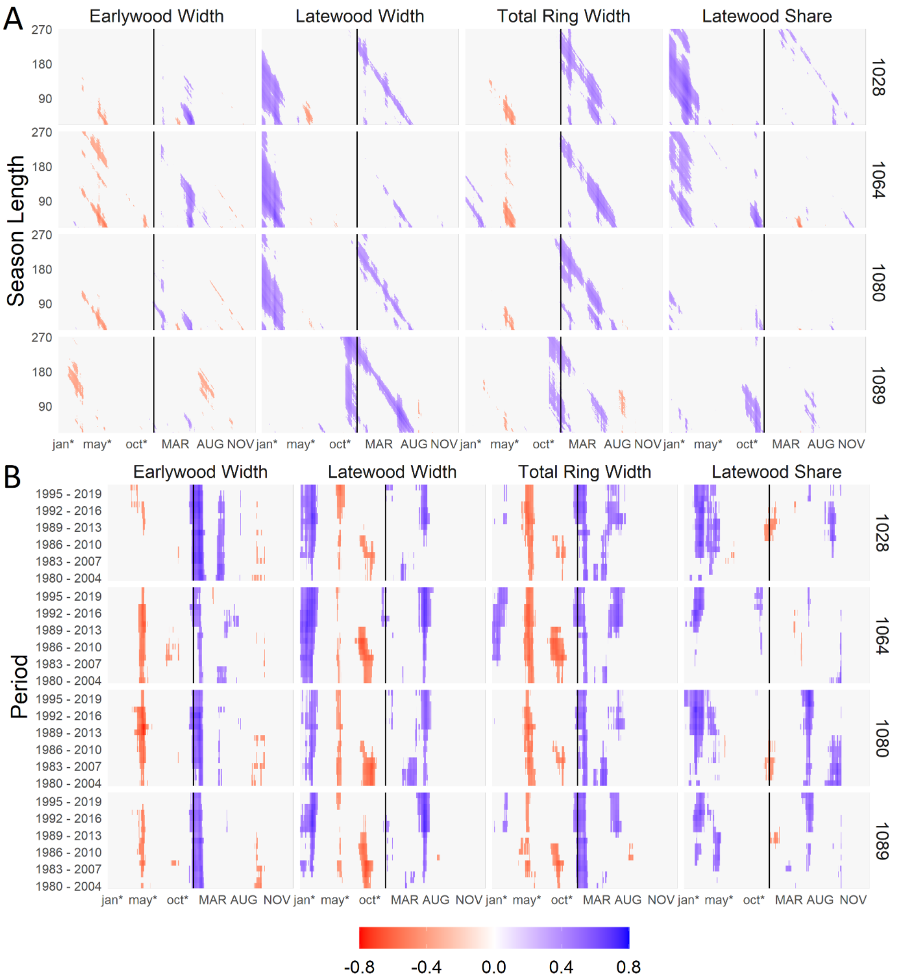

Fig. 7: Climate growth correlations between studied tree-ring proxies and aggregated SPEI using the variable response window from 21 to 270 days. B) Climate growth correlations between tree-ring parameters and 60-day SPEI, where correlations were calculated for sub-periods of 25 years, from juvenile (1980 – 2004) to adult phases (1996 - 2020). Months with lowercase letters and '*' represent previous growing season. Only correlations with $p < 0.05$ are shown. The reference position of plotted correlations is the end of time windows.

4 Discussion

4.1 The importance of provenance on overall growth qualities

The four analysed Douglas-fir provenances were found to be suitable for plantation establishment in SW Slovenia with a sub-Mediterranean climate. As reported by Smolnikar (2018), all provenances originated from the low-altitude western coast of Washington, with the Cathlamet provenance (P-1089) showing the best combination of good growth, survival rate, and log quality. Our analysis showed that when selecting the most promising provenance for planting based on these criteria, a change in growth rate from juvenile to adult phase should be considered. Only by combining climate-growth analysis with measurements of external tree features (such as diameter etc.) can we compare and assess the suitability of specific provenances for planting in current and future climates. Additionally, a visual assessment of log quality does not provide an insight into the wood structure (density, homogeneity of radial growth, intra-annual density fluctuations and other wood characteristics), which defines its usability for sawn timber or its end use. In addition to having the largest annual radial increments, provenances 1064 and 1080 also had the most homogeneous growth in the adult phase. Due to systematic planting in provenance trials and the fact that this particular trial was not thinned, the findings of the study will not necessarily translate directly to trees in more natural stands. However, in the context of the data from this provenance trial, neither mortality nor vitality can explain the superior radial growth of provenances 1064 and 1080 in the adult phase compared to the other two analyzed provenances and why this trend is not consistent throughout the analyzed period (see Table 2 and Figure 3).

4.2 Wood characteristics across growth phases

Since wood characteristics, and consequently, wood properties are age related (Dinwoodie 1981), we distinguished between juvenile and adult wood in the analysis. Juvenile wood is formed in the early stages of tree radial growth and is generally of inferior quality compared to the relatively stable structure of adult wood. In conifers, juvenile wood is characterised by shorter tracheids having thinner secondary walls and a larger microfibril angle in the S2 layer, and it usually contains a lower proportion of latewood. This is reflected in different physical and mechanical wood properties compared to adult wood, such as lower wood density, transverse shrinkage, and strength, which limit its end use (Blohm et al. 2016). Despite that, juvenile wood of Douglas-fir is economically important and its properties have to be considered due to the shortening of the rotation periods on commercial plantations, which consequently leads to a higher proportion of juvenile wood (Blohm et al. 2016).

The higher latewood proportion in juvenile wood (48%) compared with the latewood proportion in adult wood (45%) found in our study contradicts previous findings. Giagli et al. (2017) observed a coordinated age-related decrease of RW and EWW, while the LW proportion gradually increased with tree age; from 30% in the juvenile phase to almost 50% in adult wood. In Germany, a lower latewood percentage (34%) was reported in juvenile wood compared with adult wood (Blohm et al. 2016). These discrepancies in findings can be attributed to provenance specifics and/or environmental conditions. More southern provenances tend to have a higher proportion of latewood as an adaptation to drought conditions, since thicker latewood cells with smaller lumens prevent hydraulic failure (Eilmann et al. 2013). Our site is located in the sub-Mediterranean area well supplied with water throughout the year, which could allow a long growing season that can extend into the autumn, as already previously reported for conifers in similar environments (Prislan et al. 2016). To the best of our knowledge, no data on the seasonal dynamics of xylogenesis are available for Douglas-fir, but it can be inferred from tree-ring widths, which are consistent with the values provided by other studies for productive Douglas-fir (Eilmann et al. 2013).

The differences in earlywood and latewood widths between provenances appear consistent across both growth phases, indicating that differences between provenances are not directly climate-related and are consistent throughout the growing season. All three measured ring-related parameters (RW, EWW, LWW) exhibited more variation in the adult phase of growth than in the juvenile phase. Different climatic sensitivity across growth phases, changing growing conditions, or the effect of changing competition pressure over time could explain this pattern. Competition between individual trees was more pronounced in the later stages of growth, since the trees had a relatively large growing area (2.5 x 2.5 m) available immediately after the establishment of the trial. The sampled trees in the current study were mostly dominant trees at the time of sampling, although at least some of them were not constantly dominant throughout their lifespan. The LW fraction exhibited less variation than RW, EWW or LWW overall, with some individual trees exhibiting a consistently higher latewood share than others. Whether this is directly related to the geno- or pheno-type of individual trees could be an interesting direction for future research.

Due to the differences found in RW between provenances, we also expected to find some differences in resistance-drilling wood density. This was expected because wood density in softwoods is directly related to RW (Dinwoodie 1981; DeBell et al. 2004). However, we found no differences in wood density across the four provenances. One possible explanation for this lack of differences could be directly related to the method and/or the device we used for assessing wood density. If another method/tool were to be used (such as X-ray or high-frequency densitometry), the results could be different and this should be examined in future research, possibly using X-ray density measurements for a side-by-side comparison of methods. However, such methods are relatively time-consuming and expensive when compared to resistance drilling. An alternative (and equally plausible) explanation is that no differences in wood density exists between provenances. No differences were found in the latewood share between provenances in the current study. It is therefore quite possible that this was directly reflected in wood density, since latewood fraction can be used as an indicator of wood density in softwood species.

4.3 Climate-growth relationship

Climate-growth analysis showed that dry conditions in the previous growing season were favourable for radial growth in the following year, while dry conditions in the current growing season limited radial growth, but again, promoted growth in the next growing season (Figure 7 and Supplementary Material). Such relationships are commonly reported for conifers (e.g. Sun et al. 2021) and could be explained by the carry-over effect related to carbohydrates and other nutrients, which are stored and are available for growth in the next growing season. Namely, photosynthetic activity, even at a reduced rate, may still occur in dry conditions or during mild winter conditions (Lassoie and Salo 1981).

An adjustment of cambial rhythm to the months with favourable weather conditions is necessary to avoid a potential water shortage. Wet conditions in spring are beneficial and result in wider annual increments. Thus, earlier spring cambial reactivation provides a longer growing season without water stress, which could enhance radial growth. Information on seasonal radial growth dynamics is not known for Douglas-fir at the selected location; however our previous studies on conifers in the (sub)Mediterranean shows that cambial rhythm in this region is more complex than in temperate locations (Prislan et al. 2016). In the Mediterranean, cambial activity (and consequently xylem growth) in conifers is more plastic compared to colder regions, such as temperate or boreal climates. It may generally exhibit two interruptions, one during winter triggered by low temperature and one during summer due to a precipitation deficit coupled with high temperature (e.g., Liphschitz and Lev-Yadun (1986); Deslauriers et al. (2017)). Thus, an autumnal resumption of cambial cell production can occur in the case of favourable growing conditions. Such bimodal xylem growth is reflected in intra-annual density fluctuations (IADFs) (de Luis et al. 2007). IADFs are characterized by the occurrence of latewood-like cells within earlywood or earlywood-like cells within latewood (de Luis et al. 2007). Drastically unfavourable environmental conditions for tree growth, i.e., severe lack of precipitation throughout the year, result in specific wood anatomical features, such as locally missing rings or dark rings (Novak et al. 2016). No missing rings or dark rings were detected in our case. IADFs occurred occasionally only in one (P-1028), two (P-1064 and P-1080) or three individual (P-1089) trees in the juvenile phase. No IADFs were identified in the adult phase. The lack of anatomical anomalies and rather wide RW, on the one hand suggests that environmental conditions are favourable for radial growth of Douglas-fir on the studied site. Conversely, this could also be a direct result of only sampling dominant trees, which experience less stress than subdominant trees when resources are scarce.

Douglas-fir is reported to be a highly productive and relatively undemanding tree species that copes well with prolonged drought periods (Eilmann and Rigling 2012). It has been explained by a more effective stomatal control mechanism compared to other conifer species (Lassoie and Salo 1981), which may constitute a water-saving strategy under temporary dry conditions (Eilmann et al. 2013). In addition, stomatal functioning and photosynthetic capacity in Douglas-fir have been observed to recover immediately after the relief of soil water deficits. This and the ability to fix a significant amount of carbon dioxide during mild winter conditions could explain the wide distribution range of Douglas-fir (Lassoie and Salo 1981). However, a recent study by Duarte et al. (2016) shows a limited physiological plasticity of Douglas-fir after exposure to elevated temperature. This would prevent it from full recovery in the case of heat waves, which may become more frequent and severe in the coming years. In this case, the capacity of a tree to maintain its photosynthetic potential and minimize water loss will be crucial (Duarte et al. 2016). The differences in the findings could be attributed to the age of the studied trees; in the case of Lassoie and Salo (1981) the study was performed on adult trees, whereas in the case of Duarte et al. (2016) on young saplings. However, the drought tolerance and productivity of Douglas-fir also depend on its geographical origin, as demonstrated by Isaac-Renton et al. (2014). Based on the high share of latewood proportion linked with a lower cavitation risk, the analyzed provenances in the current study indicate a high potential to cope with drought.

As far as different provenances are concerned, we observed that P-1089 showed no significant response to wet spring conditions from the previous growing season, in contrast to the other three examined provenances. We assume that current climatic conditions at a given location are the most favourable for radial growth of P-1089, consequently its growth is less restricted by climate and thus more resistant to dry conditions although it originates from a location well supplied with precipitation (annual amount = 2102 mm), also in the spring period (Figure 1). In addition, our study site has a very similar temperature pattern and mean annual temperature to the region from which P-1089 originated (Figures 1 and 2).

Information in the literature on the age-related climate response of different studies is inconsistent. For example, few differences were found in response to climate between trees of different ages of *Pinus nigra* and *Pinus uncinata* (Liñán et al. 2011) and *Pinus cembra* (Esper et al. 2008). In addition, the main limiting climate factors constrained tree growth equally regardless of the age group. Other studies reported that growth trends and climatic sensitivity differ between young and old trees; annual increments are generally wider in young trees, which also show higher climatic sensitivity (e.g., Colangelo et al. 2021). In the juvenile phase trees usually exhibit different cambial and radial growth rhythms than in the adult phase; in the former age group cambial growth period is usually longer, which results in wider xylem increments (Rossi et al. 2008).

5 Conclusions

The current study demonstrates that provenances for future planting should be selected by using a variety of criteria. Whether planting Douglas-fir to improve the timber quality/quantity from future forests, or to simply improve the overall stand resilience of existing stands by including individual Douglas-fir trees in existing stands, the visible and invisible features of individual trees and their provenances should be considered. In addition to DBH, other factors to consider include survival rate and vitality, present and past productivity, growth homogeneity, and intraannual density fluctuations. As well as providing useful information on age-related radial and volume growth, tree-ring characteristics also include a treasure trove of often overlooked and underutilized information (e.g., IADFs). Tree age and future climate-change scenarios (including extreme weather events) on a regional level should be considered when assessing the suitability of provenances for certain parts of Europe because they may greatly affect the long-term performance of provenances under future European environmental conditions (St Clair and Howe 2007). The results of the current study indicate that provenances could potentially be selected according to the chosen rotation period of a stand, due to the differences found between radial growth across the two growth phases. When considering shorter rotations (30+ years), different provenances could be chosen to maximize volume growth than when considering longer rotation periods (60+ years). Existing provenance trials remain extremely valuable and should be monitored long-term, since the growth and vitality may change over the years, as demonstrated in the current study.

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Appendix A Additional tables and figures

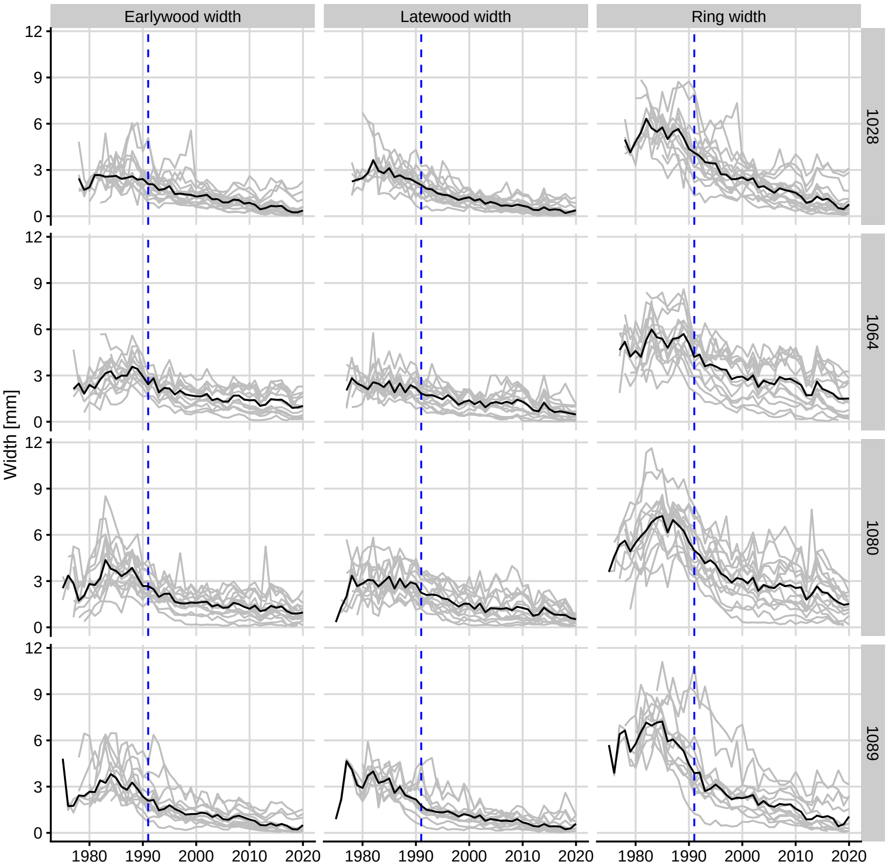

Fig. A1: Raw chronologies.

Table A1: Supplemental information on gathered chronologies. EPS stands for "expressed population signal", one of key metrics commonly used in dendrochronology that indicates the amount of variance within a population chronology. Rbar is a similar metric and is calculated as mean inter-series correlation. See Wigley et al. (1984) for more information.

Parameter	IUFRO code	n	Minimum year	Maximum year	rbar	eps	sd	mean
Earlywood Width	1028	18	1978	2020	0.739	0.978	0.88	1.41
Earlywood Width	1064	13	1977	2020	0.702	0.967	0.87	1.95
Earlywood Width	1080	15	1975	2020	0.708	0.971	1.11	2.06
Earlywood Width	1089	12	1975	2020	0.891	0.989	1.12	1.74
Latewood Width	1028	18	1978	2020	0.845	0.988	0.95	1.30
Latewood Width	1064	14	1977	2020	0.757	0.976	0.77	1.52
Latewood Width	1080	15	1975	2020	0.778	0.98	0.97	1.80
Latewood Width	1089	12	1975	2020	0.846	0.983	1.17	1.54
Total Ring Width	1028	18	1978	2020	0.833	0.987	1.74	2.70
Total Ring Width	1064	14	1977	2020	0.796	0.981	1.53	3.40
Total Ring Width	1080	15	1975	2020	0.811	0.983	1.91	3.86
Total Ring Width	1089	12	1975	2020	0.905	0.99	2.18	3.28
Latewood Share	1028	18	1978	2020	0.162	0.746	0.08	0.45
Latewood Share	1064	14	1977	2020	0.33	0.867	0.08	0.44
Latewood Share	1080	15	1975	2020	0.166	0.731	0.09	0.46
Latewood Share	1089	12	1975	2020	0.161	0.668	0.09	0.46

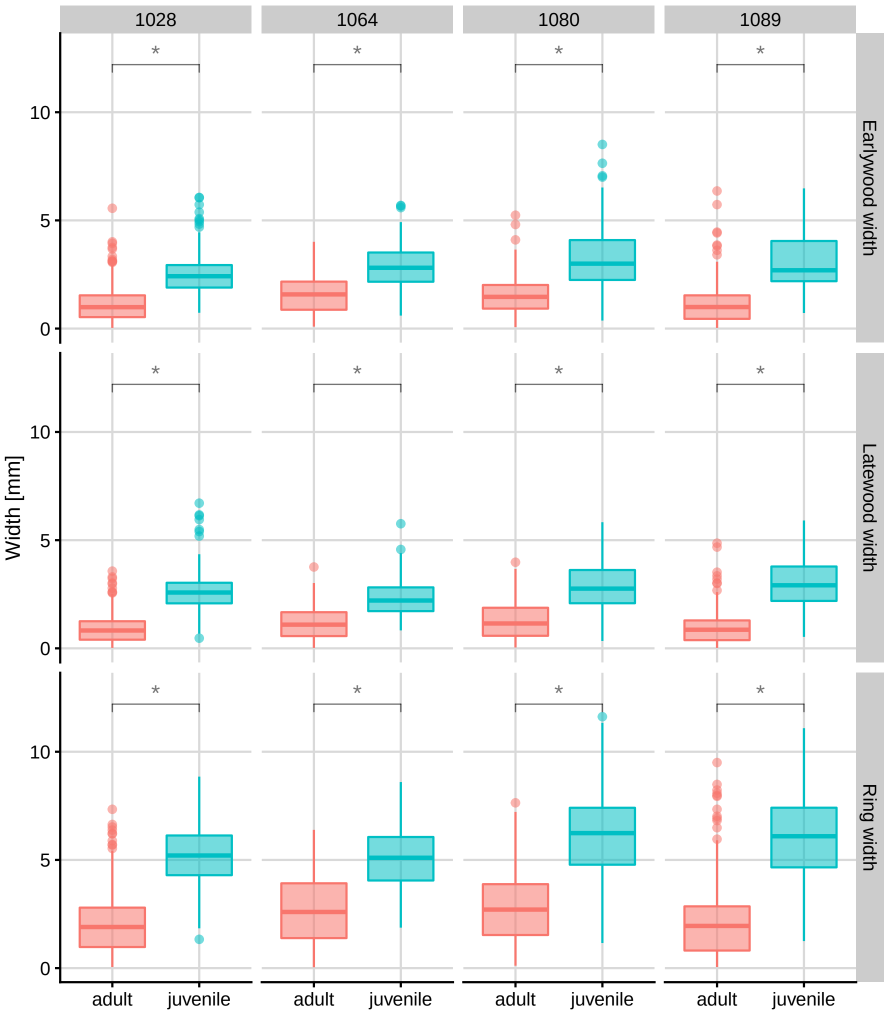

Fig. A2: EWW, LWW and RW by phase and provenance. The comparison of means between growth phases was made using a Kruskal-Wallis test and statistical significance is marked with a * symbol ($p < 0.05$).

Table A2: RW data by growth phase and provenance, displaying mean values and cofficients of variation in brackets.

Phase		1028	1064	1080	1089
adult	EW	1.11 (68)	1.55 (51)	1.50 (54)	1.12 (78)
	LW	0.90 (68)	1.16 (61)	1.32 (67)	0.93 (75)
	RW	2.02 (65)	2.62 (55)	2.81 (57)	2.11 (76)
juvenile	EW	2.58 (40)	2.87 (35)	3.24 (43)	3.15 (43)
	LW	2.68 (38)	2.32 (35)	2.86 (39)	2.97 (35)
	RW	5.24 (28)	5.11 (29)	6.11 (30)	6.10 (31)

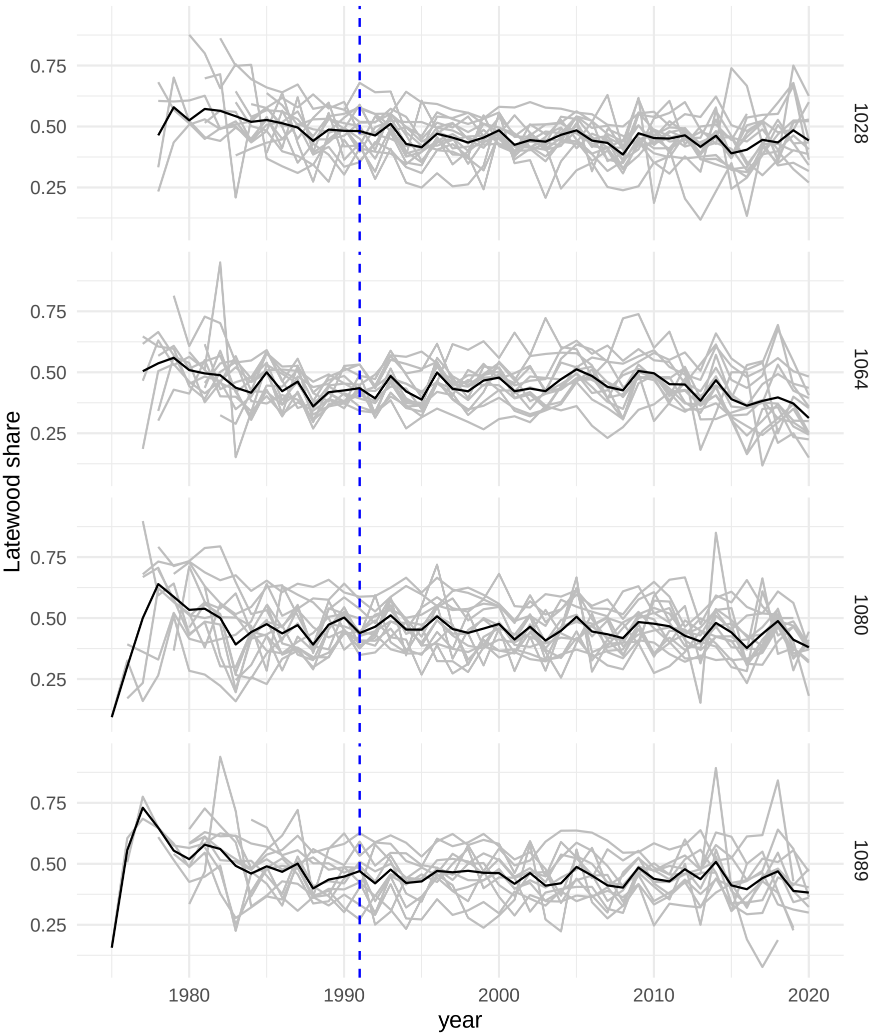

Fig. A3: Raw chronologies of latewood share by provenance.

Table A3: Latewood share by provenance, displaying mean values and coefficients of variation in brackets.

Phase	1028	1064	1080	1089
adult	0.45 (19)	0.44 (23)	0.45 (21)	0.44 (23)
juvenile	0.51 (22)	0.46 (23)	0.47 (30)	0.49 (24)

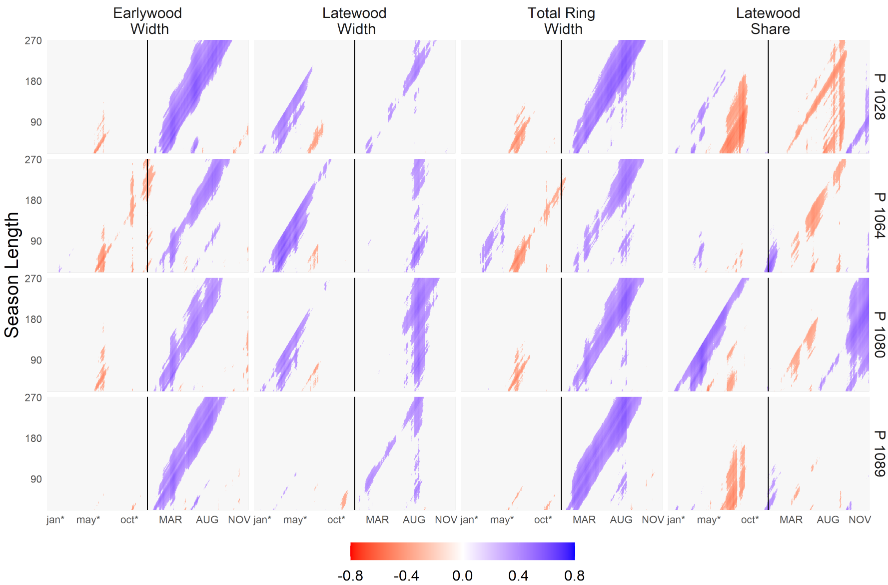

Fig. A4: Correlations between growth and precipitation for the four analyzed provenances. Months with lowercase letters and '*' represent previous growing season. Only correlations with $p < 0.05$ are shown. The reference position of plotted correlations is the end of time windows.

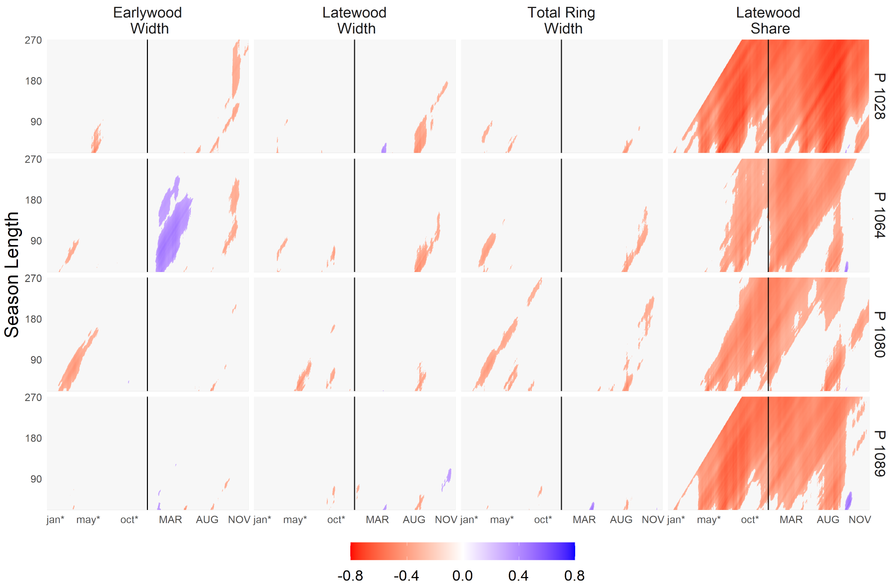

Fig. A5: Correlations between growth and temperature for the four analyzed provenances. Months with lowercase letters and '*' represent previous growing season. Only correlations with $p < 0.05$ are shown. The reference position of plotted correlations is the end of time windows.

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Declarations

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- Availability of data and materials: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.
- Authors' contributions: All authors contributed to the study conception and design. Material preparation and data collection were performed by Polona Hafner and Luka Krajnc. The analysis was done by Luka Krajnc and Jernej Jevšenak. The first draft of the manuscript was written jointly by all authors and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.