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Abstract: Foliar plasticity in response to ontogeny, location within the plant and environmental changes is widespread among long-lived organisms. To quantify phenotypic variation in needle morphology and anatomy in response to a climate gradient, we compared contrasted populations of *Pinus canariensis* grown in five sites inside and outside the natural distribution area of the species. Most needle and growth traits were strongly affected by site. In general, site xericity increased the relative area of the dermal and transfusion tissues and decreased mesophyll and endodermis. Within each site, provenances from less productive locations tended to show longer needles, less relative area of dermal tissues but higher relative area of mesophyll and transfusion tissue than provenances from fertile origins. Although sclerophylly increased with aridity, no genetic differences were found for this trait thus apparently the ontogenetic delay of some provenances in xeric environments was not related with the formation of tougher needles. Several patterns of phenotypic response to different environments were shown. In general all traits were plastic but the degree of plasticity was much higher in traits related with growth than foliar traits. These results, combined with formerly published research suggest that highly plastic populations rather than narrowly specialized ones have been selected in this species to cope with the complex interaction of environmental factors in its habitat.

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1 **Intraspecific variation and plasticity in growth and foliar morphology along a**
2 **climate gradient in the Canary Island pine.**

3

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5

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12

13 **Abstract**

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15 changes is widespread among long-lived organisms. To quantify phenotypic variation in
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17 contrasted populations of *Pinus canariensis* grown in five sites inside and outside the
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31 factors in its habitat.

32

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35 *canariensis*.

36

37 **INTRODUCTION**

38

39 Leaves exhibit a great variability consistent with the expected developmental flexibility
40 of long-lived organisms in responding to environmental variation (Sultan 1987).
41 Plasticity in foliar morphology and physiology depending on ontogeny, location within
42 the plant and as a response to environmental changes is widespread. Dissimilarities of
43 sun and shade leaves is one of the best-known and most easily observed examples of
44 foliar plasticity as well as the reduction of leaf size with increasing environmental
45 stress, accompanied by a decrease in specific leaf area and an increase in leaf thickness
46 (Givnish 1984; Cunningham et al. 1999). Since leaf morphological, anatomical and
47 physiological traits are often found to vary together (Niinemets et al. 1998), energy gain
48 and plant production are influenced by leaf size, shape and cell distribution. For
49 example, a higher leaf mass area and the ratio of palisade to mesophyll thickness are
50 correlated with an increase of water use efficiency and photosynthetic rates under high

51 temperatures in *Quercus ilex* (Gratani et al. 2003), whereas the decline in
52 photosynthesis with tree age is closely related to changes in proportion of mesophyll,
53 vascular bundle and stomatal density (Greenwood et al. 2008).

54 The structure of pine needles reflect xeromorphic characteristics based on a high ratio of
55 dry mass per surface area, a sclerified epidermis covered by epicuticular waxes, the
56 presence of a sheath of hypodermal tissue, the deeply sunken stomata, the homogeneous
57 mesophyll and the existence of a suberized endodermis and a transfusion tissue (unique
58 in pines) surrounding the vascular bundles. Similar leaf construction costs have been
59 assessed for leaves with differentiated life-spans and from contrasted ecosystems
60 despite differences in the synthesis of the leaf compounds. It seems that allocation of
61 energy in the leaf, either chemical composition and/or leaf structure is more critical in
62 differentiation between species (Villar and Merino 2001). Defensive compounds such as
63 lignin, which avoid water loss and provide stiffness, are expensive to synthesize, thus it
64 could be thought that needle structure vary depending on resource availability and
65 environmental conditions and can influence survival or growth. Moreover the cost of
66 sclerophylly has been postulated to be one of the causes of the delay in heteroblastic
67 phase change of *Juniperus occidentalis* (Miller et al. 1995) or *Pinus canariensis*
68 (Climent et al. 2006).

69 *Pinus canariensis* is the only endemic pine of the Canary Islands. Despite its small
70 distribution area, topography, island colonization pattern and within island
71 differentiation have favoured a complex genetic structure and a high level of haplotypic
72 diversity (Gómez et al. 2003). Genetic differentiation within species is often a key
73 aspect in adaptation to geographic variation (Bongarten and Teskey 1987; Ducrey et al.
74 2008). Geographical dependence of survival (López et al. 2007), ontogeny (Climent et
75 al. 2006) and traits related to fire response (Climent et al. 2004) of this species has been

76 already assessed. Furthermore, in a previous study we observed distinct needle anatomy
77 and morphology in natural populations of Canary Island pine spread throughout the
78 ecological range of the species (López et al. 2008). The apparently adaptation of natural
79 populations to their specific environment confounded environmental with genetic
80 factors. Consequently, our first objective was to separate intraspecific genetic
81 differentiation from phenotypic plasticity of those traits by growing several populations
82 in a common garden experiment replicated over several sites with contrasting
83 environments conditions. Secondly, we checked if there is any evidence of intraspecific
84 divergence in plasticity inside and outside the natural range of the species. Finally, we
85 were interested in the relationship between heterophyllic plasticity and the delay of the
86 heteroblastic phase change (change from the juvenile to the adult phase) in xeric
87 environments.

88

89 **Material and methods**

90

91 *Plant material and trial sites*

92 Four contrasted provenances (Table 1), ten trees per provenance, were sampled in five
93 locations of two multi-site provenance trials of *Pinus canariensis* in Tenerife (Canary
94 Islands, Spain) and Israel (Table 2; see more details of the provenance trials in López et
95 al. 2007). The two experimental sites in Tenerife have similar soils and mean annual
96 temperatures, 13.8 °C, but they differ in rainfall, 795 mm / year plus the water added by
97 the fog in Realejos (TFW) and 460 mm in Fasnia (TFD). In Israel, the experimental
98 sites differed in both, climate and soil conditions, 720 mm and a mean annual
99 temperature of 16.5 °C in Biria (ISRW), 19.8 °C and 542 mm in Ben Shemen (ISRM),
100 and 20.1 °C and 499 mm in Ein Dor (ISRD). The bulky and clayey soil of ISRM

101 hampered plant growth. Temperature and rainfall data were obtained from the
102 Worldclim database (Hijmans et al. 2005). Besides elevation, temperature, precipitation
103 and drought period, an indirect site index, the sapwood area per hectare (Gs), was used
104 to characterize environmental conditions of the provenances. This index accounted
105 better for variation in climatic parameters that occur at very short distances due to the
106 topography and the variable amount of water carried by trade winds (more details in
107 Climent et al. 2004).

108 From each tree, 24 needles were taken from the south half of the crown at the same
109 height (about 1.5 m) from the ground. Six needles per tree were fixed in FAA (5%
110 formalin, 5% acetic acid, 90% alcohol) until taken to the laboratory and the rest were
111 used to assess leaf mass per projected area (LMA).

112 Survival, height and polycyclism were compared in the five study sites six years after
113 planting while age and height of heteroblastic change (i.e. change from juvenile to adult
114 phase) were only available in the two locations of the Canary Islands (more details in
115 Climent et al. 2006; López et al. 2007).

116

117 *Morphological and Anatomical measurements*

118 LMA was calculated from 18 needles of each sampled tree. Needle projected area was
119 obtained with a scanner. The images were analyzed using Scion image for Windows
120 (Scion corporation, Frederick, Maryland, USA). Needle samples were then dried at 40
121 °C for 5 days to determine leaf dry mass and leaf mass per unit area (in milligrams per
122 square centimetre).

123 Needle length (NL) was measured with a caliper. Cross-sections of the central portion
124 of three needles per tree were obtained with a sliding microtome, stained with safranin-
125 fast green and mounted following a standard method (Johansen 1940). Sections were

126 observed through an optical microscope and digitalized. Needle width (NW) and the
127 areas corresponding to the following tissues were measured using Scion Image software
128 (Scion corporation, Frederick, Maryland, USA): total cross section (CROSS), epidermis
129 together with hypodermis (HYP), mesophyll (MES), sum of resin canals lumen (RES),
130 endodermis (END), transfusion tissue (TRANS), xylem (XYL) and phloem (PHLO).
131 Needle slenderness was obtained as NL / NW and the relationship between water
132 conduction and photosynthesising parenchyma was calculated as XYL / MES .

133

134 *Data analysis*

135 Statistical analyses were conducted on the individual-tree mean values for each trait.
136 The analyses were performed with Statistica (StatSoft, Tulsa, OK). The effects of the
137 site, the provenance and the interaction site x provenance on the morphological,
138 anatomical and field performance variables were tested by a General Linear Model
139 equation. The percentage of variation explained by each factor was calculated with the
140 variance components, assuming all the factors were random.

141 Relationships between morphological and anatomical variables were checked using
142 Spearman's rank correlation coefficients and principal component analysis (PCA). Once
143 PC were obtained a Varimax rotation was applied to analyse the relationship among
144 those traits. Spearman's correlation coefficients were determined between average
145 values of needle and field traits of each provenance with climatic variables at origin.

146 Patterns of phenotypic response (termed reaction norms) were obtained plotting the
147 mean values of a given trait against the climatic gradient represented by the length of
148 the drought period (dp) of the trial sites. A General Linear Model including the driver of
149 the reaction norm (dp) was applied to test the parallelism and intersections of the
150 reaction norms. In addition, we used a Plasticity Index (PI) based on the difference

151 between maximum and minimum means of each trait among the trial sites divided by
152 the maximum mean value (Valladares et al. 2000). This index was calculated for
153 provenance responses in the Canary Islands and Israel independently.

154

155 **RESULTS**

156

157 *Needle morphology*

158 Site was the main source of variation for length and needle slenderness and the only
159 significant effect for leaf mass per area (Table 3). Needle length and slenderness
160 decreased with xericity. The longest needles were found in TFW, mean value of 15.36
161 cm, while the shortest in ISRD, mean value of 10.13 cm (Fig. 1a). On the contrary, leaf
162 mass per area was much higher in the three Israeli sites and ISRW almost doubled the
163 mean value of TFW, 23 mg/cm² versus 12 mg/cm² respectively (Fig. 1c). Needle width
164 was apparently unrelated to rainfall or drought period in the sites of origin (Fig 1b).
165 Needle width and needle length were strongly correlated ($r = 0.78$) whereas no
166 correlation was found between them and leaf mass per area.

167

168 *Needle anatomy*

169 Site, provenance and the interaction site x provenance were significant for all traits
170 (Table 3). Needle cross sectional area showed the most dramatic differences in TFW
171 between the extreme provenances, Esperanza and Tirma, and the intermediate ones,
172 Guancha and Vilaflor. In the other sites, Tirma maintained the highest value while
173 Guancha showed the smallest cross sectional area in ISRM and Arico in ISRD. The
174 relative area occupied by the hypodermis plus epidermis increased considerably in the
175 three Israeli sites. Within each site, the percentage of hypodermis increased with

176 provenance site index (Fig. 2, Fig. 3). An opposite pattern was showed by the
177 percentage of mesophyll which was lower in the dryer, Israeli sites and generally
178 decreased with site index (Fig. 2, Fig. 3). A high site effect was also encountered for the
179 percentage of transfusion tissue and percentage of endodermis (34% and 45% of the
180 explained variation respectively). Both traits were apparently related with dryness of the
181 experimental sites but whereas transfusion tissue was lower in the wet sites (7.95% in
182 ISRW compared to 12.20% in ISRD), endodermis increased in these locations (14.01%
183 in ISRW versus 8.93% in ISRM). The most striking differences in the relative area of
184 the resin canals among provenances were displayed in ISRW where the percentage of
185 area of the resin canals of Esperanza was almost 2.5 times higher than Tirma (Fig. 2).
186 Relative area of phloem and xylem were highly correlated ($r = 0.94$). Site x provenance
187 interaction was high for both traits explaining more than 40% of the variation (Table 3).

188

189 *Principal Component analysis*

190 Four principal components had eigenvalues higher than 1 and explained 79.33% of the
191 total variance of morphological and anatomical traits. The PC1 explained 30.67% of the
192 total variance and was negatively related to needle length and width, cross sectional area
193 and relative area of endodermis and vascular bundle and positively with relative area of
194 hypodermis and transfusion tissue. The PC2 (22.00% of the variance) had high positive
195 factor loads for relative area of mesophyll and negative for relative area of hypodermis
196 and resin canals (Fig. 4). The PC3 (16.37% of the variance) was mostly correlated to the
197 vascular bundle while the PC4 (10.29% of the variance) was positively related to the
198 endodermis and mesophyll and negatively to transfusion tissue and leaf mass per area.
199 The PC1 separated the two wet sites, more than 700 mm rainfall per year, from the rest,
200 whereas the PC2 divided the trial sites in Israel from those in the Canary Islands which

201 mainly differed in the length of the drought period and the temperature range (Table 2).
202 When we focused on provenances, the first axis divided those in Tenerife from the only
203 provenance in Gran Canaria which grows in a considerably less fertile location ($G_s =$
204 $15.9 \text{ m}^2 \text{ ha}^{-1}$). Tirma and Vilaflor had positive coordinates on the second axis while
205 Esperanza and Guancha had negative.

206

207 *Field performance*

208 Site was the main source of variation for survival, height and polycyclism (Table 4).
209 Although the provenance effect was always significant, the percentage of variation
210 explained by it was never higher than 3.5%. The three variables were higher in the wet
211 site of Israel. Survival ranged from 44% in ISRD to 86% in ISRW. Polycyclism was
212 almost negligible in ISRM while in ISRW more than 70% of trees showed a second
213 flush. Variation in height was remarkable, from 9.6 m in TFD to 24.9 m in ISRW. It is
214 worth to note the high growth achieved in ISRD, 21.1 m, even higher than growth in
215 TFW, 20.0 m (Table 5). Genetic differences for survival were only significant in TFW
216 and ISRM where Tirma displayed higher survival rates than Guancha. Scarce genetic
217 differentiation was also found for height and polycyclism, as a whole, Guancha grew
218 better while Tirma grew slower and tended to be more polycyclic.

219 Heteroblastic phase change was earlier in TFW than in TFD but the height at this
220 change was not significantly different between both sites (Table 4). The divergence
221 among provenances was only evident in the wet site where Esperanza and Guancha
222 displayed a more precocious heteroblastic change and with lower height than Tirma.
223 Age or height at heteroblastic change did not show any connection with needle traits.

224

225 *Influence of the climate of origin on needle traits and field performance*

226 The site index at the seed source was strongly correlated with relative area of
227 mesophyll, hypodermis and resin canals but with different sign. As fertility rose, the
228 percentage of mesophyll decreased ($\rho = -1$) and the percentage of resin canals and
229 hypodermis increased ($\rho = 1$). This index was also negatively correlated with survival (ρ
230 $= -1$) and polycyclism ($\rho = -1$) but it was not with height. Needle length was positively
231 related to seed-source mean annual temperature ($\rho = 1$) while temperature range was
232 negatively related to relative area of endodermis ($\rho = -1$). Leaf mass per area was
233 positively related to length of the drought period ($\rho = 1$). An increase in 3.2 months of
234 drought period from the driest to the wettest provenance was associated with a 22%
235 increase in LMA.

236

237 *Assessment of Plasticity*

238 All provenances showed significant phenotypic plasticity for foliar traits as showed the
239 significant influence of the trial location. Trends of phenotypic responses differed
240 between Canary Islands and Israel trial sites for relative area of the dermal tissues, resin
241 canals, mesophyll and vascular bundle.

242 In general the degree of plasticity (calculated with the PI) was similar inside and outside
243 the natural range of the species except for the vascular bundle, resin canals, and
244 polycyclism frequency which showed higher indexes in Israel. Nevertheless, levels of
245 plasticity varied widely among traits. Traits related with growth were much more plastic
246 than needle traits. Among these last ones, needle length, LMA and relative area of the
247 transfusion tissue were the most plastic. The covariance analysis showed divergences
248 between reaction norms of the four provenances for all foliar traits except for relative
249 area of endodermis and transfusion tissue in Israel. In the Canary Islands, the reaction
250 norms of Esperanza, the most fertile provenance, followed an opposite direction to the

251 others: an increase in the length of the drought period meant a rise in relative area of
252 dermal tissues, endodermis, vascular bundle and resin canals but the decline in relative
253 area of mesophyll and transfusion tissue. On the other hand, in Israel, intraspecific
254 differences among reaction norms were more pronounced and not only Esperanza but
255 also Tirma, the provenance from the least fertile origin, were significantly different
256 from the others.

257

258 **Discussion**

259

260 The patterns of variation encountered are scarcely trivial. It is most striking that both
261 site (trial location) and provenance had very visible effects on almost all variables, with
262 significant interactions and several patterns of phenotypic response to different
263 environments.

264

265 *Foliar and field traits responses to the environmental gradient*

266 The majority of needle and field traits were strongly affected by site (Tables 3, 4)
267 reflecting that high phenotypic plasticity is widespread in this species as formerly
268 postulated (López et al. 2007). Plasticity depends on the level of organization in the
269 same plant. It seems to increase with complexity since it was higher in traits related to
270 physiology and growth than in morphological traits (Valladares et al. 2000; the present
271 work).

272 Leaf mass per area ratio, widely used as a sclerophylly index (Paula and Pausas 2006),
273 increased with xericity, consistently with its recognised role in the adaptation to low
274 water availability in woody plants (Niinemets 2001), through the reduction of leaf
275 transpiration, avoidance of tissue compression and improvement of leaf recovery after

276 drought-induced cavitation (Salleo et al. 1997). The reduction of needle length, though,
277 seems to be more related to annual rainfall than to drought period and for example,
278 longer needles were reported in ISRW comparing with TFD. Concerning anatomical
279 traits, the most consistent difference across sites was the relative area of the dermal
280 tissues, which increased almost linearly with xericity while the mesophyll displayed an
281 opposite pattern. Contrasting patterns were also exhibited by the endodermis and the
282 transfusion tissue but in this case, annual rainfall instead of drought period in the trial
283 sites appeared to be more explicative.

284

285 *Genetic differentiation within environments*

286 Except for LMA, all traits were significantly different between provenances. In general,
287 provenance differentiation was less pronounced in the extreme sites of the
288 environmental gradient based on the length of the drought period. This reduction of
289 genetic differentiation in more extreme environments is a rather consistent trend in
290 genetic experiments of forest trees. In general, provenances from infertile sites
291 accounted for a higher relative area of the mesophyll and transfusion tissue but invested
292 less resources in dermal tissues and endodermis. It is claimed that species from
293 unproductive habitats allocate proportionally less nitrogen to photosynthesis (Field and
294 Mooney 1986) and therefore to the mesophyll cells. However, while this assessment is
295 coherent with the observed patterns (including the reduction of needle size), the
296 intraspecific genetic differentiation was the opposite in the Canary Islands pine, i.e.
297 needles of the dry provenances, Vilaflor and Tirma, had longer needles and invested
298 more resources in mesophyll and transfusion tissue. We suggest that these provenances
299 could be able to maintain higher photosynthesis rates linked to a wider relative area of
300 mesophyll cells (Parkhursts 1986) and longer needles.

301

302 *Intraspecific differences in phenotypic plasticity*

303 Every population showed plastic responses of foliar traits, growth and survival but the
304 direction and degree of phenotypic change across environments differed among traits
305 (Table 6). The neutral genetic diversity found in the studied populations (Vaxevanidou
306 et al. 2006) indicated a certain degree of isolation and a high differentiation among
307 populations within each island. Particularly a boundary of sharp genetic change in
308 haplotypic frequencies separated Guancha from the other three provenances.
309 Nevertheless, for the phenotypic traits analyzed here, Esperanza was the most distinct
310 population both inside and outside the natural range of the species. Plasticity differences
311 among provenances are difficult to explain in terms of specific adaptations and are more
312 easily considered as a consequence of non-adaptive internal constraints. In fact, we
313 found little relationship between height, polycyclism, survival and foliar traits.
314 Although plastic responses of plants to changing abiotic factors might increase fitness
315 and in heterogeneous environments selection usually favour adaptive plasticity over
316 genetic differentiation (Valladares et al. 2002), injurious and neutral plasticity have
317 been also reported and canalization can increase fitness in highly dynamic and
318 unpredictable, both in time and space, ecosystems (Alpert and Simms 2002).

319

320 *Functional interpretation of anatomical traits*

321 LMA, dermal and transfusion tissues were positively related to the first multivariate
322 axis of the PCA, functionally linked to sclerophylly, while relative area of the vascular
323 bundle, with chiefly a conductive function, the endodermis, which controls the transport
324 of transpiration water for xylem to stomata (Scholz and Bauch 1973) and traits related
325 to size are negatively related, agreeing with the general tendency of reducing needle

326 dimensions as a consequence of environmental stress (Richardson and Rundel 1998).
327 These correlations would confirm the important role of the transfusion tissue in drought
328 adaptation of this species as proposed in the previous study with natural populations
329 (López et al. 2008). In addition, this component separated the three sites with less
330 annual precipitation from the wet sites in both trials. This grouping of anatomical and
331 morphological traits matched our previous results with natural populations
332 corroborating that size and position of needle tissues reflect adaptations to diverse
333 environmental conditions (Pachepsky et al. 1995).

334 Results do not support that ontogenetic delay is caused by the cost of leaf sclerophylly
335 in this species. Other differences in resource allocation (i.e. leaf, root or stem biomass)
336 should be investigated to explain the high ecotypic variation for heteroblastic change
337 and the highly significant correlation with survival at the population level (Climent et
338 al, 2006; López et al 2007).

339 Our findings indicate not only that needle morphology is plastic in the Canary island
340 pine, but also that different reaction norms facing a climatic gradient have been selected
341 among four contrasted populations. Considering previous results on heteroblasty,
342 survival and height growth (Climent et al. 2006, López et al. 2007), highly plastic
343 populations rather than narrowly specialized ecotypes, seem to have been favoured in
344 the Canary Islands pine, allowing this species to cope with the highly heterogeneous
345 environment (both over short geographical distances and over time) of its natural
346 habitat.

347

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423

424 Figure legends

425 Fig. 1. Mean (\pm SE) length (a), width (b) and leaf mass per area (c) of four provenances
426 of *P. canariensis* at five trial sites. -▲- Esperanza, -○- Guancha, --*-- Vilaflor, -■-
427 Tirma.

428

429 Fig. 2 Relative area (in percentage) occupied by needle tissues at five trial sites. Bars
430 represent the standard error of the mean. -▲- Esperanza, -○- Guancha, --*-- Vilaflor,
431 -■- Tirma.

432

433 Fig. 3 Cross sections of canary pine needles of the provenance Esperanza in two
434 contrasted sites TFW (a) and ISRW (b). Grey arrows shows the hypodermis and black
435 dotted arrows shows the transfusion tissue.

436

437 Fig. 4 Principal Components Analysis. Percentage of explained variation and projection
438 of the original variables, trial sites and provenances on the factor plane. Bars correspond
439 to the standard errors of the mean values of all individual trees in each site or of all trees
440 of each provenance.

Table 1. Location and ecological characteristics of the four provenances of *Pinus canariensis* used in this study.

Pa, annual precipitation; T, mean annual temperature; Tr, annual temperature range; Dp, drought period; Gs, sapwood area per hectare.

Provenance / Trial Site	Latitude (N)	Longitude (W)	Elevation (m)	Pa (mm)	T (°C)	Tr (°C)	Dp (months)	Gs (m ² h ⁻¹)
Esperanza	28°25'	16°23'	1100	630	14.7	17.4	4.79	36.6
Guancha	28°22'	16°40'	700	940	12.7	14.4	3.6	26.6
Vilaflor	28°11'	16°38'	1900	505	13.2	22.2	5.36	15.9
Tirma	28°01'	15°42'	850	380	18	20.6	6.83	9.8

Table 2. Location and climatic characterisation of the trial sites.

T: mean annual temperature, Tr: annual temperature range, P: precipitation, Ps: Spring precipitation, Psm: Summer precipitation, Pa: Autumn precipitation, Pw: Winter precipitation, Dp: drought period.

Site	Island/District	Latitude	Longitude	Elevation	T	Tr	P	Ps	Psm	Pa	Pw	Dp
TFW	Tenerife	28°21'N	16°36'W	1575	14.3	21.1	795.0	173.2	21.2	259.6	341.0	4.07
TFD	Tenerife	28°16'N	16°29'W	1720	11.4	21.0	460.0	75.3	4.0	170.6	210.1	4.82
ISRW	HaZafon	32°58'N	35°29'E	874	16.5	24.9	723.0	145.0	0	102.0	476.0	6.20
ISRM	HaMerkaz	31°57'N	34°55'E	62	19.8	24.1	542.0	83.0	0	96.0	363.0	6.70
ISRD	HaZafon	32°39'N	35°25'E	104	20.1	24.6	499.0	169.0	0	83.0	335.0	7.00

Table 3. Percentage of the explained variation and significance values from the GLM to determine the sources of variation for the anatomical and morphological traits.

F values with asterisks are significant (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), ns not significant.

Source	NL	NW	LMA	CROSS	HYP	MES	END	TRANS	XYL	PHLO	RES
Site	22.65 ***	12.22 ***	57.17 ***	17.08 ***	46.75 ***	42.61 ***	45.41 ***	34.00 ***	40.48 ***	35.04 ***	34.23 ***
Provenance	9.87 ***	ns	ns	23.27 ***	22.41 ***	7.39 ***	0.48 **	15.47 ***	0.10 ***	0.10 ***	11.92 ***
Site x Prov	11.66 ***	23.11 ***	22.97 ***	16.67 ***	9.61 ***	18.51 ***	14.35 ***	15.04 ***	41.30 ***	43.49 ***	14.42 ***

Table 4. Percentage of the explained variation and significance values for field performance traits.

F values with asterisks are significant (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), ns not significant. †

Calculated only at TFW and TFD.

Source	Survival	Height	Polycyclism	Th†	Hh†
Site	10.28 ***	64.31 ***	23.83 ***	17.44 ***	ns
Provenance	2.09 **	3.28 **	3.42 **	10.82 ***	9.70 *
Site x Prov	ns	ns	3.59 *	8.60 *	7.76 *

Table 5. Mean (\pm SE) survival, height, polycyclism, time at heteroblastic change (Th) and height at heteroblastic change (Hh) in the trial sites.

† Calculated only at TFW and TFD.

Site	Survival	Height (cm)	Polycyclism	Th† (year)	Hh† (cm)
TFW	0.78 \pm 0.04	200 \pm 8	0.65 \pm 0.06	1.9 \pm 0.20	35.0 \pm 2.1
TFD	0.65 \pm 0.05	96 \pm 7	0.36 \pm 0.06	3.5 \pm 0.22	35.2 \pm 2.3
ISRW	0.86 \pm 0.03	249 \pm 10	0.71 \pm 0.10		
ISRM	0.72 \pm 0.04	120 \pm 7	0.04 \pm 0.07		
ISRD	0.44 \pm 0.05	211 \pm 11	0.37 \pm 0.08		

Table 6. Mean Phenotypic Plasticity Index ($PI = (\max - \min) / \max$) of the four provenances of *Pinus canariensis* in the provenance trials of the Canary Island (upper number) and Israel (lower number).

Provenance	NL	NW	LMA	CROSS	HYP	MES	END	TRANS	XYL	PHLO	RES	H	POL
Esperanza	0.34	0.07	0.21	0.28	0.08	0.10	0.09	0.07	0.05	0.06	0.26	0.56	0.89
	0.55	0.08	0.11	0.15	0.06	0.04	0.34	0.47	0.30	0.22	0.53	0.53	1
Guancha	0.08	0.01	0.31	0.09	0.01	0.07	0.30	0.31	0.19	0.19	0.18	0.28	0.06
	0.10	0.01	0.32	0.24	0.11	0.01	0.38	0.44	0.38	0.33	0.37	0.37	1
Vilaflor	0.30	0.06	0.38	0.10	0.02	0.05	0.43	0.36	0.17	0.17	0.02	0.32	0.41
	0.29	0.08	0.30	0.29	0.10	0.02	0.43	0.37	0.33	0.78	0.55	0.55	1
Tirma	0.09	0.02	0.45	0.12	0.08	0.17	0.47	0.30	0.28	0.28	0.19	0.53	0.40
	0.38	0.03	0.27	0.10	0.02	0.08	0.41	0.27	0.33	0.59	0.51	0.51	0.84

Figure

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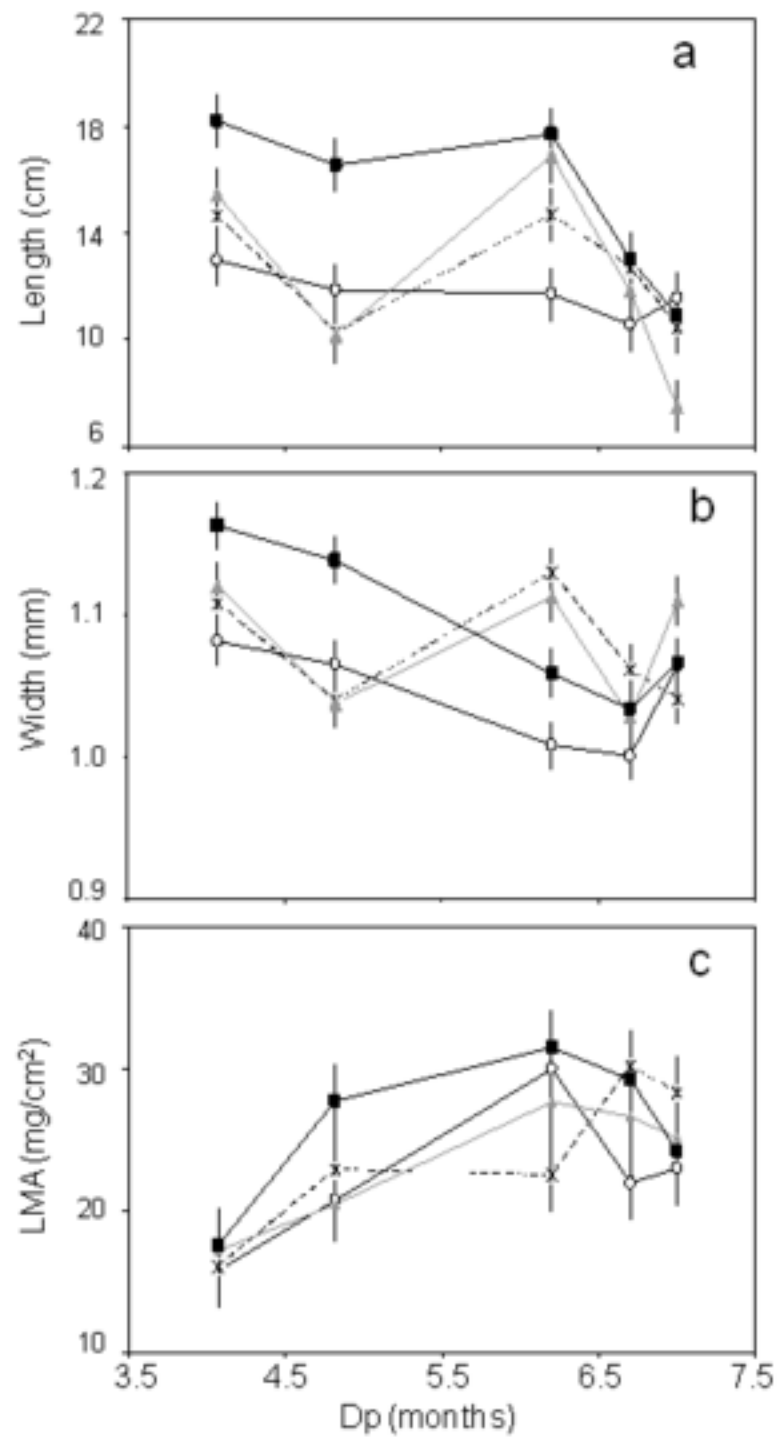
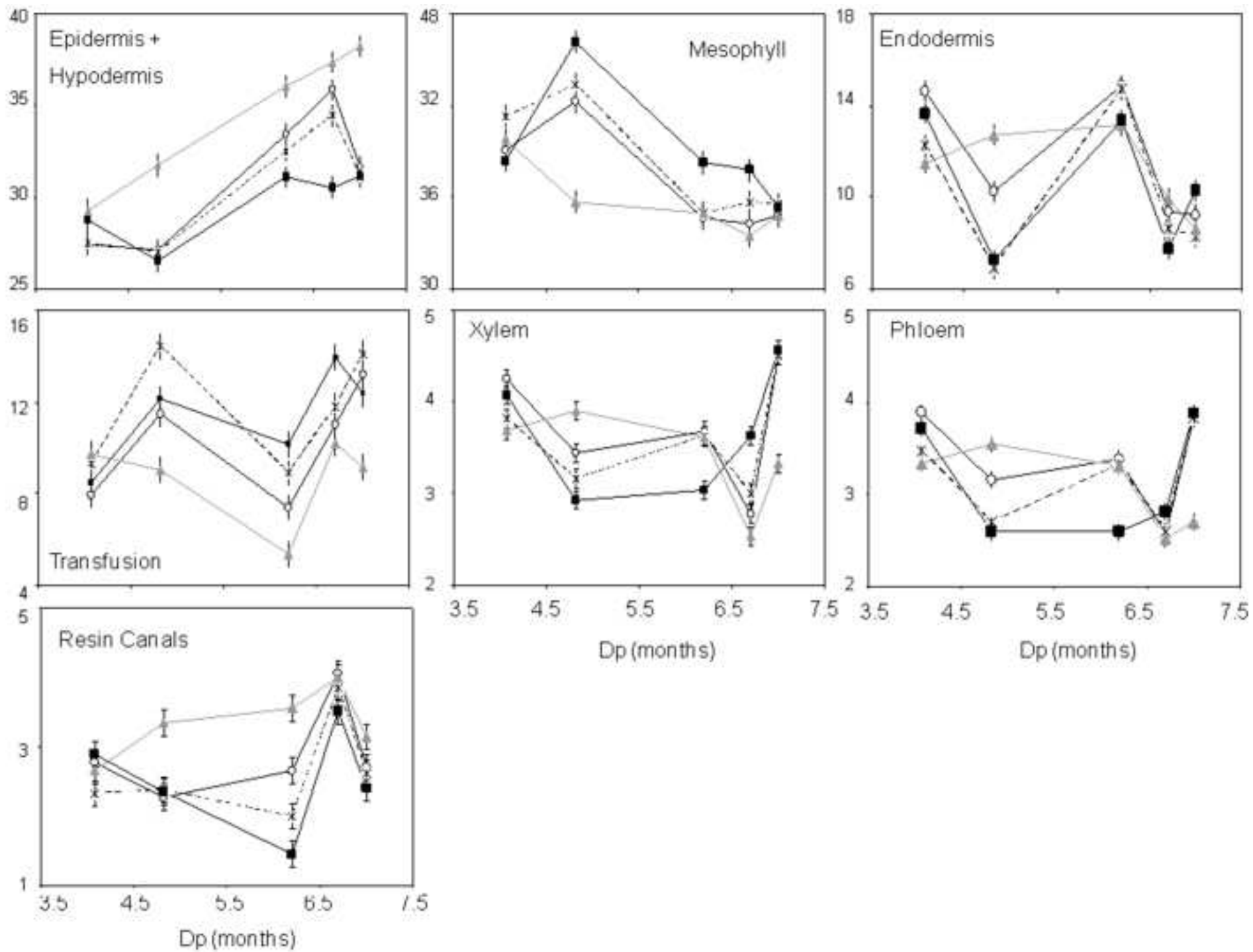
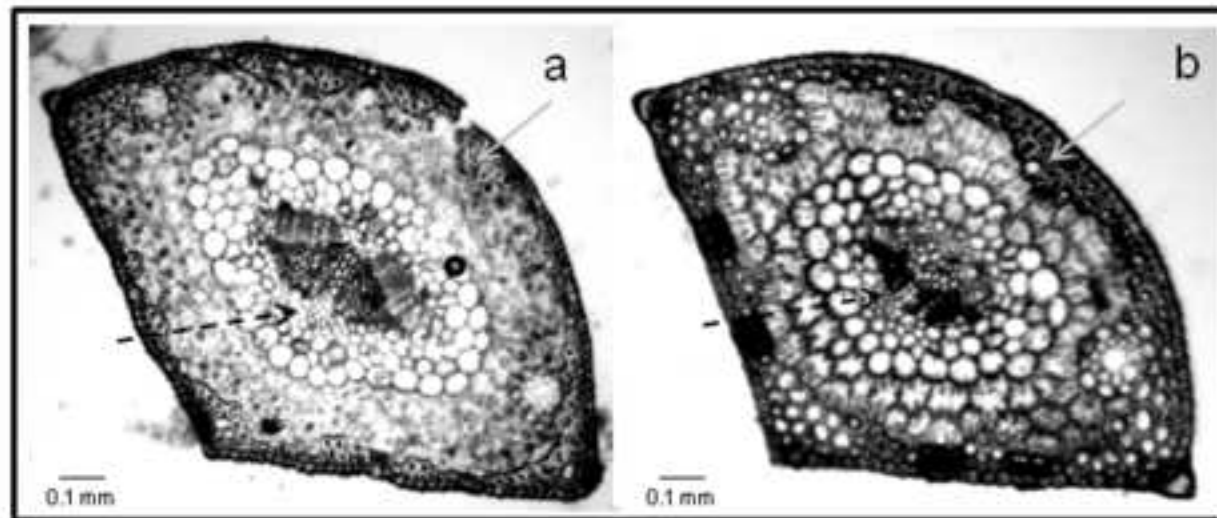


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