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ECOTYPIC VARIATION AND PLASTICITY OF GROWTH, SURVIVAL AND ONTOGENY IN PROVENANCES OF CANARY ISLANDS PINE

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Abstract

Height, survival and ontogeny (juvenile, intermediate or adult stages) were measured during the first six years after planting in a provenance trial of Pinus canariensis *established in four sites in Canary Islands (Spain). We could observe an ecotypic variation pattern related to seed origin that affected survival in the less favourable sites as well as heteroblasty in the trial as a whole. Provenances from drier and warmer areas presented in general retarded ontogeny and better survival rates. Height growth showed a predominance of phenotypic plasticity (site factor) against the differentiation among provenances. In addition, total height exhibited higher variation among provenances, even neighbouring ones, than among ecological regions.*

INTRODUCTION

The Canary Islands pine (*Pinus canariensis* C. Sm.) is the only endemic pine of the Canary archipelago. Its natural distribution area is restricted to the western islands and it grows from near the sea level to about 2500m. It colonizes volcanic soils and it is able to live in climates that range drastically. Pine forests on north-facing slopes experiment humid conditions thanks to the frequent fogs induced by the trade winds, whereas the south-facing slopes are exposed to dry and partly semi-arid climates.

Most pine species starts to produce adult needles from the second growing season. However, a great amount of Mediterranean pines, like *Pinus canariensis*, maintain the juvenile stage longer. During the first developmental stage, seedlings of Canary Islands pine exhibit short solitary and glaucous primary needles while dark green secondary needles appear grouped in dwarf shoots. The change between the phases, heteroblastic phase change (HPC), involves an alteration from free growth to fixed growth resulting in the formation of a terminal bud and it is independent from the reproductive phase change. Between both stages, juvenile and adult, an intermediate stage can be considered, without bud formation but with both, juvenile and adult leaves.

Previous studies have demonstrated morphological and structural differences between adult and juvenile needles to avoid water loss [1, 2]. Due to the wide ecological amplitude of this species, we expect different field performances between juvenile and mature plants and among different populations. Therefore, the objective of this paper is to study patterns of growth, survival and heteroblastic phase change and their relationships in *Pinus canariensis* from several seed sources (provenances), covering the whole geographical and ecological range of the species.

MATERIAL AND METHODS

Data used in this study were collected in a common garden experiment with 19 natural populations planted at four sites, two in Tenerife and other two in Gran Canaria. (figure 1 and table 1). Sampled population covered the whole ecological range of Canary pine, from semi-arid stands with 300 mm of rain per year to mixed pine forest with more than 1500 mm per year. The design of all the experimental plots was randomised completed blocks. The experimental sites in Tenerife have similar soils and temperatures but they differ sharply in average rainfall; while in the North site (Tw) the average rainfall is about 750 mm, in the South site (Td) is only 425 mm. In Gran Canaria, variation is even bigger, from 800 mm in the wetter site, also in the north of the island (GCw) to 250 mm in the dryer site, in the south (GCd).

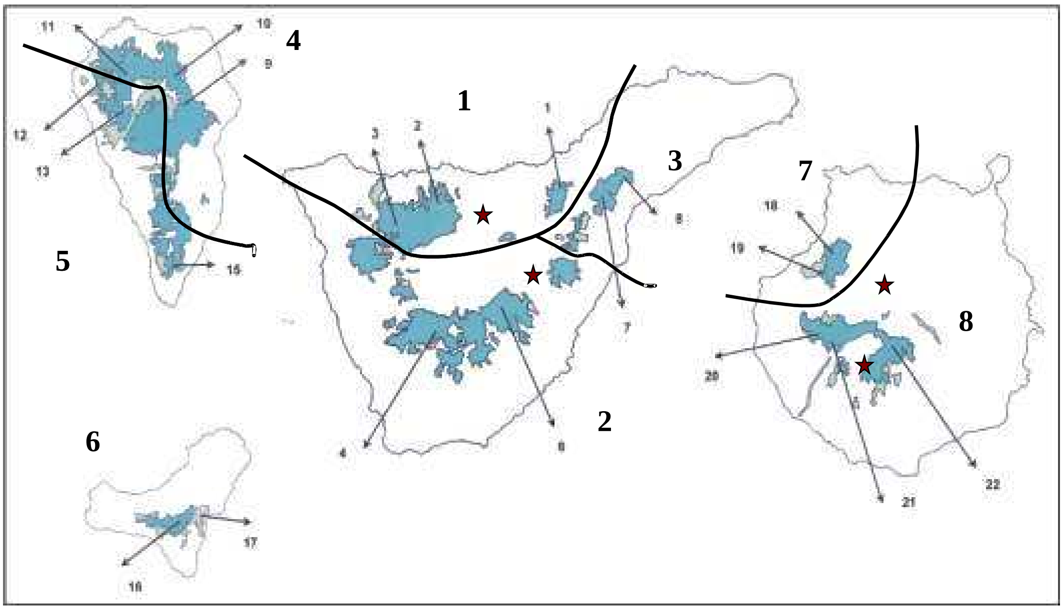

Fig. 1. Trial sites (stars), sampled populations (small numbers), ecological regions (in bold) and Gs value in m^2/ha (brackets).

Table 1. Location and ecological features of trial sites.

Trial site	Island	Ecol. Region	Gs (m^2/ha)	Lat (N)	Long (W)	Altitude
Los Realejos	Tenerife	1	26.6	28º 21’	16º 36’	1575
Fasnia	Tenerife	2	15.9	28º 16’	16º 29’	1720
Llanos de la Pez	Gran Canaria	8	6.2	27º 58’	15º 35’	1725
Tirajana	Gran Canaria	8	6.2	27º 54’	15º 38’	1259

Due to the great differences in rainfall and temperatures that occur at very short distances because of topography and the trade winds and also because of the limited meteorological network, climatic data in Canary Islands are not easy to obtain. For those reasons, to characterize sites and provenances, an indirect index has been used, the average sapwood area per hectare (Gs), which has demonstrated to be highly correlated to different phenotypic features of this species [3] (figure 1). According to this index eight ecological regions are distinguished: three in Tenerife, two in Gran Canaria and La Palma and one in El Hierro (figure 1). The most productive regions with more than 30 m^2 of sapwood per hectare are located in the north facing slopes of Tenerife and La Palma, while the least productive with less than 10 m^2/ha are both located in Gran Canaria.

Survival and height were measured in the four trial sites every year after planting (in the winter of 1999) until 2004. In addition to these measurements, ontogenetic score was followed in Tenerife locations during the same period. Two variables related to heteroblastic change were evaluated, height and age at HPC. General lineal models approach to ANOVA were used to separate environmental and genetic factors influencing the phenotypic traits. First of all we analyzed the experimental plots separately considering as factors block, ecological region and provenance nested in ecological region [a] and then the trial as a whole including the factor site and considering block nested in site [b]. In all the analysis plant height at the moment of plantation was included as a covariate in order to remove possible differences due to the nursery conditions. Linear regressions were used to determine the relationship of total height and survival with the site quality (Gs).

$$Y_{ijk} = \mu + B_i + R_j + P_k(R_j) + \xi \, H_{1ijk} + \varepsilon_{ijk\,[a]}$$

$$Y_{ijkl} = \mu + S_i + B_i(S_i) + R_j + P_k(R_j) + \xi \cdot H_{1ijklm} + \varepsilon_{ijklm\,[b]}$$

Where µ is the general mean, S the deviation due to the site, B the effect of the Block, R the effect of the Ecological Region, P the effect of the Population within each Ecological Region, H1 the height at the moment of plantation, included as a covariate and e the error.

RESULTS AND DISCUSSION

Survival

When sites were considered separately, no differences among ecological regions were found in Tw. However, we observed two different common behaviours in the other sites. Plants from ecological regions with higher Gs, consequently from more favourable sites, showed lower survival rates whereas those with lower Gs survived better. Mortality in GCd was much higher than in the rest of the sites, presenting a micro-spatial variation, which the experimental design was unable to remove, therefore the differences between provenances in this site seemed to be a consequence of environmental, rather than genetic factors, despite the fact, we could see a similar pattern to the other site in Gran Canaria and the dry site in Tenerife ones (figure 2a).

When all locations were considered together, site was the most important factor, explaining the 17% of the variation, the seed source, considering both the ecological region and the provenance, only accounts for the 7.47% (table 2).

In spite of the huge ecological disparity between Td and GCw, divergences among provenance for survival rates decreased with time and in the last year differences in survival rates weren't significant, although the surviving percentage of each provenance was different, thus provenances had different rates of mortality depending on the site.

It's good to note that once went over the first developmental stage, mortality almost disappeared so this species has to be considered in afforestation programs in dry environments due to the great potential resistance of some provenances.

A strong relationship was found between survival in Td and Gs. The lowest Gs the highest survival (figure 2c) thus in this site the correlation between site index of the seed source and survival was practically linear which meant that provenances from drier and warmer areas survived better than those from more favourable locations.

Height

No differences in growth patterns of the seed sources were found in GCw and Td. In the extreme sites, Tw and GCd, only plants from ecological region number 8, the worst one, were significantly different. Furthermore, this ecological region had the best rate in GCd and the worst in Tw (data not shown).

Again, when we considered all the sites together, site was the most important factor, accounting for more than the 72% of the variation. Provenances accounted for more variation than ecological regions (table 3). This meant more variability intra regions than inter regions, which matched the results obtained with molecular markers [4], cone morphology [5] or traits related to fire [3].

As it was expected growth in Tw was remarkably higher than in the rest of the sites and it seemed than in the future, differences between this site and the others will be increased (figure 2b). Once more, GCw and Td had similar scores although the ranking of the tallest provenances was different. The hard conditions of GCd, not only because the scarce annual rainfall and lack of influence of the trade winds but also because the type of soil, have as a consequence the low rates of growth.

No relationships were found between growth and survival or the site index anywhere. In contrast to the results in other provenance trials of *Pinus* [6, 7 and 8] where a higher growth meant usually lower survival, specially in extreme conditions of drought or cold.

The lack of relationship between growth and mortality allows the choice of different provenances adaptable to a wide spectrum of ecological conditions.

The trees analyzed were still young but previous studies have asserted a good correlation between some phenotypic traits little influenced by competition as height, not diameter much more sensitive to changes in competition, in young and old trees [9], thus it is possible that differences in growth between populations remain being almost insignificant.

Table 2. Analysis of variance for Survival considering all the sites.

Source of Variance	Sum of Squares type III	Degrees of Freedom	Mean Square	Explained variation
Site	8.8500	3	2.9500	17 %
Block (Site)	6.6346	24	0.2764	12.71 %
Region	2.6276	7	0.3754	5.03 %
Pop (Region)	1.2747	13	0.0980	2.44%
H1	3.0803	1	0.0803	5.90 %
Residual	29.5528	509	0.0581	56.63 %
Total (corr.)	52.1820	557		

Table 3. Analysis of variance for Survival considering all the sites.

Source of Variance	Sum of Squares type III	Degrees of Freedom	Mean Square	Explained Variation
Site	1143267	3	381088.999	72.90 %
Block (Site)	66440.133	24	2768.339	4.24 %
Region	7583.181	7	1083.312	0.49 %
Pop (Reg)	15878.873	13	1221.452	1.01 %
H1	577.797	1	577.797	0.04 %
Residual	334710.082	478	700.23	21.34 %
Total (corr.)	1598545.11	526		

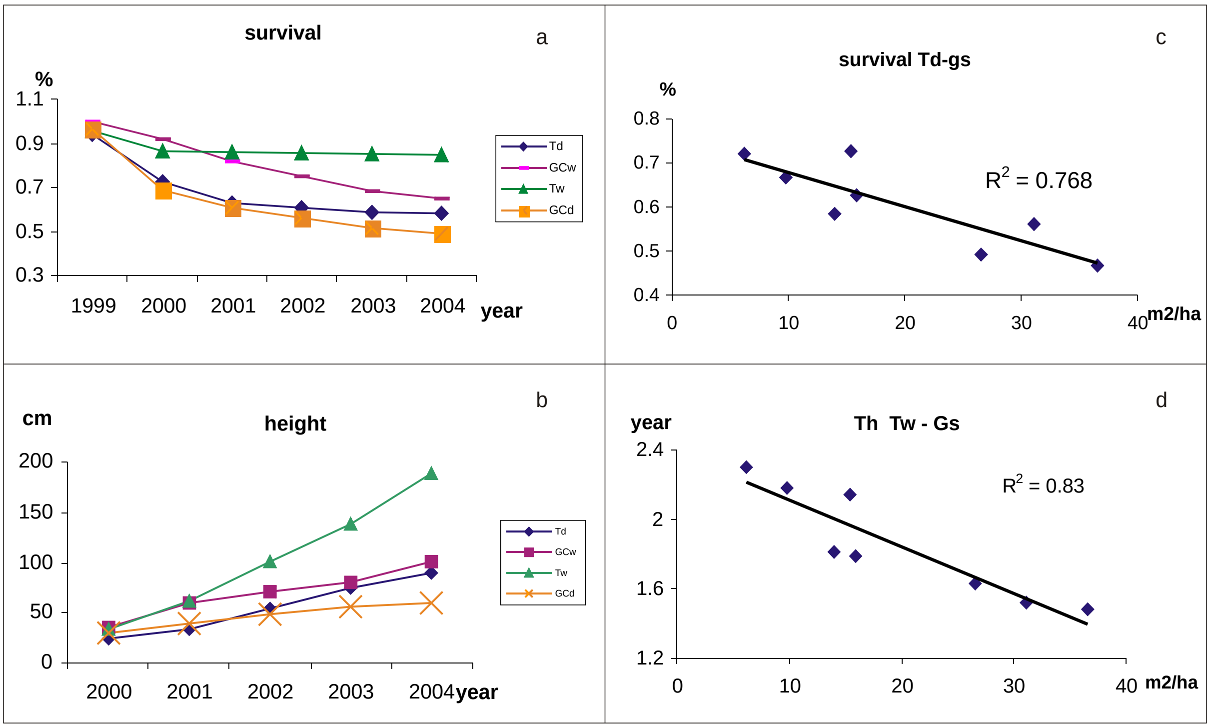

Fig. 2. a) and b) Evolution of survival and height in the four sites until 2004. c) and d) Correlations of survival in Td and age at heteroblastic phase change (Th) with site quality (Gs), per ecological region.

Heteroblastic Phase Change

Ontogenetic scores were only followed in Tw and Td. HPC started significantly earlier and progressed at higher rate in the wet site (figure 3). While in 2001 more than the 72% were adults in this site, only the 22% were adults in the dry site, and the year after in contrast with the 95% of adults in Tw, the 66% in Td. On the other hand, in 2001 the 57% remained juvenile in Td and only the 8% in Tw. It should be noted that even in 2004, plants in juvenile and intermediate states remained in the dry site.

On the contrary, when we considered height at heteroblastic phase change, it was more related to the seed source than to the site. This meant that plants reached the adult condition at the same height independent of the site. Only three ecological regions seemed to be plastic considering this character, 1, 3 and 4, which were those with higher value of site index.

Although no significant differentiation among sites was found for height at HPC, ecological regions were significantly different and accounted for almost the 10 % of the variation of this trait. Those with higher site index became adult at lower height (data non shown).

A good correspondence was found between Gs and Th in the North Site. Provenances from sites with higher Gs (better sites) showed accelerated ontogeny, meaning that they became adult earlier (figure 2d).
It's worth noting that no correlations were found between height at heteroblastic phase change and total height. Thus, achieving adult stage earlier didn't mean higher growth rates for the years after.

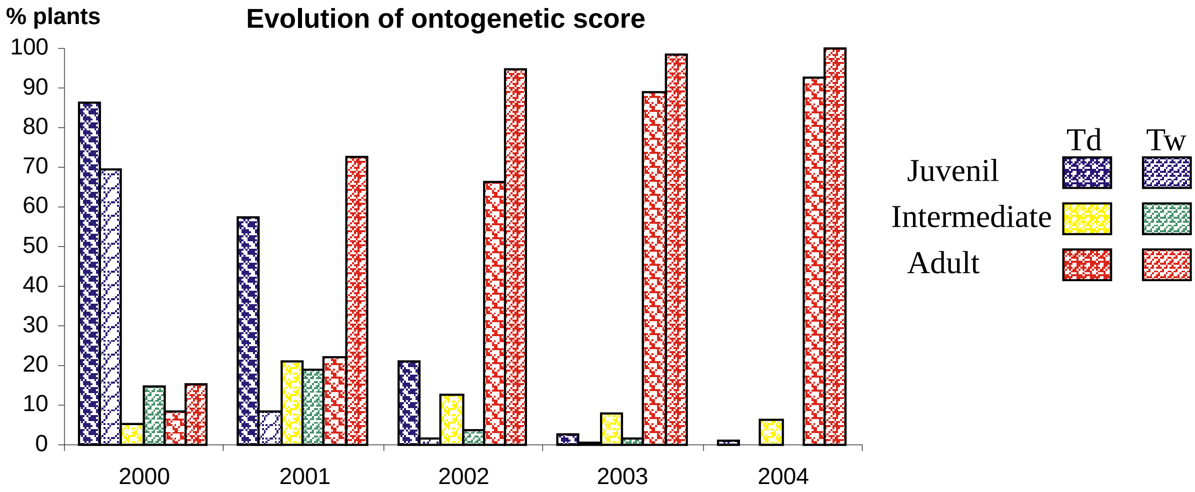

Fig. 3. Evolution of Ontogenetic score in Td and Tw.

CONCLUSIONS

Seed origin affected survival in the less favourable sites (with lower Gs) as well as heteroblasty in the trial as a whole. However, height growth showed a predominance of phenotypic plasticity (site factor) and exhibited higher variation among provenances, even neighbouring ones, than among ecological regions. The lack of correlation between growth and survival allows the choice of different provenances for sites with different ecological conditions. These were the first results of still young trees. While survival is already known, growth rate may change with age. Future measurements may suggest better recommendations of certain provenances to different planting sites, although the traits studied tolerate some confidence on conclusions in accordance with the results of other species of *Pinus*.

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