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ORIGINAL PAPER

Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate

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Abstract Dendrochronology generally assumes that climate–growth relationships are age independent once the biological growth trend has been removed. However, tree physiology, namely, photosynthetic capacity and hydraulic conductivity changes with age. We tested whether the radial-growth response to climate and the intra-annual density fluctuations (IADFs) of *Pinus pinaster* Ait. varied with age. Trees were sampled in Pinhal de Leiria (Portugal), and were divided in two age classes: young (<65 years old) and old (>115 years old). Earlywood and tree-ring width of young *P. pinaster* trees were more sensitive to climate influence while the response of latewood width to climate was stronger in old trees. Young trees start the growing season earlier, thus a time window delay occurs between young and old trees during which wood cells of young trees integrate environmental signals. Young trees usually have a longer growing season and respond faster to climate conditions, thus young *P. pinaster* trees presented a higher frequency of IADFs compared with old trees. Most of the IADFs were located in latewood and were positively correlated to autumn precipitation. The radial-growth response of *P. pinaster* to climate and the IADFs frequency were age dependent. The use of trees with different age to create a tree-ring chronology for climate studies can increase the resolution of climatic signals. Age-dependent responses to climate can also give important clues to predict how young and old trees react to climate change.

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Introduction

The number of tracheids produced by the cambium, their lumen area, and the thickness of cell walls are controlled by both physiological processes and environmental conditions (De Micco et al. 2007; Jardon et al. 1994; Nicault et al. 2001; Rossi et al. 2008; Vaganov et al. 1996). High temperatures in spring promote the synthesis of cell wall components, but reduce the time of tracheid development in the secondary wall thickening zone and as a result, the early tracheids have thin cell walls (Nicault et al. 2001). The formation of latewood occurs in the summer and is influenced by water stress and photoperiod (Vaganov et al. 2006). The increased time length of cell wall material deposition results in the formation of tracheids with thick walls (De Micco et al. 2007; Uggla et al. 2001).

Besides the normal transition between earlywood and latewood in tree rings, intra-annual density fluctuations (IADFs) can occur. IADFs are characterized by latewoodlike cells within the earlywood and earlywoodlike cells within the latewood (Fritts 2001). These structures are formed in response to changing climatic conditions during the growing season (Masiokas and Villalba 2004) and their radial position within the ring is determined by the time the triggering factor occurred (Campelo et al. 2007). In *Pinus pinea* L., growing under a Mediterranean climate, earlywood like cells within latewood were positively correlated to above-average precipitation in September or October (Campelo et al. 2007). *Pinus nigra* Arn. growing in the Austrian Alps showed earlywood IADFs positively correlated with a wet April, dry May and wet June (Wimmer et al. 2000).

The inclusion of IADFs in dendrochronological studies allows a more detailed analyses of climatic events within the growing season (Wimmer et al. 2000). However, in the literature it is suggested that younger trees have higher IADF frequency than older trees (Copenheaver et al. 2006; Masiokas and Villalba 2004; Rigling et al. 2002; Villalba and Veblen 1994), since younger trees have a longer growing season (Rossi et al. 2008) and respond faster to changing environmental conditions (Villalba and Veblen 1994). Few studies have investigated whether climate–growth response is consistent across different age classes. Some studies showed that the climate signal was maximized in older trees (Carrer and Urbinati 2004; Rossi et al. 2008; Yu et al. 2008). Linderholm and Linderholm (2004) found that older trees were more sensitive to summer temperature, while younger trees were more responsive to temperatures in the peak of the growing season.

Most of the age-dependent tree-ring growth response studies were held under subarctic climate (Szeicz and Macdonald 1994) or high-altitude environments (Rossi et al. 2008; Yu et al. 2008), where the growing season is short (2–3 months) and tree growth is mainly limited by temperature. However, the response of tree growth to climate according to tree age has not yet been investigated under a Mediterranean climate, where water stress is the main limiting factor and the growing season is longer (6–8 months). The aims of the present study were to analyse whether the response of earlywood, latewood and tree-ring width to climate and the frequency of different types of IADFs in *Pinus pinaster*, growing under a Mediterranean climate, were age dependent.

Materials and methods

Study area

The study areas were located in Mata Nacional de Leiria, in the northwest coast of Portugal (Fig. 1). It is a managed forest of *P. pinaster* growing on sand dunes. The climate is typical Mediterranean with a strong oceanic influence, characterized by dry summers and maximum precipitation in autumn and winter, with mean annual temperature of 15°C and mean annual precipitation of 720 mm (Fig. 2). Climate data was obtained from the nearest meteorological stations, Cabo Carvoeiro and Alcobaça (Fig. 1). Two forest stands were selected, located at approximately 5 km apart, at the same altitude, with similar stand density but with trees of different age: young (<65 years old) and old (>115 years old) trees. Sixty dominant trees of *P. pinaster* were sampled in 2007, 30 for the young category and 30 for the old category.

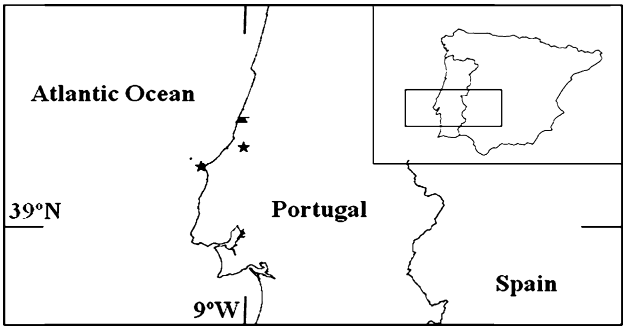

Fig. 1 Location of the study areas and meteorological stations (*star*). The *full* and *open triangles* represent the sampling areas of old and young trees, respectively

Tree-ring data

Two cores were taken per tree, at breast height, with an increment borer, in the north–south direction. Afterwards the cores were air dried, mounted on a wooden support and sanded with progressive finer sand paper to highlight tree-ring patterns.

Tree rings were visually cross-dated using standard dendrochronological techniques (Stokes and Smiley 1996). Earlywood, latewood and tree-ring width were measured to the nearest 0.01 mm using a linear table, LINTAB (Frank Rinn S.A., Heidelberg, Germany) and the program TSAP-Win (Rinn 2003). The crossdating accuracy was then checked using the program COFECHA (Holmes 1994). Trees exhibiting correlation values with the master chronology below 0.4 were excluded. In the end, 20 trees remained in the young category and 22 in the old one.

To remove age-related growth trends and competition a two-step detrending was applied to each individual series, using the program ARSTAN (Briffa and Cook 1990; Cook 1985). In the first step, a negative exponential or a straight line with slope ≤ 0 was fitted to each individual ring-width series. In the second step, a smoothing cubic spline curve with a 50% frequency cut-off and response period of 60 years was fitted to the dimensionless series. To remove the previous year effect, an autoregressive model was fitted to the standardized indices. Finally, to reduce the influence of isolated outlier values, a biweight robust estimate of the mean was applied and a residual chronology obtained. Several descriptive statistics were used to compare the age-class residual chronologies (Table 1).

Response function analyses

The relation between climate and earlywood, latewood and tree-ring widths, for the period 1942–2006, was investigated by bootstrapped response function analyses using the program PRECON (Briffa and Cook 1990; Fritts 1999; Serre-Bachet 1990). This procedure is a particular multiple

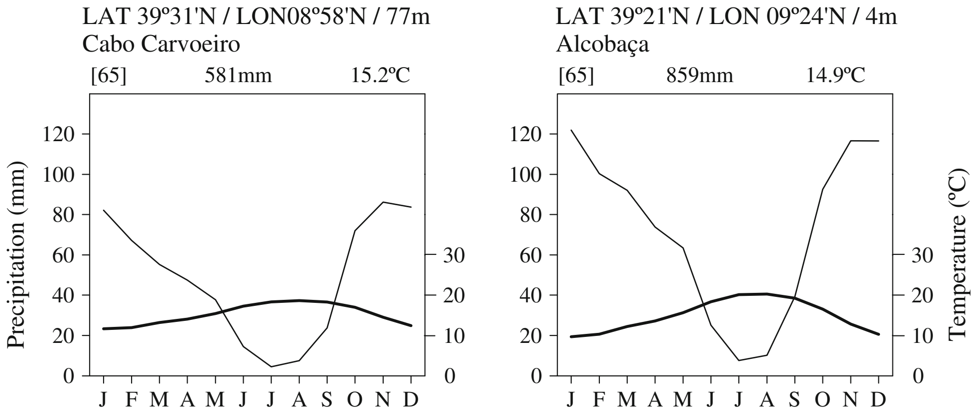

Fig. 2 Climate diagram of the meteorological stations closer to the study sites for the period of 1941–2006. The diagrams consist of precipitation (mm, *thin line*) and temperature (°C, *thick line*). Data from Instituto Nacional de Meteorologia, Portugal

Table 1 Descriptive statistics of earlywood, latewood and tree-ring width chronologies

	Old			Young		
	Ring width	Earlywood	Latewood	Ring width	Earlywood	Latewood
Start	1818	1818	1818	1933	1933	1933
End	2006	2006	2006	2006	2006	2006
Lengh (years)	189	189	189	74	74	74
Raw ring width (1/100 mm)	220	136	84	264	180	84
Residual chronologies						
Mean sensitive	0.23	0.22	0.33	0.21	0.22	0.29
Standard deviation	0.20	0.20	0.27	0.19	0.20	0.25
Skewness	0.10	0.16	0.33	0.10	0.15	0.36
Kurtosis	0.01	0.33	0.10	−0.12	−0.35	−0.09
First order autocorrelation	0.02	0.05	−0.03	0.00	0.03	0.03
Common interval analysis (1942–2006)						
No. of trees (no. of cores)	21 (41)	21 (41)	21 (41)	12 (16)	12 (16)	12 (16)
Rbt	0.29	0.29	0.30	0.39	0.34	0.37
EPS	0.91	0.90	0.90	0.89	0.86	0.88
Variation of first eigenvector (%)	35	32	34	44	39	42

regression model where the independent variables (mean monthly temperature and total monthly precipitation) are first transformed in principal components, to remove the possible interactions between them. The dependent and the independent data sets were drawn by 999 random samplings with replacement from the original data (Guiot 1990, 1991). For each iteration, the dependent data was used to construct a model to predict the relation between tree-ring width and climatic variables (calibration) and the independent data was used to verify the accuracy of the model obtained (verification). The result is a measure of the strength of the climate-forcing signal relation (Briffa and Cook 1990). The significance of each regression coefficient was provided by the ratio between the average value estimated from the result of 999 simulations and its standard deviation (Briffa and Cook 1990). When the ratio is ≥2, ≥2.58 or ≥3.3, the significance of the corresponding regression attains 95, 99, or 99.9% of probability, respectively. Finally, the overall significance of the model reaches 95% of probability when the average of the multiple correlation values is at least twice its standard deviation, as in the case of the partial regression coefficients (Guiot 1991).

Intra-annual density fluctuations

The correctly dated cores were visually examined for IADFs using a stereomicroscope magnifying up to 25-fold. IADFs were easily distinguished from annual tree rings, as illustrated in Fig. 3, since IADFs showed a non-sharp transition in opposite to the annual rings boundary (Fritts 2001). The IADFs were classified based on the radial position within the ring: Type E with latewoodlike cells within the earlywood, Type L with earlywoodlike cells within the latewood and type L$^+$ with earlywoodlike cells between latewood and earlywood of the next tree ring

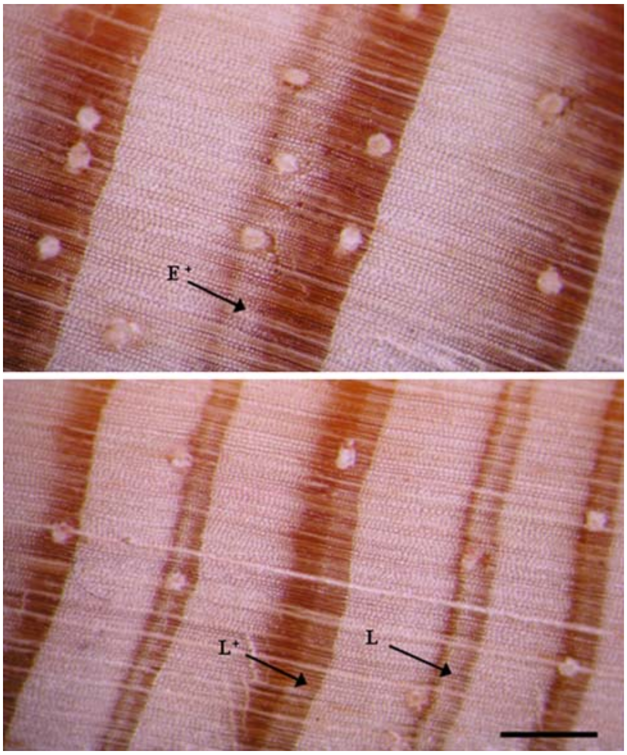

Fig. 3 Anatomical structure and relative position within a tree ring of the different types of intra-annual density fluctuations (IADFs) in *Pinus pinaster* (magnification ×16), the *bar* represents 1 mm

(Campelo et al. 2007). Because of the variability of IADFs tangentially and vertically within the tree rings along the stem the IADFs were only considered when present in both the cores, in the same tree ring (Kuo and McGinnes 1973).

The frequency of IADFs per year, F, was calculated as the ratio:

$$F = N/n$$

where N is the number of trees that showed an IADF type in a given year and n is the total number of observed trees. The changing of the sample depth, n, in time created a bias, which was addressed by the adjustment proposed by Osborn and Jones (1997) by calculating an adjusted IADFs frequency:

$$f = Fn^{0.5}$$

where f is the stabilized IADF frequency.

Results

Tree-ring chronologies

The residual chronologies are present in Fig. 4, the total time span of the residual chronologies extend from 1818 to 2006 for the old trees and from 1933 to 2006 for the young trees.

The parameters calculated with ARSTAN to characterize the chronologies are presented in Table 1. Mean sensitive was higher for latewood. The expressed population signal (EPS) was above the critical value of 0.85 proposed by Wigley et al. (1984) for both the age-categories, indicating a strong common signal. The EPS value measures the degree to which a particular chronology drawn from a finite number of trees portrays the theoretical chronology based on an infinite population (Wigley et al. 1984).

Climate–growth relationships

The bootstrapped response functions, calculated for the period 1942–2006, are presented in Fig. 5 and describe the relationship between the residual chronologies and climate. Response function analysis showed that climate accounted for a high amount of variance in ring-width chronologies, ranging from 56 to 65% (Table 2) and it was higher in young trees for earlywood and tree-ring width and in old trees for latewood width.

Tree-ring width of young trees responded positively to precipitation in January and May and to temperature in March but negatively to July and August temperatures (Fig. 5). The old trees showed a positive response toward May and October precipitation.

Earlywood width, in both the age-categories, showed a positive response to May precipitation and a negative one to May temperature (Fig. 5). In young trees, earlywood width also showed a positive response to March temperature and a negative one to August temperature. Earlywood width of old trees showed a negative response to April temperature and a positive one to September temperature.

Latewood width in young trees was enhanced by precipitation in previous December, January and September (Fig. 5). Regarding the temperature effect, latewood width of young trees exhibited a positive response to March temperature and a negative one to July and August temperature. In old trees, latewood width showed a positive response to precipitation in previous December, January, May and October.

Intra-annual density fluctuations

Young trees showed the highest stabilized frequency of IADFs, being the type L^+ the most frequent (Table 3). IADFs located within the earlywood were less frequent. Occasionally, more than one type of IADF was observed in the same tree ring.

The distribution of IADFs in relation to calendar years is shown in Fig. 6. The distribution of IADFs type E is not shown since few trees exhibit this type of IADF.

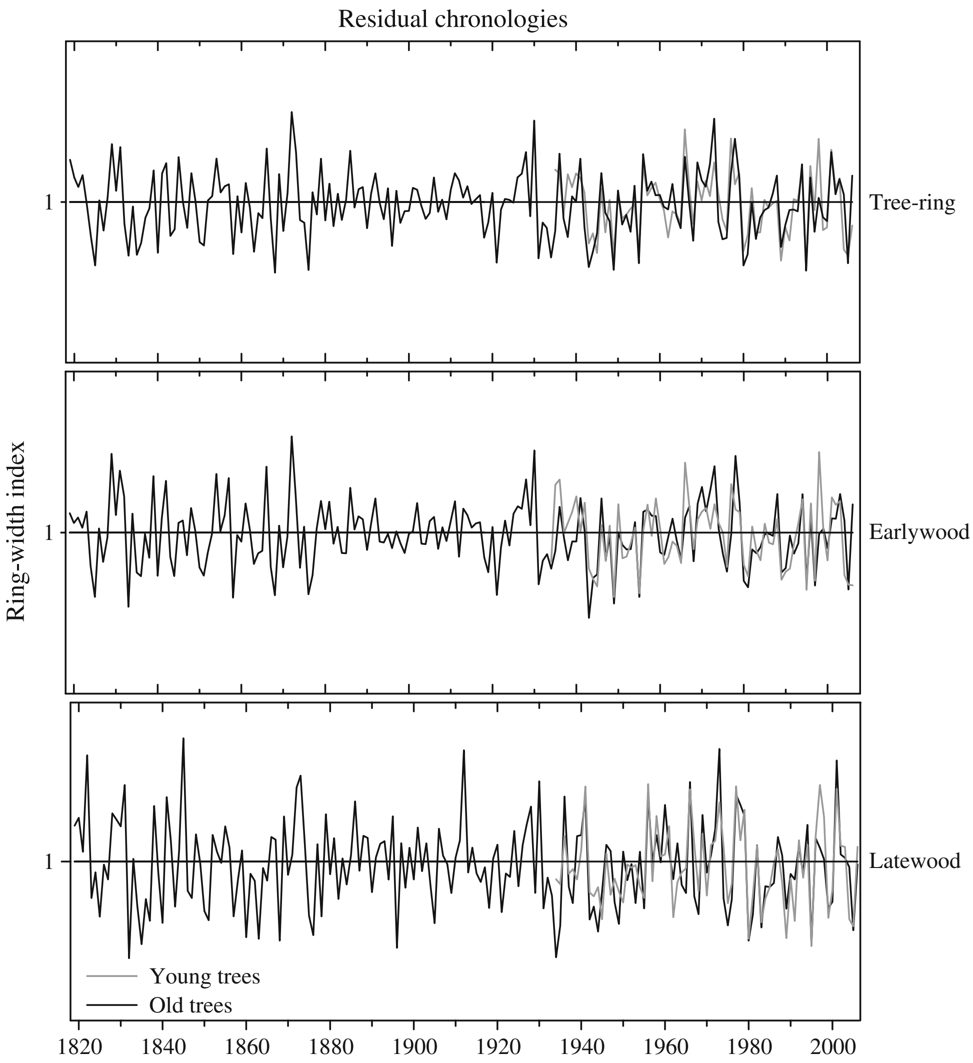

Fig. 4 Residual ring-width indices of *Pinus pinaster* for the period of 1900–2006 (*black line* old trees, *gray line* young trees)

The stabilized frequency of IADF type L ranged from 0 to 2 in the young trees and from 0 to 2.32 in the old ones. For the IADF type L^+ the frequency distribution ranged from 0 to 2.23 in young trees and from 0 to 1 in the old ones.

Spearman's correlation coefficients between the chronologies of stabilized IADFs frequencies and total monthly precipitation and mean temperature were analysed from January to December of the current year (Fig. 7). In young trees, IADF type L was positively correlated to March and September precipitation and negatively correlated to March and November temperatures. In old trees, IADF type L was negatively correlated with May precipitation and positively with October precipitation. IADF type L^+ in young trees was positively correlated with precipitation in February, September and October, whereas in old trees IADF type L^+ was positively correlated to precipitation in October and December and with November temperature.

Discussion

Response function analyses showed that earlywood and tree-ring width of young *P. pinaster* trees were more sensitive to climate influence while the response of latewood width to climate was stronger in old trees. Rossi et al. (2008) showed that old conifer trees started their growing season later, compared to young trees. If this is also true for *P. pinaster*, it is expected that younger trees start responding to climatic conditions earlier. The response of young *P. pinaster* trees to March temperature could be related to an earlier start of the cambial activity, with a longer period for earlywood formation. Latewood is initiated by photoperiod and water stress (Vaganov et al. 2006). The efficiency of water translocation through a tree declines with increasing age and/or height, due to a non-optimal network of xylem conduits with a tapered structure (Anfodillo et al. 2006; Ryan et al. 2006; West et al. 1999). As a result, water deficits may become more pronounced

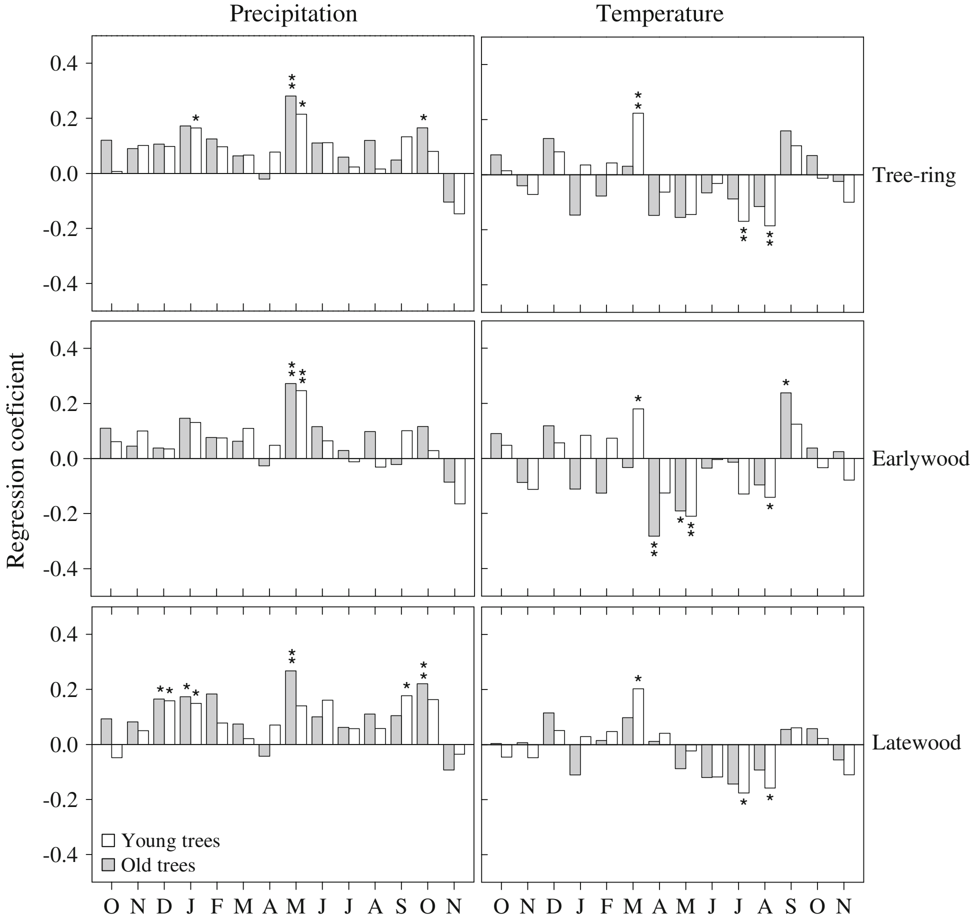

Fig. 5 Response function analyses of earlywood, latewood and tree-ring width residual chronologies for *Pinus pinaster* young and old trees and monthly climatic data (*closed bars* old trees, *open bars* young trees) from October $_{(t-1)}$ to November $_{(t)}$ in the period from 1942–2006. Significance classes * $P < 0.05$, ** $P < 0.01$

Table 2 Calibration and verification regression coefficients of the response function analyses and percentage of variance explained by climate

	Correlation coefficient of calibration	Correlation coefficient of verification	Percentage of variance explained by climate	Overall significance of the model
Tree-ring				
Young	0.859 ± 0.035	0.514 ± 0.141	65	$P < 0.001$
Old	0.818 ± 0.050	0.414 ± 0.161	58	$P < 0.05$
Earlywood				
Young	0.851 ± 0.037	0.478 ± 0.150	63	$P < 0.01$
Old	0.812 ± 0.047	0.361 ± 0.161	57	$P < 0.05$
Latewood				
Young	0.816 ± 0.050	0.354 ± 0.163	56	$P < 0.05$
Old	0.828 ± 0.049	0.435 ± 0.157	59	$P < 0.01$

with age and this is reflected in the higher response of latewood width to climate, as observed in older trees of *P. pinaster*.

In both the age classes, high precipitation in May induced the formation of wider earlywood bands and consequently, wider tree rings. Although in the Mediterranean climate the majority of the precipitation does not typically fall in May (Touchan et al. 2007), it provides the necessary moisture and optimum temperatures for photosynthesis, with earlywood being formed mainly during this month (Lebourgeois 2000). This was also reported for *P. pinaster* in central Spain (Bogino and Bravo 2008), for *Pinus nigra* in southeastern Spain (Martín-Benito et al. 2008) and for *P. pinea* in the south of Portugal (Campelo et al. 2007).

Temperatures in May had a negative effect on earlywood width of both the age classes, and April temperature also produced a negative effect on old trees (Fig. 5). High

Table 3 Descriptive statistics of the IADFs distribution

	Old	Young
Number of trees (cores)	22 (44)	20 (40)
Trees with IADFs	22	18
Number of rings analysed	1,064	1,250
Number of missing rings	8	90
Rings with IADFs (%)	12.31	19.84
Rings with IADFs type E (%)	0.19	1.92
Rings with IADFs type L (%)	5.17	4.24
Rings with IADFs type L^+ (%)	6.95	13.76

temperatures in spring can induce water stress, which in turn will limit the photosynthetic capacity of plants by inducing stomatal closure to avoid water loss (Baquedano and Castillo 2007). Tree-ring and latewood width of young trees were sensitive to high temperatures in July and August. High temperatures in summer, associated with low precipitation, reduce cambial activity and radial cell expansion (Antonova and Stasova 1997; Deslauriers and Morin 2005).

In dendrochronology, the incorporation of special ring features such as IADFs can improve the resolution of the climate signal within the growing season (Wimmer 2002).

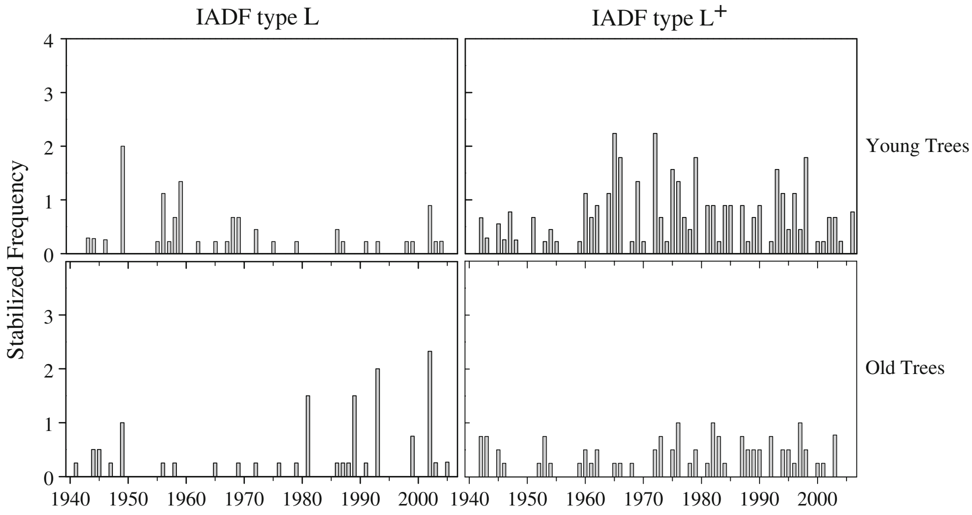

Fig. 6 Stabilized IADF frequency in relation to calendar year

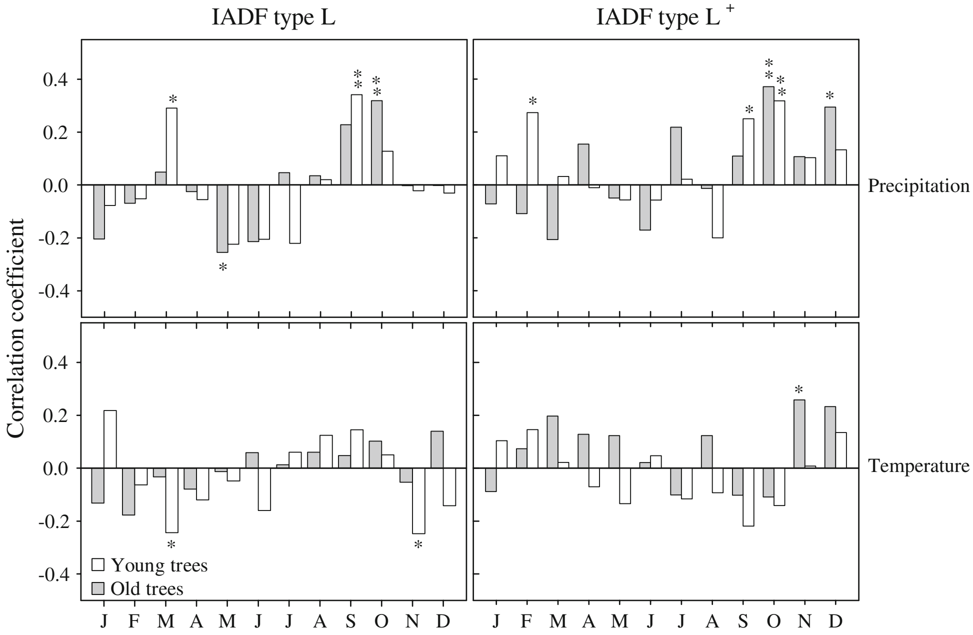

Fig. 7 Correlation coefficient between the master chronology of standardized IADFs frequency of young and old trees and monthly climatic data (*closed bars* old trees, *open bars* young trees) from 1941–2006. Significance classes * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

IADFs were shown to be a useful tree-ring feature to reconstruct monthly precipitation (Wimmer et al. 2000). Several studies with the genus *Pinus* showed a good correlation between IADF formation and climate (Campelo et al. 2007; De Micco et al. 2007; Rigling et al. 2001; Wimmer et al. 2000). However, Rigling et al. (2002) were unable to correlate the climate and IADFs formation in *P. sylvestris* growing in Siberia. Due to the short growing season in Siberia (2–3 months), the mean monthly climatic data was probably not sufficiently precise to describe the IADF formation.

Total IADF frequency was higher in young than in old *P. pinaster* trees (Table 3). Several studies have also shown that IADFs were more frequent in wider and younger tree rings (Copenheaver et al. 2006; Rigling et al. 2001; Villalba and Veblen 1994). This could be due to a faster response of young trees to changing factors (Villalba and Veblen 1994) and/or to a longer growing season of young trees (Rossi et al. 2008). In *P. pinaster* of both age classes, IADFs were mainly correlated with precipitation in autumn (Fig. 7). A wet autumn associated with favorable temperatures, resumes cambial activity resulting in the formation of an IADF (Wimmer et al. 2000). The increase of water availability will increase the turgor of xylem cells under differentiation, blocking the thickening of cell walls, producing earlywood like cells within latewood (Wimmer et al. 2000). This indicates that lignification can switch on and off in response to environmental conditions (De Micco et al. 2007). Most of the IADFs were of type L^+. The accumulation of substances in cell walls close to the end of the growing season, when climatic conditions are less favorable, can be affected and tracheids do not reach full maturity, looking like earlywood cells.

When comparing the latewood width response function analyses with the IADFs correlations we can observe that the climatic signal is slightly different (Figs. 5, 7). In young trees, latewood width and IADF type L responded to September precipitation, and IADF type L^+ responded to both September and October precipitation. In old trees, latewood width responded to October precipitation while IADF type L was correlated to October precipitation and IADF type L^+ to October and December precipitation and November temperature. Therefore, IADFs can detail and reinforce the climatic signal of latewood width chronologies in the Mediterranean climate.

To our knowledge, this is the first study to show an age-dependent tree-ring growth response in a water limited ecosystem. Earlywood and tree-ring width of young *P. pinaster* trees were more sensitive to climate, while latewood width response to climate was stronger in old trees. This is probably related to the fact that young trees start the growing season earlier, thus a time window delay occurs between young and old trees during which only young trees integrate environmental signals. Age-dependent responses to climate can give important clues to predict how differently young and old trees react to climate change. Young *P. pinaster* trees seem to be more sensitive to summer temperatures than old trees. Therefore, the predicted increase in summer temperatures in the Mediterranean region can alter the functioning and structure of *P. pinaster* forests. Further studies including other species and areas of the Mediterranean Basin are needed to fully understand how trees of different age respond to climate change and how this can affect Mediterranean forest ecology.

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