Accepted Manuscript in Agricultural and Forest Meteorology, v. 256-257, pp. 220-230.

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Authors: Jorge Aldea, Felipe Bravo, Javier Vázquez-Piqué, Álvaro Rubio-Cuadrado, Miren del Río

DOI: https://doi.org/10.1016/j.agrformet.2018.03.013

Please cite this article as: Aldea, J., Bravo, F., Vázquez-Piqué, J., Rubio-Cuadrado, A., del Río, M., 2018. Species-specific weather response in the daily stem variation cycles of Mediterranean pine-oak mixed stands. Agric. For. Meteorol. 256-257, 220-230.

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Authors: Aldea, J.[a,b], Bravo, F.[a,b], Vázquez-Piqué, J.[c], Rubio-Cuadrado, A.[d], Río, M. del[e,a]

[a] Sustainable Forest Management Research Institute, University of Valladolid - INIA, Avda. Madrid, s/n, 34004, Palencia, Spain.

[b] Departamento de Producción Vegetal y Recursos Forestales, ETS de Ingenierías Agrarias. Universidad de Valladolid, Palencia, Spain.

[c] Department of Agroforestry Sciences , Escuela Técnica Superior de Ingeniería, University of Huelva, Campus Universitario de La Rábida, Palos de la Frontera, 21819. Huelva. Spain.

[d] Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid. Ciudad Universitaria, s/n, 28040, Madrid, Spain.

[e] Department of Silviculture and Forest Management, INIA, Forest Research Centre, Ctra.A Coruña, km 7.5, 28040 Madrid, Spain.

Corresponding author: Aldea, J. email: jorge.aldea@uva.es

Highlights:

- Maximum daily radial variation for pine occurred in spring, but in summer for oak
- Number of spring daily cycles with radial increment was higher for pine than oak
- Species responded differently to air temperature according daily radial variation
- Rain increased daily radial variation and cycle duration in both species
- Water availability limited daily radial increment for both species

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[a] Sustainable Forest Management Research Institute, University of Valladolid - INIA, Avda. Madrid, s/n, 34004, Palencia, Spain.

[b] Departamento de Producción Vegetal y Recursos Forestales, ETS de Ingenierías Agrarias. Universidad de Valladolid, Palencia, Spain.

[c] Department of Agroforestry Sciences , Escuela Técnica Superior de Ingeniería, University of Huelva, Campus Universitario de La Rábida, Palos de la Frontera, 21819. Huelva. Spain.

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Abstract

Climate change forecasts are particularly severe for the western Mediterranean Basin, where rising temperatures and decreased precipitation could increase the frequency of drought events. Understanding the specific weather drivers of radial variation in Mediterranean mixed forest stands will allow us to better predict the ecological and production alterations that may result from climate change. Here, we studied species differences in stem daily radial variation cycles and daily radial increment of Mediterranean pine-oak (*Pinus pinaster-Quercus pyrenaica*) mixed stands over three climatically contrasted years (2012-2014) at two sites with dissimilar drought conditions. Our aim was to uncover differences in the weather drivers of daily radial variation for the two co-existing species. High-resolution point dendrometers were installed in dominant oak and pine trees, so that daily radial variation cycles were analyzed. Linear mixed models were fitted to analyze species-specific response to weather. Air temperature leads to radial stem-size changes in daily variation cycles with different species responses. Precipitation increased daily radial variation and cycle duration in the same way for both species. Daily radial increment and number of cycles with increment phase during spring was mostly higher for pine than oak, and water availability was the most important control factor for the phase mentioned. Differences in species response to weather conditions may offset the usual low production of pure oak coppice Mediterranean stands and highlight the role of mixed forests as a possible adaptation strategy for climate change.

Highlights:

- Maximum daily radial variation for pine occurred in spring, but in summer for oak
- Number of spring daily cycles with radial increment was higher for pine than oak
- Species responded differently to air temperature according daily radial variation
- Rain increased daily radial variation and cycle duration in both species
- Water availability limited daily radial increment for both species

Keywords: climate change, drought, high-resolution dendrometers, tree water deficit, *Pinus pinaster*, *Quercus pyrenaica*

1. Introduction

Climate change may impact Mediterranean forests harshly (Dankers and Hiederer, 2008). Changes in extreme climatic conditions, such as more frequent and severe summer droughts, might affect the provision of goods and forest services (Hanewinkel et al., 2012). Climate change could influence biodiversity and ecosystem functioning through phenological alterations (Büntgen et al., 2015), species-specific distribution range shifts (Peñuelas et al., 2007), changes in forest production (Linares and Camarero, 2012; Pretzsch et al., 2014) and subsequent changes in carbon storage (Vayreda et al., 2012).

Projected climate changes give urgency to the need for a better understanding of the effects of meteorological factors on growth in Mediterranean forests. Rising temperatures and drought events seem to be the key causes of tree decline in Mediterranean forests, despite tree acclimation to cope with climate change through phenological changes and increased water-use efficiency (Hartmann et al., 2015; Natalini et al., 2016; Peñuelas et al., 2011).

In this context, mixed forest stands could play an important role in preventing or reducing adverse changes. Mixed species stands might be more stable than monospecific ones, because of their greater resilience and resistance to biotic and abiotic factors (Guyot et al., 2016; Knoke et al., 2008; Pretzsch et al., 2013) and their higher temporal stability (Jucker et al., 2014; del Río et al., 2017). Mixtures could increase resistance and resilience in extreme drought conditions through complementary use of water resources based on species niche partitioning and alterations in water-use efficiency (Forrester, 2014). Although studies have shown contrasting results depending on species composition and site conditions, the positive effect of mixing species seems relevant to drought-prone sites (Grossiord et al., 2014; Forrester et al, 2016).

Monitoring stem radial variations can provide insight into intra-annual stem dynamics and improve our understanding of climate impacts on tree physiology and growth processes (Deslauriers et al., 2007; Drew and Downes, 2009; King et al., 2013). Continuous or high-resolution dendrometer recordings provide valuable information on tree stem radial variation along with the possibility of studying tree response to environmental influences at a high temporal resolution (Siegmund et al., 2016). High-resolution dendrometers are commonly used for studying seasonal tree growth dynamics, uncovering the environmental parameters that drive tree growth, and monitoring aspects of tree water balance such as water use and drought stress (Van der Maaten et al., 2016; Zweifel, 2016; Zweifel et al., 2016). Consequently, automatic dendrometers are now widely used to provide high-resolution stem variation data on coniferous and broadleaf trees from boreal to tropical forests (King et al., 2013). However, because these analyses often involve short observation periods, they do not accurately capture radial variations under contrasting weather conditions (King et al., 2013).

The handful of studies that have reported on seasonal variations in tree stem radius in Mediterranean areas mostly confirm the dominant role of temperature as the major constraint on radial increment in short time scales, and of precipitation effects in monthly scales (Camarero et al., 2010; Gutiérrez et al., 2011; Vieira et al., 2013). High-resolution stem diameter variation studies on mixed forests in this region are also infrequent. Sánchez-Costa et al., (2015) found contrasting growth and water use strategies in four co-occurring Mediterranean species, and Camarero et al., (2010) reported species-specific differences in xylogenesis patterns in mixed stands of *Juniperus thurifera* L., *Pinus halepensis,* and *Pinus sylvestris* L. However, very little research is available concerning daily radial variation cycles in mixed stands, so remains unclear in the Mediterranean climate.

Recent studies have shown that the Mediterranean tree species *Pinus pinaster* Ait. and *Quercus pyrenaica* Willd are highly vulnerable to intense drought events (Gea-Izquierdo et al., 2013; Prieto-Recio et al., 2015). *P.pinaster* is one of the most common pine tree species in Spain and usually establishes spontaneous mixed stands with *Q.pyrenaica*. Consequently, forest management strategies during the second half of the twentieth century included re-introducing pine into oak coppice stands. These co-occurring species show different successional and phenological traits: light-demanding pine species are dominant in early successional stages, while deciduous oak is a moderately shade-tolerant tree that predominates in the late-successional stage. Studies of radial variation cycles focusing on these species are insufficient, with the exception of Vieira et al. (2013), who worked with *P.pinaster* for one year only (2010). A previous study by Aldea et al., (2017) on the same stands used in the current work, showed species differences in radial increment patterns and positive effects from heavy thinning. However, these were based on data from band dendrometer measurements, which have lower temporal resolution.

For the research presented here, we used high-resolution dendrometer data to investigate species-specific tree responses to contrasted meteorological conditions in Mediterranean pine-oak mixed forest stands during the 2012-2014 period. The aims of the present study were 1) to show species differences in daily radial variation cycles, 2) to uncover species-specific weather responses in daily radial variation cycles and 3) to identify the weather variables that drove radial increment. We tested the hypotheses that (i) daily radial variation cycles varied according to seasons and species; (ii) differences were due to species responding differently to weather conditions and (iii) temperature and water availability were the main factors limiting radial increment, as expected in Mediterranean areas.

2. Materials and methods

2.1. Study sites

The study took place at two experimental sites with different drought conditions in central Spain: Lubia (Soria; 41º 39’ N, 2º 29’ W) and San Pablo de los Montes (Toledo; 39º 31’ N, 4º 16.6’W). The Lubia site was located at an altitude of 1,134 m.a.s.l. on a continental plateau. It has a sub-humid continental Mediterranean climate with an annual rainfall of 512 ± 133 mm, of which 100 ± 49_ mm falls during the summer drought period, between June and August (AEMET, 2016; Spanish State Meteorological Agency). Annual mean temperature is 10.0 ± 1.6 ºC and the hottest month is July, with an average temperature of 18.9± 2.9 ºC. Frost occurs from September to May.

The site at San Pablo de los Montes was established in the Montes de Toledo mountain range at 1,102 m.a.s.l. It has a continental Mediterranean climate, average rainfall of 469±_122 mm and a marked summer drought between June and August, with 49 ± 51 mm recorded rainfall (AEMET, 2016). Annual mean temperature is 12.9± 0.6 ºC and the hottest month is July, with an average temperature of 23.9± 1.1 ºC. Frost occurs from November to March.

The Walter-Lieth annual aridity index (WAI) was calculated using the ‘BIOdry’ R package (Lara et al., 2013), based on historical climate records (1981-2010; AEMET, 2016) that revealed drought differences for the sites: WAI of 0.22 for Lubia and 0.65 for San Pablo de los Montes. Hereafter, we will refer to these sites as WAI-0.22 and WAI-0.65, respectively.

The forest stands at both sites were generated by afforestation over a *Q. pyrenaica* coppice stand in the 1970s. The ground was prepared by bulldozer screefing, followed by strip sowing with *P.pinaster*. Today, these stands are a mixed even-aged forest composed of these two species arranged in strips and with closed canopy cover.

2.2. Stem radial variation and climatic measurements

Three dominant trees per species and site (twelve trees in total) were selected for installation of electronic point dendrometers. The pine trees chosen for sampling were 268.8 mm (standard deviation (sd) of 15.3 mm) in diameter at breast height and 11.2 m (0.7 m sd) high, while the oaks were 94.5 mm (7.3 mm sd) in diameter and 7.4 m (0.8 m sd) high. All trees were similar in age and there were no significant differences in species diameter or height between sites.

In autumn 2011, we installed electronic point dendrometers (Depfor, University of Huelva, details are available in Vázquez-Piqué et al., 2009) with a resolution of 1 μm in the selected trees to measure stem radial variation at breast height. Dead outermost layers of the bark were slightly removed to reduce the influence of hygroscopic bark swelling and shrinkage on dendrometer measurements. Data loggers were programmed to record measurements every 15 min for the entire 2012-2014 study period.

Site weather variables were continuously monitored using a variety of sensors. Air temperature, relative humidity and dew point were recorded at 15 min resolution using a data logger (HOBO U12 4-External Channel) placed at the WAI-0.22 site. A weather station (HOBO) was installed at the WAI-0.65 site to record air temperature, relative humidity, rainfall, solar radiation and wind speed. Additionally, temperature, precipitation and radiation records were compiled using hourly data from the AEMET automatic network stations (Lubia-Ceder 2044B and San Pablo de los Montes 3298X) located 6 km and 5 km from the WAI-0.22 and WAI-0.65 sites, respectively, to fill gaps in the climate information. Mean vapor pressure deficit was also estimated from former weather measurements, and we applied indirect method described by Zweifel et al., (2005), to calculate tree water deficit by tree and year, using dendrometer measurements to quantify drought stress based on potential linear growth during periods of stem shrinkage (Zweifel et al., 2016).

Summer drought was severe in 2012 at the WAI-0.22 site, while 2013 and 2014 had high spring and autumn rainfall, respectively (Figure 1). Conversely, summer drought was present in all sampling years at WAI-0.65, but precipitation was very low at both sites during winter and spring of 2012.

Figure 1. Climograms of sampling years by site.

2.3. *Data analysis*

2.3.1. *Radial stem variation cycle approach*

The sub-hourly dendrometer values were averaged to hourly resolution to link them with environmental variables, as well as to identify and correct errors or wrong measurements. Gaps of short duration (lower than a day, longer gaps remained unfilled) and abrupt jumps were corrected using an ARIMA model for the trend series from the same tree and season (Van der Maaten et al., 2016).

Daily radial variation series for each tree and year were processed individually according to the stem cycle approach (Deslauriers et al., 2011; Drew and Downes, 2009; Van der Maaten et al., 2016, 2013), which splits radial variation cycles into three different phases: (1) contraction, the period between the first maximum radius and the next minimum radius; (2) expansion, the period from the minimum to the next morning maximum; and (3) stem radial increment, part of the expansion phase from the time when the stem radius exceeds the morning maximum until the subsequent maximum (Figure 2).

Stem radial increment (mm) and duration (hours) of the radial increment phase in the daily variation cycles were calculated for each tree and year. We also defined several metrics based on sinusoidal waveform characteristics, in order to explore features of full daily radial variation cycles (Figure 2). The difference between local maximum and minimum stem radius in the daily cycle is the amplitude of the cycle (mm), i.e., the maximum daily radial variation for a full cycle. Similarly, the period variable was defined as the duration, or the time (hours) required to complete a full cycle. The statistics extraction from cycle, gap filled and environmental linked was performed using ‘dendrometeR’ R package (Van der Maaten et al., 2016).

Figure 2. Schematic representation of stem daily radial variation cycle, divided into three distinct phases: contraction (grey dots), expansion (white and black dots) and stem radial increment (black dots). Daily amplitude coincides with the magnitude of radial expansion (Rmax - Rmin). Period is the duration of full cycle.

To better describe stem radial variation throughout the year, dendrometer series were divided into five periods or seasons according to Vieira et al., (2013): winter dormancy, during which radius variation was around zero; spring growth, from the start of positive radial increment until the spring maximum; pre-summer contraction, when the daily increment was negative; summer dormancy, when radial increment ceased and autumn, when rehydration occurred and radial increment increased rapidly in a short period of time. Radial variation cycles were defined as a symmetrical sinusoidal waveform for better visualization of daily seasonal cycles.

Species and season differences in amplitude and period for full daily cycles were calculated by applying non-parametric statistics based on global rankings, which compute simultaneous confidence intervals and adjusted p-values based on Tukey contrasts for repeated measurements. Similarly, we calculated species and year differences in magnitude (mm), duration (hours) and number of cycles with the radial increment phase using the *npar.t.test* and *mctp.rm* functions from ‘nparcomp’ R package (Konietschke et al., 2015).

2.3.2. Weather effect on stem radial variation cycle and increment phase

Linear mixed models were fitted to determine the influence of meteorological variables on the amplitude and period of radial variation cycles, and on the magnitude of the increment phase. To better understand the influence of meteorological variables on the increment phase, especially when growth takes place, the model was also fitted for two different time scales: annual and spring. Mean, sums (when necessary), maximum, and minimum values of meteorological variables were calculated for full cycles. The structure of the linear mixed model was as follows:

$$\boldsymbol{log(\rho_{ijk} + 1) = \alpha_0 + f(weather) + (\alpha_1 + f(weather)) * oak + \omega_k + u_{jk} + v_{ijk} + \varepsilon_{ijk}} \qquad [1]$$

where $\boldsymbol{\rho}_{\mathbf{ijk}}$ is the amplitude (mm), period (hours) of full radial variation cycle or daily radial increment (mm), for tree *i* in site *j* and year *k* (mm); $\boldsymbol{\alpha_0}$ and $\boldsymbol{\alpha_1}$ are the intercept regression coefficients for pine and oak, respectively*;* $\boldsymbol{f(weather)}$ is a linear function of weather variables; $\boldsymbol{oak}$ is a dummy variable with values of 1 for oak and 0 for pine; $\boldsymbol{\omega}_{\mathbf{k}}$ ~N (0, $\boldsymbol{\sigma_k}$) is the year random effect; $\boldsymbol{u_{jk}}$ ~N (0, $\boldsymbol{\sigma}_{\mathbf{j}\boldsymbol{k}}$) is the site random effect; $\boldsymbol{v_{ijk}}$~N (0, $\boldsymbol{\sigma_{ijk}}$) is the tree random effect and $\boldsymbol{\varepsilon_{ijk}}$~N (0, $\boldsymbol{\sigma}_{\mathbf{e}}$) is the error term for each individual *i* in each site *j* for year *k*.

Additionally, previous scatter plots were analyzed to check for possible non-linear relationships between response and weather variables. The best random and fixed effect structures were fitted by restricted and maximum likelihood, respectively. Explanatory variables were chosen based on stepwise model selection using Akaike information criterion (AIC) to find the most parsimonious model. Multicollinearity of environmental variables was controlled by variance inflation factor values. Serial autocorrelation was assessed by partial and autocorrelation function plots, and several serial correlation structures were evaluated (autoregressive, moving average, and a mixed autoregressive-moving average model) to account for residual autocorrelation. A variance function for modeling heteroscedasticity was used for several structures (exponential, power, and constant plus power of the absolute value of the variance covariate) (Pinheiro and Bates, 2000).

3. *Results*

Cumulative annual radial increment patterns confirmed a marked bimodal pattern for both species regardless of the year (Figure 3) as a consequence of summer drought, which is typical in Mediterranean environments (Albuixech et al., 2012; Camarero et al., 2010). Cumulative intra-annual radial increment patterns differed between species and among years. Pine species always presented a higher spring and autumn asymptotic parameter than oak, along with a greater spring increment rate. Low precipitation in autumn 2011 and spring 2012 provoked an extreme drought in 2012 at both locations, resulting in low cumulative radial increment for both species. However, high winter or spring rainfall during 2013 and 2014 increased annual cumulative radial increment, despite summer drought (Figure 3).

Figure 3. Mean observed cumulative radial increment values for each species for the three sampling years. Filled area shows confidence intervals (95%).

3.1. Seasonal differences in stem radial variation cycles

Trees generally revealed a synchronous shrinking and swelling cycle response at the site level (data not shown) corresponding to daytime, when trees transpire quickly, and nighttime, when processes leading to water depletion or replenishment occur rapidly. Comparisons of mean full cycles throughout the year reveal variation among seasons and species (Figures 4 and 5). The lowest amplitudes were observed in winter, regardless of species (p-value lower than 0.01). Oak had the highest amplitude during pre-summer and summer, while amplitude was greatest for pine in spring, when growth occurs (p-value lower than 0.01 for both cases). Amplitude was higher for pine than oak during winter and spring, but the opposite occurred in pre-summer and summer (p-value lower than 0.01). However, period was always lower for pine than oak (p-value lower than 0.01), except in pre-summer and summer, when there were no differences between species (p-value 0.65). The cycle period was higher during winter and autumn, and lower in summer (p-value lower than 0.05).

Figure 4. Mean daily radial variation cycles by season and species.

Figure 5. Differences in amplitude (mm), period (hours) and onset of contraction phase for daily radial variation cycles by species and season. Error bars indicate confidence intervals (95%) and asterisk denotes significant differences between species.

3.2. Weather effect on amplitude and period of stem radial variation cycles

Models fitted for weather drivers of amplitude and period showed the importance of air temperature and rain (Table 1 and Figure 6). A non-linear relation (expressed as logarithm plus five to avoid mathematical indeterminacy) was found between amplitude, period, and air temperature. Water deficit was also related to high radial cycle amplitude, which supports summer observations. The effect of air temperature on the amplitude of daily cycles differed between species. In both species, amplitude increased with increasing air temperature (from 6º C for oak), though pine presented a more moderate trend (Figure 6). Amplitude also increased in oak species at air temperatures below 6.0 ºC, according to the fitted model in Table 1. Furthermore, though period was affected by air temperature, precipitation had a drastically higher impact on both species.

Table 1. Model fitted for amplitude and period of stem radial variation cycles (Eq. 1). Significant parameters are in bold. $\boldsymbol{\alpha_0}$ and $\boldsymbol{\alpha_1}$ are the intercept regression coefficients for pine and oak respectively; T_{air} is air temperature (ºC); P is daily precipitation(mm); Wd is water deficit (mm); $\boldsymbol{\sigma_k}$ is standard deviation for year random effect; $\boldsymbol{\sigma_{jk}}$ is standard deviation for site random effect; $\boldsymbol{\sigma_{ijk}}$ is standard deviation for tree random effect; $\boldsymbol{\sigma_e}$ is standard deviation for error term; $\boldsymbol{\varphi}$ and $\boldsymbol{\theta}$ are autoregressive and moving average for ARMA(1,1) residual serial correlation parameters; $\boldsymbol{\delta_1}$ and $\boldsymbol{\delta_2}$ are function parameters used to model residual variance as an exponential function of the variance covariate vector ($\boldsymbol{g_{ijk}}$) for amplitude: $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{2\delta_1 g_{ijk}}}$ or constant plus a power for period: $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2}$

Parameter	Amplitude		Period	
	Coefficient	p-value	Coefficient	p-value
$\boldsymbol{\alpha_0}$ (pine)	$1.18\cdot10^{-2}$	0.178	**2.995**	**<0.001**
$\boldsymbol{T_{air}}$(pine)	$1.63\cdot10^{-4}$	0.662	**$-7.32\cdot10^{-3}$**	**0.002**
$\boldsymbol{log(T_{air}+5)}$ (pine)	**$1.05\cdot10^{-4}$**	**0.021**	**$9.94\cdot10^{-2}$**	**0.005**
$\boldsymbol{\alpha_1}$ (oak)	**$8.85\cdot10^{-2}$**	**<0.001**	$2.25\cdot10^{-1}$	0.066
$\boldsymbol{T_{air}}$(oak)	**$3.69\cdot10^{-3}$**	**<0.001**	$-2.41\cdot10^{-3}$	0.517
$\boldsymbol{log(T_{air}+5)}$ (oak)	**$-5.30\cdot10^{-2}$**	**<0.001**	$-4.98\cdot10^{-2}$	0.3945
$\boldsymbol{P}$	**$1.52\cdot10^{-3}$**	**<0.001**	**$4.34\cdot10^{-2}$**	**<0.001**
$\boldsymbol{Wd}$	**$1.70\cdot10^{-1}$**	**<0.001**	0.0811916	0.098
$\boldsymbol{\sigma_k}$ (year)	$1.14\cdot10^{-6}$		$1.26\cdot10^{-6}$	
$\boldsymbol{\sigma_{jk}}$(site)	$1.15\cdot10^{-6}$		$2.76\cdot10^{-2}$	
$\boldsymbol{\sigma_{ijk}}$(tree)	$2.34\cdot10^{-7}$		$2.31\cdot10^{-2}$	
$\boldsymbol{\sigma_e}$(error)	$1.62\cdot10^{-2}$		$2.78\cdot10^{-5}$	
$\boldsymbol{\varphi}$	0.961		-0.340	
$\boldsymbol{\theta}$	-0.663		0.285	
$\boldsymbol{\delta_1}$	11.151		$2.06\cdot10^{-6}$	
$\boldsymbol{\delta_2}$	----		7.668	

Fig. 6.Species-specific effect of air temperature on amplitude of daily radial variation cycles (left). Air temperature and precipitation effects on period of radial variation cycles for both species (right). Simulation from the fitted linear mixed models for the air temperature and precipitation range. "Wet" weather corresponded to the 95th percentile of daily precipitation range and "Dry" weather corresponded to no rain.

3.3. Species differences in the spring radial increment phase

Radial increment phase was more frequent in spring time, when it is possible to ensure that xylem growth occurs. Hence, spring was the most interesting period for analyzing radial increment. Daily radial increment and number of cycles with a radial increment phase varied with years and species in spring (Figure 7). However, no remarkable differences in the duration of the increment phase between species were found (results not shown). Daily radial increment showed significant differences between species (higher for pine) during 2013 and 2014 at the WAI-0.65 site (p-value lower than 0.01, Figure 7), and only in spring 2013 at the WAI-0.22 site (p-value 0.02). The number of cycles with increment phase was always higher for pine, regardless of site and year (p-value lower than 0.01), except in 2013 at the WAI-0.65 site (Figure 7). The number of cycles with increment phase was also lower in the 2012 drought year, regardless of species and site (p-value lower than 0.01), but with no significant differences for oak at the WAI-0.22 site.

Figure 7. Differences of daily radial increment and number of cycles with increment phase in spring by site, year, and species. Error bars indicate confidence intervals (95%), asterisk denotes significant differences between species.

3.4. *Weather drivers of the radial increment*

The results from the fitted model for daily radial increment (Eq. 1) are shown in Table 2. Statistically significant weather variables that were included in the final model for spring time were mean air temperature (Tair; ºC), solar radiation (SR; 10KJ/m^2), and accumulated rainfall per daily cycle (P; mm). Two additional variables, water deficit (Wd; mm) and mean vapor pressure deficit (VPD; kPa), were significant when all annual periods were taken into account. Mean air temperature, solar radiation, and the amount of rainfall caused higher radial increments. In the annual analysis, however, was negatively affected by water deficit and high vapor pressure deficit values, which were especially acute during summer time.

Table 2. Model fitted for annual and spring daily radial increment (Eq. 1). Significant parameters are in bold. $\boldsymbol{\alpha_0}$ *and* $\boldsymbol{\alpha_1}$ *are the intercept regression coefficients for pine and oak, respectively;* T_{air} *is air temperature (ºC);SR is solar radiation (10KJ/m*^{2}*); Wd is water deficit (mm); VPD is mean vapor pressure deficit (kPa); P is daily precipitation(mm);* $\boldsymbol{\sigma_k}$ *is standard deviation for year random effect;* $\boldsymbol{\sigma_{jk}}$ *is standard deviation for site random effect;* $\boldsymbol{\sigma_{ijk}}$ *is standard deviation for tree random effect;* $\boldsymbol{\sigma_e}$ *is standard deviation for error term;* $\boldsymbol{\varphi}$ *and* $\boldsymbol{\theta}$ *are autoregressive and moving average for annual and spring residual serial correlation parameters from AR(1) and ARMA(1,1), respectively;* $\boldsymbol{\delta_1}$ *and* $\boldsymbol{\delta_2}$ *are function parameters used*

to model residual variance as constant plus a power of the absolute value of the variance covariate (g_{ijk}): $Var(\varepsilon_{ijk}) = \sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2$

Parameter	**Annual**		**Spring**	
	Coefficient	**p-value**	**Coefficient**	**p-value**
α_0 **(pine)**	$\mathbf{7.38\cdot10^{-3}}$	**<0.001**	$\mathbf{5.98\cdot10^{-3}}$	**0.002**
T_{air}	$\mathbf{5.15\cdot10^{-4}}$	**<0.001**	$\mathbf{9.76\cdot10^{-4}}$	**<0.001**
SR	$\mathbf{4.33\cdot10^{-4}}$	**<0.001**	$\mathbf{6.38\cdot10^{-4}}$	**<0.001**
Wd	$\mathbf{-1.68\cdot10^{-2}}$	**<0.001**	n.s.	n.s.
VPD	$\mathbf{-4.39\cdot10^{-3}}$	**<0.001**	n.s.	n.s.
P	$\mathbf{2.55\cdot10^{-3}}$	**<0.001**	$\mathbf{1.68\cdot10^{-3}}$	**<0.001**
α_1 **(oak)**	$\mathbf{-2.57\cdot10^{-3}}$	**0.002**	$\mathbf{-8.12\cdot10^{-3}}$	**<0.001**
σ_k **(year)**	$3.36\cdot10^{-7}$		$1.46\cdot10^{-3}$	
σ_{jk}**(site)**	$1.08\cdot10^{-3}$		$4.08\cdot10^{-8}$	
σ_{ijk}**(tree)**	$7.88\cdot10^{-4}$		$3.17\cdot10^{-7}$	
σ_e**(error)**	1.58		2.18	
φ	0.43		$8.77\cdot10^{-1}$	
θ	----		$-6.29\cdot10^{-1}$	
δ_1	$2.01\cdot10^{-3}$		$1.96\cdot10^{-3}$	
δ_2	1.15		1.32	

Interaction between weather variables and species was not significant, so the species dummy variable only affected the intercept (α_1). The value of this coefficient was negative regardless of the analysis time scale, showing the species growth effect of lower radial increment for oak than pine. Therefore, species responded to identical weather variables in the same way (linearly) but with higher radial increment reaction for pine species.

4. *Discussion*

4.1. *Species-specific stem radial variation cycles by seasons*

The dynamics of the stem size cycles might provide valuable information about water status (reversible process) and radial tree growth (irreversible process) (Turcotte et al., 2011; Vieira et al., 2013; Zweifel, 2016). We found differences in radial variation cycles across seasons and species, which support our first hypothesis. Differences observed in amplitude and period features from daily cycles provide insights into the relative changes in transpiration and/or soil water status over time (King et al., 2013).

We observed stem contraction generally from early morning until evening, reflecting the daily cycle of water uptake and loss, as in previous studies (King et al., 2013; Vieira et al., 2013). Several authors have found that most diurnal stem shrinkage occurs in the cambial zone, bark, and phloem, and that diurnal variation in the xylem cylinder is relatively small (Drew and Downes, 2009). Thus, differences between species in spring amplitude (Figures 4 and 5) could be related to higher pine crown area and leaf surface, which facilitate higher transpiration. Steppe et al., (2006) reported a close link between transpiration and sap flow, suggesting that spring amplitude differences might also be due to growth differences (higher for pine than oak, Table 2). Our results showed that the greatest amplitude in the daily variation cycle for pine occurred in spring. However in the findings of Vieira et al. (2013), this occurred in pre-summer, similar than oak species in the current study. Increased transpiration due to high air temperatures leads to elevated demand for water, which is scarce in summer time and provokes extreme contraction from shrinkage (King et al. 2013).

Therefore, our results appear to reveal species-specific responses to summer water stress, which could be related to different physiological mechanisms for coping with water stress. Oak anisohydric strategy involves high transpiration rates that are maintained during drought, eventually causing impairment of tree water status and higher radial cycle contraction. Accordingly, Sánchez-Costa et al., (2015) reported very low sap flow density regulation under drought conditions for similar Mediterranean oak species. Generally lower temperatures and photoperiods during autumn induced a decrease in physiological activity, leading to low amplitude and high period in daily radial cycles (Figures 4 and 5). Although Vieira et al., (2013) showed lower amplitude for pine in autumn, we observed the lowest amplitudes in winter regardless of species, which better corroborates with Biondi and Rossi, (2015). During winter, when no wood formation occurs, the circadian cycle of stem size becomes more erratic (Biondi and Rossi, 2015). Although photosynthesis may be observed for conifers during winter, air temperature is the dominant factor determining stem size fluctuations. This is attributed to water osmotic movement due to temperature changes near the sap freezing point (King et al., 2013; Zweifel et al., 2000). However, unlike what commonly occurs at high altitudes and latitudes, the cycles were not inverted at our study sites. This indicates that the sap did not reach the freezing point, as Vieira et al., (2013) also reported in a Mediterranean location.

Furthermore, differences in winter cycle period between species – which are higher for oak than pine (Figures 4 and 5) – could be due to anatomical differences (sapwood, cell walls, and vessels) that govern water relocation and are directly related to the higher hygroscopicity of oak compared to pine (Popper et al., 2005).

4.2. *The role of temperature and rain on daily radial variation cycles*

We found that temperature drove differences between species in amplitude cycles, whereas the effect of precipitation was similar (Figure 6 and Table 1). This partially demonstrated our second hypothesis. Changes in amplitude or period related to freezing and swelling have been observed in other species (King et al., 2013; Turcotte et al., 2011). Although available soil water certainly plays a role in the dynamics of tree water movement (higher amplitude), stem contraction is more closely linked to temperature (evapotranspiration demand in summer and thermal contraction in winter).

The relation between air temperature and stem cycle amplitude in our study showed clear increases in amplitude with increased temperature, as found by King et al., (2013) for larch and spruce. This suggests a higher contraction phase due to the depletion of stem water reserves in response to greater evaporative demand, which is driven by warmer temperatures. Similarly, increased water deficit resulted in a greater amplitude of the radial variation cycle (Table 1), which could also explain the high amplitude during summer time (Figures 4 and 5). Turcotte et al., (2011) reported that water deficit during the day led to a pronounced contraction phase for boreal black spruce. Thus, amplitude differences between species at high temperatures may indicate the abovementioned species-specific responses to water stress. We also found that rain increased the amplitude cycles (Table 1) and was related to rehydration processes, as in previous studies (Deslauriers et al., 2007; Vieira et al., 2013).

Amplitude of radial variation cycles during wintertime was related to different species-specific responses to freezing events (Figure 6 and Table 1): pine decreased in amplitude, while oak increased. Vieira et al., (2013), reported a similar pattern for maritime pine in a Mediterranean area, while King et al., (2013) reported amplitude increment for spruce and larch at freezing temperatures, which resembled the behavior of oak. The different response pattern for pine could be due to very rare winter temperatures below -5ºC at both sites. Similarly, higher amplitude for pine in a large temperature range might be related to higher radial increment rates, especially in spring (Figure 3 and Table 2).

However, species did not show a different response to weather variables for the duration of full daily radial cycle (Table 1). Thus, only weather variables (temperature and rain) controlled the period of radial variation cycles, as reported by Vieira et al., (2013).

Here, we found that period decreased with increased temperature. Thus, when temperatures are especially high and the days are longer during pre-summer and summer, transpiration rates may be also high, causing faster contraction and higher recovery duration (results not shown), resulting in a compressed wave period (Figures 4 and 5). Deslauriers et al., (2007) demonstrated demonstrates that vapor water deficit had a direct effect on the duration and amplitude of the contraction phase, which may corroborate our results.

Additionally, the fitted model (Table 1) indicated that the period of radial variation cycles decreased at air temperatures below 8.5 ºC. We suggest that temperatures close to freezing may generate a faster contraction phase due to thermal response, leading to radial variation cycles with a compressed period. Although air temperature certainly plays a role in the radial variation cycle period, precipitation is more closely linked to higher period duration because of rehydration (Figure 6).

4.3. Meteorological drivers of radial increment

We expected species-specific responses to weather in radial increment phase based on different water status regulation strategies – anisohydric vs. isohydric behavior – and/or water uptake efficiency differences between the species. However, the two species responded to the same weather variables and in the similar way (linearly) modifying radial increment. This finding agrees with that of Sánchez-Costa et al., (2015) who reported coordinated responses of transpiration, water storage dynamics, and growth-based water use efficiency in Mediterranean pine and oak species. Conversely, in a previous study we found species-specific intra-annual radial increment responses to weather variables (Aldea et al., 2017). This may be explained by methodological and precision differences in estimating radial increment (biweekly rate vs. daily cycle analysis).

Overall, pine responded to weather with higher radial increment compared to oak (Table 2), which again supports partial acceptance of the second hypothesis. This may be related to differences in reproduction methods (seed vs. coppice), tree competition (higher for oak) or efficiency in using resources (early vs. late successional species). The number of daily cycles with increment phase was also higher for pine (Figure 7), except in 2013 at WAI-0.65, indicating species-specific growth phenology. Stomatal control tends to keep water status stable, especially in isohydric plants (Jones, 2007), giving pine trees the ability to store extra water storage in tissues or withdraw stored water from the stem. Oak trees are anisohydric; they maintain high transpiration rates regardless of soil water availability, so fewer cycles with increment phase would be expected.

The third hypothesis was confirmed: temperature, precipitation, and water deficit had an important role in driving radial increment, though solar radiation and vapor pressure deficit also affected it. Several authors have found positive correlations between air temperature and radial increment (Deslauriers et al., 2003; King et al., 2013; Van der Maaten et al., 2013), though other works report the opposite due to elevated transpiration rates, especially in summer (Deslauriers et al., 2007; Oberhuber et al., 2014).

Our results corroborated that precipitation is an important factor in radial increment in Mediterranean areas, as it allows growth and/or replenishment of internal water reserves in trees. Precipitation events increase available soil water, which is essential for photosynthesis and growth, but there is also evidence that rain plays a role in the stem rehydration process. The difficulty in differentiating these two effects with dendrometers leads to overestimation of the role of rain (Biondi and Rossi, 2015; King et al., 2013; Turcotte et al., 2011).

At the tree physiological level, the negative effect of high vapor pressure deficit concurs with other studies (Aldea et al., 2017; Oberhuber et al., 2014; Van der Maaten et al., 2013) and can be explained by increased evapotranspiration, which inhibits cell enlargement and growth (Oberhuber et al., 2014). Water deficit is also related to climate variables which influence transpiration (Oberhuber et al., 2015). This suggests that drought from June to August is a highly prominent factor in limiting growth for both species, as we observed for 2012. Though solar radiation promotes radial increment and could be related to photosynthesis and eventual growth, it may also increase transpiration rates, stem water movement and subsequent stem contraction (Duchesne and Houle, 2011; King et al., 2013).

5. *Conclusions*

The results of our study provided insight into environmental control of intra-annual radial increment in co-occurring species exposed to drought. The same weather variables drove radial increment for both species, though pine response was greater. This may directly impact stand dynamics and composition, especially in light of the predicted increase in aridity resulting from climate change in the Mediterranean region.

Air temperature and rain altered the amplitude and period for daily stem radial variation cycles, while water availability (rain vs. water deficit) seemed to be crucial for the radial increment phase. Thus, the increased temperatures and higher frequency of drought events that are forecasted for the Mediterranean region may alter radial variation cycles and decrease radial increment rates for both species. Forest management strategies that enhance radial growth in stands (especially for oak trees) are needed to offset possible ecological changes affecting species survival and the decreased production that may accompany global warming predictions.

6. Acknowledgments

This work was supported by funding from the Spanish Ministry of Economy and Competitiveness, through the research projects AGL2011-29701-C02-01, AGL2011-29701-C02-02, AGL2014-51964-C2-1-R and AGL2014-51964-C2-2-R. Jorge Aldea's work was funded by a partnership grant of the University of Valladolid and Banco Santander. The authors acknowledge all those who participated in the installation and implementation of dendrometer measurements, especially Raquel Onrubia, Javier Rodríguez, Eduardo Ballesteros and the Forestry Services of the Toledo and Soria provinces, where the sampling took place. Special thanks to Jose Riofrío, Nicolás Cattaneo, and Wilson Lara for the modeling and statistical suggestions. We also acknowledge the external reviewers for English correction. The authors also thank to Spanish State Meteorological Agency (AEMET) of the Ministry of Agriculture, Food and Environment for granting access to the meteorological data.

7. References

AEMET, 2016. Spanish State Meteorological Agency. Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente. Gobierno de España. [WWW Document]. Valores Clim. Norm. 1981–2010. URL www.aemet.es

Albuixech, J., Camarero, J.J., Montserrat-Marti, G., 2012. Dinamica estacional del crecimiento secundario y anatomia del xilema en dos Quercus mediterraneos que coexisten. For. Syst. doi:10.5424/fs/2112211-12076

Aldea, J., Bravo, F., Bravo-Oviedo, A., Ruiz-Peinado, R., Rodríguez, F., Del Río, M., 2017. Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands. Agric. For. Meteorol. 237, 371–383. doi:10.1016/j.agrformet.2017.02.009

Biondi, F., Rossi, S., 2015. Plant-water relationships in the Great Basin Desert of North America derived from Pinus monophylla hourly dendrometer records. Int. J. Biometeorol. doi:10.1007/s00484-014-0907-4

Büntgen, U., Egli, S., Galván, J.D., Diez, J.M., Aldea, J., Latorre, J., Martínez-Peña, F., 2015. Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. Fungal Ecol. doi:10.1016/j.funeco.2015.03.008

Camarero, J.J., Olano, J.M., Parras, A., 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytol. doi:10.1111/j.1469-8137.2009.03073.x

Dankers, R., Hiederer, R., 2008. Extreme Temperatures and Precipitation in Europe: Analysis of a High-Resolution Climate Change Scenario. Italy.

del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., et al. 2017. Species interactions increase the temporal stability of community productivity in Pinus sylvestris–Fagus sylvatica mixtures across Europe. Journal of Ecology, 105 (4): 1032-1043.

Deslauriers, A., Morin, H., Urbinati, C., Carrer, M., 2003. Daily weather response of balsam fir (Abies balsamea (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). Trees - Struct. Funct. doi:10.1007/s00468-003-0260-4

Deslauriers, A., Rossi, S., Anfodillo, T., 2007. Dendrometer and intra-annual tree growth: What kind of information can be inferred? Dendrochronologia. doi:10.1016/j.dendro.2007.05.003

Deslauriers, A., Rossi, S., Turcotte, A., Morin, H., Krause, C., 2011. A three-step procedure in SAS to analyze the time series from automatic dendrometers. Dendrochronologia. doi:10.1016/j.dendro.2011.01.008

Drew, D.M., Downes, G.M., 2009. The use of precision dendrometers in research on daily stem size and wood property variation: A review. Dendrochronologia. doi:10.1016/j.dendro.2009.06.008

Duchesne, L., Houle, D., 2011. Modelling day-to-day stem diameter variation and annual growth of balsam fir (Abies balsamea (L.) Mill.) from daily climate. For. Ecol. Manage. doi:10.1016/j.foreco.2011.05.027

Forrester, D.I. 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. For Ecol Manage 312:282–292

Forrester, D.I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., Grossiord, C., 2016. Drought responses by individual tree species are not often correlated with tree species diversity in European forests. Journal of Applied Ecology 53, 1725-1734.

Gea-izquierdo, G., Fernández-de-uña, L., Cañellas, I., 2013. Forest Ecology and Management Growth projections reveal local vulnerability of Mediterranean oaks with rising temperatures. For. Ecol. Manage. 305, 282–293. doi:10.1016/j.foreco.2013.05.058

Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Chećko, E., Forrester, D.I., Dawud, S.M., Finér, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., Gessler, A., 2014. Diversity does not always improve adaptation of forest ecosystems to extreme drought. Proceedings of the National Academy of Sciences. 111, 14812-14815

Gutiérrez, E., Campelo, F., Camarero, J.J., Ribas, M., Muntán, E., Nabais, C., Freitas, H., 2011. Climate controls act at different scales on the seasonal pattern of Quercus ilex L. stem radial increments in NE Spain. Trees - Struct. Funct. doi:10.1007/s00468-011-0540-3

Guyot, V., Castagneyrol, B., Vialatte, A., Deconchat, M., Jactel H., 2016. Tree diversity reduces pest damage in mature forests across Europe. Biol. Lett. 12: 20151037

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., Zimmermann, N.E., 2012. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Chang. 3, 203–207. doi:10.1038/nclimate1687

Hartmann, H., Adams, H.D., Anderegg, W.R.L., Jansen, S., Zeppel, M.J.B., 2015. Research frontiers in drought-induced tree mortality: Crossing scales and disciplines. New Phytol. doi:10.1111/nph.13246

Jones, H.G., 2007. Monitoring plant and soil water status: Established and novel methods revisited and their relevance to studies of drought tolerance, in: Journal of Experimental Botany. doi:10.1093/jxb/erl118

Jucker, T., Bouriaud, O., Avacariei, D. & Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecology Letters, 17, 1560–1569

King, G., Fonti, P., Nievergelt, D., Büntgen, U., Frank, D., 2013. Climatic drivers of hourly to yearly tree radius variations along a 6°C natural warming gradient. Agric. For. Meteorol. doi:10.1016/j.agrformet.2012.08.002

Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. Eur. J. For. Res. 127, 89–101. doi:10.1007/s10342-007-0186-2

Konietschke, F., Placzek, M., Schaarschmidt, F., Hothorn, L.A., 2015. nparcomp : An R Software Package for Nonparametric Multiple Comparisons and Simultaneous Confidence Intervals. J. Stat. Softw. doi:10.18637/jss.v064.i09

Lara, W., Bravo, F., Maguire, D.A., 2013. Modeling patterns between drought and tree biomass growth from dendrochronological data: A multilevel approach. Agric. For. Meteorol. 178–179, 140–151.

Linares, J.C., Camarero, J.J., 2012. From pattern to process: Linking intrinsic water-use efficiency to drought-induced forest decline. Glob. Chang. Biol. 18, 1000–1015.

Natalini, F., Alejano, R., Vazquez-Piqué, J., Cañellas, I., Gea-Izquierdo, G., 2016. The role of climate change in the widespread mortality of Holm oak in open woodlands of Southwestern Spain. Dendrochronologia 38:51-60. http://dx.doi.org/10.1016/j.dendro.2016.03.003.

Oberhuber, W., Gruber, A., Kofler, W., Swidrak, I., 2014. Radial stem growth in response to microclimate and soil moisture in a drought-prone mixed coniferous forest at an inner Alpine site. Eur. J. For. Res. doi:10.1007/s10342-013-0777-z

Oberhuber, W., Kofler, W., Schuster, R., Wieser, G., 2015. Environmental effects on stem water deficit in co-occurring conifers exposed to soil dryness. Int. J. Biometeorol. 59, 417–426. doi:10.1007/s00484-014-0853-1

Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Glob. Ecol. Biogeogr. doi:10.1111/j.1466-8238.2010.00608.x

Peñuelas, J., Ogaya, R., Boada, M., Jump, A.S., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30, 829–837. doi:10.1111/j.2007.0906-7590.05247.x

Pinheiro, J.C., Bates, D.., 2000. Mixed-effects models in S and Splus. Springer, New York.

Popper, R., Niemz, P., Eberle, G., 2005. Untersuchungen zum Sorptions- und Quellungsverhalten von thermisch behandeltem Holz. Holz als Roh - und Werkst.

doi:10.1007/s00107-004-0554-2

Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. Nat. Commun. 5, 4967.

Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. Plant Biol. doi:10.1111/j.1438-8677.2012.00670.x

Prieto-Recio, C., Martín-García, J., Bravo, F., Diez, J.J., 2015. Unravelling the associations between climate, soil properties and forest management in Pinus pinaster decline in the Iberian Peninsula. For. Ecol. Manage. 356, 74–83. doi:10.1016/j.foreco.2015.07.033

Sánchez-Costa, E., Poyatos, R., Sabaté, S., 2015. Contrasting growth and water use strategies in four co-occurring Mediterranean tree species revealed by concurrent measurements of sap flow and stem diameter variations. Agric. For. Meteorol. doi:10.1016/j.agrformet.2015.03.012

Siegmund, J.F., Sanders, T.G.M., Heinrich, I., van der Maaten, E., Simard, S., Helle, G., Donner, R. V., 2016. Meteorological Drivers of Extremes in Daily Stem Radius Variations of Beech, Oak, and Pine in Northeastern Germany: An Event Coincidence Analysis. Front. Plant Sci. 7, 733. doi:10.3389/fpls.2016.00733

Steppe, K., De Pauw, D.J.W., Lemeur, R., Vanrolleghem, P.A., 2006. A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. Tree Physiol. doi:10.1093/treephys/26.3.257

Turcotte, A., Rossi, S., Deslauriers, A., Krause, C., Morin, H., 2011. Dynamics of depletion and replenishment of water storage in stem and roots of black spruce measured by dendrometers. Front. Plant Sci. 2, 21. doi:10.3389/fpls.2011.00021

Van der Maaten, E., Bouriaud, O., van der Maaten-Theunissen, M., Mayer, H., Spiecker, H., 2013. Meteorological forcing of day-to-day stem radius variations of beech is highly synchronic on opposing aspects of a valley. Agric. For. Meteorol. doi:10.1016/j.agrformet.2013.07.009

Van der Maaten, E., Van der Maaten-Theunissen, M., Smiljanic, M., Rossi, S., Simard, S., Wilmking, M., Deslauriers, A., Fonti, P., von Arx, G., Bouriaud, O., 2016. DendrometeR: Analyzing the pulse of trees in R. Dendrochronologia. doi:10.1016/j.dendro.2016.06.001

Vayreda, J., Martinez-Vilalta, J., Gracia, M., Retana, J., 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. Glob. Chang. Biol. 18, 1028–1041.

Vázquez-Piqué, J., Martín-Tapias, R., Gónzalez-Pérez, A., 2009. Desarrollo, características y aplicaciones de un dendrómetro potenciométrico para la medición continua del crecimiento diametral de especies arbóreas. Actas del V Congr. For. Español. SECF y _Junta Castilla y León, Ávila. 11.

Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2013. Seasonal and daily cycles of stem radial variation of Pinus pinaster in a drought-prone environment. Agric. For. Meteorol. doi:10.1016/j.agrformet.2013.06.009

Zweifel, R., 2016. Radial stem variations - a source of tree physiological information not fully exploited yet. Plant, Cell Environ. doi:10.1111/pce.12613

Zweifel, R., Haeni, M., Buchmann, N., Eugster, W., 2016. Are trees able to grow in periods of stem shrinkage? New Phytol. doi:10.1111/nph.13995

Zweifel, R., Item, H., Häsler, R., 2000. Stem radius changes and their relation to stored water in stems of young Norway spruce trees. Trees - Struct. Funct. doi:10.1007/s004680000072

Zweifel, R., Zimmermann, L., Newbery, D.M., 2005. Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiol. 25, 147–156.

Figures captions

Figure 1. Climograms of sampling years by site.

Figure 2. Schematic representation of stem daily radial variation cycle, divided into three distinct phases: contraction (grey dots), expansion (white and black dots) and stem radial increment (black dots). Daily amplitude coincides with the magnitude of radial expansion (Rmax - Rmin). Period is the duration of full cycle.

Figure 3. Mean observed cumulative radial increment values for each species for the three sampling years. Filled area shows confidence intervals (95%).

Figure 4. Mean daily radial variation cycles by season and species.

Figure 5. Differences in amplitude (mm), period (hours) and onset of contraction phase for daily radial variation cycles by species and season. Error bars indicate confidence intervals (95%) and asterisk denotes significant differences between species.

Fig. 6.Species-specific effect of air temperature on amplitude of daily radial variation cycles (left). Air temperature and precipitation effects on period of radial variation cycles for both species (right). Simulation from the fitted linear mixed models for the air temperature and precipitation range. "Wet" weather corresponded to the 95th percentile of daily precipitation range and "Dry" weather corresponded to no rain.

Figure 7. Differences of daily radial increment and number of cycles with increment phase in spring by site, year, and species. Error bars indicate confidence intervals (95%), asterisk denotes significant differences between species.

Table 1

Table 1. Model fitted for amplitude and period of stem radial variation cycles (Eq. 1). Significant parameters are in bold. $\boldsymbol{\alpha_0}$ *and* $\boldsymbol{\alpha_1}$ *are the intercept regression coefficients for pine and oak respectively;* T_{air} *is air temperature (ºC); P is daily precipitation(mm); Wd is water deficit (mm);* $\boldsymbol{\sigma_k}$ *is standard deviation for year random effect;* $\boldsymbol{\sigma_{jk}}$ *is standard deviation for site random effect;* $\boldsymbol{\sigma_{ijk}}$ *is standard deviation for tree random effect;* $\boldsymbol{\sigma_e}$ *is standard deviation for error term;* $\boldsymbol{\varphi}$ *and* $\boldsymbol{\theta}$ *are autoregressive and moving average for ARMA(1,1) residual serial correlation parameters;* $\boldsymbol{\delta_1}$ *and* $\boldsymbol{\delta_2}$ *are function parameters used to model residual variance as an exponential function of the variance covariate vector (*$\boldsymbol{g_{ijk}}$*) for amplitude:* $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2 \cdot e^{2\delta_1 g_{ijk}}}$ *or constant plus a power for period:* $\boldsymbol{Var(\varepsilon_{ijk}) = \sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2}$

Parameter	Amplitude		Period	
	Coefficient	p-value	Coefficient	p-value
$\boldsymbol{\alpha_0}$ (pine)	$1.18\cdot10^{-2}$	0.178	**2.995**	**<0.001**
$\boldsymbol{T_{air}}$(pine)	$1.63\cdot10^{-4}$	0.662	$\mathbf{-7.32\cdot10^{-3}}$	**0.002**
$\boldsymbol{log(T_{air}+5)}$ (pine)	$\mathbf{1.05\cdot10^{-4}}$	**0.021**	$\mathbf{9.94\cdot10^{-2}}$	**0.005**
$\boldsymbol{\alpha_1}$ (oak)	$\mathbf{8.85\cdot10^{-2}}$	**<0.001**	$2.25\cdot10^{-1}$	0.066
$\boldsymbol{T_{air}}$(oak)	$\mathbf{3.69\cdot10^{-3}}$	**<0.001**	$-2.41\cdot10^{-3}$	0.517
$\boldsymbol{log(T_{air}+5)}$ (oak)	$\mathbf{-5.30\cdot10^{-2}}$	**<0.001**	$-4.98\cdot10^{-2}$	0.3945
$\boldsymbol{P}$	$\mathbf{1.52\cdot10^{-3}}$	**<0.001**	$\mathbf{4.34\cdot10^{-2}}$	**<0.001**
$\boldsymbol{Wd}$	$\mathbf{1.70\cdot10^{-1}}$	**<0.001**	0.0811916	0.098
$\boldsymbol{\sigma_k}$ (year)	$1.14\cdot10^{-6}$		$1.26\cdot10^{-6}$	
$\boldsymbol{\sigma_{jk}}$(site)	$1.15\cdot10^{-6}$		$2.76\cdot10^{-2}$	
$\boldsymbol{\sigma_{ijk}}$(tree)	$2.34\cdot10^{-7}$		$2.31\cdot10^{-2}$	
$\boldsymbol{\sigma_e}$(error)	$1.62\cdot10^{-2}$		$2.78\cdot10^{-5}$	
$\boldsymbol{\varphi}$	0.961		-0.340	
$\boldsymbol{\theta}$	-0.663		0.285	
$\boldsymbol{\delta_1}$	11.151		$2.06\cdot10^{-6}$	
$\boldsymbol{\delta_2}$	----		7.668	

Table 2

Table 2. Model fitted for annual and spring daily radial increment (Eq. 1). Significant parameters are in bold. $\boldsymbol{\alpha_0}$ *and* $\boldsymbol{\alpha_1}$ *are the intercept regression coefficients for pine and oak, respectively;* T_{air} *is air temperature (ºC);SR is solar radiation (10KJ/m*^{2}*); Wd is water deficit (mm); VPD is mean vapor pressure deficit (kPa); P is daily precipitation(mm);* $\boldsymbol{\sigma_k}$ *is standard deviation for year random effect;* $\boldsymbol{\sigma_{jk}}$ *is standard deviation for site random effect;* $\boldsymbol{\sigma_{ijk}}$ *is standard deviation for tree random effect;* $\boldsymbol{\sigma_e}$ *is standard deviation for error term;* $\boldsymbol{\varphi}$ *and* $\boldsymbol{\theta}$ *are autoregressive and moving average for annual and spring residual serial correlation parameters from AR(1) and ARMA(1,1), respectively;* $\boldsymbol{\delta_1}$ *and* $\boldsymbol{\delta_2}$ *are function parameters used to model residual variance as constant plus a power of the absolute value of the variance covariate (*$\boldsymbol{g_{ijk}}$*):* $\boldsymbol{Var(\varepsilon_{ijk})} = \boldsymbol{\sigma_e^2(\delta_1 + |g_{ijk}|^{\delta_2})^2}$

Parameter	**Annual**		**Spring**	
	Coefficient	**p-value**	**Coefficient**	**p-value**
α_0 (pine)	**$7.38\cdot10^{-3}$**	**<0.001**	**$5.98\cdot10^{-3}$**	**0.002**
T_{air}	**$5.15\cdot10^{-4}$**	**<0.001**	**$9.76\cdot10^{-4}$**	**<0.001**
SR	**$4.33\cdot10^{-4}$**	**<0.001**	**$6.38\cdot10^{-4}$**	**<0.001**
Wd	**$-1.68\cdot10^{-2}$**	**<0.001**	n.s.	n.s.
VPD	**$-4.39\cdot10^{-3}$**	**<0.001**	n.s.	n.s.
P	**$2.55\cdot10^{-3}$**	**<0.001**	**$1.68\cdot10^{-3}$**	**<0.001**
α_1 (oak)	**$-2.57\cdot10^{-3}$**	**0.002**	**$-8.12\cdot10^{-3}$**	**<0.001**
σ_k (year)	$3.36\cdot10^{-7}$		$1.46\cdot10^{-3}$	
σ_{jk}(site)	$1.08\cdot10^{-3}$		$4.08\cdot10^{-8}$	
σ_{ijk}(tree)	$7.88\cdot10^{-4}$		$3.17\cdot10^{-7}$	
σ_e(error)	1.58		2.18	
φ	0.43		$8.77\cdot10^{-1}$	
θ	----		$-6.29\cdot10^{-1}$	
δ_1	$2.01\cdot10^{-3}$		$1.96\cdot10^{-3}$	
δ_2	1.15		1.32	

Figure 1

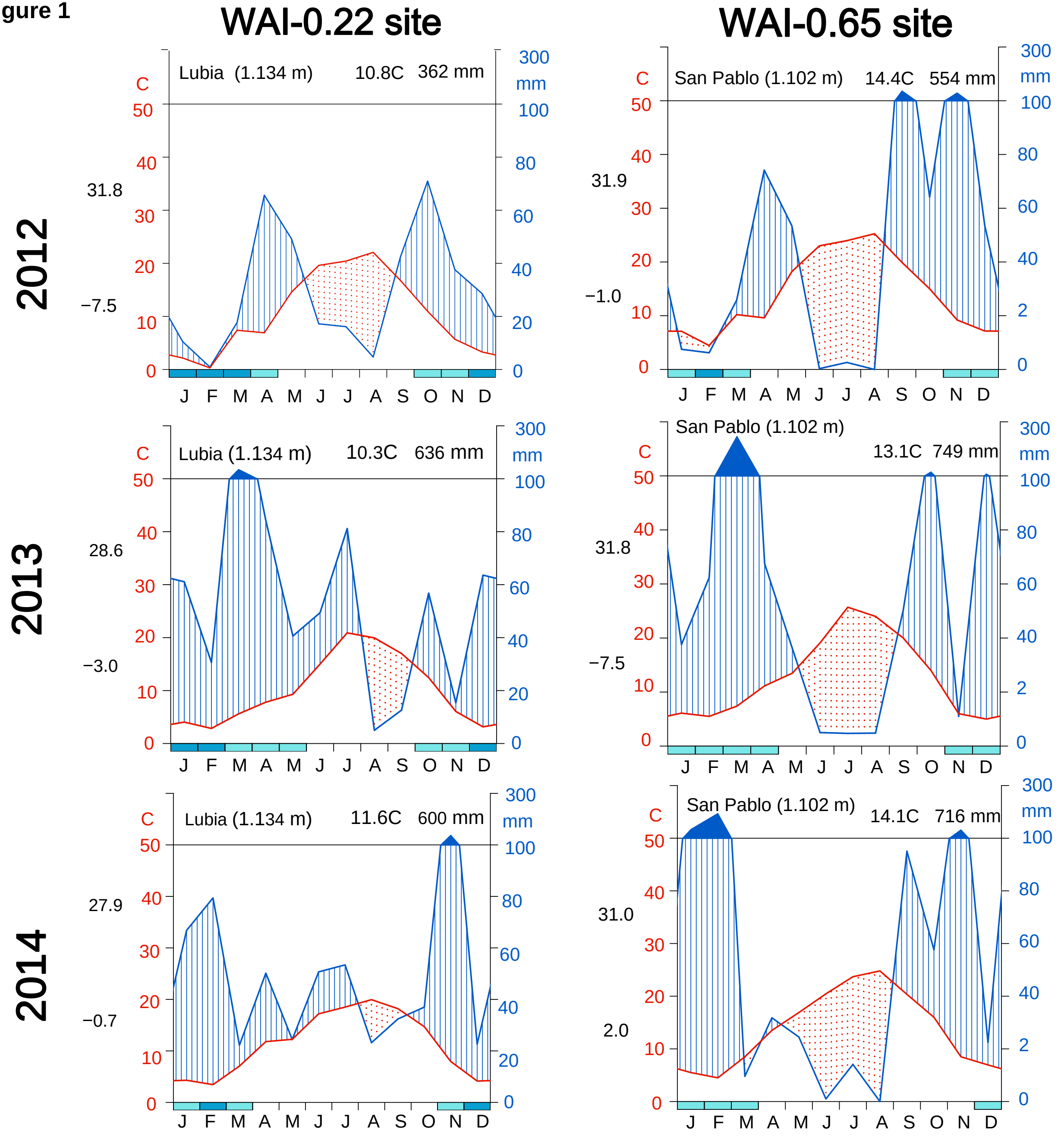

WAI-0.22 site
WAI-0.65 site
2012
2013
2014
Lubia (1.134 m)
10.8C 362 mm
31.8
−7.5
San Pablo (1.102 m)
14.4C 554 mm
31.9
−1.0
Lubia (1.134 m)
10.3C 636 mm
28.6
−3.0
San Pablo (1.102 m)
13.1C 749 mm
31.8
−7.5
Lubia (1.134 m)
11.6C 600 mm
27.9
−0.7
San Pablo (1.102 m)
14.1C 716 mm
31.0
2.0
C
0
10
20
30
40
50
mm
0
20
40
60
80
100
300
2
J F M A M J J A S O N D

Figure 2

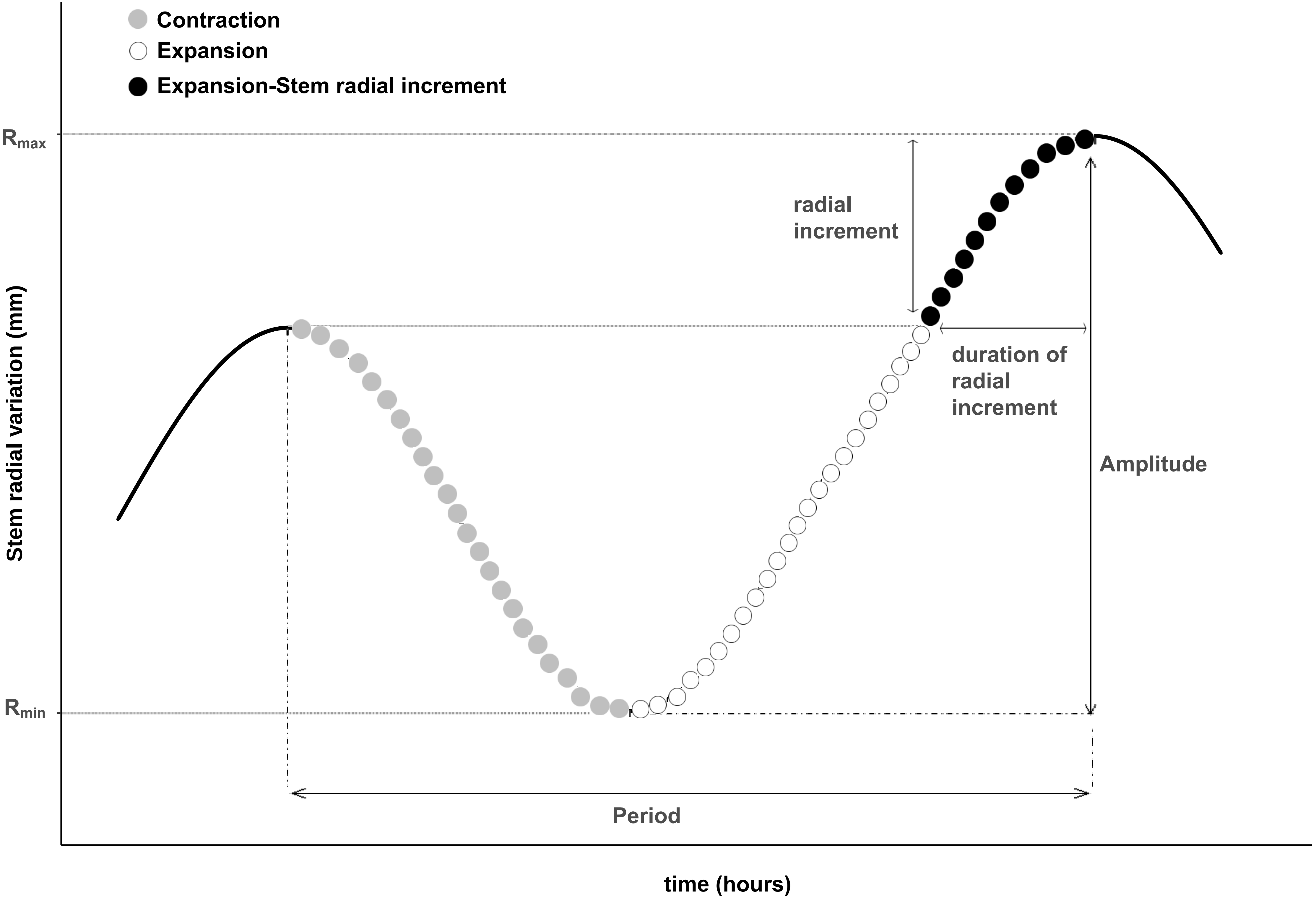
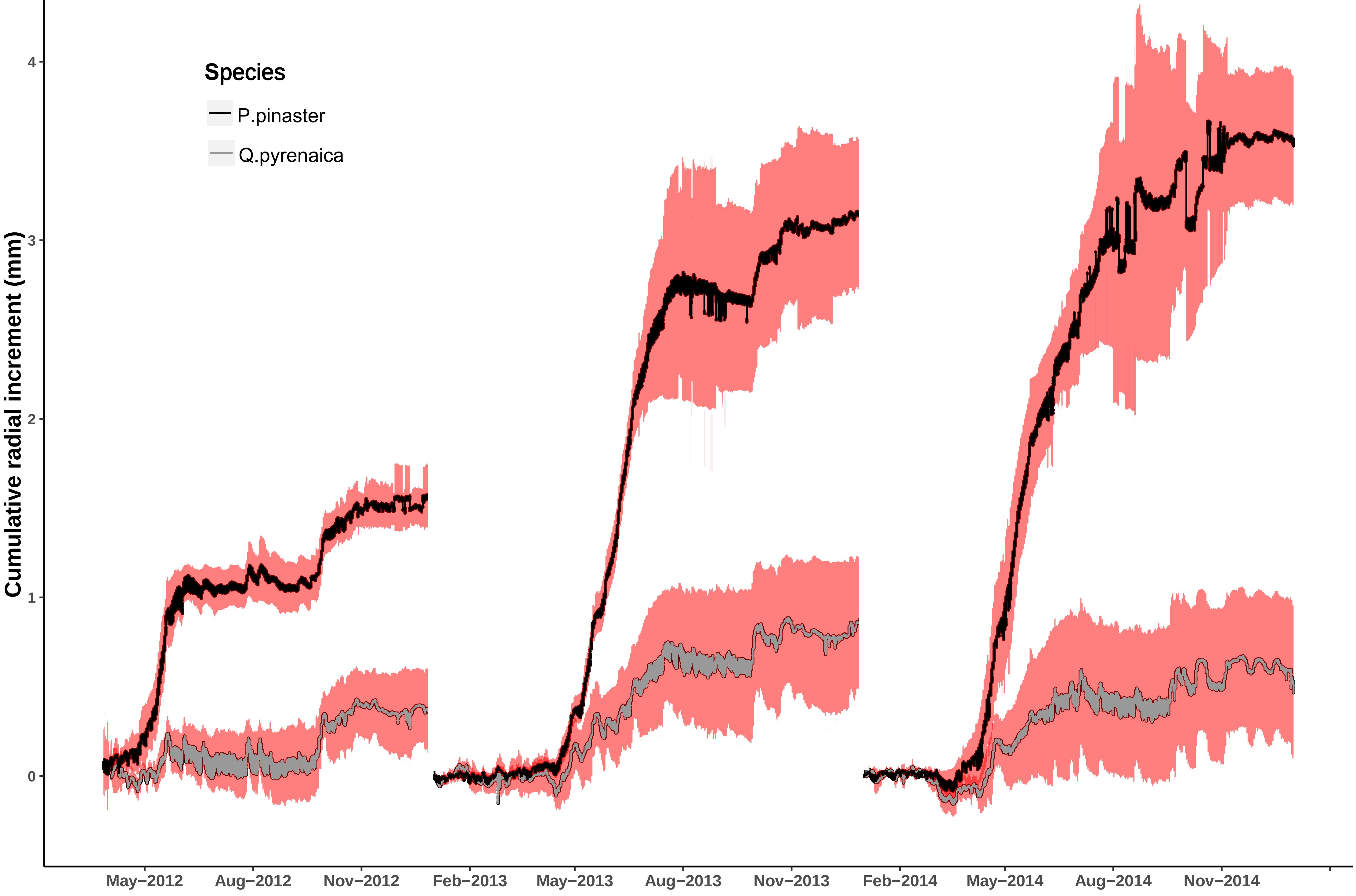

Contraction
Expansion
Expansion-Stem radial increment
Rmax
Rmin
Stem radial variation (mm)
radial increment
duration of radial increment
Amplitude
Period
time (hours)

Figure 3



Species
P.pinaster
Q.pyrenaica
Cumulative radial increment (mm)
4
3
2
1
0
May−2012
Aug−2012
Nov−2012
Feb−2013
May−2013
Aug−2013
Nov−2013
Feb−2014
May−2014
Aug−2014
Nov−2014

Figure 4

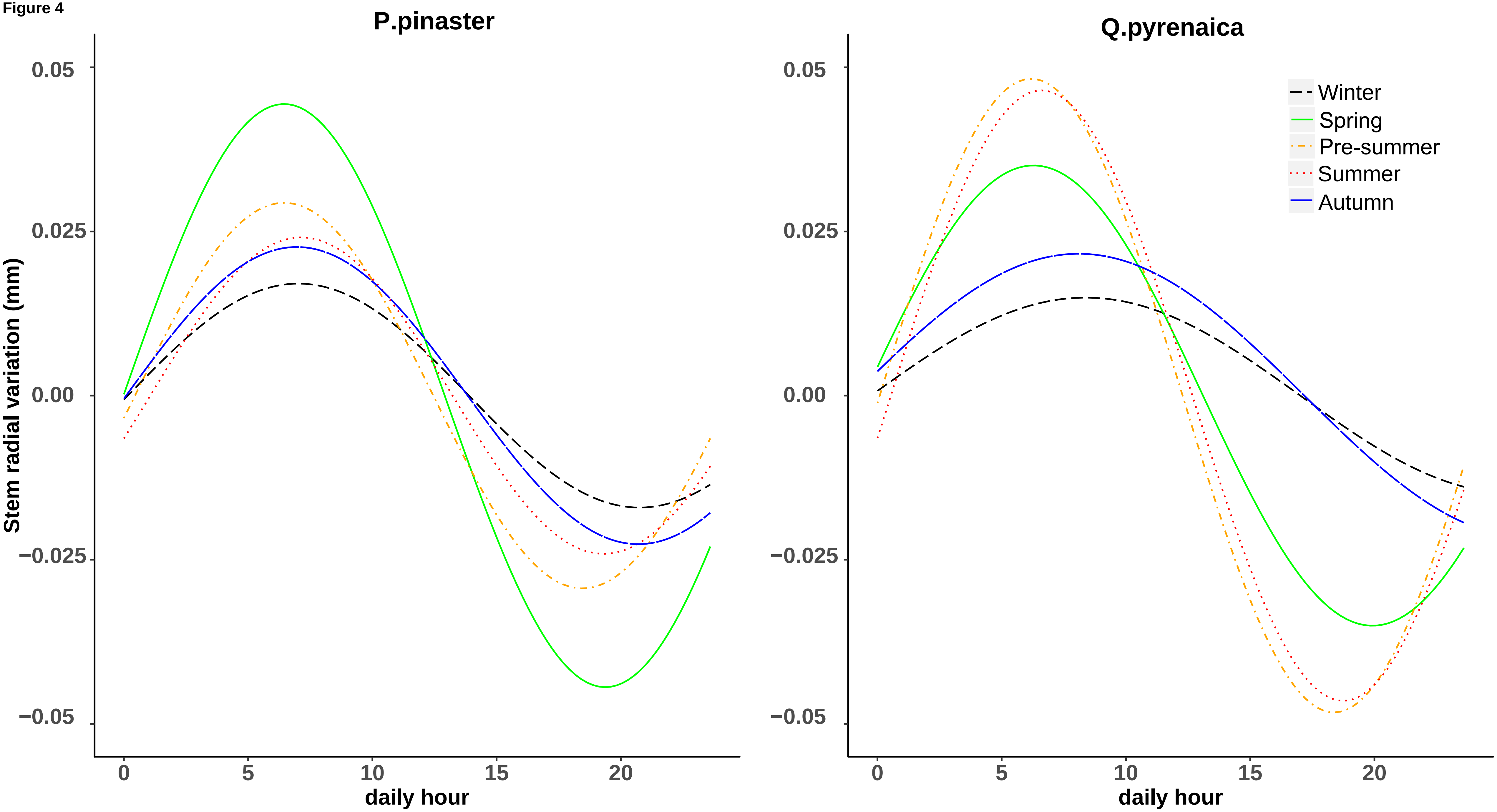

P.pinaster
Q.pyrenaica
Stem radial variation (mm)
0.05
0.025
0.00
−0.025
−0.05
0
5
10
15
20
daily hour
Winter
Spring
Pre-summer
Summer
Autumn

Figure 5

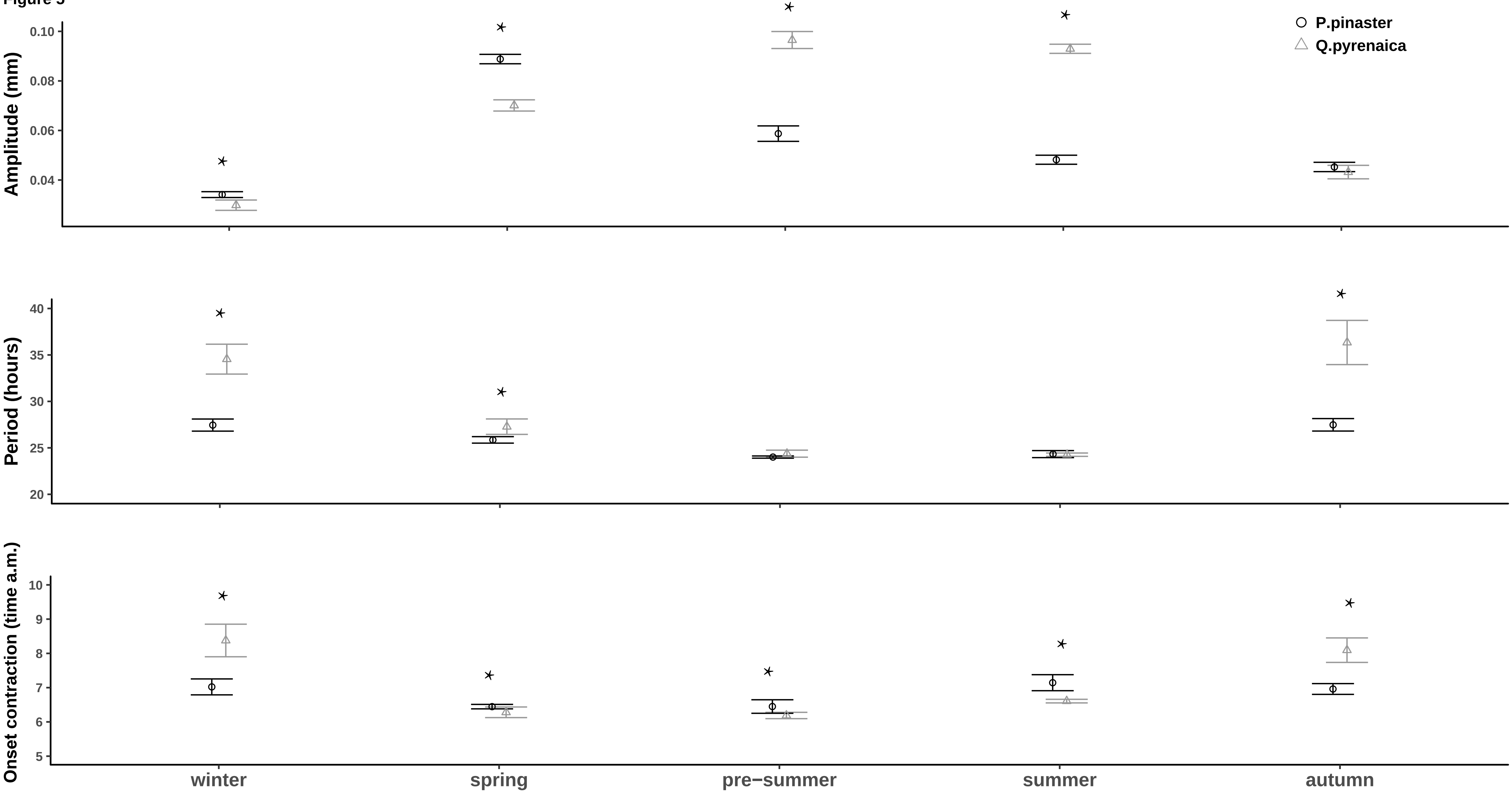
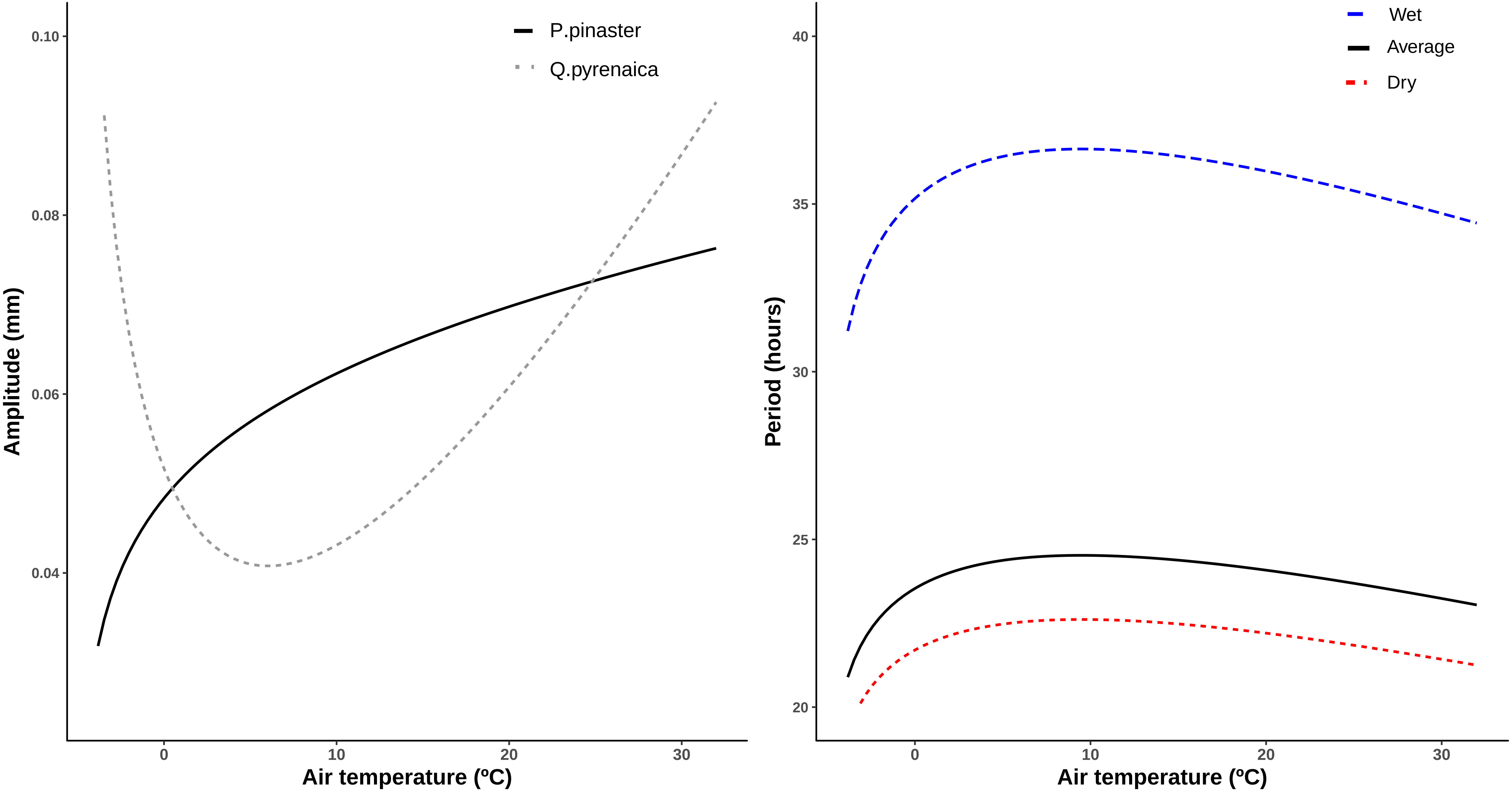
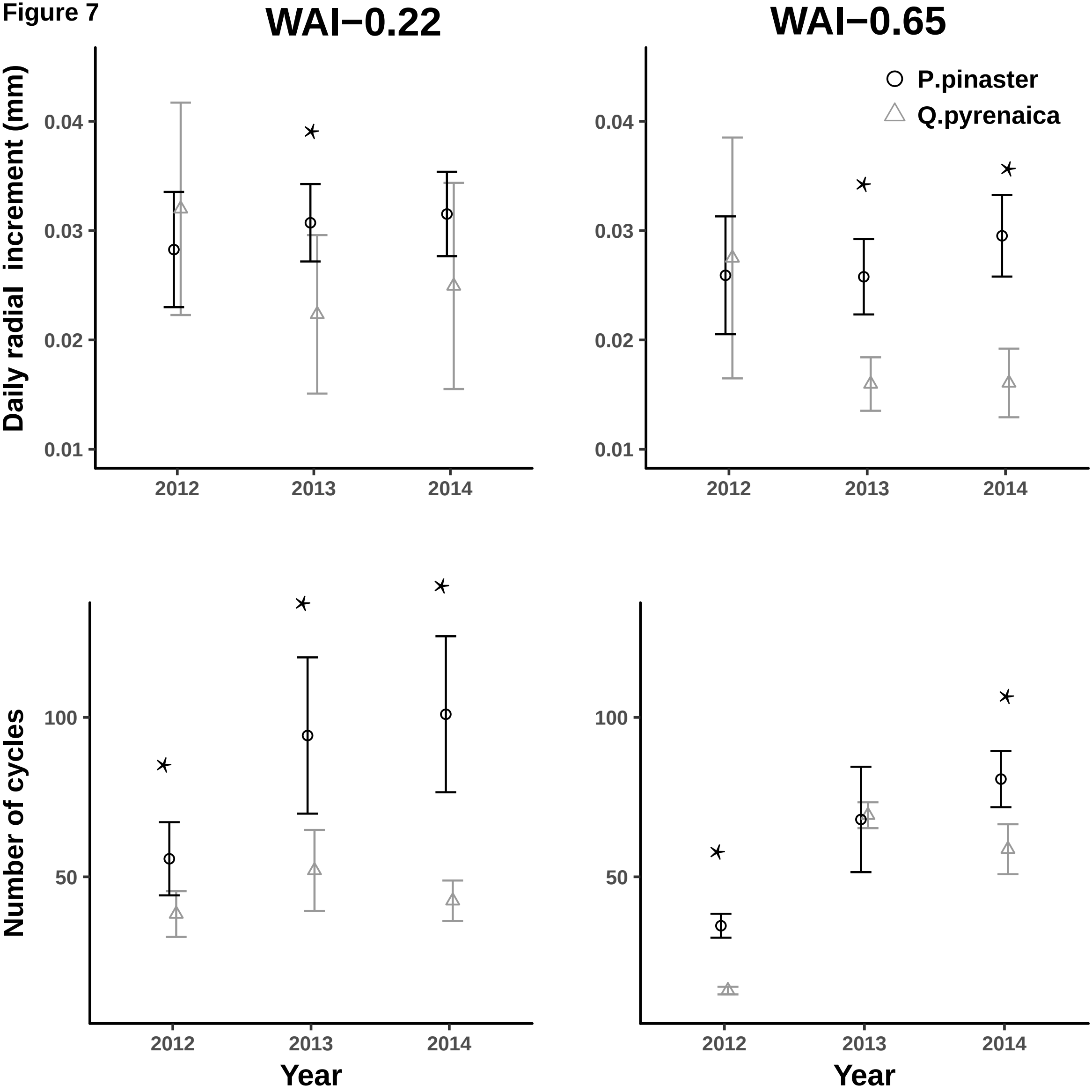

Amplitude (mm)
0.10
0.08
0.06
0.04
P.pinaster
Q.pyrenaica
Period (hours)
40
35
30
25
20
Onset contraction (time a.m.)
10
9
8
7
6
5
winter
spring
pre−summer
summer
autumn

Figure 6



P.pinaster
Q.pyrenaica
0.10
0.08
0.06
0.04
Amplitude (mm)
0
10
20
30
Air temperature (ºC)
Wet
Average
Dry
40
35
30
25
20
Period (hours)
0
10
20
30
Air temperature (ºC)

Figure 7


WAI−0.22
WAI−0.65
P.pinaster
Q.pyrenaica
Daily radial increment (mm)
0.04
0.03
0.02
0.01
2012
2013
2014
Number of cycles
100
50
Year
Year