

Contrasting ecotypic differentiation for growth and survival in *Pinus canariensis*

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Abstract. We tested genetic and environmental effects and their interaction on the behaviour of 21 provenances of *Pinus canariensis* Chr. Sm. Ex DC from the Canary Islands and three seed sources from Israel at seven study sites covering a wide range of ecological conditions. Survival and growth traits (height, diameter and polycyclism) and their relationship with environmental parameters were assessed to evaluate their adaptive value and establish patterns of variation of the species inside and outside its natural distribution area. The results showed a high level of ecotypic differentiation for survival. As a general pattern, seed sources from favourable environments exhibited lower survival rates at dry sites than those from harsh environments ($r = -0.76$, $P < 0.05$, between survival and site index at the seed source). By contrast, growth traits presented a high phenotypic plasticity, scarce differentiation among seed sources and a negligible genotype \times environment interaction. With few exceptions, local provenances from the Canary Islands did not stand out for survival or growth when compared with the rest at each trial site, whereas local seed sources from Israel were among the best growing and survived better at the experimental sites in this country. Therefore, the possibility of a locally adapted land race in Israel is discussed. We also discuss the low geographic differentiation for growth in the Canary Islands pine in the light of the current knowledge of the species' life history and the potential use of this species in reforestation programs in semi-arid environments.

Introduction

In the last decades, forest researchers have postulated that multi-site provenance trials are one of the most appropriate tools to estimate the response of forest trees to the alteration of environmental conditions within the ongoing global climate change (Mátyás 1994; Schmidting 1994; Sáenz-Romero *et al.* 2006). These trials allow evaluation of both the response of the different seed origins in the same environment and the reaction of the same seed origin across field environments. Unfortunately, given that the main focus is on production, extreme- and poor-yield sites are frequently excluded from the experimental design of these plantations. However, the predicted and current climate changes in some areas, such as the Mediterranean basin, strongly support the need to make quick assessments of the adaptability of forest reproductive materials to drier and warmer conditions. For example, in *Pinus pinea*, a considerable decrease of cone production, endangering natural regeneration, has been recently postulated following a neat rainfall reduction of 1.8 mm per year from 1960 to 2000 in inland Spain (Mutke *et al.* 2005).

The capacity of a forest species to adapt to different environments depends, in the mid- and long-term, on its genetic variability (additive genetic variance) which facilitates changes in the genetic structure through selection and migration. In

the short-term, the individual phenotypic plasticity, that is, the ability of a genotype to produce different phenotypes in contrasting environments, can allow quick acclimatisation through physiological and developmental changes (Eriksson *et al.* 1993; Sultan 2000a). The ability of an organism to alter its morphology and physiology as a response to environmental changes is not necessarily adaptive; however, in some cases, particularly when resources are scarce, these modifications seem to be unavoidable (Wells and Pigliucci 2000). In heterogeneous and unpredictable ecosystems such as Mediterranean regions, adaptive plasticity can be considered an advantage, especially for plants (Bradshaw 1965). The evaluation of the behaviour of forest species by assessing their phenotypic plasticity under contrasted environments will shed some light onto for the deployment and the conservation of forest genetic resources (Matheson and Cotterill 1990). This knowledge would pave the way for a fundamental breakthrough to mitigate problems concerning erosion and degradation that Mediterranean forest areas frequently undergo.

Although fitness can be measured almost directly in annual plants or plants with short reproductive cycles (Sultan 2000b), it is difficult to assess the adaptive value (in the strict biological sense) of different traits in forest trees because of their long lifespan, delayed maturity and complex morphological

and ontogenetic constraints (Chambel *et al.* 2005; Petit and Hampe 2006). These facts, together with size-related yield traits, have led to the wide use of tree height as a proxy to adaptation. Moreover, survival constitutes a second necessary fitness component which is complementary to tree size.

Little correlation has been found between neutral genetic diversity and diversity assessed through quantitative traits in forest species (González-Martínez *et al.* 2002). Thus, field trials represent a necessary approximation to the adaptive differentiation of species or populations and complement patterns of neutral genetic variation.

Pinus canariensis (Canary Island pine) is the only endemic pine of the Canary archipelago. Its natural distribution area is restricted to the western islands where it grows from near sea level up to ~2500 m. It colonises volcanic soils and is able to live in climates that range drastically, from desert-like environments with annual rainfall of less than 300 mm to mixed forests of pines and broadleaves with more than 1500-mm rainfall. Within the biggest islands and owing to the topography and the variable influence of the humid Trade Winds from the north-east, differences in water availability among populations and ecological regions are remarkable. Pine forests on north-facing slopes experience humid conditions, whereas those on south-facing slopes are exposed to dry and partly semi-arid climates where Saharan wind invasions are frequent. This extreme ecological variation has directed the study of both molecular and morphological traits at the population level (Korol *et al.* 1999; Gil *et al.* 2002; Gómez *et al.* 2003; Climent *et al.* 2006; Vaxevanidou *et al.* 2006).

Even though *P. canariensis* forests have never been managed and their traditional exploitation (essentially a source of wood, logs, resin and pitch) no longer exists, these forests play two key ecological roles. First, they contribute significantly to the water cycle by capturing the horizontal precipitation through mist-capturing while preventing erosion in highly sensitive soils because of the huge steepness of the territory and the short and intense rainfall events prevailing in a large part of the area. Second, the ability of the species to resprout, and the presence of serotinous cones and thick bark, endow this species with an extraordinary adaptation to fire and volcanism (Climent *et al.* 2004). *P. canariensis* forests constitute the only forest cover in large areas of the Archipelago where the growth and survival of other tree species is extremely unlikely. Human activities have caused a considerable regression of pine forests since the 15th century (Serra and Cionarescu 1960). The risk of extinction for some marginal populations in extreme environments containing high genetic variability, and the need to conserve this species, have already been discussed (Vaxevanidou *et al.* 2006).

Outside its natural area, *P. canariensis* is a well known ornamental tree on the Mediterranean coast and California (Ruiz de la Torre 1971). As an exotic forest species, the main areas are located in Morocco (~7000 ha) and Israel. Since the beginning of the last century in Israel, special attention has been paid to this species not only because of its adaptation to fire but also because of its tolerance to drought. Today, *P. canariensis* stands are also present with different purposes and extension in South Africa, Australia, Cyprus, Greece, Italy, USA, Canada, Chile, Argentina and Mexico.

Both the potential use of this species within and outside the Canary Islands and the conservation of its natural genetic resources depend on its adaptability to different or changing environments. Previous studies related to the species' natural variation have revealed high differentiation among populations in sapwood and heartwood size (Climent *et al.* 1998, 2002a, 2003), traits related to fire adaptation (Climent *et al.* 2004), heteroblasty (Climent *et al.* 2006) and cone morphology (Gil *et al.* 2002). The aim of the present study was to build and expand the knowledge of *P. canariensis* populations by assessing their performance (growth, survival and polycyclism) under highly contrasting field environments within and outside the natural distribution of the species, and to provide knowledge on seedling transfer in ecological restoration, tree breeding and conservation of genetic resources.

Materials and methods

Materials

The present study is based on two multi-site provenance trials of *Pinus canariensis* raised from the same seed lots, one in Canary Islands and the other one in Israel. Sampled population covered the whole ecological range of the species (Table 1), from semi-arid stands with 300 mm of rain per year to mixed pine forest with more than 1500 mm per year. In each population, cones were collected from 25 trees spaced at least 100-m intervals. An identical number of seeds per mother tree was mixed, and divided among trials, both for Israel or the Canary Islands. In the Israeli trial, three local seed sources from trees planted during the 1920s were also tested. The seeds were sown and raised in plastic containers in a nursery for 1 year. In December 1998 (Israel) and December 1999 (Canary Islands), 1-year-old seedlings were transplanted at the field-test sites. Fourteen of the 24 provenances were shared between both trials, 21 of them were from stands in the Canary Islands and the other three were from Israeli stands.

To characterise environmental conditions of the provenances, we used temperature and rainfall data extrapolated from meteorological stations throughout the distribution area of the species (Blanco *et al.* 1989) as well as an indirect site index at the ecological region level, the average sapwood area per hectare (Gs) (more details in Climent *et al.* 2004, 2006). According to this index, eight ecological regions were distinguished, three in Tenerife, two in Gran Canaria and La Palma and one in El Hierro (Fig. 1). The most productive regions with more than 30 m² Gs were located in the north-facing slopes of Tenerife and La Palma, whereas the least productive regions with less than 10 m² ha⁻¹ were both located in Gran Canaria. In addition to the eight ecological regions proposed, we have considered a new region, Number 9, to include the three Israeli seed sources. Given that these last seed sources were the first generation after plantation of the alloctonous material, we avoided making any inference about their environmental conditions.

Site description

In the Canary Islands, the provenance test was established with 21 natural populations (19 shared among all sites) planted at four sites, two in Tenerife (TFW and TFD) and the other two in

Table 1. Ecological regions and site index, sampled provenances, climatic characterisation and trial sites of each provenance
Pa, annual precipitation; T, mean annual temperature; Tr, annual temperature range; Dp, drought period; Gs, average sapwood area per hectare

Ecological region (Gs, m ² ha ⁻¹)	Provenance	Elevation (m)	Pa (mm)	T (°C)	Tr (°C)	Dp (months)	Test site
1 (26.6)	1. La Orotava	1500	1090.1	13.5	21.6	2.88	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	2. La Guancha	700	939.9	12.7	14.4	3.6	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	3. Garachico	1300	590	12.1	14.4	4.31	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
2 (15.9)	4. Vilaflor	1900	505	13.2	22.2	5.36	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	5. Adeje	1900	480.1	12	22.2	5.28	TFD, GCW, ISRW
3 (36.6)	6. Arico	1600	420.1	11.4	21	4.94	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	7. Candelaria	1300	1214.9	13.8	19.9	3.96	TFW, TFD, GCW, GCD
4 (31.1)	8. La Esperanza	1100	629.7	14.7	17.4	4.79	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	9. Punta Llana	1900	890	15.7	21.4	5.18	TFW, TFD, GCW, GCD
5 (14.0)	11. Garafia	1500	1015.1	16.5	19.1	5.12	TFW, TFD, GCW, GCD
	12. Punta Gorda	800	690.1	17.2	14.6	5.5	TFW, TFD, GCW, GCD
6 (15.4)	13. Taburiente	1000	719.9	14	18	5.12	TFW, TFD, GCW, GCD
	14. El Paso	1100	920	14.1	18	4.78	TFD, GCW
	15. Fuencaliente	1050	800.1	15.1	14.7	5.6	TFW, TFD, GCW, GCD
	16. S. Salvador	1000	450.1	16.4	15.7	6.66	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	17. R. de las Playas	900	580	15.6	15.7	5.7	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
7 (9.8)	18. Tamadaba	1100	598.8	15.5	20.8	4.92	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	19. Tirma	850	379.6	18	20.6	6.83	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
8 (6.2)	20. Mogán	900	334.7	17.6	21.9	7.52	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	21. Tejeda	950	439.7	16	22.3	6.43	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD
	22. Tirajana	950	414.7	14.6	22.4	6.29	TFW, TFD, GCW, GCD, ISRW, ISRM, ISRD

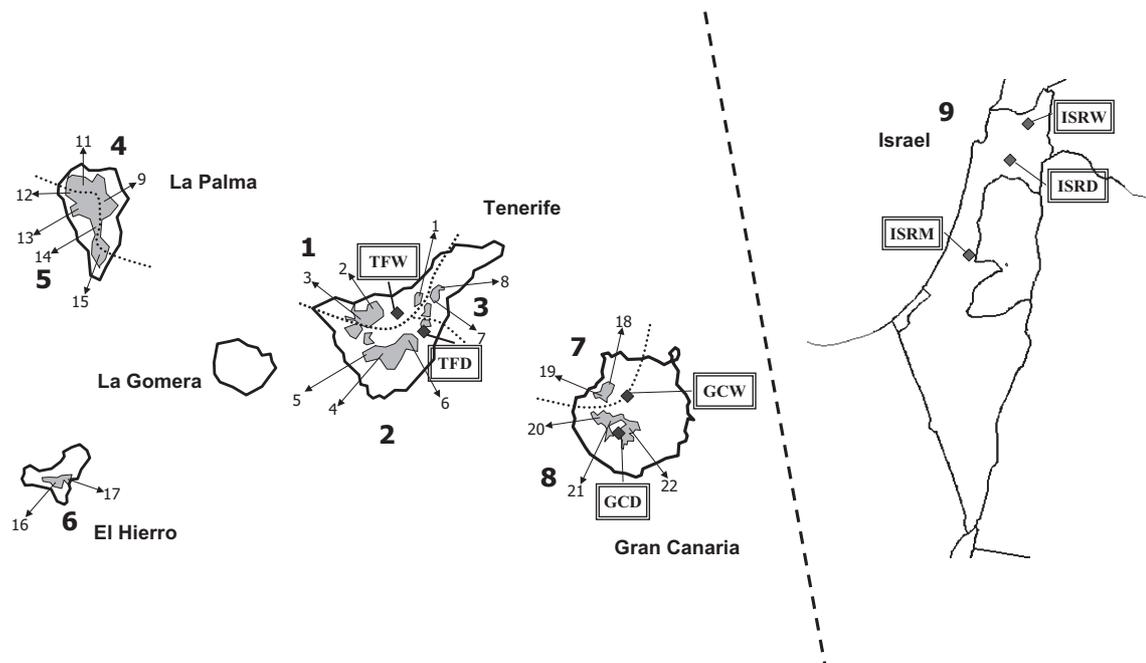


Fig. 1. Location of the sampled provenances of *Pinus canariensis* (small numbers) and trial sites (diamonds) in Canary Islands, Spain and Israel. Dotted lines are the limits of the ecological regions (bold numbers).

Gran Canaria (GCW and GCD). The experimental sites in Tenerife have similar soils and temperatures but they differ sharply in water availability, precipitation at TFW is $\sim 795 \text{ mm year}^{-1}$ plus the water added by the fog, which can be more than the incident rainfall (Aboal *et al.* 2000), facing 460 mm in TFD. In Gran Canaria, the wet site, Llanos de la Pez

(GCW), is located in the centre-north of the island. The driest site, Tirajana in the south (GCD), combines an arid environment with very compact and stony soil. In Israel, the three sites (ISRW, ISRM, ISRD) differ in rain and soil conditions. In Biria (ISRW), near the border with Lebanon, the mean annual rainfall is more than 720 mm with a mean annual temperature

of 16.5°C. Ben Shemen, the most southern site (ISRM) and Ein Dor (ISRD) have comparable mean annual temperatures (~20°C). Although the precipitation is higher in ISRM, this site has a bulky and clayey soil, hampering plant growth (Table 2).

Experimental design and variable description

In the Canary Islands sites, the experimental design followed an α -lattice resolvable design (Williams *et al.* 2002), with seven replicates of each provenance and five or seven incomplete blocks with three or four provenances each. Within each replicate, each provenance is represented by four trees in a square plot, with a spacing of 2 × 2 m. Survival and height were measured in the four trial sites every year after planting (in the winter of 1999) until 2004. In the final year, numbers of whorls, basal diameter and fructification were also assessed.

For survival assessment, all dead plants shortly after planting and those few plants in TFW severely affected by insect pests were withdrawn from further analyses after checking a random relationship of this type of mortality with provenances. Also, the few plants that were recorded as dead in one measurement but recovered by basal resprouting in the successive measurements were also withdrawn.

The smaller elongation of secondary flushes when compared with the first, spring flush, aided the detection of polycyclism. A previous study had shown that at the age of five, *P. canariensis* had reached the vegetative mature state even in a dry environment (Climent *et al.* 2006). Thus, we assumed that between 2002 and 2005, the growth of all the plants of the experiment had already attained the typical cyclic, preformed adult habit in pines, and therefore, in each vegetative period the tree formed at least one whorl. We considered polycyclism as a categorical binary variable: '0' if there were only one whorl per year, and '1' if the tree showed more than one whorl in a year (i.e. higher number of whorls than years of age).

Linear logistic models were constructed for both polycyclism and survival by using the proc GLIMMIX of SAS (SAS Institute Inc., Cary, NC, USA) for generalised linear models (GLM). A binomial distribution of the data was assumed and a logit function was used as link function.

Together with the analyses per site (Model I), an overall analysis of the 19 common provenances was conducted to assess

site differences and to evaluate the interaction site × ecological region (Model II), as follows:

$$\log[Y_{ijkl}/(1 - Y_{ijkl})] = \mu + E_j + P_i(E_j) + R_k + B_1(R_k) + \epsilon_{ijkl}, \quad (I)$$

$$\log[Y_{ijklm}/(1 - Y_{ijklm})] = \mu + S_m + E_j + P_i(E_j) + R_k(S_m) + B_1(R_k) + S_m \times E_j + \epsilon_{ijklm}, \quad (II)$$

where Y_{ijklm} stands for the value of the i th provenance (P), at the j th ecological region (E), in the k th replicate (R), in the l th block (B, random factor) and in the m th site (S); μ is the general mean and ϵ_{ijklm} is the error term.

A GLM approach to ANOVA was performed for the variables height and diameter of the provenances at each trial site (Model III). Site effect and the interaction site × ecological region were also checked, including both factors in a subsequent analysis (Model IV). In all the analyses plant height at the time of planting was included as a covariate in order to remove possible non-genetic differences during the nursery stage. The models for both analyses were as follows:

$$Y_{ijkl} = \mu + E_j + P_i(E_j) + R_k + B_1(R_k) + H_{ijkl} + \epsilon_{ijkl}, \quad \text{and} \quad (III)$$

$$Y_{ijklm} = \mu + S_m + E_j + P_i(E_j) + R_k(S_m) + B_1(R_k) + S_m \times E_j + H_{ijkl} + \epsilon_{ijkl}, \quad (IV)$$

where acronyms have the same meaning as in the preceding models. In Models III and IV, H_{ijkl} is height at the time of planting.

The percentage of variation explained by each fact was calculated with the variance components, assuming all the factors were random.

In the Israeli trial, measurements were made in 2002 (5 years old) and 2005 (8 years old), when (in addition to height and survival) we also evaluated the diameter and the number and height of whorls to estimate the frequency of polycyclic shoot growth, and reconstructed the height in the previous years. The provenances were arranged in rows with three to five replications. As there were no blocks to control within-site variability, after the GLM analysis with provenance as the only factor, residuals were checked to assess spatial correlation. Since this correlation was low, we decided to analyse data as completely randomised designs. As for the Canary Islands trial, the sites were first considered separately and then all together to

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 (m)	T (°C)	Tr (°C)	P (mm)	Ps (mm)	Psm (mm)	Pa (mm)	Pw (mm)	Dp (months)
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
GCW	Gran Canaria	27°58'N	15°35'W	1725	14.6	27.8	649.6	69.0	5.2	215.2	360.2	5.21
GCD	Gran Canaria	27°54'N	15°38'W	1259	17.8	20.3	319.7	38.4	1.9	108.2	171.2	7.68
ISRW	HaZafon	32°58'N	35°29'E	874	16.5	24.9	723.0	145.0	0	102.0	476.0	6.20
ISRD	HaZafon	32°39'N	35°25'E	104	20.1	24.6	499.0	169.0	0	83.0	335.0	7.00
ISRM	HaMerkaz	31°57'N	34°55'E	62	19.8	24.1	542.0	83.0	0	96.0	363.0	6.70

assess the influence of the site and the genotype \times environment interaction.

Linear regression models were developed to determine the relationship of phenotypic traits and Gs. Partial correlations were studied to relate patterns of provenance differentiation to independent climatic variables of seed sources.

Results

Survival

In the Canary Islands trial, the highest survival rates were reached in TFW and the lowest in GCD (Fig. 2A). Despite the high ecological disparity between TFD and GCW, differences for survival decreased with time, and were not significant in the last year. In the final year (2004), three site groups could be distinguished from multiple range test: one with TFW, another one with TFD and GCW, and the last one with GCD. Ecological-region effect was significant at all sites (Table 3), with two different common behaviours. Plants from ecological regions with lower Gs, and thus from less favourable conditions of origin, showed higher survival rates than plants from stands with higher Gs, except for ecological region Number 4, whose survival rates were similar to those from drier regions. A strong correlation ($r = -0.76$, $P < 0.05$) was found between survival and Gs, with a rather linear relationship (Fig. 3). Provenance effect was generally less significant than ecological-region effect. Notably, the local provenances did not show the highest survival at any site; they generally showed intermediate values, except in TFW where the local provenance even had the lowest survival rate.

In the Israeli trial, survival was as high as at the best sites in the Canary Islands. Differences for survival between ISRW and ISRM were only evident for two ecological regions, Numbers 2 and 9, whereas the remaining sites showed similar values. At ISRD, however, few plants of all ecological regions survived compared with the other two sites, 43% v. 68% (ISRW) and 61% (ISRM). Seed-source effects were much lower than in the Canary Islands trials, and they were only significant in ISRM (Table 3). However, unlike the Canary Islands, no relationship was found with Gs. Two of the three Israeli seed sources stood out because of their high survival rates, nearly 70%, at the three sites (Fig. 4).

The combined analysis showed, consistent with the results of the Canary Islands trials, that site provided the highest contribution to the total variance (Table 4). However, in this case, it was the provenance that had a significant effect instead of the ecological region (Table 4). Partial correlations among growth traits and climate variables of the provenances were non-significant, except for survival and the annual temperature range in GCD ($r = 0.68$). The joint analysis for all the study sites, with the 14 provenances both in Israel and Canary Islands, revealed significant effects on survival for all factors (Table 4). The significant site \times ecological region interaction indicated a different genetic response of the different ecological regions to the effect of the environment. In particular, plants from ecological regions with higher Gs (indicating favourable growth conditions) had consistently higher survival rates at the most favourable sites, whereas the rest showed no apparent relationship with the climatic

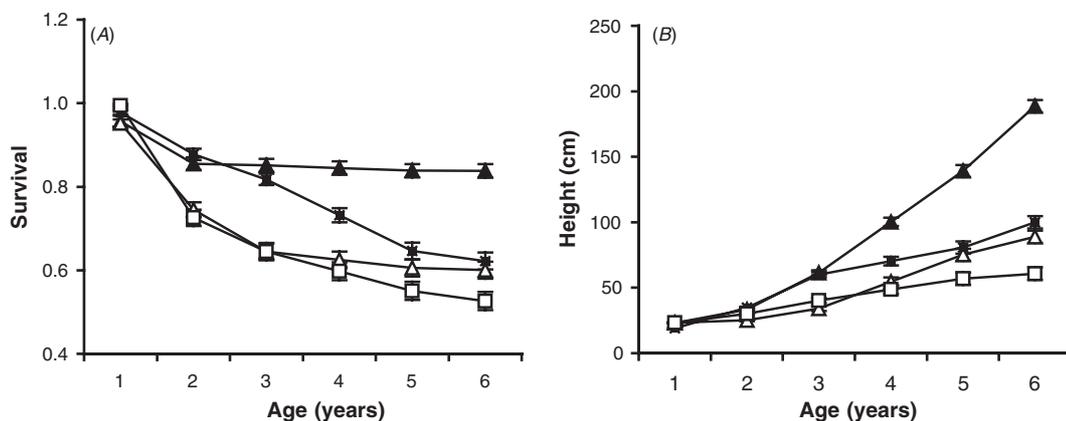


Fig. 2. Trajectory of (A) survival and (B) growth of *Pinus canariensis* at the four trial sites at the Canary Islands, Spain. Vertical bars correspond to the standard errors of the mean values of all individual trees at each site. TFW (▲), TFD (△), GCW (■), GCD (□).

Table 3. Percentage of the explained variation and significance values from the generalised linear models to determine the sources of variation for survival of *Pinus canariensis* at seven trial sites

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant

Source	TFW	TFD	GCW	GCD	ISRW	ISRM	ISRD
Ecological region	11.31**	7.20**	11.15**	5.12**	n.s.	1.02*	n.s.
Replicate	11.10*	n.s.	8.14*	32.40***			
Provenance (ecological region)	n.s.	12.77*	n.s.	8.88*	n.s.	25.66**	n.s.
Block (replicate)	12.11	23.77	5.86	9.22			

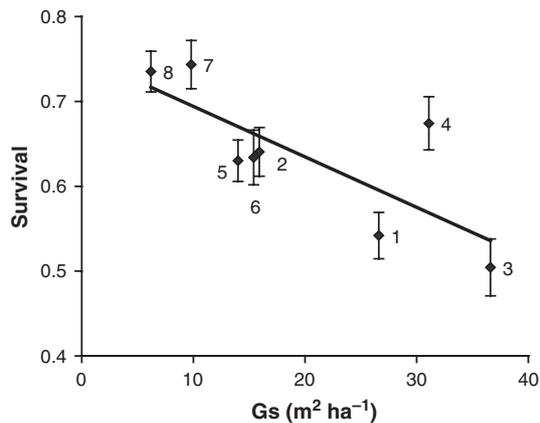


Fig. 3. Correlation between mean values of survival of *Pinus canariensis* of the ecological regions and the indirect site index (Gs, sapwood area per hectare) trials in the Canary Islands and Spain. Bars represent the standard error of the mean pooling data from all the experimental sites.

conditions of the experimental sites, contributing most to the interaction.

Growth

In the Canary Islands, site was the main source of variation, with the highest growth rates in the wettest sites, especially in TFW (Fig. 2B). By contrast, differences in height or diameter, owing to the seed source, were generally very scarce (Table 5). Only at the extreme sites, TFW and GCD, was there a significant effect of the ecological region on height and diameter (Table 5) and, even in this case, only plants from the least fertile ecological region, Number 8, were significantly different from the rest. Notably, this ecological region had the highest growth rate at the driest site (GCD) and the lowest at the wettest site (TFW). The local provenances had the best growth in TFW and GCW, whereas local provenances did not stand out at the two drier sites. Genetic differences among provenances for polycyclism were significant only at the wettest sites (Table 6). In TFW, four ecological regions showed a value of polycyclism higher than 0.6; these included three regions of Tenerife (1, 2, 3) and the northern region of Gran Canaria (region Number 7).

In the Israeli trial, plants grew better than those at the Canary Islands. Plants were taller at the wettest site (ISRW), whereas the lowest growth for both height and diameter was observed at the intermediate site (ISRM) (Fig. 5). As for the Canary Islands trials, divergences among ecological regions or provenances for height growth and diameter were very small. Again, it was at the wet site where some ecological regions (e.g. region Number 8) were distinguished more significantly from the rest. Provenances accounted for more variation than ecological regions, although the percentage of the variability explained by this factor was only moderate (less than 13% at all the sites, Table 5). In contrast with the Canary Islands trials, the local Israeli seed sources showed high growth rates at all three sites (Fig. 5). Both the frequency of polycyclism and the effect of seed sources were higher in ISRW, where every tree in Ecological regions 6 and 7 showed at least one second-flush. Again, ISRD showed higher rates for this trait than did ISRM.

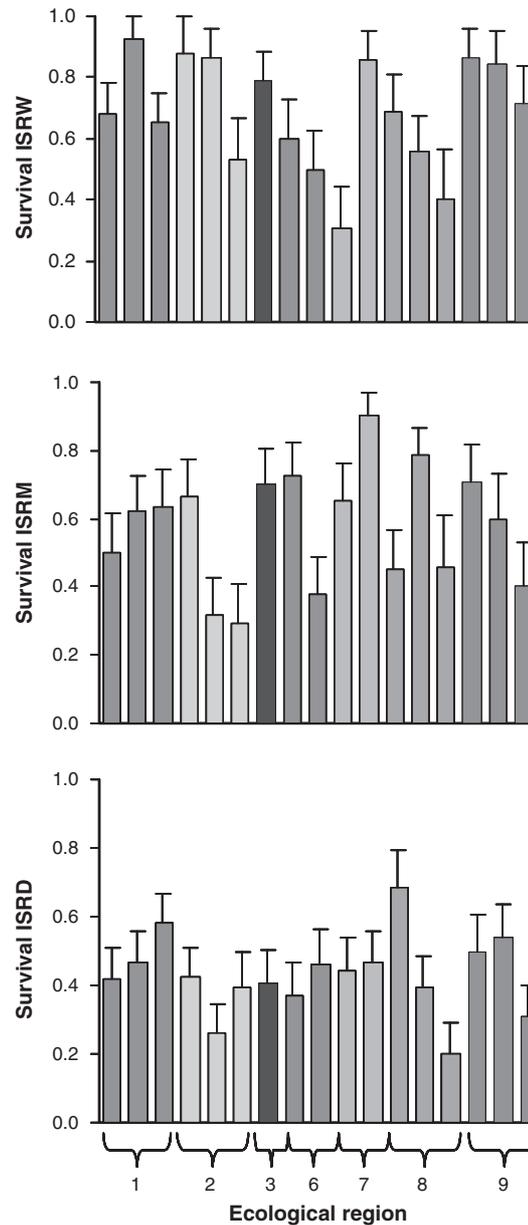


Fig. 4. Mean survival rates and standard errors of the different provenances of *Pinus canariensis* grouped by ecological region at the Israeli sites.

The joint analyses, with the 14 provenances shared across both trials and all sites, confirmed that site was the most important factor, whereas seed-source effects and the site \times region interaction, even when significant, explained an extremely low proportion of the variance (Table 4), indicating a similar plastic response among seed sources. Polycyclism seemed to be less influenced by the environment and more dependent on the seed source than height or diameter.

Partial correlations among height and mean annual temperature range were significant in TFW ($r = -0.73$), GCD (0.60) and ISRW ($r = -0.77$). At ISRW, height was also correlated with the mean annual temperature ($r = 0.65$). Interestingly, height at TFD was negatively correlated with

Table 4. Percentage of the explained variation and significance values for survival (surv), polycyclism (pol), height (h) and diameter (d) of *Pinus canariensis*Data correspond to all sites of the Canary Islands, Spain (19 provenances) and Israel (17 provenances) and to the joint analysis of both trials (14 provenances). H1, height at the time of planting. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant

Source	Canary Islands				Israel				Joint analysis		
	surv	h	d	pol	surv	h	d	pol	surv	h	pol
Site	23.48***	78.77***	64.71***	33.10***	19.83***	68.10***	23.02***	64.19***	17.95***	68.07***	48.72***
Ecological region	6.43***	n.s.	n.s.	n.s.	n.s.	0	0	6.46***	1.40***	0	2.96*
Provenance (ecological region)	n.s.	0.42*	n.s.	n.s.	7.69**	1.74***	1.61**	n.s.	2.85*	1.67***	n.s.
Replicate (site)	14.40***	2.10***	1.89***	4.50*							
Block (replicate)	3.44	2.03	8.94	11.26							
Site × Ecological region	5.10***	0.87*	n.s.	5.13*	n.s.	1.98***	0.50	6.77**	9.29***	1.16*	6.85*
H1		n.s.	n.s.								

Table 5. Sources of variation and percentage of explained variation from the general linear models for growth at seven trial sitesh, height; d, diameter; H1, height at the time of planting. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Source	TFW		TFD		GCW		GCD		ISRW		ISRM		ISRD	
	h	d	h	d	h	d	h	d	h	d	h	d	h	d
Ecological region	15.83***	1.98*	8.69	0	2.48	0	20.32**	0.35*	6.34**	5.67**	4.77**	0.30	0.56	0
Replicate	8.73*	0	0	4.64	0	0.09	6.038**	5.06						
Provenance (ecological region)	12.14*	0.18	32.99**	2.95	17.74*	2.42	7.46*	9.74	12.55**	12.34**	10.93*	0	4.70	0.40
Block (replicate)	2.87	18.34	3.64	23.74	4.10	11.64	9.57	14.20						
H1	**	***	***	***			*							

Table 6. Percentage of the explained variation and significance values for polycyclism of *Pinus canariensis* at seven trial sites* $P < 0.05$; ** $P < 0.01$; n.s., not significant

Source	TFW	TFD	GCW	GCD	ISRW	ISRM	ISRD
Ecological region	1.93**	n.s.	n.s.	n.s.	62.17**	56.58**	n.s.
Replicate	n.s.	n.s.	n.s.	n.s.			
Provenance (ecological region)	18.18**	n.s.	14.42*	n.s.	n.s.	n.s.	42.30*
Block (replicate)	13.46	39.82	23.02	17.45			

the annual precipitation ($r = -0.61$) and the with length of the drought period ($r = -0.59$), and with altitude ($r = -0.61$) at GCD. Significant partial correlations between diameter and climatic variables were detected at only two sites: at GCW with annual precipitation ($r = -0.54$) and length of the drought period ($r = -0.62$), and mean annual temperature range ($r = -0.73$) at ISRW.

In all the studied variables, the interaction between site and ecological region was low, less than 2%.

Discussion

All previous knowledge on the geographic variation of *P. canariensis* has led researchers to expect a high level of

ecotypic differentiation for the traits considered. However, the first-ever analysis of a multi-site provenance trial for this species, with populations from the entire natural range presented in this paper, has confirmed this expectation for survival but not for growth. The fact that plants from favourable, wet environments exhibited a lower survival in dry conditions can be postulated as a general pattern for the species, since it runs in parallel with previous results obtained at the two Tenerife sites (Climent *et al.* 2006) and also at an extremely harsh site remote to the actual natural distribution of the species (Climent *et al.* 2002b). Nevertheless, plants from favourable ecological regions tended to have a more consistent behaviour, whereas the rest of the plants showed

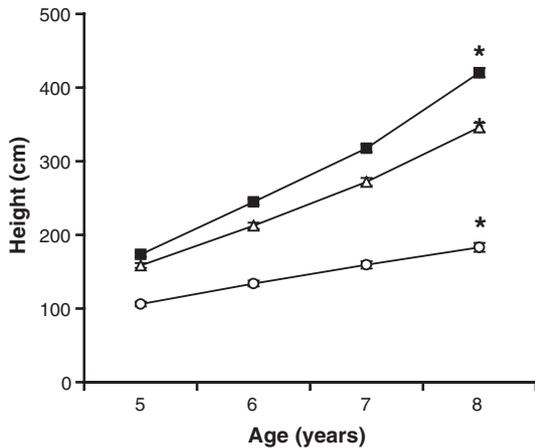


Fig. 5. Trajectory of height growth of *Pinus canariensis* during the last 4 years in the trial in Israel. Values are the mean + s.e. for all trees at each experimental site. Asterisks indicate the mean value of the Israeli provenances. ISRW (■), ISRM (○), ISRD (△).

a less strict relationship with the climatic conditions of the experimental sites.

Previous results based on the two sites in Tenerife revealed a low significance of populations and ecological regions for height growth (Climent *et al.* 2006). In the present work, even when we expanded the study to highly contrasted site conditions both inside and outside the range of distribution of the species, the results confirmed the trend observed at only two sites. The graphic analysis revealed that reaction norms of the ecological regions for height growth were not only parallel, as a consequence of the low genotype × environment interaction (Schlichting 1986; Dejong 1990), but almost coincidentally, reflected the extremely low genetic variation owing to the seed origin (Fig. 6). Moreover, only the least fertile ecological region, Number 8, showed a distinct growth behaviour at the most extreme sites. This ecological region seemed exceptionally well adapted to the climatic dryness and poor soils of its area of origin, which showed the lowest values of the indirect site index (Gs, 6.2), of the entire natural area of distribution of the species.

Together with its high survival in harsh conditions, this seed source ranked the best for growth at the least fertile sites and the worst at the most fertile, resulting in a relatively flat reaction norm, i.e. less plasticity facing the environmental gradient. This result is congruent with a rather general trend in plants; namely, that genotypes adapted to harsh environments tend to present a conservative behaviour in favourable environments. As has been postulated, this may be due to the evolutionary costs of stress tolerance, making it impossible to benefit from better growth conditions (Bloom *et al.* 1985; Lortie and Aarssen 1996; Sáenz-Romero *et al.* 2006). Confirming this trend, the ecological correlations obtained, even when based in provenance means (not all significantly different), revealed an opposite tendency for growth between the wettest and the driest sites. Favourable climatic conditions of origin were related to good performance at the best site but poor performance at the harsh site. This result was consistent with the specialisation hypothesis (Lortie and Aarssen 1996) and constitutes an indirect reflection of an underlying genotype × environment interaction for growth, which was not detected as significant by statistics.

Seed-source effects (ecological region + provenance) for all traits were even smaller in the Israeli trial. The lack of a proper field array and a lower number of trees per ecological region and provenance led to higher experimental errors ruling out genetic effects (Williams *et al.* 2002). Although the variation in the survival within an ecological region seemed to be more important than that among regions in the Israeli trial, this could be attributed to uncontrolled factors. The favourable performance of the local seed sources in the Israeli trial is worth noting, especially when compared with the generally inconspicuous behaviour of the local provenances at the Canary Islands trial. The fact that these local seed sources in the Israeli trial stood out only after the selection of parental trees, following the initial reforestation, could be considered as the beginning of a local land race (Zobel *et al.* 1988). However, we cannot discard that epigenetic factors or maternal effects may have contributed to the high performance of these materials at the first stages of development (Johnsen and Skroppa 1996; Lopez *et al.* 2003). Moreover, some authors confer the better performance of the local land races to artificial selection (Lopez *et al.* 2001). Performance

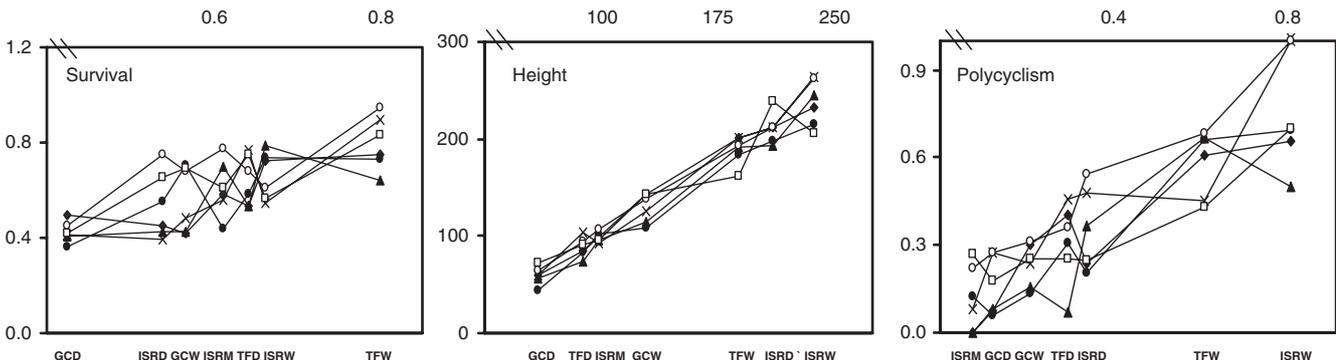


Fig. 6. Reaction norms of the six ecological regions shared by the trials in the Canary Islands, Spain, and Israel on the survival, height and polycyclism of *Pinus canariensis* in the joint analysis. Values of the x-axis represent the mean value obtained for all seed sources at each site for Ecological regions 1 (◇ in black square), 2 (●), 3 (▲), 6 (×), 7 (○) and 8 (□).

of the local land races varied widely among regions, species and traits. For example, in Argentina, opposite behaviour in the growth potential of the local races was observed when compared with North American native provenances of Douglas fir and Ponderosa pine (Rehfeldt and Gallo 2001). Stem straightness of the land races was superior to that of the natural provenances. Trees from the natural provenances grew better in *Casuarina equisetifolia* spp. *equisetifolia* but stem straightness of the land races was superior (Pinyopusarek *et al.* 1996), whereas land races were among the best-growing in *Eucalyptus camaldulensis* (Pinyopusarek *et al.* 1996) in Thailand.

Among phylogenetically closely related species (Mediterranean pines, *sensu* Klaus 1989), extremely different combinations of population divergence, phenotypic plasticity and genotype \times environment interaction ($g \times e$) for growth have been found: high overall plasticity, ecotypic divergence and very high $g \times e$ interaction in *P. pinaster* (Alía *et al.* 1995, Alía *et al.* 1997; González-Martínez *et al.* 2004), very high overall plasticity but low ecotypic divergence and low $g \times e$ in *Pinus halepensis* (Chambel *et al.* 2005), and very high overall plasticity but scarce or null ecotypic divergence and $g \times e$ in *P. pinea* (Court-Picon *et al.* 2004; Chambel *et al.* 2005). Therefore, the fact that *P. canariensis*, *P. pinea* and *P. halepensis* showed a similar high plasticity rather than divergence among populations for vegetative growth may represent a common solution to cope with the increasing heterogeneity of their Mediterranean environments after glaciations.

The high genetic differentiation found with neutral molecular markers (Gómez *et al.* 2003; Navascues *et al.* 2006), heteroblasty (Climent *et al.* 2006) and survival (the present paper), contrasted with the low differentiation for growth, suggest a more intensive selection for traits related to colonisation capacity. The recurrence of intense perturbations in the Canarian forest ecosystems, both at a geological (Carracedo and Day 2002) and historical time scale (Climent *et al.* 2004), facilitates the possible colonisation of new territories by *P. canariensis*, as postulated to explain the pine–broadleaves dynamics in other similar ecosystems (Agee 1998). Hence, a high competitive ability in the first developmental stages probably has less adaptive advantages than does adult endurance, when facing those perturbations.

Polycyclic growth is frequent among pine species, particularly those growing in favourable habitats where several suitable vegetative periods throughout the year occur (Allen and Wentworth 1993; Lascoux *et al.* 1994; Isik *et al.* 2002; Pardos *et al.* 2003). However, even at the most favourable sites of our trial, the frequency of a second-flush was scant, which again reinforces the idea of a low adaptive value of height growth in *P. canariensis*. Furthermore, the most shade-intolerant Mediterranean pine species, namely *P. pinaster*, *P. halepensis* and *Pinus brutia*, are also the most polycyclic (as deduced from Alía *et al.* 1997; Isik *et al.* 2002 and Pardos *et al.* 2003), in contrast to *P. pinea*, which is more shade tolerant (Awada *et al.* 2003) and mostly monocyclic (Mutke *et al.* 2003). However, although *P. canariensis* is extremely shade intolerant (Arévalo and Fernández-Palacios 2005; Climent *et al.* 2006), its clear monocyclic tendency again might be related to its conservative life strategy.

The differences in life-history traits found in natural populations could explain the variation in survival and growth among seed sources as shown in this paper. Mesic stands have higher fire recurrence than dry stands, which has been postulated to be adaptively related to a higher investment in bark and nutrient reserves in populations from wet locations, allowing their resilience owing to their resprouting ability (Climent *et al.* 2004). By contrast, in the driest places, drought is the main restrictive factor for survival, particularly in the first stages of development (Gieger and Leuschner 2004). Thus, plants tend to invest more resources in root development instead of height growth (Bongarten and Teskey 1987; Cregg 1994). The different level of divergence among seed sources for different traits could thus be explained by different patterns in resource allocation between plants adapted to rich and poor environments, as suggested for heteroblastic phase change (Climent *et al.* 2006).

The loss of valuable genetic resources from the forest because of the regression or extinction of some populations has been pointed out for several *Pinus* species such as *P. oocarpa* (Sáenz-Romero *et al.* 2006), *P. sylvestris* (Rehfeldt *et al.* 2002; Rebetetz and Dobbertin 2004), *P. contorta* (Rehfeldt *et al.* 1999) and *P. halepensis* (Atzmon *et al.* 2004). If we take the accepted models of climate change into account, in similar latitudes to those of Canary Islands, a temperature rise between 3 and 5°C and a sharp decrease in precipitation can be expected this century (Lal *et al.* 2002; Castro *et al.* 2005). A recent study (Sperling *et al.* 2004) postulated a drying trend across the Trade Wind inversion. In this scenario, our results may contribute to implementation of *in situ* genetic conservation programs for some ecological regions. According to the results of the present study, natural regeneration could be affected by the low survival of some provenances, particularly those from currently favourable regions more susceptible to drought, thus endangering some stands. Furthermore, conservation of the driest provenances (ecological region Number 8) is highly recommended because of their adaptability to extreme environments and because of the singularity of some populations, including interesting relicts, as shown with molecular markers (Vaxevanidou *et al.* 2006). Differences among provenances and ecological regions suggest the need to maintain the identification of seed sources (base materials) at least at the ecological-region level. The lack of genetic correlations between growth and survival would allow a combined selection for both traits, thus encouraging the interest on this species as a promising forest species in moderately dry Mediterranean climate zones, such as Israel or south-western Australia. The good performance of the Israeli local provenances after only one generation corroborates this potential.

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