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The Impact of Climate Change on Anatomical Characteristics of Silver Fir and European Beech Wood from Three Sites in the Carpathians, Romania

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Abstract

Structural adaptations of wood to environmental conditions play a crucial role in shaping its mechanical and hydraulic properties, which are vital for the performance and survival of fir and beech. In this study, we investigated how site-specific climatic conditions influence tree-ring widths and wood-anatomical traits of fir and beech in the Carpathians. Increment cores were collected from three forest stands across the Carpathians, each characterized by distinct climate regimes. We developed chronologies for mean tree-ring width (MRW), mean lumen area of vessels/tracheids (MLA), cell density (CD), relative conductive tissue area (RCTA), and, for fir, mean tangential cell wall thickness (CWTTAN), covering the period from 1980 to 2016. By comparing MRW and wood-anatomical traits with climatic variables—daily minimum and maximum temperatures and daily precipitation sums from E-OBS climate data—we identified clear differences among the three sites. The relationships between tree-ring widths and wood-anatomical traits varied between fir and beech, reflecting species-specific responses to local climate conditions. Notably, beech appeared more sensitive to warm summer temperatures, while fir was comparatively less affected. Evaluating the variability in radial growth and wood anatomy is essential for understanding the plasticity of fir and beech under diverse environmental conditions, and represents a first step toward predicting their responses to future climate scenarios.

Keywords: *Abies alba*; *Fagus sylvatica*; dendrochronology; radial growth response; wood anatomy

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Academic Editor: Juan M Rubiales

Received: 11 August 2025
Revised: 18 September 2025
Accepted: 18 September 2025
Published: 21 September 2025

Citation: Adamič, P.C.; Prislan, P.; Levanič, T.; Jevšenak, J.; Kašpar, J.; Čater, M. The Impact of Climate Change on Anatomical Characteristics of Silver Fir and European Beech Wood from Three Sites in the Carpathians, Romania. *Forests* **2025**, *16*, 1497. https://doi.org/10.3390/f16091497

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1. Introduction

The anatomy of xylem provides insights into the allometry and ecophysiological performance of trees that cannot be inferred from conventional parameters such as ring width or wood density [1]. Although general anatomical features are species-specific and

genetically determined, their actual characteristics vary across different parts of the xylem rings due to diverse external influences [2]. Trees respond to environmental conditions through structural modifications in the wood, which significantly affect their mechanical and hydraulic properties, thereby influencing tree performance and survival [3,4]. While numerous studies have examined the impact of environmental factors on the radial growth of fir and beech, limited knowledge exists regarding how temperature and precipitation variability influence xylem structure in these species [5–8].

Growth dynamics under drought conditions often manifest as reduced tree-ring width, resulting from reduced cell division rates or premature cessation of cambial activity [9–12]. Anatomical changes in the wood, such as alterations in cell lumen and wall morphology, also occur under drought stress [13,14]. However, the implications of these anatomical changes for wood structure and tree function under increasing climate variability remain largely unexplored.

The Carpathian Mountains represent one of Europe's most complex mountain landscapes, shaped by the interplay of numerous environmental factors. Global warming presents significant challenges to mountain ecosystems and their associated services, as these regions are particularly vulnerable to climate change. This underscores their importance in environmental research as sensitive indicators of biodiversity shifts [15,16]. During the twentieth century, mountain ecosystems experienced above-average warming [17], with projections indicating continued warming and increased climate extremes. According to Micu et al. [16], the most pronounced temperature rise is expected during summer, with most Carpathian regions anticipated to be 2.5–3.0 °C warmer in 2021–2050 compared to 1961–1990. In terms of precipitation, winters are projected to become significantly drier, while autumns may experience increasing trends.

European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) are expected to remain dominant tree species in mid- and high-elevation European forests [18]. Despite its ecological plasticity and functional adaptability, beech is sensitive to drought, as evidenced by studies conducted in southern Europe [19]. Recent research using provenance trials has investigated the variability of beech anatomical traits across Europe [5,20]. Climatic conditions influence not only ring width and vessel size in beech, but also vessel arrangement. Humid conditions promote wider rings and larger vessels, whereas dry conditions have the opposite effect. Under high precipitation, vessel area typically increases in the early part of the tree-ring, remains stable, and then declines sharply toward the end. In contrast, under water deficit, beech wood exhibits a semi-ring porous structure, with vessel area peaking at approximately 25% of the ring width before rapidly decreasing [9]. Consequently, projected changes in temperature and precipitation under climate change scenarios are expected to affect both tree-ring width and wood structure in beech [7].

Silver fir, a key conifer species in European mountain forests, is prevalent in cold temperate zones [21]. Its ecotypes exhibit considerable variation in resistance to frost, drought, and shade [17]. Unlike beech, the anatomical responses of fir remain relatively understudied. Larysch et al. [22] found that fir was unaffected by spring drought and demonstrated a strong capacity to respond rapidly to improved growing conditions, highlighting the plasticity of wood formation in conifers under extreme environmental stress [23–25]. However, summer drought severely disrupted cell enlargement, with rates significantly reduced. Prolonged drought negatively impacted cell wall area throughout the growing season, with both wall thickening and duration declining for several weeks. Drought conditions also led to reduced cell production, limiting the conductive area for water transport, and resulting in smaller cells due to low turgor pressure [22].

Under normal climatic conditions, the formation of typical tree-ring structures in conifers is only marginally influenced by climate, suggesting a strong developmental

control over xylogenesis [26]. Cuny et al. [27] introduced new quantifications and mechanistic models of wood formation kinetics that explain tree-ring structure formation in Norway spruce, Scots pine, and silver fir. Similar studies on other conifers, such as those by Ziaco et al. [28], demonstrated that drought significantly affects cell enlargement and final tracheid size in pine and spruce species. Tracheid morphogenesis—comprising cell enlargement and wall thickening—occurs sequentially during the growing season and is influenced by climatic conditions in successive periods, indicating that distinct morphogenetic mechanisms govern different tracheid traits [29].

Warming tends to increase lumen area in conifers, enhancing water transport efficiency but also elevating the risk of cavitation, whether induced by drought in summer or freezing in winter. The combined effects of warming and elevated CO_2 alter tracheid dimensions, with more pronounced changes in latewood, thereby affecting wood density, mechanical support, and stem water-holding capacity [30]. Studies on spruce and beech confirm high interannual variability and sensitivity of xylem ring width to temperature and precipitation, with species- and site-specific responses. Water availability emerged as the most critical factor influencing tissue- and species-specific responses to local weather conditions [31].

This study builds upon a broader research initiative investigating the responses of fir and beech to climate variability in the Carpathians [32–35]. In this study, we focus specifically on wood-anatomical adaptations in both species, providing an additional perspective on how fir and beech respond to environmental conditions in this region. The primary objective is to examine the influence of site-specific climatic factors—particularly temperature and precipitation—on wood-anatomical traits in fir and beech.

We anticipate that fir and beech will exhibit distinct responses to climatic variables across the selected sites. Previous research has emphasized beech's vulnerability to drought, whereas conifers typically adopt more conservative water-use strategies and possess xylem anatomical characteristics—such as smaller conduit diameters and thicker cell walls—that confer greater resistance to drought-induced cavitation [36]. Accordingly, we hypothesize the following: (H1) wood-anatomical traits (e.g., cell size, cell wall thickness, density, and distribution of water-conducting cells) differ between the selected sites for both species; (H2) relationships between tree-ring width and wood-anatomical traits are consistent across sites for each species; (H3) fir and beech respond differently to climatic variables, with fir exhibiting greater drought tolerance than beech.

Evaluating the variability in radial growth and wood-anatomical traits across different sites is essential for assessing the plasticity of these species under diverse environmental conditions. This represents a critical step toward predicting their responses to future climate scenarios.

2. Materials and Methods

2.1. Study Site and Climate Data

In the Carpathian Mountains, three sites with mature fir–beech stands—Gorj, Vrancea, and Suceava—located between 830 and 985 m above sea level, were selected and analyzed. All sites are situated in managed forests with natural regeneration of both species and represent optimal growing conditions for silver fir and European beech. The favorable ecological conditions of these areas are reflected in their rich biodiversity and high diversity of plant and animal species [37]. Positioned at the intersection of Atlantic and continental climate zones, the region is predominantly influenced by a western climate type characterized by anticyclonic weather patterns [38]. For detailed information on weather conditions, study sites, and sampled trees, see Figure 1 and Table 1. Geologically, flysch dominates the eastern and outer Western Carpathians, while crystalline and volcanic rocks are typical of the inner band, and metamorphic rocks prevail in the Southern Carpathians [39,40]. The

easternmost site, Vrancea, is steeper and rockier than the others, resulting in shallower soils. Detailed soil sampling conducted by Dařenová et al. [34] classified the soil type at all sites as Cambisols.

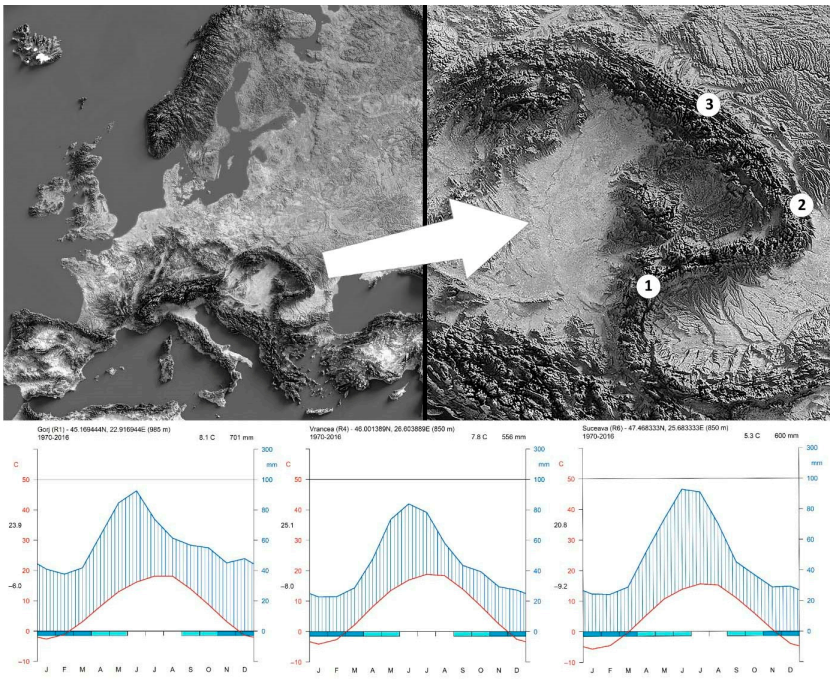

Figure 1. Geographical locations and climate diagrams of selected sites, i.e., 1—Gorj, 2—Vrancea, 3—Suceava. Climate diagrams are based on E-OBS daily climate datasets for the period from 1970 to 2016.

Table 1. Characteristics of the research site locations, representing the local site conditions (CGP—canopy gap fraction, MAT—mean annual air temperature, and MAP—mean annual precipitation), as well as sampled tree characteristics (N—number of trees and DBH—mean diameter at breast height).

County	Plot	Elevation (m)	Latitude	Longitude	Slope Inclination (%)	Exposure	CGP (%) *	MAT (°C)	MAP (mm)	N *A. alba* *F. sylva.*		Average DBH (cm) *A. alba* *F. sylva.*	
Gorj	Tismana	985	45°10′10″	22°55′1″	10–15	E-SE	7.04	8.1	701	15	15	63.9	63.7
Vrancea	Soveja	830	46°0′5″	26°36′14″	20–25	SE	8.75	7.8	556	16	15	56.9	54.2
Suceava	Frumosu	850	47°28′6″	25°40′60″	15–20	SW	7.18	5.3	600	16	15	78.9	54.0

* Canopy gap fraction was estimated in 2023 from hemispherical photographs according to Dařenová et al. [34].

We used E-OBS daily climate data (version 30.0e) on a 0.1° regular grid [38] to extract mean, minimum, and maximum daily temperatures, as well as daily precipitation sums from the nearest grid points. All sites receive between 550 and 700 mm of annual precipitation, with a peak in June and a minimum in January. Gorj, the southernmost site, experiences the highest average temperatures and the greatest precipitation. The E-OBS climate database is based on daily climate data collected from ground-based observation stations operated by national meteorological services between January 1950 and December 2019 [41]. For this study, we extracted climate data from 1980 to 2016 for further analysis.

2.2. Sample Collection and Preparation

Samples (cores) of beech and fir were collected in 2017 from healthy trees with no visible signs of stem damage or any kind of declining tree vitality. The criteria for the selection of trees were as follows: (1) adult trees of the second (dominant trees) and third class (co-dominant trees) according to Kraft classes; (2) they must form the canopy of the stand; (3) the trunk must be free of visible damage up to a height of at least 4–5 m;

and (4) crown transparency must not exceed 30%. At each site, 15 mature dominant fir and beech trees were sampled using a standard 5 mm increment borer (Haglöf Sweden, Långsele, Sweden). Two cores were taken from each tree and carefully placed in straws for transport.

The cores were dried under load for fourteen days to prevent bending, mounted and glued to a wooden support, and sanded with increasingly finer sandpaper with a grit of 180 to 600. The cores were scanned using the ATRICS [42] imaging system, and the annual radial increments were measured to the nearest 0.01 mm using CooRecorder and CDendro software, which also served as quality control for the measured tree-ring widths. Sampled trees were from at least 91 to 234 years old for fir and 124 to 260 years old for beech. In general, the trees in Gorj were the oldest and the trees in Suceava the youngest, with the beech being older than the fir on all sites. The MRW sequences were visually and statistically synchronized with PAST-5. Quality control was also performed by verification and correction. We calculated correlations between trees in CDendro and created a plot chronology that we compared with individual trees. Any tree-ring width sequence that did not fit into the plot chronology was corrected in CooRecorder and returned to the data pool. In three cases with obvious anomalies in tree-ring width, the cores were excluded from further processing. We paid attention to missing and false tree rings and rotated sections of the cores.

2.3. Laboratory Methods and Quantitative Analysis of Wood Anatomy

Quantitative wood anatomy analysis was performed on five to six randomly selected cores per site. We used random selection with the goal of capturing population-level anatomical variability, acknowledging the trade-off with climate signal strength. The small sample size, which can be explained by the relatively high effort required to obtain such data, has nevertheless been reported in several studies to have meaningful and robust correlations with environmental parameters for both wood anatomy and shrub-ring data [43]. Since the same cores were used for MRW measurements, they were first soaked in water before removal from the wooden holders. The samples were prepared for imaging under a transmitted light microscope at the Laboratory for Wood Anatomy at the Slovenian Forestry Institute according to the protocol suggested by von Arx et al. [44], i.e., each core was split into subsamples of similar length to fit on the microscope slide.

From each beech subsample, 15 to 20 µm thick transverse sections were cut with a sledge microtome using OLFA-80 × 9 mm replacement blades [45]. Fir samples were dehydrated in a graded series of ethanol and infiltrated with UltraClear (Avantor Performance Materials, Deventer, the Netherlands) and paraffin (Paraplast plus, Leica Biosystems, Richmond, CA, USA) and embedded in paraffin blocks to stabilize the samples for further processing [46]. Embedding the samples in paraffin helps to prevent damage to the cell structures during cutting, and as the fir samples were brittle, different protocols were used compared to the beech. Transverse sections of 20 µm thickness were cut with a LeicaRM 2245 rotary microtome (Leica Microsystems, Wetzlar, Germany) using Leica 819 Low Profile Microtome blades (Leica Biosystems, Nussloch, Germany). The sections of both species were transferred to object glasses, and the paraffin was subsequently washed out with UltraClear and ethanol. The sections were stained with a water mixture of safranin and Astra blue. After staining, sections were dehydrated and permanently fixed between two glass slides with Euparal mounting medium. To prevent the sections from buckling, which impairs a uniform focus when capturing an image, a small magnet was placed on the top of the slide with the coverslip to keep the sections flat and avoid air bubbles during drying. High-resolution images (beech: 0.514 pixel/µm, fir: 2.056 pixel/µm) of the sections were obtained using a Leica DM 4000 B light microscope (Leica Microsystems, Wetzlar,

Germany) at 50× magnification, a Leica DFC 280 digital camera (Leica Microsystems, Wetzlar, Germany), and LAS image analysis software (Leica Application Suite). The image sequences of the xylem rings were acquired with at least 25% of the overlapping area and then stitched together using PTGui v11.16 Pro (New House Internet Services B.V., Rotterdam, The Netherlands). The panoramic images were then processed using Image-Pro Plus 7.1 image analysis software and ROXAS (v3.0.437) [44,47], which provides cell (vessels for beech and tracheids for fir) dimensions (e.g., lumen size, cell wall thickness) and relative position within the dated growth ring for all selected cells [29].

Based on this, we calculated chronologies of (1) mean tree-ring width (MRW), (2) mean vessel/tracheid lumen area (MLA), (3) tracheid or vessel density (CD), (4) relative conductive area (RCTA), and (5) for fir also mean thickness of tangential cell walls (CWTTAN) for a minimum of the last 39 years and then used the period between 1980 and 2016 for the analyses with climate variables.

2.4. Statistical Analysis

Individual MRW were standardized to remove long-term trends using a cubic smoothing spline of 67% with a frequency cutoff of 50% in the R program's dplR library [48]. All other wood-anatomical chronologies were also standardized, resulting in detrended series: MRWi, MLAi, CDi, RCTAi, and CWTTANi. Raw chronologies were used to assess differences in wood-anatomical characteristics between sites.

To test for significant differences in tree-ring characteristics, i.e., mean tree-ring width (MRW), mean vessel/tracheid lumen area (MLA), tracheid or vessel density (CD), relative conductive area (RCTA), and mean tangential cell wall thickness (CWTTAN), either parametric or non-parametric statistical tests were applied depending on the distribution and variance homogeneity of the data. Specifically, linear mixed-effects models (LMMs) with site as a fixed effect and year as a random effect were used when the assumptions of normality and homoscedasticity were satisfied. In cases where these assumptions were violated, the non-parametric Friedman test was applied. Post hoc pairwise comparisons were corrected using the Bonferroni adjustment for multiple testing.

To assess the influence of site-specific climatic conditions on wood-anatomical traits and tree-ring widths, we applied repeated measures ANOVA (rm-ANOVA). This statistical approach was used to evaluate differences in mean tree-ring width (MRW), cell density (CD), relative conductive tissue area (RCTA), tangential cell wall thickness (CWTTAN), and mean lumen area (MLA) across the three study sites. The rm-ANOVA allowed us to account for within-subject variability over time and test for site-specific effects while considering the repeated nature of the measurements taken from individual trees over multiple years.

To examine relationships between wood-anatomical traits, we used LMMs fitted with the lmerTest package in R. Analyses were based on yearly averages per site to ensure consistent temporal resolution. Each model included site (Gorj, Suceava, Vrancea) as a fixed effect and year as a random intercept to account for temporal dependency. To assess site-specific relationships, we estimated marginal slopes (trends) and pairwise contrasts using the *emtrends ()* function from the emmeans package. All statistical analyses were conducted in R version 4.5.1.

Correlations between climate variables and growth parameters were assessed using the *daily_response ()* function from the R (version 4.5.1) package dendroTools [49], applied independently to each species and tree-ring parameter. Daily values of precipitation, maximum temperature, and minimum temperature were considered and aggregated into seasonal windows ranging from 7 to 60 days, covering the period from the previous June to the current October. Pearson's correlation coefficients were calculated for the

years 1980–2016 using 1000 bootstrap samples. Only correlations with $p < 0.05$ were retained to infer statistically significant relationships between climate and wood-anatomical characteristics.

3. Results

3.1. Differences in Wood-Anatomical Characteristics Between Sites

Chronologies of MRW were similar at the Suceava and Vrancea sites, with some peaks and declines matching well, while the Gorj site has a very different chronology for both species and generally has the lowest MRW (Figure 2; Table 2). All MRW chronologies appear to be declining between 1980 and 2016, except for beech at the Gorj site, which has been increasing since 2002. In Vrancea, there has been the largest decrease in MRW for both species in recent years. In Suceava, the MRW of beech was significantly lower than that of fir, while the MRW in Vrancea and Gorj is similar for both species. CD and RCTA of vessels are lower than those of tracheids, while the MLA of vessels is higher than that of tracheids. CWTTAN of tracheids increases with time and is therefore inversely proportional to the MRW of the fir.

Table 2. Mean ring width (MRW), relative conductive area (RCTA), cell density (CD), mean lumen area (MLA), and tangential cell wall thickness (CWTTAN) of fir and beech with descriptive statistics across sites.

Species	Site	Wood-Anatomical Characteristics	Mean	±SD	AC1
Abies alba	Suceava	MRW	4654.9	916.3	0.706
		RCTA	43.3	2.8	0.556
		CD	882.9	59.3	0.510
		MLA	515.5	56.1	0.568
		CWTTAN	5.8	0.3	0.520
	Vrancea	MRW	2262.8	913.0	0.764
		RCTA	39.5	3.5	0.485
		CD	1017.1	121.3	0.680
		MLA	417.5	69.2	0.583
		CWTTAN	5.8	0.4	0.535
	Gorj	MRW	1159.4	322.5	0.751
		RCTA	41.7	2.8	0.365
		CD	836.5	59.4	0.548
		MLA	517.1	59.5	0.475
		CWTTAN	6.1	0.3	0.329
Fagus sylvatica	Suceava	MRW	2638.5	518.1	0.421
		RCTA	18.3	1.4	0.493
		CD	113.1	5.8	0.344
		MLA	1627.4	98.8	0.439
	Vrancea	MRW	2301.6	780.9	0.662
		RCTA	20.5	1.8	0.532
		CD	119.4	10.3	0.545
		MLA	1726.8	102.7	0.396
	Gorj	MRW	1340.8	600.1	0.698
		RCTA	22.3	2.1	0.577
		CD	134.8	15.3	0.581
		MLA	1689.5	135.5	0.461

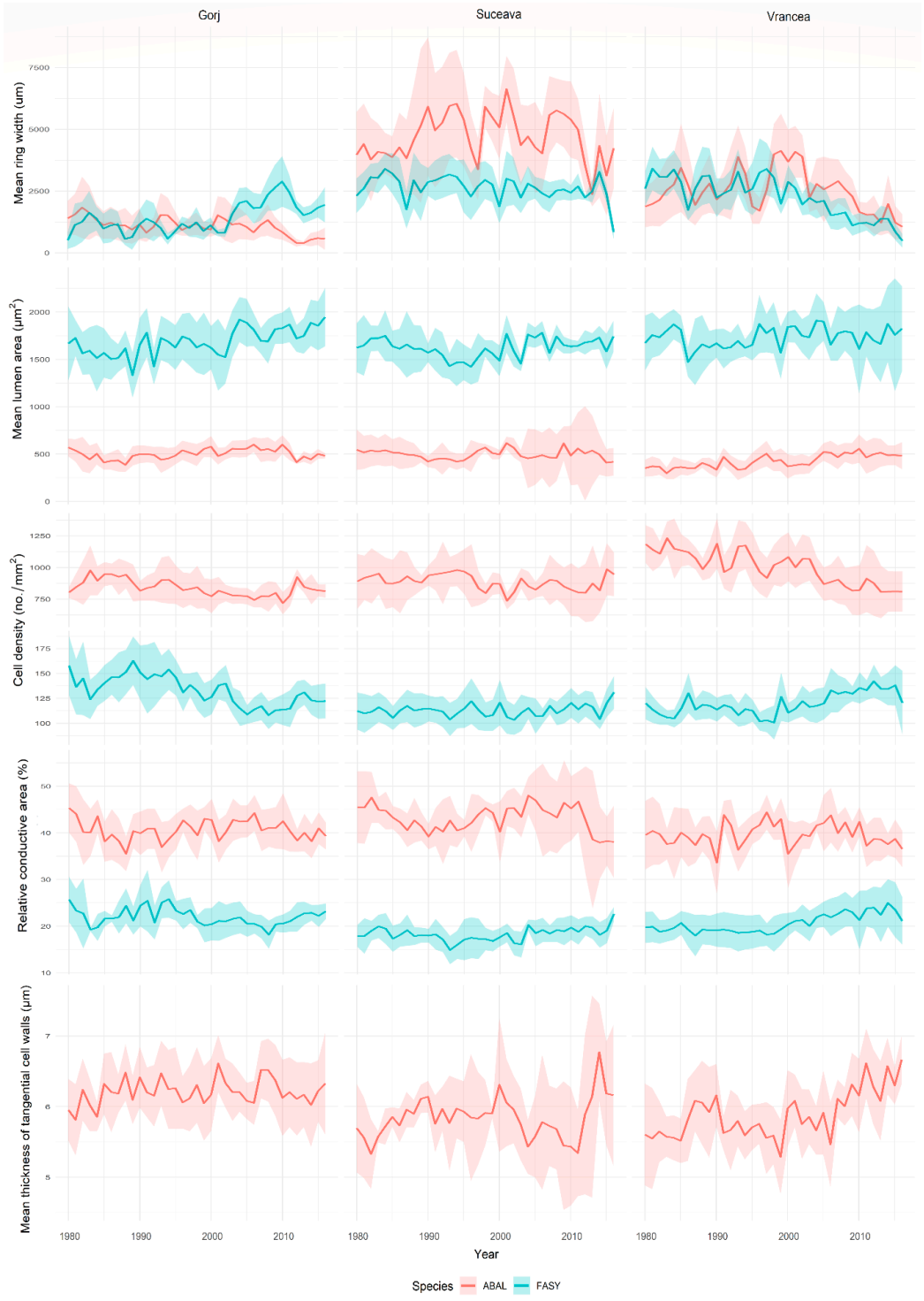

Figure 2. Chronologies of mean tree ring width and wood-anatomical characteristics in fir (ABAL) and beech (FASY) at studied sites.

The widest MRW for fir was measured in Suceava, followed by Vrancea and Gorj; all differences were statistically significant (Figure 3A). MLA of tracheids was similar in Suceava and Gorj, but significantly lower in Vrancea (Figure 3B). RCTA was comparable in Vrancea and Gorj, but significantly higher in Suceava (Figure 3C). CD differed significantly across all sites, with the highest values measured in Vrancea, followed by Suceava, and the lowest in Gorj (Figure 3D). CWTTAN was highest in Gorj, but significantly lower in Suceava and Vrancea (Figure 3E).

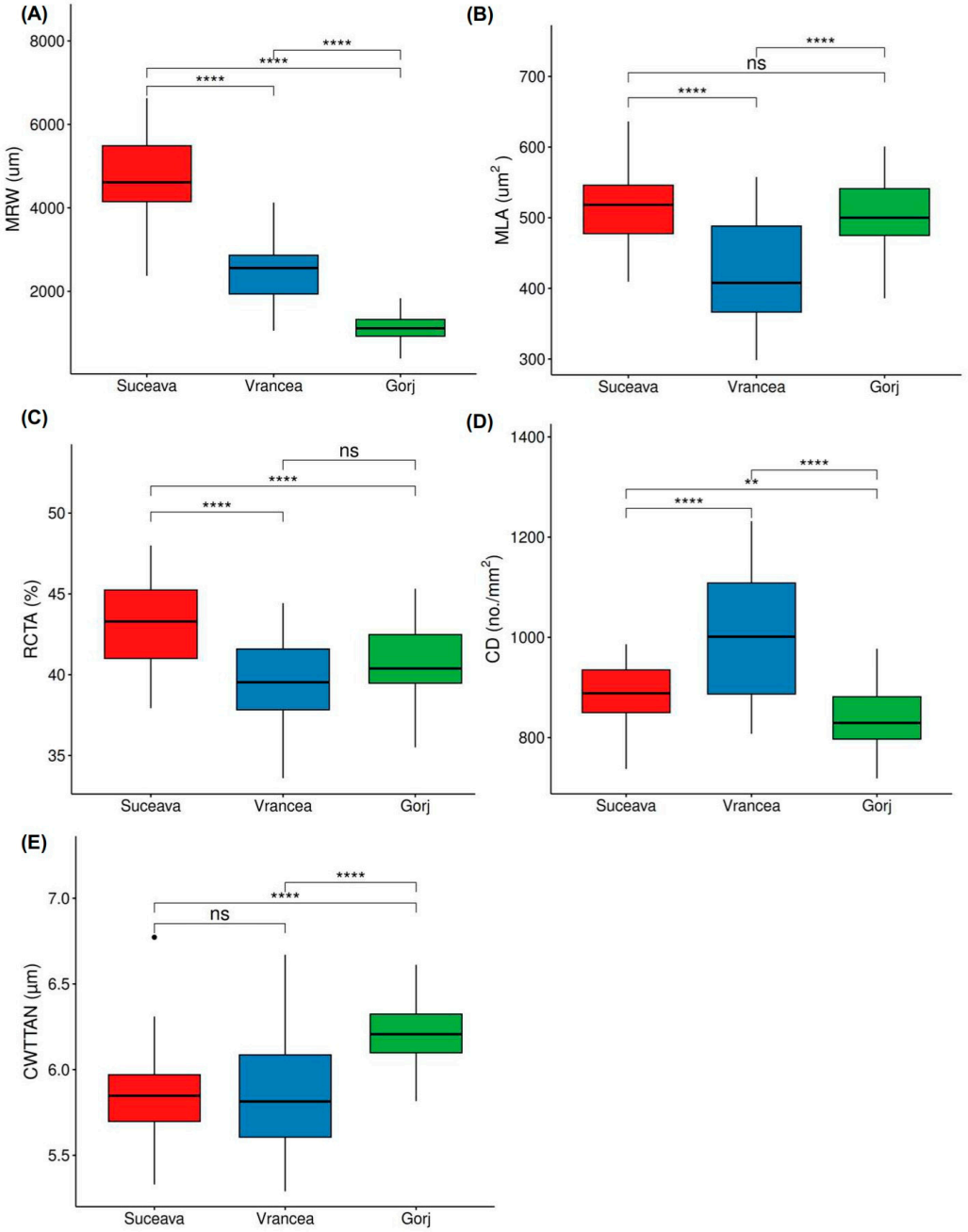

Figure 3. Differences among the sites in (**A**) mean ring width (MRW), (**B**) mean lumen area (MLA), (**C**) relative conductive area (RCTA), (**D**) cell density (CD), and (**E**) tangential cell wall thickness (CWTTAN) in fir analyzed by rm-ANOVA or the Friedman test. The significance level of the differences in tree-ring characteristics between sites is marked by ns—not significant. ** $p < 0.01$, and **** $p < 0.0001$. For summary of statistical tests, see Table A1.

The differences between sites in MRW of beech were similar to the differences in MRW of fir—statistically significant, highest in Suceava and lowest in Gorj (Figure 4A). MLA of vessels was similar in Vrancea and Gorj, but significantly lower in Suceava (Figure 4B). CD and RCTA values of beech differed significantly at all sites, with the highest values in Gorj and the lowest in Suceava (Figure 4C,D).

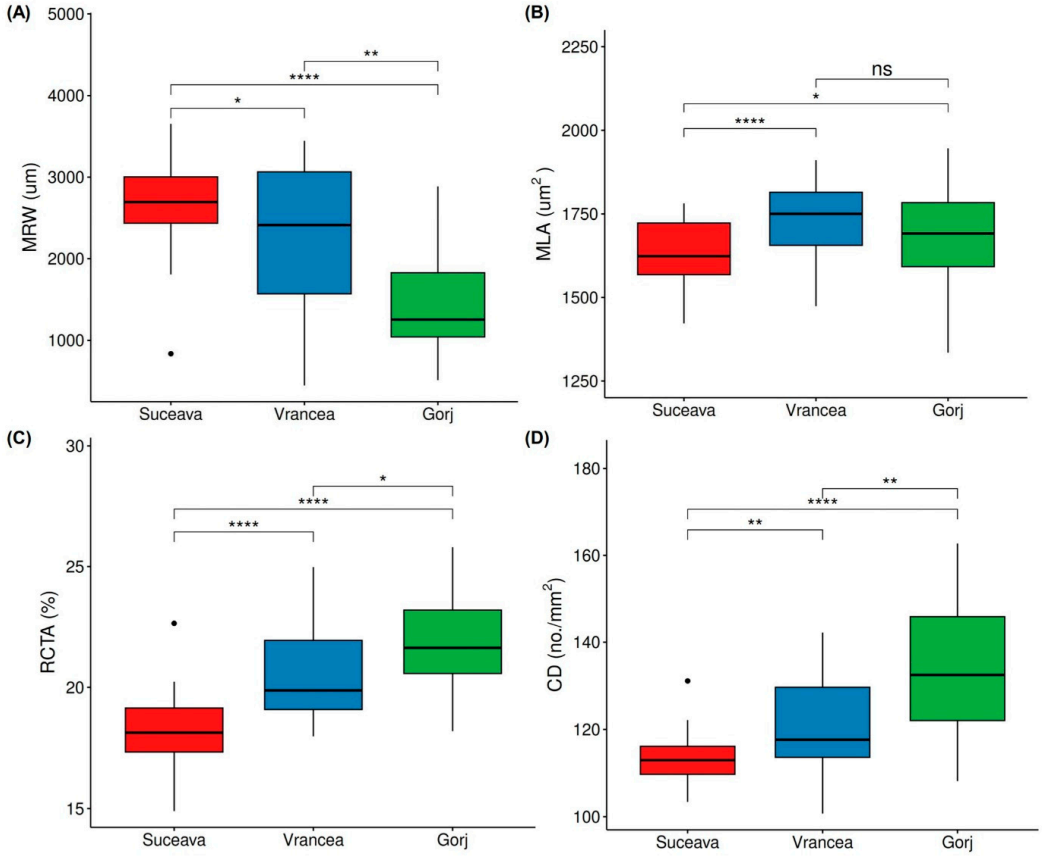

Figure 4. Differences among the sites in (**A**) mean ring width (MRW), (**B**) mean lumen area (MLA), (**C**) relative conductive area (RCTA), and (**D**) cell density (CD) in beech analyzed by rm-ANOVA or the Friedman test. The significance level of the differences in tree-ring characteristics between sites is marked by ns—not significant. * $p < 0.05$, ** $p < 0.01$, and **** $p < 0.0001$. For summary of statistical tests, see Table A1.

The correlation between CD and MRW in fir was significant and positive only in Vrancea (Figure 5A; detailed descriptions of the models in Tables A2 and A4), while the correlation between CWTTAN and MRW was significantly negative in Vrancea and positive in Gorj (Figure 5D). The relationships between RCTA vs. MRW and CD vs. MRW in fir showed no significant correlations (Figure 5B,C). The analysis revealed a significant negative correlation between RCTA vs. CD, MLA vs. CD, and CWTTAN vs. RCTA at all sites (Figure 5E,F,I). In Vrancea, there is a significant negative correlation between CWTTAN and CD (Figure 5G) and a significant positive correlation between CWTTAN and MLA, while in Suceava, there is a negative correlation between CWTTAN and MLA (Figure 5H).

The measured vessel traits in beech generally showed more significant correlations between wood-anatomical traits and MRW than those of fir (Figure 6; detailed descriptions of the models in Tables A3 and A5). A negative relationship between MRW and CD and between MRW and RCTA was observed at all sites, suggesting that narrower rings contain higher density vessels and have a larger relative conducting area (Figure 6A,B). Consequently, RCTA and CD showed a significant positive relationship at all sites; higher CD resulted in higher RCTA (Figure 6C), which is in contrast to the correlation in fir. Gorj was the only site where there was a significant positive correlation between MRW and MLA and a significant negative correlation between CD and MLA, suggesting that vessels are larger and density is lower in wider rings, reflecting a trade-off between vessel density and size as would be expected hydraulically (Figure 6D,E).

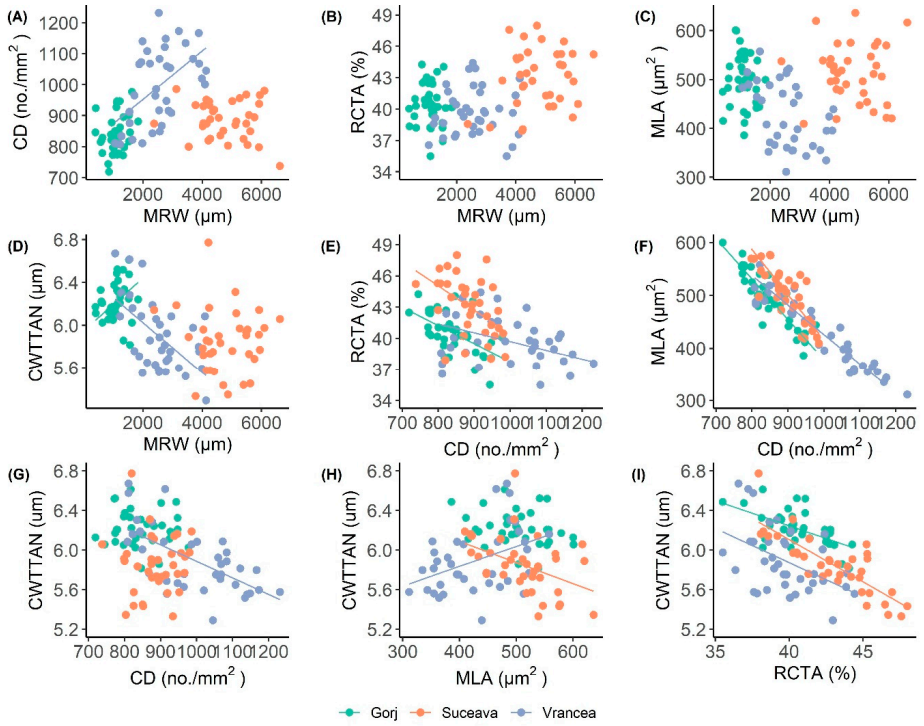

Figure 5. Relationships between wood-anatomical traits in fir at three sites (Gorj, Suceava, and Vrancea): (**A**) cell density (CD) vs. mean tree-ring width (MRW), (**B**) relative conductive area (RCTA) vs. MRW, (**C**) mean lumen area (MLA) vs. MRW, (**D**) mean tangential cell wall thickness (CWTTAN) vs. MRW, (**E**) RCTA vs. CD, (**F**) MLA vs. CD, (**G**) CWTTAN vs. CD, (**H**) CWTTAN vs. MLA, and (**I**) CWTTAN vs. RCTA. Lines represent site-specific slopes derived from linear mixed-effects models (LMMs) including year as a random effect. Only statistically supported relationships are shown. For model summaries and slope estimates, see Table A2 (LMM results) and Table A4 (emtrends results).

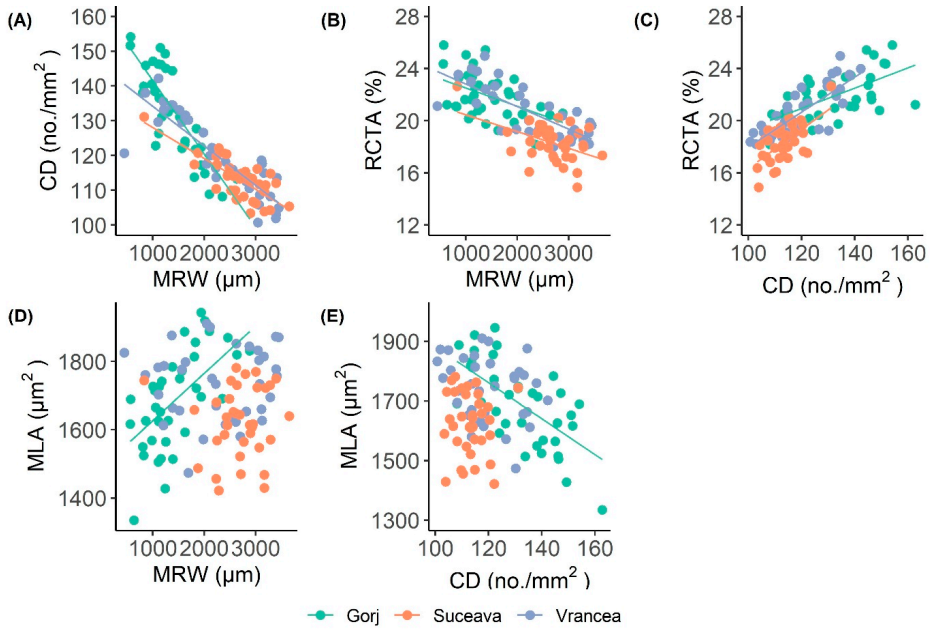

Figure 6. Relationships between wood-anatomical traits in beech at three sites (Gorj, Suceava, and Vrancea): (**A**) cell density (CD) vs. mean tree-ring width (MRW), (**B**) relative conductive area (RCTA) vs. MRW, (**C**) RCTA vs. CD, (**D**) mean lumen area (MLA) vs. MRW, (**E**) MLA vs. CD. Lines represent site-specific slopes derived from linear mixed-effects models (LMMs) including year as a random effect. Only statistically supported relationships are shown. For model summaries and slope estimates, see Table A3 (LMM results) and Table A5 (emtrends results).

3.2. The Effect of Climate Variables on Tree-Ring and Vessel Parameters

The correlation analysis between long-term daily climate data and the investigated wood-anatomical parameters in beech and fir revealed strong and statistically significant associations with temperature and precipitation across all study sites. Overall, precipitation and maximum temperature emerged as the most influential climatic factors affecting tree-ring characteristics, whereas minimum temperature showed weaker correlations, with only a few notable exceptions.

Correlations between the climate variables and the fir tree-ring characteristics were strongest in Vrancea (Figure 7). Interannual variability in MRWi was primarily influenced by winter conditions (from previous November to April—start of current growing season), with both maximum and minimum temperatures showing positive correlations. This means that tissue formation in the following year is influenced by preconditioning winter conditions. The strongest negative correlation was observed in Vrancea between maximum temperature at the beginning of the current growing season (April and May) and MLAi, as well as CDi, while RCTAi exhibited a positive correlation in this period. MLAi and CDi were positively correlated with precipitation in July and August, while CDi also showed a positive correlation with minimum temperature. CWTTANi displayed positive correlations with both minimum and, more notably, maximum temperatures in February at all sites (at Gorj also in January and at Suceava also in March). Increased wall thickness in response to warmer February temperatures implies better xylem safety, which increases resistance to drought-induced cavitation.

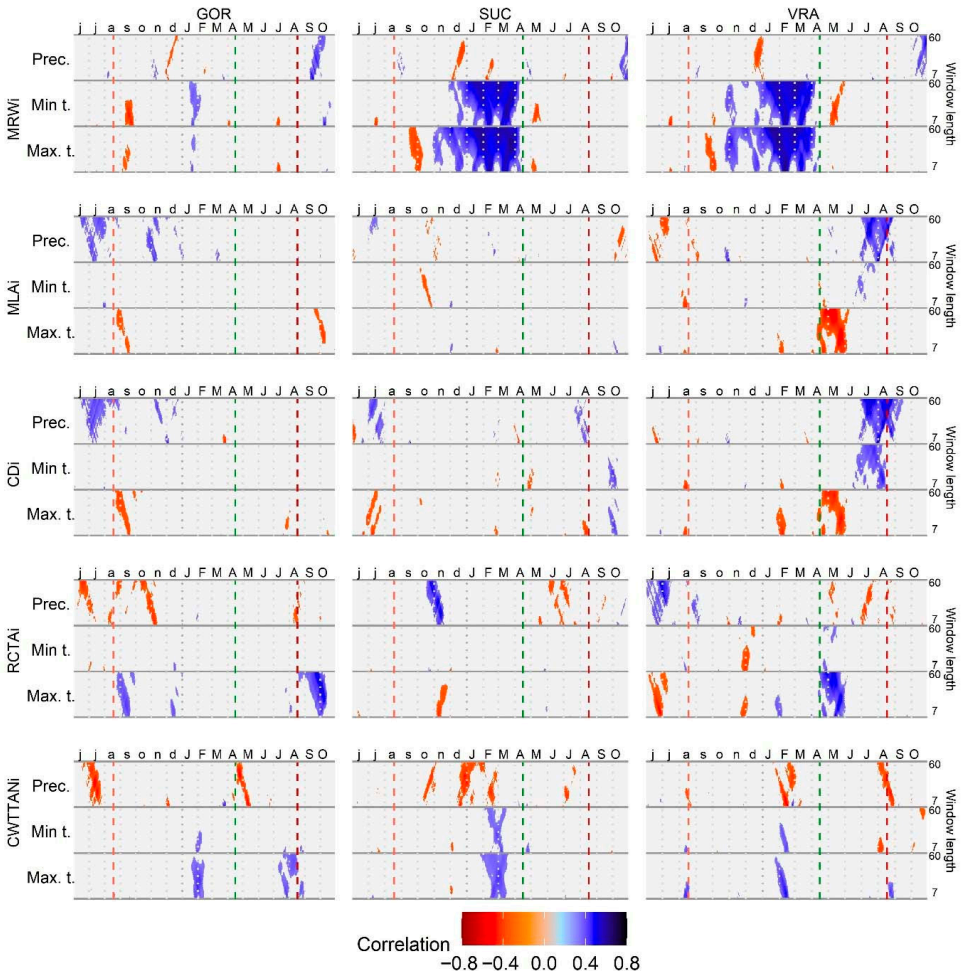

Figure 7. Correlations between standardized tree-ring chronologies for fir (mean ring width—MRWi, mean lumen area—MLAi, cell density—CDi, relative conductive area—RCTAi, and mean tangential

cell wall thickness—CWTTANi) and maximum and minimum daily temperature and daily precipitation sums at Gorj (GOR), Suceava (SUC), and Vrancea (VRA), using a time window spanning between 7 and 60 days. Vertical dashed lines from left to right depict the approximate timing of the growing season based on previous data [46]: end of previous growing season (orange), start (green), and end (red) of current growing season.

Correlations between climate variables and tree-ring characteristics in beech differed from those in fir, generally showing stronger negative relationships (Figure 8). The correlations for MRWi varied across sites: Gorj showed the weakest correlations, Suceava exhibited a negative correlation with maximum temperatures in June–July and minimum temperatures in preceding July, while Vrancea had a negative correlation with the maximum and minimum temperatures in March–April (beginning of the growing season) and July. The strongest correlations were observed in Suceava, where interannual variability in MLAi was primarily influenced by current May and June conditions, with maximum and minimum temperatures showing negative correlations. The highest positive correlation was observed in Suceava between maximum and minimum temperature in December and CDi. In contrast, correlations were least pronounced in Gorj, where the strongest positive relationships were observed between MLAi and precipitation as well as minimum temperatures in October and November.

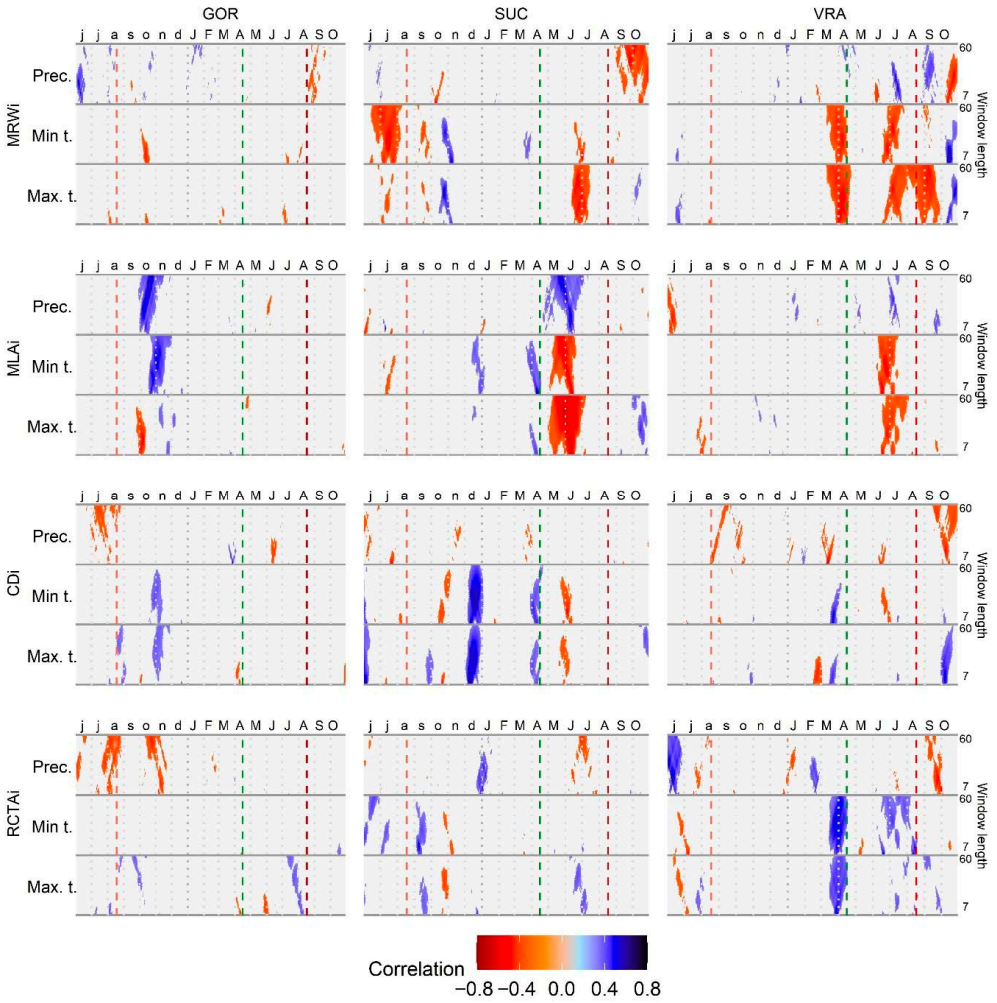

Figure 8. Correlations between standardized tree-ring chronologies for beech (mean ring width—MRWi, mean lumen area—MLAi, cell density—Cdi, and relative conductive area—RCTAi) and maximum and minimum daily temperature and daily precipitation sums at Gorj (GOR), Suceava (SUC),

and Vrancea (VRA), using a time window spanning between 7 and 60 days. Vertical dashed lines from left to right depict the approximate timing of the growing season based on previous data [46]: end of previous growing season (orange), start (green), and end (red) of current growing season.

4. Discussion

Our results show differences in wood-anatomical characteristics (e.g., MRW, CD, RCTA, CWTTAN, and MLA) at the selected sites for both investigated species, thus confirming our first hypothesis. The second hypothesis is rejected as the relationships between tree-ring widths and wood-anatomical characteristics are not similar for fir and beech at the selected sites. The third hypothesis, that beech and fir respond differently to climate variables at the selected sites, with fir being more drought-tolerant than beech, can be confirmed with significance.

4.1. Wood-Anatomical Characteristics of Fir and Beech Differ Between the Selected Sites

A comparison of MRW and wood-anatomical characteristics and their relationship to climatic factors revealed differences between three Carpathian sites that differ in their climatic regimes. In fir, significant differences in MRW and CD were found at all sites, in MLA at Vrancea, in RCTA at Suceava, and in CWTTAN at Gorj. The widest MRW for fir was measured in Suceava, the northernmost site, where there is also the greatest difference between the growth of fir and beech, with fir having a much wider MRW. The narrowest MRW was found in Gorj, the southernmost site. MLA is statistically lowest in Vrancea, the driest site with the lowest rainfall. In dry habitats, community mean conduit diameters are much narrower than in humid habitats. Narrower vessels are favored in drier environments as they are more resistant to the formation of embolism [50]. RCTA is highest in Suceava, where the water transport efficiency is the best. Wall thickness of the tracheids is significantly greater at the southernmost site, Gorj, which increases their resistance to drought-induced cavitation.

In beech, significant differences in MRW, RCTA, and CD were found at all sites. MLA is statistically lowest in Suceava, the northernmost site. The differences between sites in MLA, RCTA, and CD are not similar for fir and beech. However, the same pattern of MRW differences among sites is observed in beech, where the widest MRW is found in Suceava and the narrowest in Gorj. This could indicate that the southern areas of distribution of both species are less favorable for their growth. Statistically, RCTA and CD are highest in Gorj and lowest in Suceava. As beech has similar MLA values, it increases RCTA at a narrower MRW to maintain hydraulic capacity at a higher level. In the site chronologies, RCTA values increase slightly in Suceava and even more in Vrancea, a drier site. This means that the effect of the higher RCTA could be an effect of the production of smaller MRW due to the low humidity, which does not allow the production of a larger amount of new tissue. This means that in beech, the increasing amount of moisture can be traced from chronologies of wood-anatomical features (mainly RCTA). No such observation could be made for fir.

4.2. Relationships Between Tree-Ring Widths and Wood-Anatomical Traits

The relationships between the wood-anatomical features differ between fir and beech. The correlation between RCTA and CD is negative for fir and positive for beech at all sites. The only similar—negative—correlation is between MLA and CD in Gorj. In fir, MRW shows no significant relationship with RCTA and MLA. The analysis shows a significant negative correlation between RCTA-CD, MLA-CD, and CWTTAN-RCTA at all sites. At Vrancea, there was a significant negative correlation between CWTTAN and CD and a significant positive correlation between CWTTAN and MLA, suggesting that the tracheid

structure of fir is different under drier conditions—when the cell walls are thicker, the CD is lower and the MLA is greater. This does not apply to Suceava, where the correlation between CWTTAN and MLA was significantly negative.

The measured vessel traits in beech showed significant correlations with MRW, consistent with previous studies [5–7,51], which reported that CD and RCTA were generally smaller in wider tree rings. Consequently, a significant positive relationship between RCTA and CD was observed. Prislan et al. [52] demonstrated that CD depends on MRW and varies significantly between sites, being approximately 30% higher at the high-elevation site, where beech trees exhibited 54% narrower xylem rings. Similarly, Oladi et al. [51], studying oriental beech (*Fagus orientalis* Lipsky), found that wider tree rings contained slightly larger but substantially fewer vessels per mm^2, resulting in a negative correlation between MRW and RCTA.

In diffuse-porous beech, vessels from multiple years contribute to water transport, meaning the influence of a single tree ring on total hydraulic capacity is only partial [53]. However, a higher RCTA value in narrower rings suggests that water transport may take precedence over mechanical support, as the need for additional strength diminishes in adult trees—both ring width and density tend to decrease with increasing number of rings from the pith outward [54]. Oladi et al. [51] proposed that CD and MRW are highly influenced by environmental conditions, whereas mean lumen area (MLA) and RCTA are more endogenously regulated and thus exhibit less interannual variability [55].

Arnič et al. [7] reported similar correlations between MRW and CD, MRW and RCTA, and CD and RCTA, but found no significant relationship between MRW and MLA or between CD and MLA in beech. In contrast, our results from Gorj, the southernmost site, revealed a significant positive correlation between MRW and MLA and a significant negative correlation between CD and MLA. Beech trees appear to compensate for external environmental influences by adjusting their anatomical traits [51]. During the mature growth phase, MRW in beech is strongly influenced by external factors. Cornelius [56] and Zobel and Jett [57] argued that wood properties—and thus wood structure—are more closely linked to genetic predisposition than to tree-ring width, suggesting that genetic influence on MRW is generally limited.

The first anatomical trait to respond to changes in MRW is CD, with both being affected by the same environmental factors to which beech is particularly sensitive [58,59]. CD has also been shown to correlate more strongly with exogenous variables such as precipitation and temperature [60], as well as fluctuations in groundwater levels [61]. In contrast, vessel size and porosity are relatively stable traits, exhibiting limited variation and being primarily governed by genetic factors.

4.3. Fir and Beech Respond Differently to Climatic Variables

We used daily response functions to examine the effect of weather conditions on the tree-ring widths and vessel features. The fir show site-specific responses to climate variables. The only similar response is between MRWi and the maximum and minimum daily temperature and daily precipitation totals in Suceava and Vrancea. The comparison of fir tree-ring width with climatic variables revealed that MRWi variability is mainly influenced by winter and early spring (from November to April) conditions, with maximum and minimum temperatures showing positive correlations. As an evergreen species, fir benefits from warmer winters (with winter photosynthesis) [62], whereas beech, a deciduous species, is less affected by warm winter temperatures [32]. Correlations between the climate variables and the fir tree-ring characteristics were strongest in Vrancea, which is the driest site. The strongest negative correlation was observed in Vrancea between maximum temperature at the beginning of the current growing season (April and May) and MLAi, as

well as CDi, while RCTAi exhibited a positive correlation in this period. MLAi and CDi were positively correlated with precipitation in July and August, while CDi also showed a positive correlation with minimum temperature. CWTTANi displayed positive correlations with both minimum and, more notably, maximum temperatures in February at all sites (at Gorj also in January and at Suceava also in March). Larysch [22] reported that cell wall area was only slightly affected by low soil moisture or high temperatures compared to the direct effects of the environment on wall thickening rate during summer drought development. Correlations between climate variables and tree-ring characteristics were least pronounced in Gorj, where moisture conditions are less limited. This could be due to more mesic conditions, higher resilience, or lower climatic variability.

The results are consistent with those of Čater et al. [33], who show differences in the response of fir between Balkan and Carpathian sites. Mihai et al. [63] showed a high genetic variability within the studied fir in the Carpathians. They confirm that climate change may increase the productivity of fir at higher elevations, while climatically marginal environments and low elevations, such as the edges of the Eastern Carpathians and the Banat region, may be more at risk due to higher temperatures and lack of moisture [63]. Studies show that conifers have a greater hydraulic safety margin than flowering plants, although this also depends on the species of conifer, e.g., Pinaceae species have a significantly lower embolism resistance and safety margin than Cupressaceae [36].

Castagneri et al. [29] demonstrated that in Norway spruce (*Picea abies* (L.) H. Karst.) growing at high elevations, the wall thickness of late-formed tracheids was strongly positively correlated with temperatures in August–September, whereas low early summer temperatures negatively affected cell enlargement. At lower elevations, early summer water availability was positively associated with cell diameter. These findings suggest that climate influences cell enlargement and wall thickening through distinct morphogenetic mechanisms, resulting in different tracheid characteristics in spruce. Ziaco et al. [28] observed a general reduction in cell lumen size in spruce and pine species along a north–south gradient, likely as an adaptive strategy to drought and to mitigate the risk of xylem cavitation. Wood cellular parameters varied in response to seasonal climatic conditions, offering insights into the mechanisms of tree-ring formation and reflecting physiological adaptations to environmental stress. Their comparative analysis of average anatomical parameters across four conifer species (three pines and one spruce) revealed significant relationships between precipitation and air temperature and wood anatomy, particularly in earlywood. In contrast, the weaker correlations between climate and average latewood parameters—except for cell wall thickness—may reflect the relatively low variability of latewood cell traits across sites. It is likely that multiple environmental factors, such as soil properties, radiation balance, and snow cover dynamics, exert both direct and indirect influences on the physiological processes that govern wood anatomy and tree-ring formation.

It is possible that many environmental factors (e.g., soil properties, radiation balance, snow cover dynamics) have direct and indirect effects on the growth and physiological processes that produce wood anatomy and tree-ring widths.

Beech reacts differently to climate variables at the selected sites, showing evidence consistent with local adaptation, especially in Gorj. Only in Suceava and Vrancea is the response of MLAi to daily maximum and minimum temperatures and daily precipitation totals similar. Our study found a negative correlation between beech—MRW and maximum temperature in June and July, as well as minimum temperature in the previous July in Suceava. In Vrancea, negative correlations were observed for both maximum and minimum temperatures before the beginning of the growing season and in July. This aligns with our dendrochronological findings, which indicate that beech struggles with excessively warm summers, whereas fir is less affected. Sass and Eckstein [64] showed that vessel formation

at the beginning of cambial activity is mainly controlled by internal factors. Precipitation in the previous summer and autumn and in the current May had only a minor influence. Vessel formation towards the end of cambial activity is strongly influenced by precipitation in July and is thus more strongly determined by external factors [64].

Increased summer temperatures have a negative effect on radial growth, which can lead to growth disturbances in beech trees. This is consistent with previous observations that the beech forests in the Eastern Carpathians have changed in recent decades [65], while the old-growth beech forests in the Northwest Carpathians have remained relatively stable [66]. Martinez del Castillo et al. [67] predicted a significant decline in beech growth across Europe, ranging from −20% to more than −50% by 2090, depending on the region and climate change scenario (CMIP6 SSP1-2.6 and SSP5-8.5). Under a moderate climate change scenario (CMIP6 SSP2-4.5), beech growth will decline in the near future (2021–2050) in most parts of its range: by 12–18% in northwestern Central Europe and by 11–21% in the Mediterranean region. Climate-induced growth increases are limited where the historical mean annual temperature was below ~6 °C: a growth increase of 3% to 24% in the high-altitude areas of the Alps and the Carpathian Arc, with a northward range shift limited by water availability [68]. In contrast, Prislan et al. [52] found no significant correlation between intra-annual weather conditions and conduit characteristics of beech. Therefore, they assumed that precipitation is not a limiting factor for xylem growth and cell differentiation at sites with similar weather conditions in Europe.

With rising temperatures and constant precipitation, trees have a greater water deficit, which means that they must have higher water efficiency [69] and, consequently, adapt the anatomical properties of the wood. Provenance trials of beech confirmed that provenances from drought-prone sites cope better with water scarcity and show no negative response of mean or cumulative vessel area to summer drought [5]. Site conditions influence the climate sensitivity of beech, which is more pronounced in marginal locations or in extreme years [31]. Small vessels are generally less susceptible to cavitation [70], which can be an advantage under frequent drought conditions. However, as the smaller vessel area is not compensated by a higher vessel density, the water transport capacity is significantly lower [5]. The decrease in overall hydraulic capacity could then be behind the negative growth trends of beech predicted under future climate scenarios [67,68]. In locations where water supply is likely to be limited, drought-tolerant provenances could be planted to minimize the impact of drought on the growth of beech forests [31]. Populations growing at the southern limit of the distribution show considerable phenotypic plasticity, leading them to adjust anatomical and physiological traits in response to narrow ranges of environmental parameters. However, the distribution of beech appears to be limited to areas with at least 400 mm of precipitation during the growing season and a vapor pressure deficit (VPD) of <3 kPa, which may represent the main environmental thresholds that severely limit beech growth and thus affect its ability to cope with future environmental conditions [71]. Diaconu et al. [6] provide new insights into the plastic response of beech wood anatomy to warmer climatic conditions and showed that thinning of forest stands alters the water-conducting system to make it more resistant to hydraulic failure. Kašpar et al. [35] concluded that beech has consistently higher moisture limits throughout the Carpathians, suggesting a potentially higher vulnerability to future droughts due to its limited growth plasticity compared to fir, which appears to be better able to adapt to future conditions, especially in the north. In Central Europe, fir showed recently more increasing growth trends than beech [72]. The likely response of species to climate change will vary, which will affect their competitiveness, their existence, and, consequently, forest management decisions and measures [73].

The novelty of the study is that we monitored coexisting fir and beech on three different sites in the Carpathians. Fir and beech always respond differently to climate variables at the same locations. Interestingly, both species showed the weakest climate-growth correlations in Gorj (especially with MRWi), suggesting that climatic limitations may be less pronounced at this site. Our results provide a more detailed understanding of the effects of complex climatic conditions on the productivity of temperate mixed forests.

5. Conclusions

This study is part of a broader research initiative examining the responses of fir and beech in the Carpathians [33,34,74], and provides an additional analysis of their climate-related adaptations [32,35]. Our primary objective was to investigate how site-specific climatic conditions—namely, temperature and precipitation—influence tree-ring widths and wood-anatomical traits in beech and fir.

By comparing mean tree-ring width (MRW) and wood-anatomical characteristics (e.g., MRW, cell density [CD], relative conductive tissue area [RCTA], tangential cell wall thickness [CWTTAN], and mean lumen area [MLA]) across three Carpathian sites with distinct climate regimes, we identified clear differences in species-specific responses. The relationships between tree-ring widths and wood-anatomical traits varied between fir and beech, reflecting their differing sensitivities to local climate conditions. Our findings align with previous dendrochronological studies, confirming that beech is more vulnerable to extremely warm summers, whereas fir exhibits greater tolerance.

Author Contributions: Conceptualization, P.C.A., M.Č. and P.P.; Methodology, P.C.A., M.Č., T.L., J.J., J.K. and P.P.; Validation, P.C.A., M.Č., T.L., J.J., J.K. and P.P.; Formal Analysis, P.C.A., J.J., J.K. and P.P.; Investigation, P.C.A., M.Č., J.K. and P.P.; Resources, M.Č. and P.P.; Data Curation, P.C.A., M.Č. and P.P.; Writing—Original Draft Preparation, P.C.A. and P.P.; Writing—Review and Editing, P.C.A., M.Č., T.L., J.J., J.K. and P.P.; Visualization, P.C.A., M.Č., T.L., J.J., J.K. and P.P.; Supervision, M.Č.; Project Administration, M.Č.; Funding Acquisition, M.Č. and P.P. All authors have read and agreed to the published version of the manuscript.

Funding: The authors acknowledge the financial support from the Slovenian Research Agency (research core funding P4-0107 Program research at the Slovenian Forestry Institute, project grants No. J4-3086, J4-8216, and J4-50130) and by the Young Researcher program of the Slovenian Research Agency and by the Czech Science Foundation GAČR No. 21-47163L.

Data Availability Statement: The non-meteorological datasets presented in this study are available on request from the corresponding author. Publicly available meteorological datasets were analyzed in this study.

Acknowledgments: Sincere thanks to Saša Ogorevc from the Slovenian Forestry Institute for her work in Roxas. Thanks also to Robert Krajnc and Samo Stopar from the Slovenian Forestry Institute for their substantial contribution to field acquisition.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

MRW	Mean tree-ring width
MLA	Mean vessel/tracheid lumen area
CD	Cell (tracheid or vessel) density
RCTA	Relative conductive area
CWTTAN	Mean thickness of tangential cell walls
LMM	Linear mixed model

CGP	Canopy gap fraction
MAT	Mean annual air temperature
MAP	Mean annual precipitation
N	Number of trees
DBH	Mean diameter at breast height

Appendix A

Appendix A.1

Table A1. Summary of statistical tests assessing differences in xylem traits among three sites (Suceava, Vrancea, Gorj) for *Abies alba* (ABAL) and *Fagus sylvatica* (FASY). Tree-ring characteristics included: (I) mean tree-ring width (MRW); (II) mean vessel/tracheid lumen area (MLA); (III) tracheid or vessel density (CD); (IV) relative conductive area (RCTA); and (V) mean thickness of tangential cell walls (CWTTAN). Depending on data distribution and variance homogeneity, either the Friedman rank sum test or a linear mixed model (LMM) was applied. Test statistics and degrees of freedom (df) are reported. Pairwise comparisons between sites were corrected for multiple testing. Significance codes: **** $p < 0.0001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant.

Species	Tree-Ring Characteristic	Test (Statistic, df)	*p*-Value	Pairwise Comparison	Adjusted *p*	Significance
ABAL	MRW	Friedman (χ^2 = 74, df = 2)	<0.0001	SUC–VRA	<0.0001	****
				SUC–GOR	<0.0001	****
				VRA–GOR	<0.0001	****
	CD	Friedman (χ^2 = 31.3, df =2)	<0.0001	SUC–VRA	<0.0001	****
				SUC–GOR	<0.01	**
				VRA–GOR	<0.0001	****
	RCTA	LMM (F = 30.47, df = 2, 72)	<0.0001	SUC–VRA	<0.0001	****
				SUC–GOR	<0.0001	****
				VRA–GOR	0.07	ns
	MLA	LMM (F = 31.81, df = 2, 72)	<0.001	SUC–VRA	<0.0001	****
				SUC–GOR	1.00	ns
				VRA–GOR	<0.0001	****
	CWTTAN	Friedman (χ^2 = 32, df = 2)	<0.0001	SUC–VRA	1.00	ns
				SUC–GOR	<0.0001	****
				VRA–GOR	<0.0001	****
FASY	MRW	Friedman (χ^2 = 26.32, df = 2)	<0.0001	SUC–VRA	0.023	*
				SUC–GOR	<0.0001	****
				VRA–GOR	<0.01	**
	CD	Friedman (χ^2 = 19.68, df = 2)	<0.0001	SUC–VRA	0.009	**
				SUC–GOR	<0.0001	****
				VRA–GOR	0.002	**
	RCTA	Friedman (χ^2 = 42, df = 2)	<0.0001	SUC–VRA	<0.0001	****
				SUC–GOR	<0.0001	****
				VRA–GOR	0.042	*
	MLA	LMM (F = 11.03, df = 2, 72)	<0.0001	SUC–VRA	<0.0001	****
				SUC–GOR	0.027	*
				VRA–GOR	0.149	ns

Appendix A.2

Table A2. Summary of linear mixed-effects models (LMMs) assessing the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA, CWTTAN) and their interactions with site in fir. All models include year as a random effect. For each fixed-effect term, the estimate, standard error, degrees of freedom (df), t-value, and *p*-value are reported. Marginal and conditional R^2 values represent the variance explained by fixed effects alone and by the full model, respectively.

Model	Term	Estimate	Std. Error	df	t Value	Pr (>|t|)	R^2 Marginal	R^2 Conditional
CD ~ MRW * site	(Intercept)	854.19	39.46	97.49	21.647	0.000	0.47	0.73
	MRW	0.01	0.03	91.70	−0.372	0.711		
	siteSuceava	27.26	66.61	76.63	0.409	0.683		
	siteVrancea	−57.82	47.89	72.11	−1.207	0.231		
	MRW:siteSuceava	0.01	0.03	80.76	0.404	0.687		
	MRW:siteVrancea	0.09	0.03	78.88	2.662	0.009		
RCTA ~ MRW * site	(Intercept)	41.68	1.23	98.88	33.800	0.000	0.27	0.55
	MRW	0.00	0.00	95.47	−0.973	0.333		
	siteSuceava	−1.36	2.13	79.92	−0.638	0.525		
	siteVrancea	−1.72	1.54	74.91	−1.118	0.267		
	MRW:siteSuceava	0.00	0.00	84.44	1.481	0.142		
	MRW:siteVrancea	0.00	0.00	82.32	0.881	0.381		
CWTTAN ~ MRW * site	(Intercept)	5.95	0.13	98.40	45.240	0.000	0.39	0.64
	MRW	0.00	0.00	94.33	2.151	0.034		
	siteSuceava	0.16	0.23	78.36	0.728	0.469		
	siteVrancea	0.54	0.16	73.35	3.332	0.001		
	MRW:siteSuceava	0.00	0.00	82.90	−2.615	0.011		
	MRW:siteVrancea	0.00	0.00	80.78	−4.160	0.000		
MLA ~ MRW * site	(Intercept)	488.66	30.67	99.45	15.932	0.000	0.34	0.57
	MRW	0.01	0.03	96.81	0.393	0.696		
	siteSuceava	53.70	53.54	81.23	1.003	0.319		
	siteVrancea	36.27	38.77	76.00	0.936	0.352		
	MRW:siteSuceava	−0.02	0.03	85.91	−0.613	0.542		
	MRW:siteVrancea	−0.05	0.03	83.68	−1.773	0.080		
RCTA ~ CD * site	(Intercept)	55.20	4.19	92.09	13.167	0.000	0.42	0.68
	CD	−0.02	0.00	91.70	−3.508	0.001		
	siteSuceava	8.50	5.85	78.28	1.453	0.150		
	siteVrancea	−7.06	4.50	75.44	−1.568	0.121		
	CD:siteSuceava	−0.01	0.01	78.37	−0.870	0.387		
	CD:siteVrancea	0.01	0.01	77.16	1.745	0.085		
MLA ~ CD * site	(Intercept)	1142.87	52.17	92.24	21.905	0.000	0.87	0.92
	CD	−0.76	0.06	91.87	−12.365	0.000		
	siteSuceava	126.68	72.97	77.99	1.736	0.086		
	siteVrancea	−157.42	56.16	74.96	−2.803	0.006		
	CD:siteSuceava	−0.09	0.08	78.08	−1.052	0.296		
	CD:siteVrancea	0.21	0.06	76.74	3.189	0.002		
CWTTAN ~ CD * site	(Intercept)	6.50	0.54	99.75	12.075	0.000	0.40	0.52
	CD	0.00	0.00	99.68	−0.525	0.601		
	siteSuceava	−0.79	0.78	88.07	−1.016	0.312		
	siteVrancea	1.05	0.61	82.50	1.738	0.086		
	CD:siteSuceava	0.00	0.00	88.17	0.549	0.584		
	CD:siteVrancea	0.00	0.00	84.53	−1.924	0.058		
CWTTAN ~ MLA * site	(Intercept)	6.28	0.39	96.84	16.167	0.000	0.37	0.52
	MLA	0.00	0.00	96.55	−0.153	0.879		
	siteSuceava	0.66	0.52	90.21	1.273	0.206		
	siteVrancea	−1.24	0.45	83.25	−2.739	0.008		
	MLA:siteSuceava	0.00	0.00	90.46	−1.963	0.053		
	MLA:siteVrancea	0.00	0.00	82.76	2.234	0.028		
CWTTAN ~ RCTA * site	(Intercept)	8.28	0.72	101.94	11.442	0.000	0.56	0.57
	RCTA	−0.05	0.02	101.94	−2.860	0.005		
	siteSuceava	1.23	0.91	96.24	1.357	0.178		
	siteVrancea	0.35	0.96	91.94	0.360	0.720		
	RCTA:siteSuceava	−0.03	0.02	96.46	−1.565	0.121		
	RCTA:siteVrancea	−0.02	0.02	91.96	−0.751	0.455		

Appendix A.3

Table A3. Summary of linear mixed-effects models (LMMs) assessing the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA) and their interactions with site in beech. All models include year as a random effect. For each fixed-effect term, the estimate, standard error, degrees of freedom (df), t-value, and *p*-value are reported. Marginal and conditional R^2 values represent the variance explained by fixed effects alone and by the full model, respectively.

Model	Term	Estimate	Std. Error	df	t Value	Pr (>|t|)	R^2 Marginal	R^2 Conditional
CD ~ MRW * site	(Intercept)	162.74	2.72	101.85	59.839	0.000	0.80	0.83
	MRW	−0.02	0.00	101.51	−12.086	0.000		
	siteSuceava	−25.77	6.06	101.81	−4.251	0.000		
	siteVrancea	−17.19	4.07	96.27	−4.223	0.000		
	MRW:siteSuceava	0.01	0.00	100.02	4.591	0.000		
	MRW:siteVrancea	0.01	0.00	91.75	4.470	0.000		
RCTA ~ MRW * site	(Intercept)	23.91	0.63	102.00	37.840	0.000	0.63	
	MRW	0.00	0.00	102.00	−3.442	0.001		
	siteSuceava	−2.16	1.40	102.00	−1.548	0.125		
	siteVrancea	0.63	0.92	102.00	0.684	0.496		
	MRW:siteSuceava	0.00	0.00	102.00	0.185	0.853		
	MRW:siteVrancea	0.00	0.00	102.00	−0.665	0.507		
MLA ~ MRW * site	(Intercept)	1487.43	47.89	101.47	31.062	0.000	0.27	0.41
	MRW	0.14	0.03	100.19	4.513	0.000		
	siteSuceava	103.95	107.06	101.97	0.971	0.334		
	siteVrancea	201.45	72.59	98.27	2.775	0.007		
	MRW:siteSuceava	−0.13	0.05	101.20	−2.676	0.009		
	MRW:siteVrancea	−0.12	0.04	94.63	−3.015	0.003		
RCTA ~ CD * site	(Intercept)	11.61	1.96	100.83	5.924	0.000	0.69	0.72
	CD	0.08	0.01	100.77	5.280	0.000		
	siteSuceava	−10.24	4.55	101.87	−2.249	0.027		
	siteVrancea	−7.08	3.07	97.58	−2.303	0.023		
	CD:siteSuceava	0.07	0.04	101.81	1.836	0.069		
	CD:siteVrancea	0.06	0.02	97.48	2.303	0.023		
MLA ~ CD * site	(Intercept)	2486.75	159.75	99.07	15.567	0.000	0.31	0.41
	CD	−6.04	1.20	98.90	−5.032	0.000		
	siteSuceava	−726.43	371.74	100.74	−1.954	0.053		
	siteVrancea	−407.60	252.84	100.30	−1.612	0.110		
	CD:siteSuceava	4.84	3.20	100.55	1.513	0.133		
	CD:siteVrancea	3.18	2.02	100.25	1.571	0.119		

Appendix A.4

Table A4. Estimated site-specific slopes and pairwise contrasts of marginal trends (emtrends) extracted from linear mixed-effects models (LMMs). The models assess the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA, CWTTAN) and site-specific differences in these relationships in fir. For each model, estimated slopes are reported separately for each site (Gorj, Suceava, Vrancea), followed by Tukey-adjusted pairwise contrasts between sites. Columns include estimates, standard errors (SE), degrees of freedom (df), confidence intervals (CL), t-ratios, and *p*-values.

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	*p* Value
CD ~ MRW * site	Estimated slope	Gorj	−0.013	0.035	92.17	−0.081	0.056		
		Suceava	0.001	0.013	93.70	−0.025	0.027		
		Vrancea	0.078	0.014	94.60	0.050	0.106		
	Pairwise contrast	Gorj–Suceava	−0.014	0.034	81.62			−0.401	0.915
		Gorj–Vrancea	−0.091	0.034	79.80			−2.646	0.026
		Suceava–Vrancea	−0.077	0.017	72.17			−4.645	0.000
RCTA ~ MRW * site	Estimated slope	Gorj	−0.001	0.001	95.54	−0.003	0.001		
		Suceava	0.001	0.000	96.87	0.000	0.001		
		Vrancea	0.000	0.000	97.63	−0.001	0.001		
	Pairwise contrast	Gorj–Suceava	−0.002	0.001	84.62			−1.469	0.311
		Gorj–Vrancea	−0.001	0.001	82.52			−0.875	0.658
		Suceava–Vrancea	0.001	0.001	73.79			1.222	0.444

Table A4. *Cont.*

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	*p* Value
CWTTAN ~ MRW * site	Estimated slope	Gorj	0.000	0.000	94.77	0.000	0.000		
		Suceava	0.000	0.000	96.16	0.000	0.000		
		Vrancea	0.000	0.000	96.97	0.000	0.000		
	Pairwise contrast	Gorj–Suceava	0.000	0.000	83.87			2.594	0.030
		Gorj–Vrancea	0.000	0.000	81.83			4.130	0.000
		Suceava–Vrancea	0.000	0.000	73.36			3.157	0.006
MLA ~ MRW * site	Estimated slope	Gorj	0.011	0.027	96.86	−0.043	0.064		
		Suceava	−0.006	0.010	98.04	−0.026	0.014		
		Vrancea	−0.038	0.011	98.71	−0.060	−0.016		
	Pairwise contrast	Gorj–Suceava	0.017	0.028	86.04			0.60729	0.81653
		Gorj–Vrancea	0.048	0.028	83.81			1.75874	0.18986
		Suceava–Vrancea	0.032	0.013	74.64			2.3563	0.05433
RCTA ~ CD * site	Estimated slope	Gorj	−0.017	0.005	91.92	−0.027	−0.007		
		Suceava	−0.023	0.005	89.24	−0.034	−0.013		
		Vrancea	−0.008	0.003	92.26	−0.014	−0.003		
	Pairwise contrast	Gorj–Suceava	0.006	0.007	78.79			0.86429	0.66428
		Gorj–Vrancea	−0.009	0.005	77.59			−1.7357	0.19852
		Suceava–Vrancea	−0.015	0.006	79.90			−2.6893	0.02343
MLA ~ CD * site	Estimated slope	Gorj	−0.765	0.063	92.42	−0.889	−0.641		
		Suceava	−0.853	0.065	89.77	−0.983	−0.724		
		Vrancea	−0.560	0.033	92.76	−0.625	−0.495		
	Pairwise contrast	Gorj–Suceava	0.089	0.085	79.19			1.04513	0.55084
		Gorj–Vrancea	−0.205	0.065	77.90			−3.1705	0.0061
		Suceava–Vrancea	−0.294	0.069	80.32			−4.258	0.00016
CWTTAN ~ CD * site	Estimated slope	Gorj	0.000	0.001	99.64	−0.002	0.001		
		Suceava	0.000	0.001	98.39	−0.001	0.002		
		Vrancea	−0.002	0.000	99.79	−0.002	−0.001		
	Pairwise contrast	Gorj–Suceava	0.000	0.001	87.95			−0.543	0.85032
		Gorj–Vrancea	0.001	0.001	84.26			1.90759	0.14282
		Suceava–Vrancea	0.002	0.001	89.16			2.47074	0.04039
CWTTAN ~ MLA * site	Estimated slope	Gorj	0.000	0.001	96.80	−0.002	0.001		
		Suceava	−0.002	0.001	95.91	−0.004	−0.001		
		Vrancea	0.002	0.001	97.18	0.001	0.003		
	Pairwise contrast	Gorj–Suceava	0.002	0.001	90.96			1.93827	0.13387
		Gorj–Vrancea	−0.002	0.001	83.52			−2.2133	0.07477
		Suceava–Vrancea	−0.004	0.001	87.88			−4.486	6.5×10^{-5}
CWTTAN ~ RCTA * site	Estimated slope	Gorj	−0.051	0.018	101.94	−0.087	−0.015		
		Suceava	−0.085	0.013	101.93	−0.111	−0.059		
		Vrancea	−0.069	0.016	101.95	−0.101	−0.037		
	Pairwise contrast	Gorj–Suceava	0.034314	0.02226	96.3681			1.54184	0.27611
		Gorj–Vrancea	0.017945	0.02422	91.7898			0.74098	0.73981
		Suceava–Vrancea	−0.01637	0.02081	94.0712			−0.7866	0.71217

Appendix A.5

Table A5. Estimated site-specific slopes and pairwise contrasts of marginal trends (emtrends) extracted from linear mixed-effects models (LMMs). The models assess the relationships between wood-anatomical traits (e.g., MRW, CD, RCTA, MLA) and site-specific differences in these relationships in beech. For each model, estimated slopes are reported separately for each site (Gorj, Suceava, Vrancea), followed by Tukey-adjusted pairwise contrasts between sites. Columns include estimates, standard errors (SE), degrees of freedom (df), confidence intervals (CL), t-ratios, and *p*-values.

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	*p* Value
CD ~ MRW * site	Estimated slope	Gorj	−0.021	0.002	101.52	−0.025	−0.018		
		Suceava	−0.009	0.002	100.88	−0.013	−0.005		
		Vrancea	−0.011	0.001	101.66	−0.014	−0.009		
	Pairwise contrast	Gorj–Suceava	−0.012	0.003	100.05			−4.517	0.000
		Gorj–Vrancea	−0.010	0.002	91.89			−4.384	0.000
		Suceava–Vrancea	0.002	0.002	89.47			1.089	0.524
RCTA ~ MRW * site	Estimated slope	Gorj	−0.001	0.000	102.00	−0.002	−0.001		
		Suceava	−0.001	0.000	102.00	−0.002	0.000		
		Vrancea	−0.002	0.000	102.00	−0.002	−0.001		
	Pairwise contrast	Gorj–Suceava	0.000	0.001	97.14			−0.183	0.982
		Gorj–Vrancea	0.000	0.001	84.13			0.653	0.791
		Suceava–Vrancea	0.000	0.001	94.74			0.815	0.694

Table A5. *Cont.*

Model	Type	Site/Contrast	Estimate	SE	df	Lower CL	Upper CL	t Ratio	*p* Value
MLA ~ MRW * site	Estimated slope	Gorj	0.139	0.031	100.63	0.077	0.201		
		Suceava	0.012	0.035	99.16	−0.057	0.081		
		Vrancea	0.021	0.021	100.98	−0.022	0.063		
	Pairwise contrast	Gorj–Suceava	0.127	0.048	101.40			2.632	0.026
		Gorj–Vrancea	0.118	0.040	96.35			2.957	0.011
		Suceava–Vrancea	−0.009	0.039	86.14			−0.220	0.974
RCTA ~ CD * site	Estimated slope	Gorj	0.078	0.015	101.09	0.048	0.107		
		Suceava	0.150	0.037	100.65	0.077	0.222		
		Vrancea	0.134	0.019	101.07	0.096	0.173		
	Pairwise contrast	Gorj–Suceava	−0.072	0.040	101.86			−1.802	0.174
		Gorj–Vrancea	−0.057	0.025	98.64			−2.255	0.067
		Suceava–Vrancea	0.015	0.041	98.66			0.369	0.928
MLA ~ CD * site	Estimated slope	Gorj	−6.044	1.220	99.85	−8.464	−3.624		
		Suceava	−1.208	2.986	98.91	−7.133	4.717		
		Vrancea	−2.869	1.583	99.80	−6.009	0.272		
	Pairwise contrast	Gorj–Suceava	−4.836	3.253	101.00			−1.487	0.302
		Gorj–Vrancea	−3.175	2.064	100.79			−1.539	0.277
		Suceava–Vrancea	1.661	3.353	96.37			0.495	0.874

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