

Article

Why Intra-Annual Density Fluctuations Should Be Formed at Night? Implications for Climate–Growth Relationships in Seasonally Dry Conifer Forests

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Abstract: Trees grow at night, when the vapor pressure deficit (VPD) is low enough. Therefore, intra-annual density fluctuations (IADFs) should be formed when the VPD drops below a certain threshold. This idea is tested by assessing climate–latewood IADF relationships in six conifer species under Mediterranean climate conditions. Hourly climate and dendrometer data were analyzed for years with elevated IADF production in two species (*Pinus halepensis*, *Juniperus thurifera*). Lastly, climate–growth relationships were evaluated in two drought-prone sites to assess the relative role of minimum vs. maximum temperatures as growth drivers. Latewood IADF production was positively related to growth rate. IADFs were more abundant when monthly or 10-day long precipitation was high in the late growing season (August and September). According to dendrometer data, growth mainly occurred in early night (20–2 h) and early morning (6–8 h). This growth window corresponded to rainy periods with VPD below a minimum threshold associated with summer storms. Latewood IADFs are produced in response to these wet late-summer conditions, which could be related to bimodal growth. These associations are in line with correlations showing that high minimum (night) rather than maximum (day) temperatures reduce growth. This last idea should be further checked in drought-prone forests using global tree-ring databases.

Keywords: dendroecology; dendrometer; *Juniperus thurifera*; *Pinus halepensis*; radial growth; tree-ring features; vapor pressure deficit



Citation: Camarero, J.J. Why Intra-Annual Density Fluctuations Should Be Formed at Night? Implications for Climate–Growth Relationships in Seasonally Dry Conifer Forests. *Forests* **2022**, *13*, 1425. <https://doi.org/10.3390/f13091425>

Academic Editor: Bao Yang

Received: 2 August 2022

Accepted: 2 September 2022

Published: 5 September 2022

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1. Introduction

Forests play major roles in this planet as carbon and biodiversity reservoirs, but many of them, particularly in drought-prone areas, are increasingly stressed due to warmer conditions amplifying mortality rates and reducing productivity [1]. In the Anthropocene, forest productivity and tree radial growth are becoming increasingly more driven by water availability [2]. In this sense, a better understanding on how trees grow and respond to climate drivers at multiple temporal resolutions is needed. For instance, radial growth could be plastic enough and allow for trees adapting to changing climate conditions, including a more severe drought stress [3,4].

Dendrochronology has mainly focused on radial growth changes at annual to seasonal resolutions [5]. Xylogenesis studies have enabled reconstructing the growth phenology (amount of formed and developed cells) by repeatedly taking wood samples at weekly or biweekly periods [3,6,7]. Finally, modern, high-precision automatic dendrometers have enabled quantifying radial stem growth and water-related swelling/shrinkage dynamics at hourly and lower temporal resolutions [8,9]. However, we lack stronger linkages between growth and wood anatomy (Figure 1), and these connections should encompass several temporal scales, from the annual ring to intra-annual wood anatomical features.

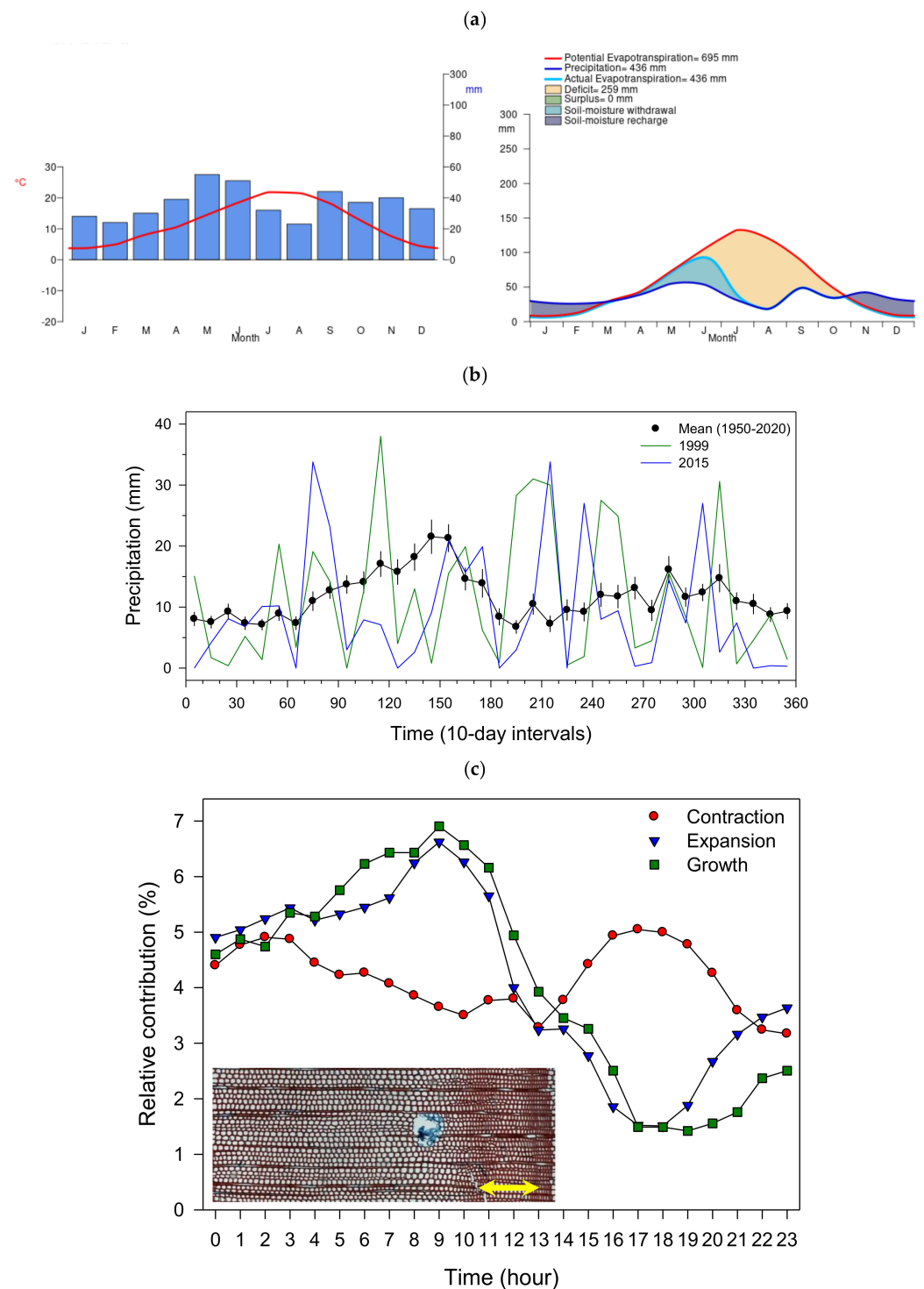


Figure 1. Temporal scales (month, 10-day intervals, hours) considered in the study of climate–IADFs relationships. Correlations were calculated considering (a) monthly, (b) 10-day, and (c) hourly climate data. In plot (a) the climate diagram of Daroca station showing typical Mediterranean conditions is presented with estimates of monthly potential evapotranspiration. In plot (b) symbols show mean ($\pm$ SE) precipitation values and color lines show precipitation values in this station for years with a high frequency of IADFs (1999, 2015). In plot (c) the hourly phases of stem contraction, expansion, and assumed growth were obtained from dendrometers attached to a *P. halepensis* tree in the Peñaflor site (see Table 1). The image in (c) shows a latewood IADF (yellow arrow) in a cross-section showing an annual ring of *P. halepensis*.

Table 1. Study species and sites where tree-ring chronologies were developed to quantify the annual percentage of IADF production in the latewood. The sites with asterisks (*) correspond to plantations. Dbh is the diameter at breast height (mean $\pm$ SD).

Tree Species	Site	Latitude N	Longitude (−W, +E)	Elevation (m a.s.l.)	Mean Temperature (°C)	Annual Precipitation (mm)	Dbh (cm)
<i>Pinus pinaster</i>	Armuña	41.08	−4.31	870	11.6	488	41.0 $\pm$ 2.3
	Bayubas	41.53	−2.89	850	10.5	527	31.2 $\pm$ 1.1
	Orera	41.30	−1.46	884	13.0	412	28.3 $\pm$ 0.9
	Prades *	41.34	1.04	807	11.8	659	24.2 $\pm$ 2.6
<i>Pinus halepensis</i>	Peñaflor	41.78	−0.71	350	13.9	356	32.3 $\pm$ 4.6
	Retuerta de Pina	41.48	−0.26	360	13.2	378	29.6 $\pm$ 2.8
	Begues	41.34	1.89	300	13.2	673	24.0 $\pm$ 0.8
<i>Juniperus thurifera</i>	Peñaflor	41.78	−0.71	345	13.9	356	17.5 $\pm$ 2.9
	Olmedilla	40.29	−0.74	1350	9.8	496	29.0 $\pm$ 2.0
	Retuerta de Pina	41.48	−0.26	360	13.2	378	25.0 $\pm$ 1.5
<i>Abies pinsapo</i>	Orcajo *	41.09	−1.51	1152	11.5	612	36.0 $\pm$ 1.9
<i>Pinus sylvestris</i>	Sierra de las Nieves *	36.65	−4.93	1400	10.8	1180	33.2 $\pm$ 1.5
<i>Cedrus atlantica</i>	Sierra de las Nieves *	36.65	−4.93	1400	10.8	1180	32.0 $\pm$ 2.0

Wood anatomical features are a promising tool to link intra-annual growth and related wood formation [10]. For instance, intra-annual density fluctuations (hereafter IADFs) or false rings have been widely studied as climate signals in many conifers, especially in areas subjected to seasonal drought such as the Mediterranean Basin [11–20] or North American regions [21–27]. Forests located in south-western USA or northern Mexico are important because they are subjected to strong seasonal drought [23–27]. In those forests, the main moisture source is the North American summer monsoon, which accounts for 30 to 50% of annual precipitation and it is characterized by abundant rainfall and storms from July to September after dry spring conditions [28]. Such episodic but potentially strong rainfalls can resume cambial growth, leading to the formation of latewood IADFs [26], as happens with late summer to early autumn precipitation in Mediterranean forests [16–18,20,29]. More importantly, monsoon rainfall can trigger bimodal growth [26], a pattern already described in Mediterranean conifers [3]. It should be stated that IADF formation and bimodal growth have been often related, but they are not necessarily linked, since bimodal growth can occur without latewood IADF production and vice versa [27].

In this study, I capitalize on the analogy between drought-prone conifer forests subjected to contrasting seasonal precipitation regimes where IADFs and bimodal growth have been observed. I compare Mediterranean forests, the main subject of this study, and north-western American forests affected by the summer monsoon. The study focuses on IADFs formed in the latewood, which can be defined as bands of earlywood-like tracheids formed in the latewood, i.e., tracheids with transversal wider lumen and thinner cell walls than latewood tracheids (Figure 1c). I assess the climate drivers of IADF formation at monthly to 10-day long scales in several sites and species. Then, I use dendrometer data to explore when growth occurs during the period of IADF formation in Mediterranean conifers (late summer to early autumn). Despite the fact that climate–IADFs relationships have been widely studied, we still lack a process-based approach showing when and how IADFs are formed in response to climate variability at multiple temporal scales. The main hypothesis is that IADF should form at night, when growth occurs [9]. Finally, I also test whether growth is more related to minimum (night) or maximum (day) temperatures at monthly scales in Mediterranean and north-western American drought-prone forests. I expect growth is more related to minimum temperatures in these sites, since growth occurs at night when a minimum value of evaporative demand or vapor pressure deficit (VPD) is not surpassed and turgor of enlarging xylem cells is high [9]. In contrast, maximum temperature may reduce soil moisture which seems to be less important to grow than VPD [9,30].

2. Materials and Methods

2.1. Study Sites and Tree Species

The production and climate drivers of latewood IADF formation were studied in six conifer species (*Pinus pinaster* Ait., *Pinus halepensis* Mill., *Juniperus thurifera* L., *Abies pinsapo* Boiss., *Pinus sylvestris* L. and *Cedrus atlantica* (Endl.) Manetti ex Carrière) inhabiting sites located across eastern Spain (Table 1, Figure S1). Study sites encompassed a wide gradient in latitude (36.65–41.78° N), longitude (4.93° W–1.89° E), elevation (300–1400 m a.s.l.) and climate conditions (mean annual temperature 9.2–13.9 °C, total annual precipitation 356–1180 mm). All study species are found in locations with Mediterranean climate conditions characterized by dry summers, wet–cool springs, autumn conditions, and cold winters, particularly in the case of inland sites. All study sites are natural forests except the *P. pinaster* Prades site, and the *A. pinsapo*, *P. sylvestris* and *C. atlantica* sites which are plantations. The *P. pinaster* and *A. pinsapo* sites are located on metamorphic substrates forming acid soils, whereas the *P. halepensis*, *J. thurifera*, *P. sylvestris* and *C. atlantica* sites are located in sites with basic soils. In the site with dendrometer data, *P. halepensis* and *J. thurifera* are the dominant tree species.

The sites where the effects of monthly climate data (minimum and maximum temperatures, total precipitation) on growth were studied are located in north-eastern Spain (41.3° N, 1.8° E, 300 m a.s.l.) and south-western USA (33.9° N, 108.5° W, 2140 m a.s.l.), respectively, and correspond to *P. halepensis* and *Pinus edulis* Engelm. stands, in that order. The mean annual temperatures and total annual precipitation are 14.7° and 11.0 °C and 588 and 393 mm in these dry-summer *P. halepensis* and wet-summer *P. edulis* sites, respectively. (Figure S2). These sites were selected because both IADF formation and bimodal growth were observed there [3,17,26].

2.2. Climate Data

In the case of the site with dendrometer data (Peñaflor), in situ meteorological data (air minimum and maximum temperatures, precipitation, and relative humidity) were obtained at hourly resolution for the period 2009–2020 using a weather station (HOBO RX3000, Onset, MA, USA). The station was located within a mixed *P. halepensis*–*J. thurifera* open forest. I calculated hourly VPDs (in kPa) using temperature and relative humidity data [30].

In the case of the sites with latewood IADF data, climate data (mean temperature, total precipitation) were obtained for the period 1970–2020 at monthly and 10-day temporal resolutions from a 1.1 km² gridded Spanish dataset [31].

In the case of the sites from north-eastern Spain and south-western USA where climate–growth relationships were compared, I used 0.5° gridded monthly climate data (mean minimum and maximum temperatures, total precipitation) from the CRU climate dataset [32].

2.3. Field Sampling and IADF Data

In the field, mature, healthy, dominant, or co-dominant trees of each species were selected for sampling. A total of 15 to 33 trees were sampled per site (Table 2). Their diameter at breast height (dbh) was measured at 1.3 m using tapes. Two increment cores by tree were taken at the same height using 5.15 mm Pressler increment borers (Häglof, Sweden) and perpendicular to the maximum slope when appropriate. At least one of the cores reached the pith or the innermost rings so as to estimate tree age at 1.3 m.

Table 2. Age and tree growth data and statistics calculated for the sampled sites. Variables' abbreviations: AR1, first-order autocorrelation; MSx, mean sensitivity; IADF, percentage of years with latewood IADFs in the mean site series.

Tree Species	Site	Age at 1.3 m (Years)	No. Trees/No. Radii	Tree-Ring Width $\pm$ SD (mm)	AR1	MSx	IADF (%)	Best-Replicated Period
<i>Pinus pinaster</i>	Armuña	88 $\pm$ 3	15/41	2.42 $\pm$ 1.28	0.68	0.29	45.8	1898–2008
	Bayubas	92 $\pm$ 4	22/46	1.48 $\pm$ 0.88	0.77	0.28	79.7	1876–2008
	Órera	87 $\pm$ 3	33/66	1.24 $\pm$ 1.11	0.73	0.47	19.7	1920–2019
	Prades	46 $\pm$ 2	25/50	1.30 $\pm$ 0.89	0.71	0.52	83.6	1975–2020
<i>Pinus halepensis</i>	Peñaflor	89 $\pm$ 3	26/52	0.94 $\pm$ 0.27	0.52	0.44	62.5	1906–2020
	Retuerta de Pina	75 $\pm$ 2	32/47	1.11 $\pm$ 0.21	0.72	0.36	47.8	1939–2020
	Begues	87 $\pm$ 3	22/43	0.98 $\pm$ 0.25	0.76	0.28	88.3	1941–2019
	Peñaflor	71 $\pm$ 2	21/42	1.21 $\pm$ 0.87	0.62	0.41	72.0	1941–2020
<i>Juniperus thurifera</i>	Olmedilla	88 $\pm$ 3	27/54	0.97 $\pm$ 0.47	0.65	0.32	44.0	1949–2019
	Retuerta de Pina	69 $\pm$ 3	32/55	1.09 $\pm$ 0.43	0.58	0.35	78.0	1964–2019
<i>Abies pinsapo</i>	Orcajo	51 $\pm$ 2	17/35	2.37 $\pm$ 1.12	0.54	0.37	87.5	1970–2019
<i>Pinus sylvestris</i>	Sierra de las Nieves	40 $\pm$ 1	20/39	4.08 $\pm$ 1.67	0.75	0.22	56.7	1983–2019
<i>Cedrus atlantica</i>	Sierra de las Nieves	37 $\pm$ 1	18/34	5.02 $\pm$ 1.25	0.56	0.22	36.7	1986–2019

Cores were air dried, mounted on wooden supports, and sanded with increasingly finer sandpaper until IADFs and ring boundaries were clearly visible under a microscope. Cores were visually cross-dated and annual ring widths were measured with a 0.01 mm resolution using a Lintab-TSAP system (Rinntech, Heidelberg, Germany). Visual cross dating was checked with the program COFECHA [33]. Detrending of ring-width data to remove age- or size-related trends was conducted by fitting either linear or exponential negative functions, then dividing measured by fitted ring-width values and obtaining ring-width indices. Then, a mean series of ring-width indices or chronology was calculated for each site using a bi-weight robust mean and the dplR package in R [34,35].

I used already developed chronologies for the sites located in north-eastern Spain and south-western USA [36,37]. The *P. halepensis* site in north-eastern Spain was located near Begues site (see Table 1). In the case of the *P. edulis* site, ring-width data were downloaded from the International Tree-Ring Data Bank corresponding to the site NM624 [38]. In these two sites, I considered the common and best-replicated 1950–2016 period.

Latewood IADFs (formed by earlywood-like cells within the latewood) were counted under the microscope. An annual frequency (%) of IADFs was calculated for each site and species by dividing the number of trees that formed IADFs by the total number of observed trees. The IADF was counted only when both cores from the tree showed it in the same annual ring [39].

Then, a sample-count-based variance correction was applied to correct the bias for the changing sample depth (number of trees) through time [40]. The period covered by latewood IADF analyses was 1950–2020 (Figure 2), although the common period for all sites was 1975–2008 (Table 2).

2.4. Dendrometer Data

Changes in stem perimeter were recorded at hourly resolution in *P. halepensis* ($n = 3$ individuals, mean dbh = 17 cm, mean age = 65 years) and *J. thurifera* ($n = 3$ individuals, mean dbh = 12.0 cm, mean age = 43 years) trees from the Peñaflor site during the 2009–2020 period. Automatic band dendrometers (DRL26C, EMS Brno, Czech Republic) were placed at 1.3 m after removing the dead bark. Dendrometers recorded variations in stem circumference every 30 min with 1 μ m resolution. These values were converted into hourly radial increment rates assuming a circular stem shape. Stem diameter variation is composed of: (1) irreversible stem diameter growth, including cell division and cell enlargement, and (2) water-related processes (swelling/shrinkage) leading to contraction and expansion depending on the water potential gradient (Figure 1c). The zero-growth concept, which assumes zero growth during periods of stem shrinkage, was used to separate irreversible growth from stem diameter contraction and expansion [8]. The percentage of hours corresponding to each phase (contraction, expansion, and growth) was calculated.

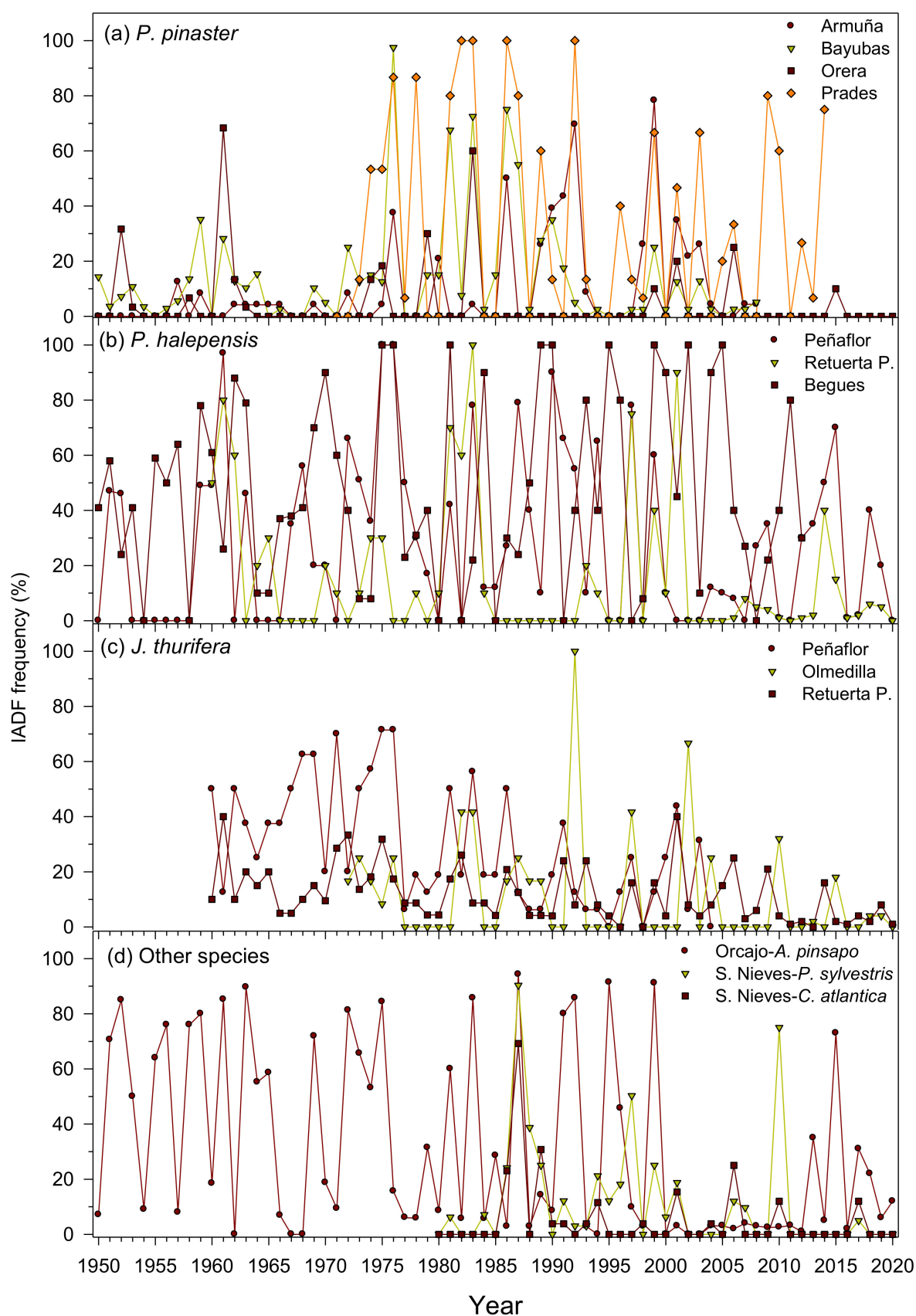


Figure 2. Mean annual frequency of latewood IADFs observed in the six study species: (a), *P. pinaster*; (b), *P. halepensis*; (c), *J. thurifera*; and (d), other species. Data correspond to the period 1950–2020.

I focused on August and September and the period of 2009–2011 because IADFs were formed in those two months and years [3,17,20]. On average, 12% and 9% of *P. halepensis* and *J. thurifera* individuals produced IADFs during that period, respectively, with maximum values observed in 2009 (35% and 21% of *P. halepensis* and *J. thurifera* individuals, respectively).

The frequency of hours with conditions favorable to growth according to [9], i.e., positive precipitation values and VPD < 0.24 kPa, were calculated. I also used climate and dendrometer data from other years (2015, 2021) to illustrate the punctual effects of late summer (August–September) storms and rainfall on climate conditions (air temperature, precipitation, VPD, relative air humidity) and changes in stem radius.

2.5. Climate–Growth Relationships

I used Pearson correlations and partial correlations to assess the relationships between monthly climate variables (mean minimum and maximum temperatures, precipitation) and growth rates (chronologies or mean series of ring-width indices) in the two sites from north-eastern Spain and south-western USA. Partial correlations were calculated between minimum and maximum temperatures to disentangle the relative contributions of each variable to explain year-to-year growth variability. Partial correlations were calculated only for months when either minimum or maximum temperatures showed significant ($p < 0.05$) correlations with ring-width indices. Correlations were calculated considering the window from prior to current October and the common 1950–2016 period.

2.6. Statistical Analyses

The Spearman correlation coefficient (r_s) was used to evaluate the relationships between tree growth rate, tree age, climate variables (mean temperature, total precipitation), and the frequency of formed IADFs. Correlations between growth rate and IADF production were calculated considering all measured ring widths, whereas the age–IADF correlation was calculated considering the maximum age of each tree and the mean number of IADFs produced by that tree, i.e., the average of the IADFs observed in the two cores of the same individual.

Correlations between climate variables and IADFs were calculated from prior to current October. To account for the high spatial variability of precipitation in Mediterranean regions, climate–IADF relationships based on 10-day long precipitation amounts were only presented for sites where meteorological stations with long-term (>30 years) precipitation records were located less than 20 km away from sampled stands. Results for the other sites are shown in the Supplementary Materials.

3. Results

3.1. Formation of IADFs in Mediterranean Tree Species: Roles of Growth Rate and Tree Age

Some species and sites showed a high frequency (>50% of years) of IADFs such as *P. pinaster* in Bayubas and Prades sites, *P. halepensis* in Begues and Peñaflor sites, *J. thurifera* in Peñaflor and Retuerta de Pina sites, *A. pinsapo* in Orcajo site, and *P. sylvestris* in Sierra de las Nieves site (Table 2, Figure 2). IADFs were frequent in wet–cool periods such as the 1970s, but they were rarely formed in dry periods such as the mid-1990s and 2000s and early 2010s when the growth rates were low. In some species and sites, there was a decrease in IADF production, such as in the case of *J. thurifera* in the Retuerta de Pina site.

Radial growth rate was positively related to IADF production in all sites and species (Table 3). Tree age was negatively related to IADF production in two *P. pinaster* sites (Armuña, Bayubas) and in two *P. halepensis* sites (Peñaflor, Begues).

Table 3. Relationships observed between tree growth rate (tree-ring width) or age and the amount of IADFs produced by trees assessed using the Spearman correlation coefficient (r_s) and its significance level (p). Note that the correlations between growth rate and IADF production were calculated considering all measured rings.

Tree Species	Site	Growth Rate			Age	
		r_s	p	No. Rings	r_s	p
<i>Pinus pinaster</i>	Armuña	0.411	<0.001	1123	−0.381	<0.001
	Bayubas	0.383	<0.001	1459	−0.599	<0.001
	Órera	0.453	<0.001	2189	−0.267	0.207
	Prades	0.351	<0.001	820	0.152	0.521
<i>Pinus halepensis</i>	Peñaflor	0.296	<0.001	955	−0.709	0.015
	Retuerta de Pina	0.181	<0.001	552	−0.246	0.217
	Begues	0.130	<0.001	1380	−0.596	0.023
	Peñaflor	0.271	<0.001	712	−0.056	0.835
<i>Juniperus thurifera</i>	Olmedilla	0.158	<0.001	748	0.320	0.338
	Retuerta de Pina	0.352	<0.001	904	−0.202	0.196
<i>Abies pinsapo</i>	Orcajo	0.198	<0.001	1708	0.275	0.210
<i>Pinus sylvestris</i>	Sierra de las Nieves	0.339	<0.001	799	0.157	0.591
<i>Cedrus atlantica</i>	Sierra de las Nieves	0.141	<0.001	691	0.241	0.223

3.2. Climate Drivers of IADF Formation in Mediterranean Tree Species

Latewood IADF formation was enhanced by wet and cool conditions due to elevated precipitation in August and September and (Figures 3 and S3–S7).

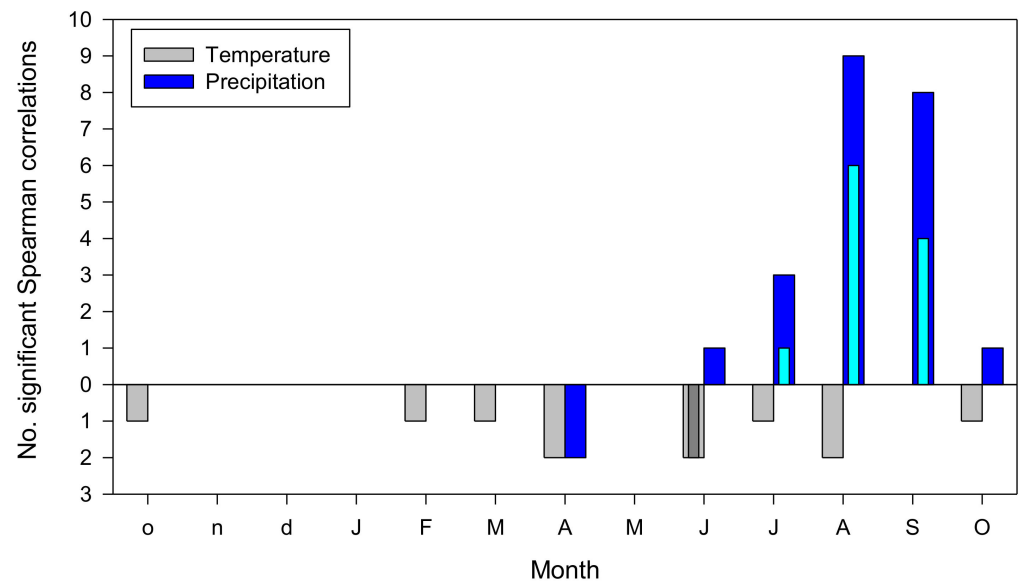


Figure 3. Summary of climate–IADF relationships calculated at monthly scale in the six study tree species. Monthly climate variables are mean temperature (grey bars) and precipitation (blue bars). Months abbreviated by lowercase and uppercase letters correspond to the previous and current years, respectively. Wide and narrow bars correspond to Spearman correlations coefficients (r_s) with significance levels lower or equal to 0.05 and 0.01, respectively.

At the 10-day scale, latewood IADF formation was related to high precipitation from late July to early August (*A. pinsapo*), or from early (*P. halepensis*) and mid-late September (*P. pinaster*, *J. thurifera*) to mid-October (*P. pinaster*) (Figures 4 and S8).

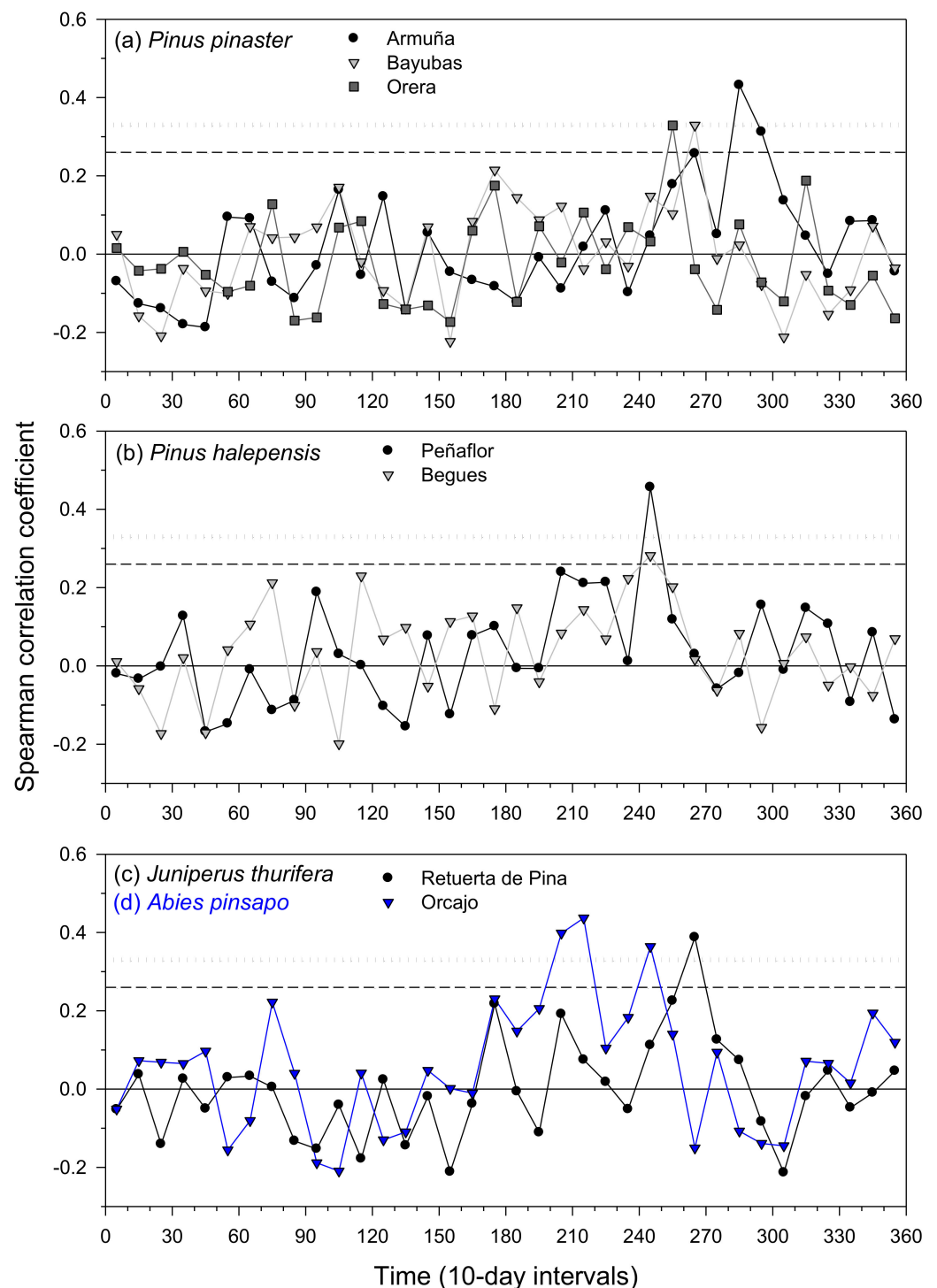


Figure 4. Summary of climate–IADF relationships calculated with 10-day long precipitation windows in the six study tree species ((a), *P. pinaster*; (b), *P. halepensis*; (c,d), *J. thurifera* (black line and symbols), and *A. pinsapo* (blue line and symbols)). These correlations were only calculated in sites where there were meteorological stations with long-term (>30 years) precipitation records located less than 20 km away from sampled sites. Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively.

3.3. Dendrometer Data at Hourly Resolution

At hourly resolution, the highest relative contribution to growth occurred from 7 to 9 h and from 7 to 12 h in *P. halepensis* and *J. thurifera*, respectively (Figures 5 and S9). Expansion also peaked in the night, whereas contraction was mainly observed from 14 to 17 h and from

16 to 21 h in *P. halepensis* and *J. thurifera*, respectively. Conditions favorable for growth were observed during night in both species, from 20 to 2 h and from 6 to 8 h (Figures 6 and S10).

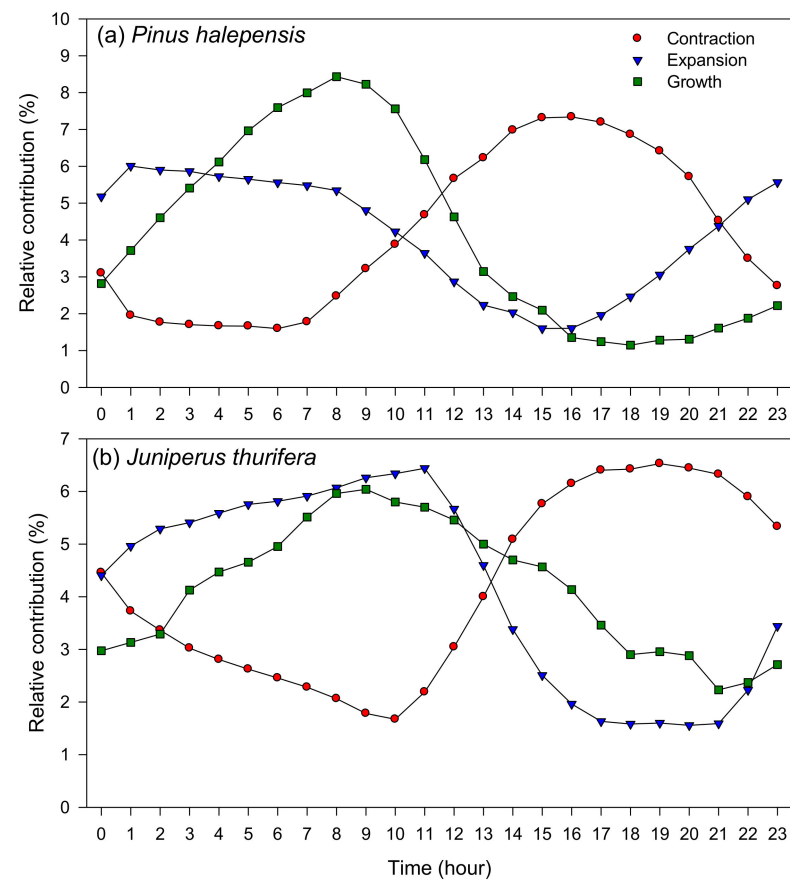


Figure 5. Contraction, expansion, and growth hourly phases based on dendrometer data corresponding to two study species ((a), *P. halepensis*; (b), *J. thurifera*) from the Peñaflor study site. Data correspond to months when most IADFs are formed (August to September) and were obtained in the Peñaflor site during the period 2009–2011.

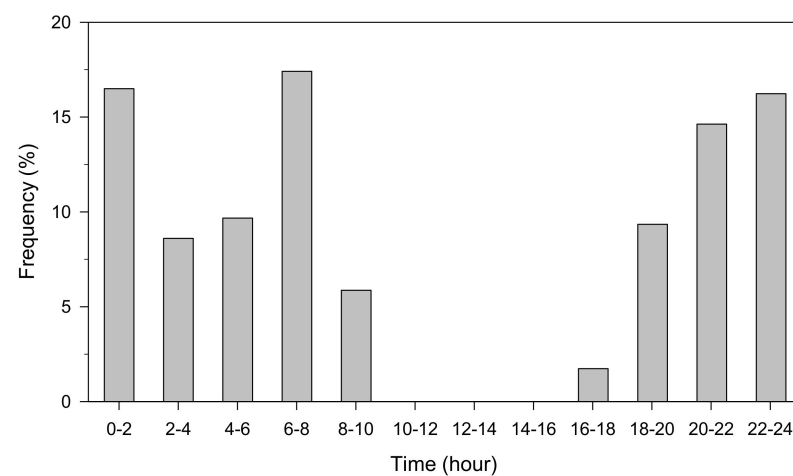


Figure 6. Frequency of hours with conditions favorable to growth, i.e., positive precipitation values and VPD < 0.24 kPa. Values were binned with 2 h classes.

The hourly growth increments observed in August and September, when IADFs are formed, often corresponded to night or early morning storms with abundant rainfall

(Figure S11). These late-summer storms lead to a sudden drop in air temperatures, increase the relative air humidity, and decrease the VPD (Figure S12).

3.4. Comparing Climate-Growth Relationships in Drought-Prone Sites

In the sites from north-eastern Spain and south-western USA, growth increased when current spring–summer or prior-to-winter and spring precipitation, respectively, did (Figure 7). Minimum and maximum temperatures showed negative associations with growth in those seasons as well as in autumn. Partial correlations indicated that growth was negatively related to spring, summer, and early autumn minimum temperatures.

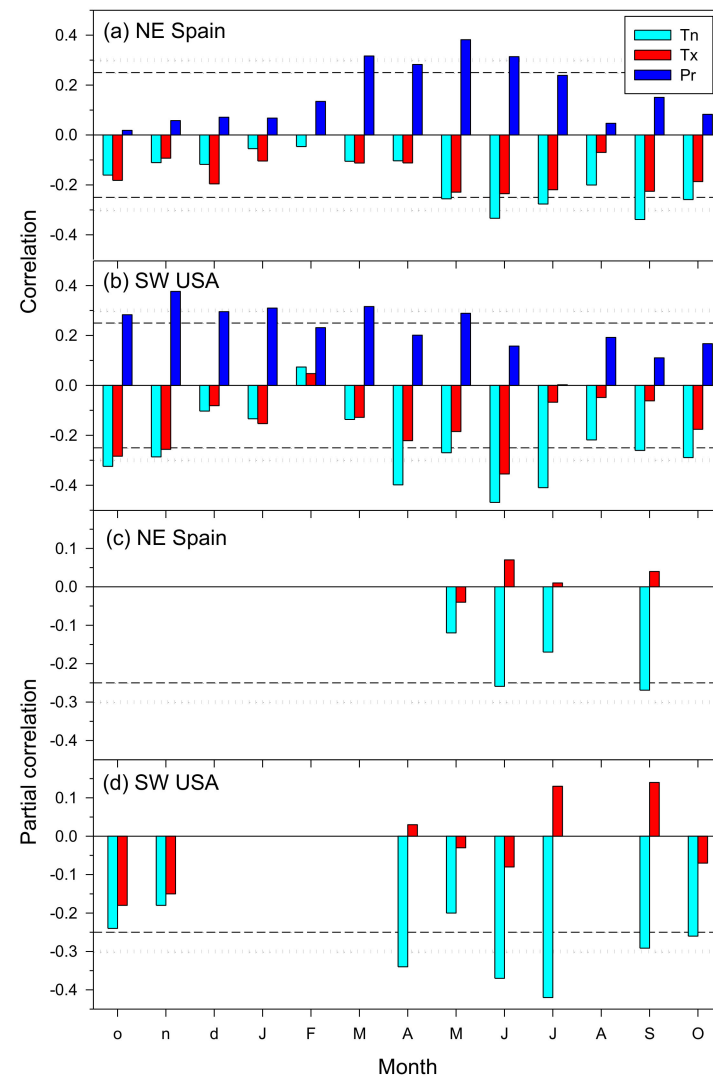


Figure 7. Climate–growth relationships assessed in two sites with different climate conditions but presenting latewood IADFs and potential growth bimodality: (a,c), *Pinus halepensis* in north-eastern Spain; (b,d), *Pinus edulis* in south-western USA. Plots (a,b) show Pearson correlations calculated between ring-width indices and climate variables (Tn, mean minimum temperature; Tx, mean maximum temperature; Pr, precipitation). Plots (c,d) show partial Pearson correlations by relating growth and minimum temperature after controlling for the influence of maximum temperature (blue bars) and vice versa (red bars). Partial correlations are only presented for months when minimum or maximum temperatures showed significant ($p < 0.05$) correlations with ring-width indices (see plots (a,b)). Months abbreviated by lowercase and uppercase letters correspond to the previous and current years, respectively. Horizontal dashed and dotted lines correspond to the 0.05 and 0.01 significance levels, respectively.

4. Discussion

4.1. IADFs Are Formed at Night and Early Morning in Response to Wet Conditions and Low VPD

In this paper, I tested the idea that latewood IADFs are formed when air temperatures and the VPD drop, i.e., during night and early morning. This hypothesis was supported by hourly climate and dendrometer taken in a *P. halepensis*–*J. thurifera* site where bimodal growth was also previously described [3]. This finding represents an addendum to recent studies showing that tree growth occurs at night when the VPD is below the 0.24 kPa threshold [9].

At monthly and 10-day temporal scales, latewood IADFs were produced in response to wet conditions in late summer and early autumn, which often correspond to night or early morning storms with abundant rainfall. In eastern Spain, these late-summer storms are generated by convective activity from the Mediterranean Sea [17]. They lead to a sudden drop in air temperatures, thus decreasing the VPD. The presented findings indicate that those conditions could reactivate cambial dynamics, increase the turgor of tracheids and their radial enlargement rate [41,42], and lead to the formation of latewood IADFs. In fact, a biophysical model of ring formation showed that changes in plant water status were the main driver of IADF formation through a direct effect on cell volume [43]. This has clear implications for forests' responses to changing climate conditions in seasonally dry areas since shifts of the dry season could affect growth, IADF production, wood density, and the capacity of trees to uptake carbon as thick, latewood cell walls [44,45]. Functionally, the shifts in the occurrence of the dry and wet season could also impact the hydraulic conductivity of the tree since the earlywood and latewood show contrasting conductivity, vulnerability to embolism, and water storage capacity [46]. For instance, the formation of more or wider latewood IADFs would increase hydraulic conductivity in late summer but also reduce the latewood water storage capacity.

The formation of IADFs from night to early morning has been mainly discussed from a meristem (cambium) perspective but should be understood considering the diurnal or circadian regulation of carbon supply and growth [47,48]. Light, plant hormones, sugar metabolism (e.g., starch degradation), and the circadian clock interact to control diurnal patterns of plant growth and carbon use by meristems. Therefore, future research could address how the carbohydrates fixed during the day are used to grow and form IADFs during the night and disentangle which environmental signals trigger these processes.

4.2. Minimum (Night) Temperature Is a Major Driver of Growth in Seasonally Dry Areas

The comparison of climate–growth relationships between the seasonally dry Mediterranean and North American conifer forests revealed that growth was mainly constrained by high minimum or night temperatures. This agrees with the inferences on IADF formation based on dendrometer data and the recent study demonstrating that growth occurs when the VPD is low enough [9]. In both study sites, high night temperatures from spring to autumn lead to VPD drops and reduced radial growth. This occurs during the peak of the growing season in spring [3,26], but also during late summer and autumn when latewood is formed.

Consequently, a high VPD could reduce cambial activity and growth either in conifers showing unimodal (spring peak) growth or in conifers from seasonally dry areas showing bimodal growth (spring and autumn peaks). If bimodality provides some adaptive advantage by growing during two wet–cool seasons [3,26,49,50], warmer conditions during night leading to elevated VPD values could lessen that benefit. The presented analyses indicate that forecasting growth and IADF formation would require considering the seasonal trends of minimum temperatures. For example, an increase in April, June, and July minimum temperatures would be detrimental to conifer growth in regions such as south-western USA and northern Mexico under the influence of the North American monsoon, but it would not affect Mediterranean conifer forests subjected to dry summer conditions. Moreover, warmer night conditions could also impair the capacity of trees to recover after previous dry seasons such as spring in North American monsoonal forests or summer in the Mediterranean

basin forests [51,52]. A rise in autumn minimum temperatures would reduce growth in both biogeographic regions and also decrease the formation of IADFs. Indeed, a significant ($p < 0.05$) increase in autumn temperatures was observed since 1950 in all study Spanish sites excepting Retuerta de Pina and Prades sites. A similar trend towards warmer autumn conditions, particularly in night, was also detected when analyzing minimum temperatures in the two compared sites from north-eastern Spain and south-western USA.

The proposed ideas on the links between tree growth and minimum temperature, a proxy of night VPD, could be further tested by comparing more conifer species and sites in seasonally dry regions. Furthermore, I also propose testing at a global scale if minimum (night) temperatures are a more important driver of tree radial growth than maximum (day) temperatures using international tree-ring databases.

5. Conclusions

Latewood IADFs were formed in response to wet conditions from late summer to early autumn in six conifer species inhabiting sites with Mediterranean climate conditions (dry summer). The formation of IADFs was also positively related to growth rate, indicating they tend to form during years with favorable (wet) climate conditions. Hourly dendrometer data taken in two species (*P. halepensis*, *J. thurifera*) showed that growth during the period of IADF formation (August–September) mainly happened in early night (20–2 h) and early morning (6–8 h), when the VPD was low enough due to summer storms. Warmer night temperatures would reduce wood production during the main growth peak in spring, but also during the second peaks in late summer and autumn, thus decreasing IADF production. Therefore, further research could investigate if growth rate and phenology (unimodal vs. bimodal patterns) are changing or shifting as a function of different seasonal increases in minimum temperature. Growth changes could be also linked to the variability in the formation of conspicuous, climate-driven, wood-anatomical features such as latewood IADFs.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13091425/s1>, Figure S1: Map of study sites; Figure S2: Climate conditions in sites where latewood IADFs are formed; Figure S3: Example of climate–IADF relationships; Figure S4: Climate–IADF relationships in *Pinus pinaster*; Figure S5: Climate–IADF relationships in *Pinus halepensis*; Figure S6: Climate–IADF relationships in *Juniperus thurifera*; Figure S7: Climate–IADF relationships in *Abies pinsapo*, *Pinus sylvestris*, and *Cedrus atlantica*; Figure S8: Climate–IADF relationships based on 10-day long precipitation windows; Figure S9: Frequency of the phases of stem contraction, expansion, and growth; Figure S10: Hourly precipitation and VPD data in August and September; Figure S11: Hourly changes in stem radial increment rates in *Pinus halepensis* and *Juniperus thurifera*; Figure S12: Hourly changes of temperature, relative air humidity, and vapor pressure deficit.

Funding: This research was funded by the SPANISH MINISTRY OF SCIENCE, INNOVATION AND UNIVERSITIES, grant number RTI2018-096884-B-C31.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are available upon request from the corresponding author.

Acknowledgments: I thank two reviewers and the editor for their comments. I also thank several colleagues for showing me some of the sampling sites and helping with data acquisition: Emilia Gutiérrez, Arturo Pacheco, Michele Colangelo, Antonio Gazol, José Bellosta, Carlos Castanao, Juan Carlos Linares, Maika Folch, and José Antonio Bonet, among others. This work is dedicated to the memory of Nemesio Camarero López who recently passed away.

Conflicts of Interest: The author declares no conflict of interest.

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