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Climatic control of intra-annual wood density fluctuations of
Pinus pinaster in NW Spain

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20

21 **Abstract** Tree rings of *Pinus pinaster* often contain intra-annual density fluctuations
22 (IADFs), which have been attributed to the succession of dry and rainy periods typical
23 of Mediterranean climate, but their formation has not been studied yet under Atlantic
24 climate. We analyzed the occurrence and climatic significance of replicated IADFs in
25 ten monospecific stands in NW Spain. The frequency of IADFs was higher than
26 previously reported for this species under Mediterranean conditions and consistently
27 decreased with increasing elevation. The formation of bands of latewood-like tracheids
28 within the earlywood was favored by dry previous August, cold previous winter and dry
29 April. Bands of earlywood-like tracheids within the early latewood were also favored by
30 low winter temperatures. However, their occurrence was geographically heterogeneous,
31 with two groups of stands being defined by their distances to the shoreline. In coastal
32 stands, cold May-August triggered IADFs formation, while in inland stands their
33 formation was favored by dry May-July. Regional winter temperatures and April water
34 balance were strongly related to the East Atlantic (EA) pattern, which greatly
35 conditioned the occurrence of IADFs in the earlywood and the early latewood. By
36 contrast, the presence of bands of earlywood-like tracheids in the late latewood was
37 independent of the EA pattern, being strongly related to warm conditions in spring and
38 especially to a wet October. The link between regional climate and the EA pattern
39 strongly controlled the physiological processes that determine intra-annual growth
40 dynamics and short-term cell enlargement of *P. pinaster* in NW Spain.

41

42 **Keywords** Dendrochronology, false tree-rings, *Pinus pinaster*, Atlantic climate, water
43 balance, East Atlantic pattern

44

45 **Introduction**

46 The integration of the effects of several environmental factors operating at multiple time
47 scales on tree-ring growth make difficult to understand the underlying mechanisms
48 responsible for triggering intra-annual cambial activity and growth dynamics (Fritts
49 2001). In fact, cambial activity in conifers may vary at a shorter time scale within the
50 growing season, leading to the formation of intra-annual bands of tracheids with
51 distinctive appearance, differing from those typical of the early- or latewood parts of the
52 ring (Vaganov et al. 2009). Like the most widely used ring-width records, small
53 variations in wood density within a tree ring are morphologically preserved in the wood
54 structure and can be easily differentiated and analyzed any time.

55 The intra-annual density fluctuations (IADFs) in conifers are areas of the tree ring
56 where wood density changes as a response to a particular combination of environmental
57 conditions that modify the rates of cambial activity (De Micco et al. 2007). The term
58 IADF includes the so-called false rings, intra-annual bands, light latewood rings and
59 double or multiple rings, which can be anatomically characterized by latewood-like
60 tracheids within the earlywood, or earlywood-like tracheids within the latewood
61 (Wimmer et al. 2000; Girardin et al. 2001; Rigling et al. 2001). The visual
62 characterization of IADFs is given by changes in the wall/lumen ratio of the tracheids,
63 which corresponds with intra-ring variations in the $^{13}\text{C}/^{12}\text{C}$ isotopic composition of
64 cellulose, suggesting that IADFs are associated to plastic responses to changes in
65 physiological stress (Park et al. 2006; De Micco et al. 2007).

66 Several external disturbance events such as insect outbreaks, and different climatic
67 triggers such as droughts, flooding, snowfall, or frosts have been identified as causes of
68 IADF formation (Rigling et al. 2002; Hoffer and Tardif 2009; Edmondson 2010). In

69 addition, individual features such as canopy position, growth rate and tree age can also
70 influence their formation (Copenheaver et al. 2006; Bogino and Bravo 2009; Vieira et
71 al. 2009). Usually, the presence of IADFs in the earlywood is related to dry springs
72 followed by moist conditions, while moist summers can cause IADFs in the latewood
73 (Wimmer et al. 2000; Bouriaud et al. 2005). A wide variety of woody species under
74 Mediterranean climate characterized by summer drought and a high inter-annual
75 variability in precipitation and temperature commonly form IADFs (Cherubini et al.
76 2003). Among these species, IADFs in the Mediterranean pines *P. halepensis*, *P.*
77 *pinaster* and *P. pinea* have been attributed to an irregular rainfall regime during the
78 growing season (Campelo et al. 2006; De Luis et al. 2007; De Micco et al. 2007;
79 Bogino and Bravo 2009).

80 *Pinus pinaster* is a forest species of the western Mediterranean basin, inhabiting a
81 wide range of environmental and physiographic conditions. Its main populations are
82 located in the Iberian Peninsula, growing in both natural and planted woodlands under
83 climatic conditions ranging from the extremely dry and warm summers of the
84 Mediterranean areas in central and southern Spain to the mild and humid climate of the
85 Atlantic coast at its western range boundary in the Iberian Peninsula (Alía et al. 1997).
86 Despite the great productive and conservational importance of *P. pinaster* under
87 Atlantic conditions, its intra-annual growth dynamics and sensitivity to limiting climatic
88 factors have not been studied in this region yet. Under Mediterranean climate, *P.*
89 *pinaster* presents IADFs in both the early- and latewood due to the succession of dry
90 and rainy periods during the growing season (Bogino and Bravo 2009; Vieira et al.
91 2009). The pronounced genetic and physiological differences between the Atlantic and
92 Mediterranean populations (Bucci et al. 2007; Correia et al. 2008), and the contrasting
93 climatic regimes of both regions, suggest that other environmental factors different from

94 the alternation between dry and wet periods may be critical for the intra-annual growth
95 dynamics of *P. pinaster* under Atlantic climate.

96 Regional climate in Spain is controlled by large-scale circulation patterns, such as
97 the North Atlantic Oscillation and El Niño-Southern Oscillation, which significantly
98 influence rainfall regimes (Rodó et al. 1997; Trigo et al. 2004). Therefore, large-scale
99 climatic patterns may also influence intra-annual growth of *P. pinaster* through
100 determining the variability of regional climate conditions in NW Spain. This study is
101 aimed at (a) characterizing the occurrence patterns of intra-annual wood density
102 fluctuations in *Pinus pinaster* over a tree-ring network at its northwestern range
103 boundary in NW Spain, and (b) identifying the regional and large-scale climatic factors
104 that drive the formation of different IADF types under Atlantic climate.

105

106 **Materials and methods**

107 Study area

108 The study area comprises the region of Galicia, NW Spain, where *P. pinaster* grows at
109 its northwestern range boundary and covers over 47% of the forested area in pure or
110 mixed stands, being one of the most important commercial woods. Since the past
111 century, this species has been extensively planted in Galicia (Fig. 1a), and the resulting
112 even-aged stands are typically managed through short rotations of 40-50 years.
113 Regional climate is temperate and humid, with a mean annual temperature of 12.7 °C
114 for the period 1967–2005, ranging between 10.1 and 14.5 °C. The mean annual
115 precipitation is 1,300 mm, ranging from 870 in the southern inland area to 1,800 mm
116 near the coast under more oceanic influence.

117

118 Climate data

119 We used monthly gridded data from the datasets of the Climate Research Unit,
120 University of East Anglia (CRU TS 3, $0.5^\circ \times 0.5^\circ$), taken from the Web site of the Royal
121 Netherlands Meteorological Institute (<http://climexp.knmi.nl/>), for mean temperature
122 (T) and total precipitation (P) for the period 1967–2006. Since maximum temperature is
123 coupled to a minimum of rainfall during summer time, precipitation data were just used
124 to calculate water balance (WB) as $WB = P - PET$, where PET is the potential
125 evapotranspiration estimated as a function of monthly mean temperatures and
126 geographical latitude (Thornthwaite 1948). Mean monthly WB ranged between -73 mm
127 in July and 145 mm in December-January, showing a tendency to water deficit from
128 June to August. To characterize the climatic determinants of IADFs formation in *P.*
129 *pinaster* at a regional scale, mean values from the $0.5^\circ \times 0.5^\circ$ grid boxes comprised
130 within the region ($7.0-9.5^\circ$ W, $42.0-44.0^\circ$ N) were calculated.

131 Monthly indices of a series of teleconnective patterns (North Atlantic Oscillation,
132 East Atlantic pattern, East Atlantic/West Russia pattern, Scandinavia pattern,
133 Tropical/Northern Hemisphere pattern, Polar/Eurasia pattern) were obtained from the
134 Web site of the NOAA/National Weather Service, Climate Prediction Center, Maryland,
135 USA (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh). Among them,
136 only the East Atlantic (EA) pattern showed significant relationships with IADFs records
137 of *P. pinaster*. EA pattern is a prominent mode of low-frequency variability structurally
138 similar to the NAO, which consists of a north-south dipole of anomaly centers spanning
139 the North Atlantic from east to west, whose positive phase is associated with above-
140 average surface temperatures in Europe (Barnston and Livezey 1987).

141 Monthly climatic variables were seasonalized to values for winter (December-
142 February), spring (March-May), summer (June-August) and autumn (September-
143 November). The considered window for exploring the relations between climate and

144 tree growth were from previous June (Jun(-1)) to current November (Nov) for monthly
145 values, while for seasonal values they spanned from previous summer (Sum(-1)) to
146 current autumn (Aut). Additionally, annual values were calculated by averaging
147 monthly values from previous October (Oct (-1)) to current September (Sep).

148

149 Sampling, tree-ring dating and tree age estimation

150 We sampled 10 monospecific stands located both at the coastal and inland areas along
151 the full elevation range of *P. pinaster* in Galicia, from sea level to 855 m (Fig. 1b, Table
152 1). We measured DBH (bole diameter at 1.30 m), and took at least two increment cores
153 per tree from 15 to 24 dominant trees per stand. The cores were air-dried, glued onto
154 wooden mounts, and polished with successively finer grades of sandpaper, until the
155 xylem cellular structure was visible in the transverse plane. The tree-ring series were
156 absolutely dated by assigning calendar years to the rings following standard procedures
157 (Fritts 2001). Total ring widths were measured under magnification to the nearest 0.001
158 mm with a sliding-stage micrometer (Velmex Inc., Bloomfield NY, USA) interfaced
159 with a computer. The software COFECHA (Grissino-Mayer 2001) was used to
160 quantitatively check for crossdating errors in the ring width series. All series with
161 potential dating errors or weakly correlated with the master site chronology were
162 corrected when possible or discarded.

163 In cores showing the pith, tree age at coring height was determined by the number
164 of crossdated rings. In partial cores showing the arcs of the inner rings, the pith was
165 located using a graphical method based on the convergence of xylem rays at the pith
166 (Rozas 2003), and the number of missing rings toward the pith was estimated by
167 extrapolating the mean growth rates from the innermost five rings in the cores. Tree age

168 was estimated based on the oldest core per tree. No corrections for the number of
169 missing rings due to coring height were performed.

170

171 Intra-annual wood density fluctuations

172 The adequately dated cores were visually examined under magnification for
173 identification of IADFs, which were distinguished from actual tree rings due to their
174 non-sharp transitions in opposite to the marked boundaries between annual rings
175 (Wimmer et al. 2000; Park et al. 2006). Based on previous definitions for *P. pinaster*,
176 IADFs were classified into three types according to their appearance and intra-ring
177 position (Vieira et al. 2009). IADFs type E were bands of latewood-like tracheids within
178 the earlywood (Fig. 2a). By contrast, IADFs types L and L+ were bands of earlywood-
179 like tracheids within the latewood (Fig. 2b), and near the transition between the
180 latewood and the earlywood of the following ring (Fig. 2c), respectively.

181 An IADF in a given ring was considered when present in at least one core per tree,
182 and was tabulated. The percent frequencies of cores and rings per stand showing IADFs
183 of types E, L, and L+ were computed as descriptive statistics of the IADF distributions.
184 The relative frequency of IADFs was calculated as $F = n_x/N$, where n_x is the number of
185 trees showing IADFs in the year x , and N is the number of trees in that year. Moreover,
186 the variance bias induced by the varying number of tree rings per year was corrected by
187 calculating the stabilized IADF frequency as $F_{stab} = F \times N^{0.5}$ (Rigling et al. 2001). F_{stab}
188 series were calculated separately for the types E, L and L+ at each stand. In order to
189 estimate the dependence of IADFs frequency on ring age and ring width, Spearman's
190 correlations between ring age, mean ring width, and F_{stab} of each IADF type, were
191 calculated.

192 We tested if the occurrence of IADFs in *P. pinaster* was independent from both
193 inter-site distances and differences between site elevations using the standardized
194 Mantel statistic (R_M). The Mantel test compares two similarity or distance matrices
195 computed for the same objects, and behaves like a correlation coefficient, being
196 bounded between -1 and 1 (Legendre and Legendre 1998). To calculate R_M we used the
197 matrices of similarity between F_{stab} chronologies and descriptive statistics of the IADF
198 distributions for the period 1967-2005, compared to the matrices of geographical
199 distances and elevation differences among stands. We used Spearman's correlation as a
200 measure of similarity between F_{stab} chronologies, and $1 - D_{\text{norm}}$ as similarity between
201 descriptive statistics, being D_{norm} the normalized difference ranging between 0 and 1
202 (Legendre and Legendre 1998). Since we compared similitude matrices with distance
203 matrices, positive and negative R_M values would indicate more and less similar patterns,
204 respectively, at increasing distances or elevation differences. The statistical significance
205 of R_M was tested by means of 9,999 random permutations of one of the distance
206 matrices, to obtain the expected distribution of the statistic under the null hypothesis of
207 independence. R_M was calculated with the Mantel function from the PopTools v3.1.0
208 add-in for Microsoft Excel (<http://poptools.org/>).

209

210 Relationships between IADFs and climate variability

211 To analyze the relationships between climate and IADFs frequency at a regional scale,
212 we excluded from the analyses those years showing IADF frequencies that did not show
213 any significant replication within a stand. We used the definition given by
214 Schweingruber et al. (1990) of "pointer year" to refer to a group of trees in which most
215 of them display an event –in our case a density fluctuation– in the same year. The most
216 conspicuous IADFs replicated amongst a significant proportion of trees at each stand

217 were considered using a significance test that identifies frequencies higher than a given
218 background value (Edmondson 2010). This background value represents the
219 approximate frequency of an entirely random inter-annual occurrence, and was
220 calculated as the ratio between all IADFs and the total number of dated rings at a given
221 stand. The frequency F was considered significant when the value $F - (F \cdot (1 - F) / N)^{0.5}$
222 exceeded the random background value (Edmondson 2010). Pointer years showing
223 significant IADFs were identified separately for the types E, L and L+ in each stand,
224 and a regional distribution was calculated for each type as the year-by-year sum of
225 significant events at all stands (Appendix S1).

226 The analyses for relating climate and IADFs frequency were performed along
227 1967–2005, the common period for all IADFs records. Due to the abundant zero values
228 in the regional chronology of IADFs type E, we calculated the anomalies of all climatic
229 variables for pointer years in comparison to the expected means in the remainder years
230 without IADFs for the period of analysis (Masiokas and Villalba 2004). Monthly,
231 seasonal and annual climatic variables were normalized, and the deviations of means
232 from years showing IADFs type E, with respect to years not showing IADFs, were
233 calculated. Standard deviations above 0.5 or below –0.5 were considered as significant
234 positive or negative anomalies, respectively. Logistic regression analysis was also used
235 to identify those independent explanatory variables with a significant effect on the
236 probability of occurrence of IADFs type E at a regional level. The model was depicted
237 by $P = 1 / (1 + e^{a + \sum b_i X_i})$, where P is the probability of an IADF occurrence ($P = 0$ indicates
238 non-pointer year, $P = 1$ indicates pointer year), a is the constant of the model and b_i are
239 the coefficients for the independent variables X_i . Logistic regression was performed by
240 a forward stepwise procedure and the best adjustment was obtained by maximum
241 likelihood (Sokal and Rohlf 1995).

242 For IADFs types L and L+, the reduced number of null values allowed the use of
243 correlation analysis to identify the main climatic variables that determined the regional
244 IADF chronologies. To account for non-normality of regional IADF pointer-year
245 chronologies, we calculated Spearman's rank correlations between the regional
246 chronologies of types L and L+ and the monthly, seasonal and annual climatic variables.
247 Additionally, to evaluate the diversity of climatic triggers at a local scale, Spearman's
248 correlations between local F_{stab} distributions and monthly gridded T and WB were
249 calculated. Finally, the relationships between regional climate variability and EA pattern
250 were explored by means of Pearson's correlation. The statistical analyses were
251 performed with the SPSS 15.0 for Windows package (SPSS Inc., Chicago IL, USA).

252

253 **Results**

254 Characteristics of trees and IADF distributions

255 The mean DBHs of dominant trees at the sampled stands varied between 29.6–66.7 cm,
256 and the mean estimated ages between 33–55 years (Table 1). The reduced standard
257 deviations of tree ages suggested an even-aged origin for the majority of the sampled
258 stands. Almost 100% of the 498 cores analyzed showed IADFs (Table 2). The
259 proportion of cores with IADFs type E was quite variable, ranging between 2.2 and
260 88.2%, while the proportion of cores with IADFs in the latewood was consistently high.
261 For IADFs type L, the proportions ranged between 58.3–100%, and 87.5–100% for the
262 type L+. A total of 19,513 tree rings were analyzed, with the proportion of rings with
263 IADFs varying between 15.9–89.5% depending on the site. The proportion of rings
264 showing IADFs type E ranged between 0.0–9.0%, while the types L and L+ were
265 comparatively more abundant, ranging between 3.7–38.8% for type L, and 7.9–66.9%
266 for type L+.

267

268 Patterns of IADFs occurrence

269 No inter-site common trends in the relationships between the frequency of IADFs and
270 tree-ring age or ring widths were found. For the IADFs type E, there were no significant
271 relationships of F_{stab} with age and ring width. For types L and L+ some correlations
272 were statistically significant, both positive and negative, but no general pattern was
273 observed (Appendices S1, S2).

274 The similitude between F_{stab} chronologies was neither related to inter-site
275 distances nor to the difference among site elevations, as shown by the Mantel test
276 (Table 3). The only exception was the IADFs type L, which showed a negative
277 relationship with inter-site distances, suggesting less similar patterns of IADFs
278 frequency when increasing distance. The statistics for IADFs distribution were
279 independent of the geographic distance, but were in general significantly and negatively
280 related to elevation differences. Additionally, negative correlations with elevation were
281 found for the proportion of cores showing IADFs types E ($R = -0.71$, $P = 0.021$) and L
282 ($R = -0.65$, $P = 0.041$). The only exception was the proportion of cores showing IADFs
283 type L+, which did not show a great inter-site variation. These results suggest more
284 frequent IADFs occurring at lower than at higher sites, irrespective of their geographical
285 position.

286

287 Climatic significance of IADFs

288 Composite regional distributions of pointer years for significant IADFs were developed
289 for each IADF type, according to the random background frequencies for pointer year
290 recognition (Appendix S1). For IADFs type E, the 16 pointer years within the period
291 1967–2005 showed below-average temperature in December and previous winter,

292 below-average water balance in previous August and April, and below-average EA
293 indices in previous December and April (Fig. 3a). According to the logistic model, the
294 independent explanatory variables with a positive effect on the probability of
295 occurrence of IADFs type E were lower EA indices in April (Wald's test $\chi^2 = 4.94$, $P =$
296 0.026 , coefficient $b = -0.009$), and reduced water balance in previous August ($\chi^2 = 4.27$,
297 $P = 0.039$, $b = -0.038$).

298 The regional record of pointer years showing IADFs of type L was significantly
299 correlated with both T and EA variability, but independent from any variation in WB
300 (Fig. 3b). Pointer years for IADFs type L were negatively correlated with winter and
301 annual T, and also with EA variation in previous December, previous winter, and its
302 annual variation. The local distributions of F_{stab} for IADFs type L were negatively
303 correlated with T in January-February and May-August at the coastal sites (CAP, COR,
304 INS, MUR, VIG), but in the period May-August positive correlations with T were
305 found at inland sites (ALO, BAR, MCU, VER) (Fig. 4a). Moreover, F_{stab} for IADFs
306 type L in these inland sites showed also negative correlations with WB in May-July. All
307 these results suggest that temperature and water availability in the growing season are
308 site-dependent triggers for IADFs type L formation, exerting contrasting local effects on
309 intra-annual cambial activity.

310 By contrast, the regional record of pointer years for IADFs type L+ is significantly
311 correlated with both T and WB variability, but independent from EA pattern (Fig. 3c).
312 Positive correlations with T in April, August, spring, and the complete year were found.
313 For WB, positive correlations were found in October and autumn, and negative
314 correlations in January and the complete year, were found. The local analysis showed
315 that, in more than 50% of the cases and without any distinction between the coastal and
316 inland stands, IADFs type L+ responded positively to T in March-May and August, and

317 also positively to WB in October (Fig. 4b). Moreover, high WB in May impacted
318 negatively on the formation of IADFs type L+.

319 According to the obtained correlations, the main regional climate driver for the
320 formation IADFs type L was previous winter T, which showed a decreasing number of
321 pointer years strongly related to the ascending trend of winter temperature (Fig. 5a). For
322 the type L+, the main climatic driver at a regional scale was autumn WB, with more
323 frequent IADFs in those years with enough water availability in autumn (Fig. 5b).

324 Several climatic factors revealed as major determinants of IADFs formation in *P.*
325 *pinaster* showed to be directly dependent on EA pattern variability. For instance, mean
326 temperature of December and winter of the previous year were highly positively
327 correlated with EA in December (Fig. 6a) and winter (Fig. 6b), respectively. In addition,
328 annual temperature was positively correlated with annual EA ($R = 0.49$, $P = 0.001$).
329 Moreover, water balance in April showed a positive correlation with April EA (Fig. 6c).

330

331

332 **Discussion**

333 Patterns of IADF occurrence

334 The frequencies of IADFs previously described for different pine species under a wide
335 variety of climatic conditions were considerably lower than those reported in this paper.
336 Under boreal or temperate climate, IADFs were observed in 9% of the tree rings at
337 maximum (Wimmer et al. 2000; Rigling et al. 2001; Copenheaver et al. 2006), and
338 under Mediterranean climate, they were observed in up to 15–32% of the rings
339 (Campelo et al. 2006; Bogino and Bravo 2009; Vieira et al. 2009). In our study, eight
340 out of ten stands showed IADFs in more than 30% of the rings, six stands in more than
341 50%, and a maximum frequency of 89.5% of the rings with IADFs was found. Despite

342 IADFs are assumed to be special features or anomalies in normal tree-ring growth, in
343 the light of the observed frequencies, IADFs are more the rule than the exception in *P.*
344 *pinaster* under mild Atlantic climate.

345 Studies on several pines, including *P. pinaster*, showed that the frequency of
346 IADFs was negatively related to tree age and positively to growth rates, being more
347 abundant in the juvenile period and during or immediately after periods with wider rings
348 (e.g., Copenheaver et al. 2006; Bogino and Bravo 2009; Hoffer and Tardif 2009; Vieira
349 et al. 2009). Our findings, however, showed no dependence among IADFs frequency,
350 cambial age, and ring width, which can be due to the reduced age of our trees in
351 comparison with other works describing age-related effects. However, age-related
352 effects can be important in determining the high frequency of IADFs observed, since the
353 sampled trees are not much older than 55 years, and IADFs frequency is usually much
354 higher for younger trees (Viera et al. 2009).

355 The frequency of IADFs was strongly dependent on elevation, with more
356 abundant IADFs at lower than higher elevations. These evidences suggest that the
357 stressful effects of specific triggering factors causing short-term reduction/reactivation
358 of cambial activity and cell enlargement decrease with increasing elevation. A longer
359 span of the growing season at a lower elevation has probably also contributed to higher
360 frequencies of IADFs.

361 As previous publications on pine species (Rigling et al. 2001, 2002; Campelo et al.
362 2006; Vieira et al. 2009), we found a higher frequency of IADFs in the latewood than in
363 the earlywood of *P. pinaster*. Reductions of cambial activity at the early growing season
364 are less likely than a later growth reactivation, probably due to the different duration of
365 growth periods for early- and latewood, and to more regular weather conditions during
366 early in the active season. In *P. halepensis* under warmer and xeric conditions,

367 earlywood formation lasts for only two months (March to April-May), while latewood
368 growth is more time-consuming, extending up to six-eight months from May-June to
369 November-December (De Luis et al. 2007; Camarero et al. 2010). Accordingly, our
370 results suggest that latewood growth of *P. pinaster* in NW Spain could last for at least
371 six months, from May to October-November.

372

373 Climatic determinants of wood density fluctuations

374 We interpret the dependency of IADFs on climate on the basis of particular
375 preconditioning and triggering climatic factors, whose combined effects produced the
376 observed fluctuations in wood density.

377 Climatic drivers for the occurrence of IADFs in the earlywood of *P. pinaster*
378 showed to be relatively heterogeneous throughout the study area, with very few IADFs
379 per stand, while a clear combination of climatic drivers for their formation was
380 identified at a regional scale. Below-average water availability in previous late summer
381 (August), or below-average temperature in previous winter (December), are
382 preconditioning factors for the formation of bands of latewood-like tracheids within the
383 earlywood. Both factors are related to the amount of carbohydrates stored in the
384 previous season and used for growth in spring (Hansen and Beck 1994; Lacoïnte 2000).
385 Water availability in summer can modulate the amount of carbohydrates at the end of
386 the growing season, considering that summer drought is not as restrictive as under
387 Mediterranean climate, while photosynthetic activity of *P. pinaster* can be inhibited by
388 low temperatures during winter (Medlyn et al. 2002). Below-average water balance in
389 April appears to be the actual triggering factor for IADFs type E, in combination to low
390 carbohydrate reserves at the beginning of the active season. Such relationships to water
391 availability in the early growing season were found for other conifers in different

392 regions. For instance, the frequency of IADFs in the earlywood of *P. nigra* in the
393 northern Alps was negatively correlated with May precipitation (Wimmer et al. 2000),
394 earlywood density of *Picea abies* in France responded strongly to fluctuations in soil
395 water reserves in late spring-early summer (Bouriaud et al. 2005), and drought in early
396 summer induced the formation of IADFs in the earlywood of the Mediterranean pines
397 *P. pinea* and *P. halepensis* (Campelo et al. 2006; De Luis et al. 2007). Moreover, carbon
398 gain in winter can be allocated to growth of fine roots, increasing their absorptive
399 capacity at the onset of following growing season (Lacointe 2000), which can contribute
400 to proper cell enlargement during the earlywood formation, and thus reduce the
401 frequency of IADFs type E. These findings highlight the importance of water deficit for
402 the short-term inhibition of cell enlargement at the beginning of the growing period,
403 which combined with a low carbon availability can induce false-rings formation in the
404 earlywood of *P. pinaster* under Atlantic climate.

405 The formation of IADFs type L are triggered by climatic conditions in late spring
406 and summer, but winter temperature regulating photosynthesis and the amount of
407 carbohydrates available for the following season seemed to be also a major
408 preconditioning. Radial growth depends on tree water status as a controlling factor for
409 the metabolism of the entire tree, but it also depends on the carbon balance as a source
410 of energy for metabolic activity and of compounds for the cambial activity (Zweifel et
411 al. 2006). In evergreen conifers, the carbon supply for needle formation and cambial
412 activity is provided by mobilization of stored reserves, complemented with new
413 photosynthates assimilated even during the cold season (Hansen and Beck 1994).
414 Relatively high rates of winter photosynthesis are stimulated by elevated temperatures
415 in the previous winter (Schaberg et al. 1998; Medlyn et al. 2002), and bands of
416 earlywood-like tracheids in the latewood seemed to occur less frequently when high

417 temperatures occurred in previous winter. Therefore, a negative carry-over effect due to
418 less stored carbohydrates seems to be detrimental for growth, probably causing an
419 inhibition of cambial activity and the earlier beginning of latewood formation due to
420 limited carbon reserves. If latewood is formed earlier, the probability of cambium
421 reactivation due to the occurrence of any favorable condition increases.

422 The climatic triggers for IADFs type L had a geographically heterogeneous
423 distribution within the study area, with two different groups of stands. In coastal stands,
424 IADFs type L were favored by low temperatures in May-August, when periods of low
425 water availability are common, though less pronounced than under a Mediterranean
426 climate (Martínez Cortizas et al. 1994). The high water use efficiency and growth
427 potential of *P. pinaster* even under moderate water stress (Correia et al. 2008), can
428 explain the greater frequency of IADFs type L if low temperatures in late spring and
429 summer alleviate drought stress and promote cambium reactivation. By contrast, a low
430 water availability coupled with high temperatures in late spring-summer increased the
431 probability of latewood IADFs occurrence in inland stands. Cambium reactivation may
432 be promoted by positive water balance at shorter time scales than the monthly periods
433 adopted in this work, as probably occurs in our inland study stands. These climatic
434 determinants for IADFs formation are not consistent with those previously described in
435 the literature, in which the combined effects of cool springs-drought summers (Hoffer
436 and Tardif 2009), or the succession of cool and warm conditions in the active period
437 (Rigling et al. 2002) facilitate the formation of IADFs. But these previous works were
438 performed in boreal pines under other limiting climatic conditions, and they did not
439 distinguish different types of IADFs according to their intra-ring position, then these
440 previous studies could not be comparable with our results.

441 Density fluctuations of type L+ were preconditioned by warm/dry conditions
442 during most of the growing season, particularly by a warm period from March to May
443 in dry years, and triggered by a wet October. This dependency on climatic factors is
444 consistent with those described for other Mediterranean pines. In *P. pinea* and *P.*
445 *halepensis*, the occurrence of a spring-summer drought combined with early autumn
446 precipitation favored the formation of IADFs in the latewood (Campelo et al. 2006; De
447 Luis et al. 2007). Moreover, Vieira et al. (2009) showed that IADFs in the late latewood
448 of *P. pinaster* under Mediterranean conditions are strongly linked to wet autumns,
449 mainly in October. This response was uniformly observed throughout our study area,
450 suggesting that the formation of IADFs type L+ responds to very specific climatic
451 factors, and has a wide geographical and even inter-specific validity among
452 Mediterranean pine species.

453 A relevant finding of this paper is that IADFs in the earlywood and the early
454 latewood of *P. pinaster* in NW Spain were strongly linked to the EA pattern, but not
455 those in the late latewood. This significant connection with EA was due to a direct link
456 between EA variation and the regional climatic drivers for the formation of IADFs at
457 the beginning and the middle of the growing season. In particular, regional climate is
458 strongly related to EA pattern for temperature in previous winter, and also for water
459 balance in April, which are major preconditioning and triggering factors, respectively,
460 for the formation of IADFs types E and L. Although some connection between tree-ring
461 growth and other large-scale patterns, like the North Atlantic Oscillation, have been
462 previously observed in southern Europe (Piovesan and Schirone 2000; Rozas et al.
463 2009), this work demonstrates for the first time a strong link between IADFs formation
464 and the EA pattern, mediated by a robust large-scale modulation of regional climate.

465

466 IADFs and growth plasticity in *P. pinaster*

467 As other Mediterranean pines, *P. pinaster* evolved during the Pliocene under
468 tropical-like climate, before the onset of the Mediterranean climate, as a component of
469 the pre-Mediterranean Arcto-Tertiary flora (Verdú et al. 2003; Petit et al. 2005). This
470 species survived to a past gradual increase of aridity during the transition to
471 Mediterranean conditions, which may have led to its characteristic growth plasticity
472 (Chambel et al. 2007). The expected growth behavior should be partially related to the
473 intra-annual reduction/reactivation of photosynthetic and cambial activities typical of
474 Mediterranean and subtropical environments showing seasonal aridity (Cherubini et al.,
475 2003). Also the vegetative cycle of Mediterranean pines is usually markedly bicyclic or
476 polycyclic, often showing two or more growth units in each annual shoot (Heuret et al.
477 2006; Barthélémy and Caraglio 2007). Polycyclism is a characteristic expressing
478 adaptation to intermittent favorable conditions for vegetative growth that is more
479 frequently expressed under Atlantic humid conditions (Alía et al. 1997). The hormone
480 indol-3-acetic acid is produced in the younger shoots and exported basipetally to induce
481 the production of xylem and regulate the developmental processes during xylogenesis
482 (Aloni 2001), so that we can hypothesize that shoot growth and cambial activity should
483 be related. Further investigations on intra-annual tree-ring growth based on high-
484 resolution dendrometer measurements and xylogenesis (e.g., De Luis et al. 2007;
485 Camarero et al. 2010), and their relationships with shoot enlargement, should inform us
486 about the physiological and ecological significance of IADFs as adaptive traits.

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488

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613 and water relations of trees: implications towards a growth mechanism. *J Exp Bot*
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620 **Table 1** Site and tree characteristics of the *P. pinaster* stands

Stand name	Code	Latitude (N)	Longitude (W)	Elevation (m)	Number of sampled trees	DBH \pm SD (cm)	Age \pm SD (yr)
Monte Aloia	ALO	42° 05'	8° 41'	530	21	46.2 \pm 9.3	33 \pm 6
A Barrela	BAR	42° 32'	7° 51'	620	24	66.7 \pm 15.4	45 \pm 4
A Capelada	CAP	43° 40'	7° 59'	340	23	45.0 \pm 9.0	42 \pm 3
Illa de Cortegada	COR	42° 37'	8° 47'	20	22	54.4 \pm 9.5	52 \pm 6
Monte Insua	INS	43° 08'	9° 09'	10	15	52.8 \pm 11.8	34 \pm 9
Marco da Curra	MCU	43° 22'	7° 53'	590	20	29.6 \pm 3.7	44 \pm 1
Muros	MUR	42° 48'	9° 04'	155	22	56.6 \pm 5.9	54 \pm 3
Trabada	TRA	43° 25'	7° 13'	640	23	45.7 \pm 6.8	50 \pm 5
Verín	VER	42° 04'	7° 33'	855	23	41.6 \pm 3.5	43 \pm 4
Vigo	VIG	42° 12'	8° 39'	365	19	59.6 \pm 8.3	55 \pm 7

621 *DBH* diameter at 1.30 m above ground

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626 **Table 2** Descriptive statistics of the IADF distributions. The period includes at least

627 five trees

Code	Period	Cores					Rings				
		N	% IADFs	% E	% L	% L+	N	% IADFs	% E	% L	% L+
ALO	1967-2006	36	100.0	33.3	97.2	100.0	1081	54.0	2.3	26.3	35.8
BAR	1961-2006	50	100.0	14.0	94.0	100.0	1951	69.7	0.7	11.9	61.9
CAP	1966-2006	45	97.8	20.0	97.8	97.8	1693	30.7	0.6	14.7	17.2
COR	1953-2005	34	100.0	88.2	100.0	100.0	1541	89.5	9.0	38.8	66.9
INS	1967-2007	26	100.0	61.5	100.0	92.3	822	45.7	2.8	13.7	34.4
MCU	1961-2006	46	100.0	2.2	97.8	100.0	1914	36.1	0.0	13.6	26.8
MUR	1951-2006	42	100.0	30.9	100.0	95.2	2172	56.2	0.8	15.7	47.5
TRA	1951-2006	48	100.0	16.6	95.8	89.6	2427	15.9	0.4	8.4	7.9
VER	1964-2006	48	95.8	27.1	58.3	87.5	1894	18.3	0.7	3.7	13.9
VIG	1951-2007	33	100.0	63.6	100.0	100.0	1563	53.0	3.0	28.3	31.3

628 *N* total number of cores or rings analyzed, % *IADFs* percentage of cores or rings

629 showing intra-annual density fluctuations, % *E*, % *L* and % *L+* percentage of cores

630 or rings showing density fluctuations of the types *E*, *L* and *L+*, respectively

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635 **Table 3** Mantel tests for the comparison of inter-site distances and differences between
 636 site elevations, with the similarities between F_{stab} site chronologies and chronology
 637 statistics for the different types of IADFs (ns: non-significant test)

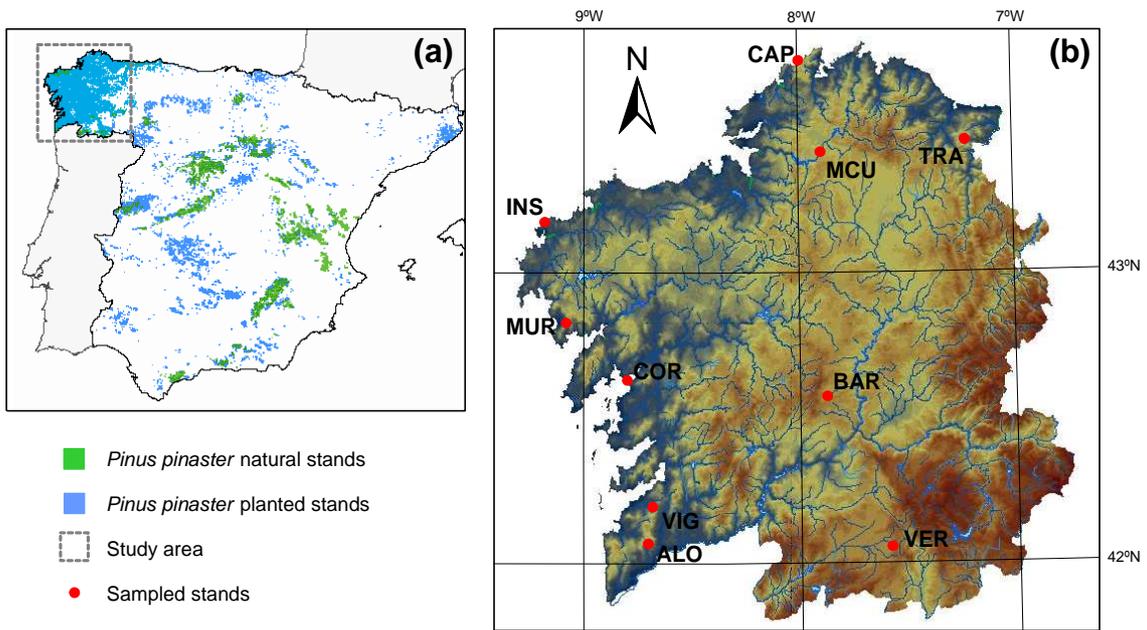
	Variables	Inter-site distances		Site elevations	
		R_M	P -value	R_M	P -value
IADF chronologies	F_{stab} E	0.08	ns	0.13	ns
	F_{stab} L	-0.30	0.021	-0.14	ns
	F_{stab} L+	-0.15	ns	0.16	ns
IADF chronology statistics	% cores E	0.01	ns	-0.73	<0.001
	% cores L	0.25	ns	-0.64	<0.001
	% cores L+	0.11	ns	-0.24	ns
	% rings IADFs	0.05	ns	-0.57	<0.001
	% rings E	-0.04	ns	-0.61	<0.001
	% rings L	0.07	ns	-0.57	<0.001
	% rings L+	0.04	ns	-0.49	0.001

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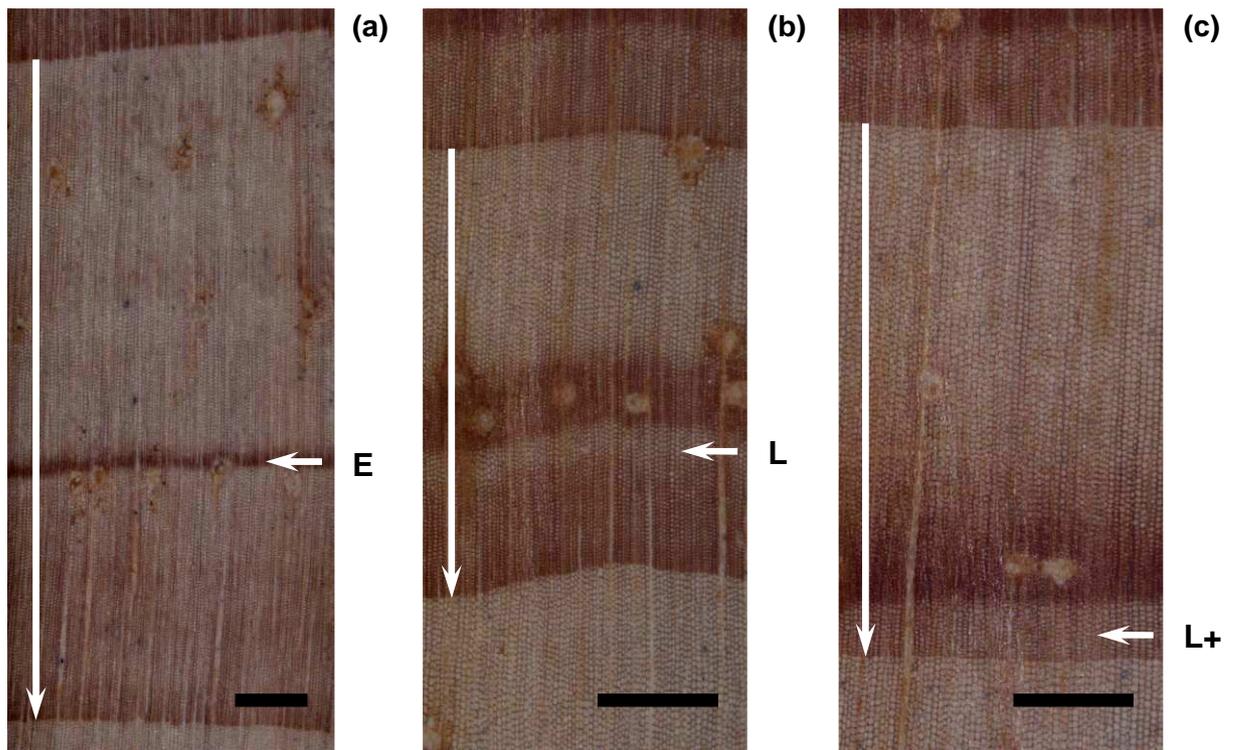
644 **Fig. 1 a** Location of the study area, and distribution of natural and planted *Pinus*
645 *pinaster* in Spain (<http://iniagis.inia.es/Pinus%20pinaster/>). **b** Location of the sampled
646 stands in Galicia, NW Spain. Stand codes are shown in Table 1.

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653 **Fig. 2** Aspect of the intra-annual wood density fluctuations of the types E **a**, L **b** and L+

654 **c** in *P. pinaster* based on their anatomical appearance and intra-ring position. Vertical

655 arrows show the extension of the complete annual ring. E: Latewood-like tracheids

656 within the earlywood. L: Earlywood-like tracheids within the latewood. L+: Earlywood-

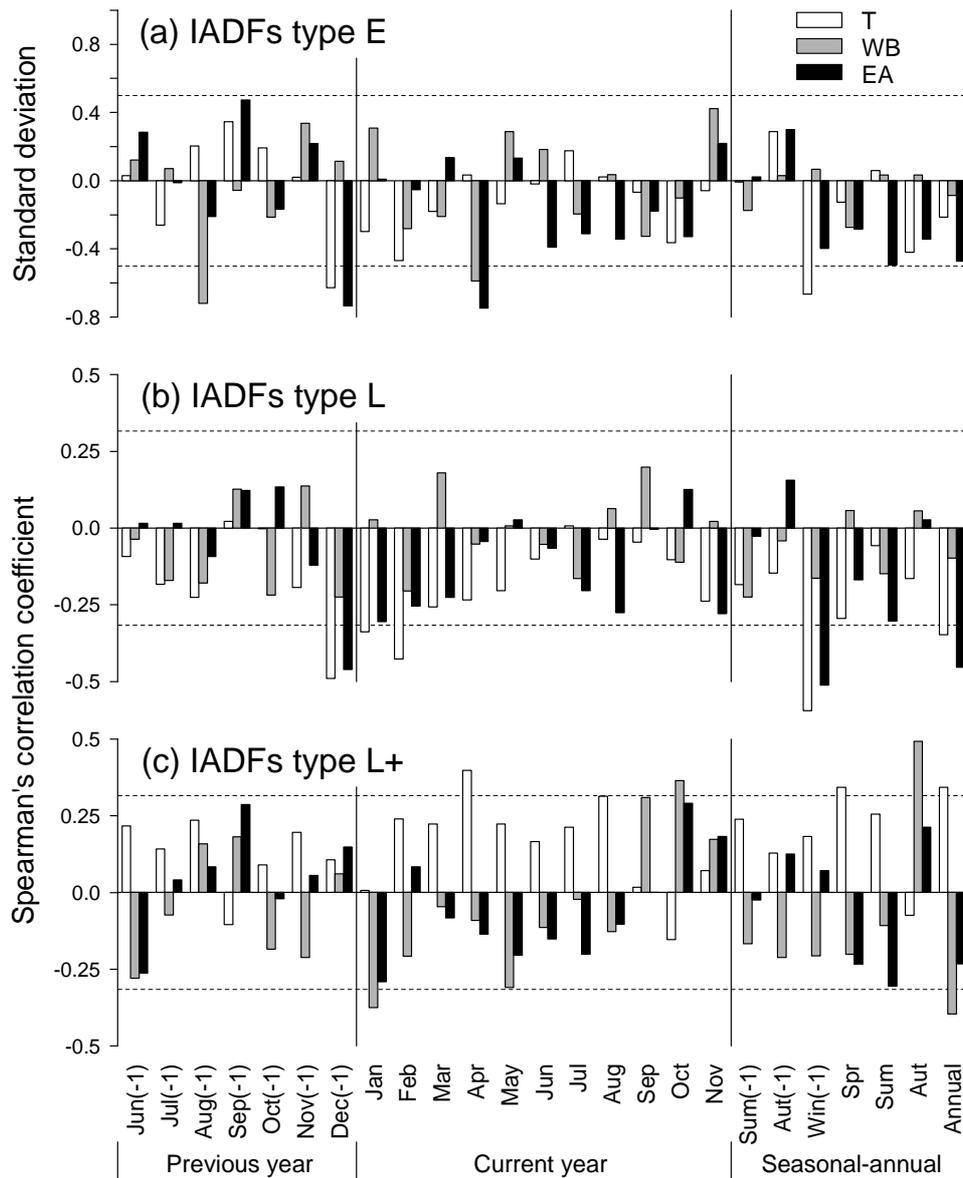
657 like tracheids near the transition between the latewood and the earlywood of the next

658 ring. Scale bars: 1 mm

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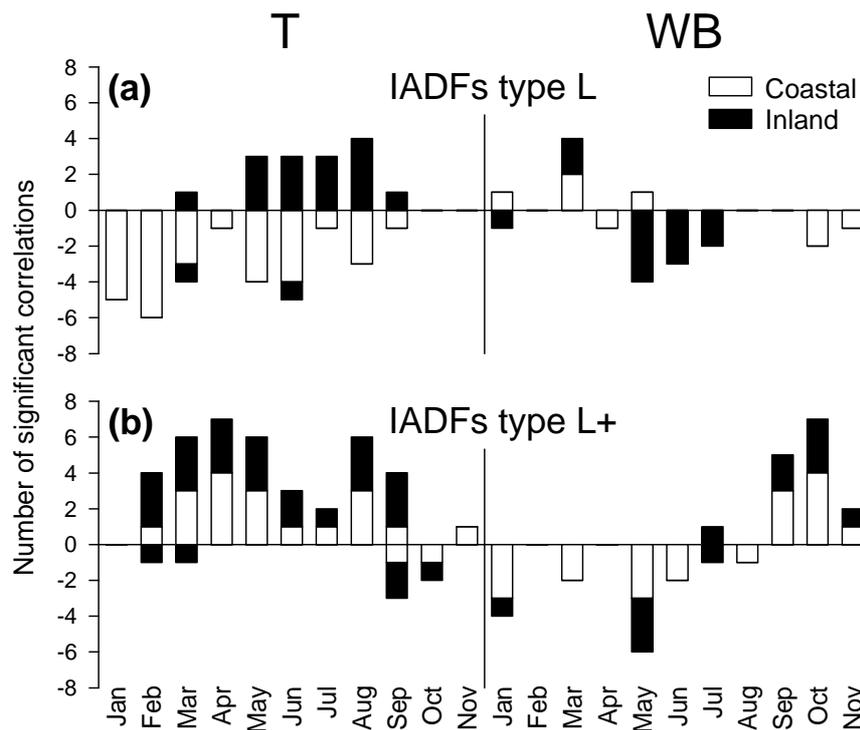


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665 **Fig. 3** Standard deviations from mean temperature (T), water balance (WB) and East
 666 Atlantic pattern (EA) in those years with significant IADFs type E **a**, and Spearman's
 667 correlation coefficients between the significant IADFs of types L **b** and L+ **c** and mean
 668 monthly, seasonal and annual T, WB and EA in the period 1967-2005. Horizontal lines
 669 indicate the standard deviations -0.5 and 0.5 , or the lowest significant ($P < 0.05$)
 670 correlation coefficient, in absolute value

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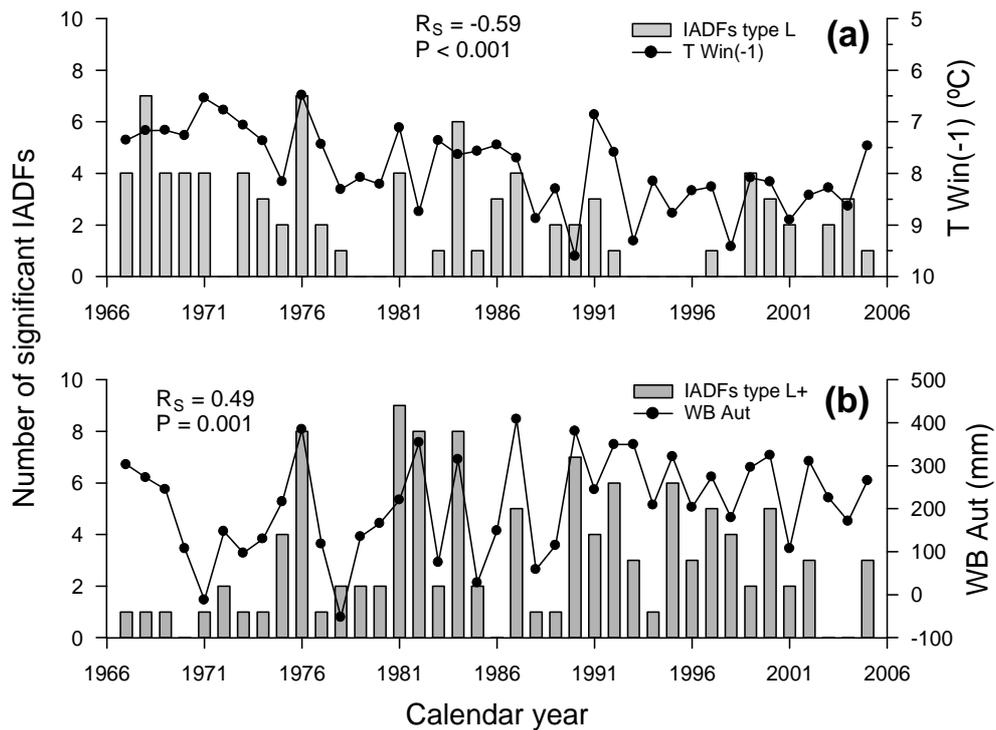
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674 **Fig. 4** Number of significant Spearman's correlation coefficients between the F_{stab}
675 chronologies for IADFs of types L **a** and L+ **b** and local gridded monthly temperature
676 (T) and water balance (WB). Coastal (CAP, COR, INS, MUR, VIG) and inland (ALO,
677 BAR, MCU, TRA, VER) stands are differentiated. Negative numbers refer to negative
678 correlations

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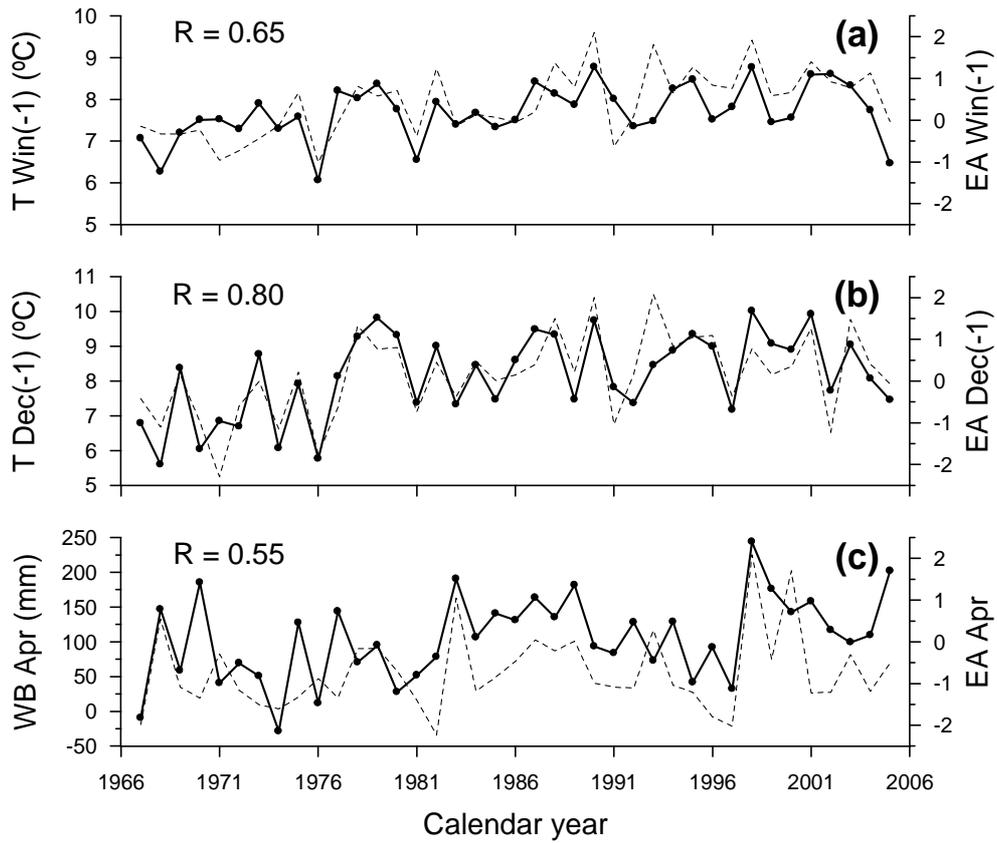
685 **Fig. 5 a** Comparison of the observed number of significant IADFs type L and mean
 686 temperature (T) in previous winter. Note the reverse scale of T axis. **b** Comparison of
 687 the observed number of significant IADFs type L+ and water balance (WB) in autumn.
 688 The Spearman's correlation coefficients (R_S) and their significance values (P) are
 689 shown

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696 **Fig. 6** Comparison of regional climatic variables for T and WB (dashed lines) and the
697 EA pattern (solid lines and dots) for previous winter T **a**, previous December T **b**, and
698 April WB **c**. Pearson's correlations (R) between EA and the regional climate series in
699 1967–2005, all of them significant at the 0.001 level, are shown

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