Genetic Variability of Scots Pine (*Pinus sylvestris*) Provenances in Spain: Growth Traits and Survival

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Plants obtained from seed of 16 Spanish and 6 German provenances of Scots pine (*Pinus sylvestris* L.*)* were installed at five trial sites distributed throughout the natural range of the species in Spain. Five years after planting (7 years of age) the experimental material was measured for total height, diameter, number of twigs at the fourth year whorl and survival. The analysis confirmed that the rate of height growth of the Spanish is lower than that of the German provenances, whereas for the other traits the best Spanish compare favourably with the Germans. Provenance by site interaction was very significant (P<0.01) for most traits. Attempts to model the interaction of Spanish provenances on height by simultaneous introduction of some climatic and geographic covariates on both factors were not successful but a multiplicative model with one bilinear term was enough to provide a sensible explanation of this interaction. Usually, provenances closest to each trial site were found better adapted than more distant ones but some provenances of close origin presented a different behaviour. Processes of adaptation and selection of these ancient populations could be considered as the main factors to cause this interaction.

1 Introduction

Scots pine (*Pinus sylvestris* L.) reaches in Spain the southern limit of its wide natural range. Spanish populations have been described as refugia of the species during glaciations. They occupy today more than 700 000 ha. About one half of this area is covered by natural and disconnected stands, different from the rest of the European populations. Analysis of isoenzymes has revealed the Spanish material to be genetically richer and more diverse than some North-European sources (Prus-Glowacki and Stephan 1994). Spanish provenances offer high resistance to drought and

several adaptations have been described, including low growth rate and branching habit. General interest comes mainly from the need to preserve genetic resources, their use for shelter plantations and their high wood quality.

Whereas performance and adaptation of Scots pine provenances has been well studied in the northern and continuous range of the species, not much information exists in the non-continuous or southern range, where more complex mechanisms of evolution could have affected the differentiation of the species. Unfortunately, Spanish material is not represented in the IUFRO series of tests of Scots pine. Up-to-date information on growth and adaptive traits of Spanish provenances seems, therefore, to be generally unavailable.

Early wide range trials did catalogue Spanish provenances as having the slowest growth (Wright and Bull 1963, Wright et al. 1966). No important provenance by environment interaction on growth traits was reported from these early trials con-

ducted outside Spain (Sweet 1964, King 1965). More recent information comes from very young experiments and/or from studies based on incomplete or non-representative samples.

The main objective of the installation of Spanish and German trials in the late eighties was to improve the knowledge of the genetic variability of the species. Spanish provenances are being tested together with German sources, that have shown excellent growth (Pardos and Stephan 1988). Trials were laid out at five sites, chosen to represent the various environments. Characters of interest in the adaptation to highly different sites and in selection for growth, survival, and branching (as related to biomass production and wood quality) are studied in the present paper. Measurements were taken five years after planting. Analysis at that age allows an early comparison and an estimate of the components of variability.
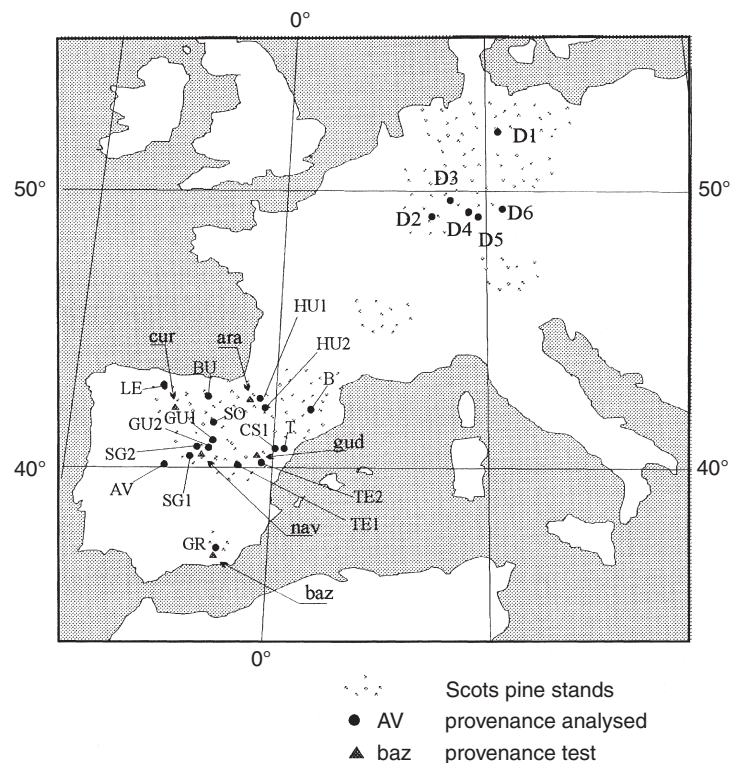

Fig. 1. Location of the origins and test sites.

2 Materials and Methods

2.1 Data

Sixteen provenances representing most regions in Spain (Catalán et al. 1991) and six from Germany were chosen for a total of $I = 22$ provenances. Morphologic features of the Spanish material have already been described (Agúndez et al. 1992a), as well as results at the nursery stage (Agúndez et al. 1992b). Table 1 is a summary describing the origin of seed and its use in the trials. See also Fig. 1.

In each origin, seed was collected from 25 mother trees more than 50 metres distant from each other. Trees were supposed to be a representative sample of each stand. Two-year-old seedlings were transplanted to $J = 5$ sites: Aragües

del Puerto (Huesca), Navafría (Segovia), Sta. Colomba de Curueño (León), Gúdar (Teruel) and Baza (Granada). Table 2 presents the main site features. The statistical design was Randomised Complete Blocks with 4 replicates. The experimental unit was a square plot with 16 trees distant $2.5 \, \text{m} \times 2.5 \, \text{m}$. Not all provenances were included at all sites (See Table 1), resulting in an incomplete overall trial. This was due to germination and survival problems, particularly of the German provenances.

The following $K = 4$ traits, measured 5 years after plantation, are considered: *Total height (H)*, at the end of the fifth growth period on the site (seven years from seed) in centimetres; *Diameter (D)*, measured in millimetres at the beginning of the second year branch whorl; *Number of branches (NB)*, at the fourth whorl on the site

Table 1. Information on the origin of seed samples and on their representation at the trial sites. The first one or two letters of the code of the Spanish provenances denote the province of origin.

Code	Origin	Altitude	Latitude	Longitude	Rainfall (mm)	Region	Representation at the trial sites ‡				
							arag	baza	cur	gudar	nava
LE	Puebla de Lillo	1550	43°04´N	05°15´W	1780	01	x	x	x	x	x
BU	San Zadornil	1000	42°50´N	03°11´W	790	02	x	x	x	x	x
HU1	Morrano	700	42°12´N	00°06´W	840	04	x	x	x	x	o
HU2	Borau	1550	42°42´N	00°35´W	1580	05	x	x	x	o	x
B	Pobla de Lillet	1100	42°14´N	01°58´W	660	07	x	o	x	o	x
SO	Covaleda	1550	41°56´N	02°48´W	1000	08	x	x	x	x	x
GU1	Galve de Sorbe	1400	41°15´N	03°07´W	810	09	x	x	x	x	x
GU2	Campisabalos	1400	41°13´N	03°12´W	810	09	x	x	x	x	x
SG1	Valsaín	1550	40°49´N	04°01´W	1170	10	x	x	x	o	x
SG2	Navafria	1600	41°00´N	03°50´W	1170	10	x	x	x	o	x
AV	Navarredonda de Gredos	1550	40°21´N	05°07´W	670	11	x	x	x	x	x
TE1	Orihuela del Tremedal	1750	40°31´N	01°38´W	1130	12	x	o	x	o	x
TE2	Gúdar	1700	40°25´N	00°41´W	750	14	x	x	x	x	x
CS	Castell de Cabrés	1150	40°45´N	00°12´E	850	15	x	x	x	x	x
T	La Cenia	1100	40°45´N	00°03´E	850	15	x	x	x	x	x
GR	Baza	2050	37°22´N	02°51´W	630	17	x	x	x	o	x
D1	Gartow	50	53°02´N	11°25´E			x	o	o	o	x
D2	Otterberg	300	49°30´N	07°45´E			x	x	o	o	x
D3	Wolfgang	177	50°09´N	09°03´E			x	o	o	o	x
D4	Wiesentheid	220	49°48´N	10°21´E			x	o	o	o	o
D5	Selb	570	50°12´N	12°10´E			x	x	o	o	o
D6	Laufen †	>900	-	-			x	o	o	o	x
	Total number						22	16	16	10	19

‡ x = presence, o = absence; † non-autochtonous material.

Table 2. Information on the trial sites.

Site	Code	Province	Altitude	Latitude	Longitude	Rain (mm)	Date of plantation	Area (ha)
Aragües	arag	Huesca (HU)	1370	42°44′N	00°37′W	1577	04-91	0.88
Baza	baza	Granada (GR)	1850	37°21′N	02°56′W	630	04-91	0.64
Curueño	cur	León (LE)	1150	42°46′N	05°21′W	1783	11-90	0.64
Gúdar	gudar	Teruel (TE)	1700	40°27′N	00°35′W	748	04-91	0.50
Navafria	nava	Segovia (SG)	1600	41°02′N	03°49′W	1170	11-90	0.76

and *Survival* (*SUR*), 5 years after planting, given by the percentage of living trees (for analysis the *arcsine($\sqrt{}$)* transformation was applied).

2.2 Statistical Methods

2.2.1 Individual and Combined Analysis of the Trials

Plot means at each site were analysed after a Randomised Complete Block design. The assumption of normality was verified for each variate with the Shapiro-Wilks W-test. Though some heteroscedasticity was noticeable in one variate a stabilising transformation was not considered indispensable as ratios between variance estimates did not exceed a factor of 10 (Patterson and Silvey 1980). The adjusted means of the provenances at each site, obtained from the individual analysis for each variate, are the entries of the I by J table, arranged by country of origin, $\{y_{pij}\}$, which was analysed after the linear model

$$y_{pij} = \mu + B_p + \pi_{pi} + \lambda_j + \varepsilon_{pij} \qquad (1)$$

with B_p being the effect of the country, $p = 1$ or 2, π_{pi} the effect of the i-th provenance from the p-th country and λ_j of the j-th site with usual assumptions about residuals ε_{pij} of normality, independence and common variance σ^2. Sum to zero side conditions are also assumed for the identifiability of the parameters. This combined analysis allows making marginal comparisons among the provenances, valid in average for the entire zone represented by the sites in the study. Multiple comparisons have been done using Tukey-Kramer intervals computed as:

$$\hat{\pi}_{pi} - \hat{\pi}_{p'i'} \pm q_{I,g;\alpha} \frac{\hat{\sigma}}{\sqrt{\bar{r}}} \qquad (2)$$

with q the studentized range at the level α, $\hat{\sigma}$ the square root of the residual mean square after fitting (1), with g degrees of freedom, and $\bar{r}$ the harmonic mean of the number of sites in which provenances, $pi, p'i'$, appear.

2.2.2 Interpretation of the Provenance by Site Interaction

To test significance of interaction from the table of adjusted means obtained from the individual analyses an F test is conducted. The test statistic is obtained by dividing the residual variance estimate from fitting model (1) by the "pooled" residual variance estimate from the individual analyses, once adjusted for taking into account that the table entries are means of 4 independent observations. The variance on the numerator includes any variability due to interaction. The variance on the denominator is usually called "pure error" variance to denote that it is free of interaction effects. If the quotient is substantially higher than 1 it should denote the presence of interaction.

In cases where the interaction appeared significant, factorial regression (Denis 1988) and multiplicative, also called biadditive, models (Mandel 1971, Denis and Gower 1994) were tried for finer interpretation. Residuals in these models are still supposed to be normal and independently distributed with mean zero and some common "pure error" variance. This part of the study devoted to the interaction includes only the 16 Spanish provenances due to the uneven representation of the German material. Accordingly, in this part the

index p is dropped. We shall now be concerned with the behaviour of specific Spanish provenances growing on each of the chosen sites.

Factorial regression requires the use of additional information on the way of covariates of provenances and sites. The covariates used in this study were: altitude, average yearly rainfall, latitude and longitude of the seed sources and of the trial sites. A regression model was fitted so that the whole set of provenance covariates was always included but a maximum of one site covariate was in the model at any one time, as the number of degrees of freedom was too small (only 4 for Site).

The joint regression model of Finlay-Wilkinson can be considered as a member of the class of factorial regression models having the site main effect as the only site covariate and none for provenances. It is written as

$$y_{ij} = \mu + \pi_i + \lambda_j + \phi_i \lambda_j + \varepsilon_{ij} \qquad (3)$$

The regression coefficient ϕ_i is interpreted by geneticists as defining the stability of the provenance.

A multiplicative model writes the interaction as the product of a score specific to the i-th provenance times another specific to the j-th site. It is thus written

$$y_{ij} = \mu + \pi_i + \lambda_j + \theta\gamma_i\delta_j + \varepsilon_{ij} \qquad (4)$$

The parameters γ_i are considered a measure of the adaptation of the i-th provenance and the δ_j of the capacity of the j-th site to produce an interactive behaviour of the provenances. The θ is a positive scale factor expressed in the same units as y. More than one multiplicative term can be used in the model up to the minimum of $I-1$ and $J-1$. Least squares estimates of the interaction parameters are based on the singular value decomposition of the matrix of additive residuals. Usual identifiability constraints and properties of estimators are described in many places (see for instance Goodman and Haberman 1990). The sum of squares of the k-th multiplicative term (*TMk)* is given by the square of the k-th singular value. To compute mean squares and approximate tests the sum of squares of each multiplicative term is divided by its parametric dimension or the number of inde-

pendent parameters contained in this term. An approximate F test is built supposing that this sum of squares distributes as a $\sigma^2\chi^2$ variable with same number of degrees of freedom and use as denominator the available estimate of the "pure error" variance.

The fit of a multiplicative model was done by the method of alternating least squares due to some incompleteness of the table (Denis 1991). Solution after convergence provided estimates that were in good agreement with those obtained by a direct singular value decomposition once the nine empty cells were filled with estimates from the additive model.

2.2.3 Clustering

A method of hierarchical agglomerative clustering was applied to the multivariate mean table of $I \times J \times K$ size. This was first proposed for a univariate approach (Corsten and Denis 1990) and then generalised to the multivariate situation (Denis and Moro 1996, Moro and Denis 1996). It is used taking as criterion the Mahalanobis distance from the origin of the Provenance plus Interaction residual vectors (Generalised total provenance sum of squares). As metric, the inverse of the "pooled error" variance-covariance matrix within sites Σ, was used. Clustering is normally stopped at the step when the accumulated criterion reaches the 5% χ^2 deviate with *(I−1)JK* degrees of freedom. The method will join provenances into groups with a similar response across sites. At the end, the bulk of the interaction is intended to be between the groups.

3 Results

3.1 Individual Analysis

The analysis of variance for each variate at each site is given in Table 3. For total height the provenance effect was significant (1%≤P<5%) at Navafría and very significant (P<1%) at the other 4 sites. For diameter it was very significant at two sites and non-significant at the other three. For number of branches it was significant or very

Table 3. Analysis of variance, general means at each site and "pooled pure error" variance estimate.

Origin		H			D			NB			SUR		
	d.f.†	Mean squares	F	P	Mean squares	F	P	Mean squares	F	P	Mean squares	F	P
Aragües													
Provenance	21	485.874	3.65	0.00	7.862	1.41	0.15	0.514	1.92	0.03	0.0487	1.50	0.11
Block	3	620.488	4.66	0.01	17.100	3.07	0.03	0.787	2.94	0.04	0.1891	5.82	0.00
Error	63	133.068			5.572			0.268			0.0325		
Mean		79.66			15.80			4.46			1.29		
Baza													
Provenance	15	434.914	9.29	0.00	5.441	1.52	0.14	1.302	4.7	0.00	0.0576	1.87	0.05
Block	3	160.602	3.43	0.02	39.620	11.05	0.00	1.961	7.07	0.00	0.0111	0.36	0.78
Error	45	46.821			3.586			0.277			0.0308		
Mean		56.46			10.51			3.87			1.29		
Curueño													
Provenance	15	319.615	10.6	0.00	5.460	3.05	0.00	0.336	1.96	0.04	0.0278	1.25	0.27
Block	3	330.558	11.0	0.00	22.483	12.57	0.00	0.592	3.44	0.02	0.0277	1.24	0.31
Error	45	29.960			1.789			0.172			0.0222		
Mean		63.39			11.99			4.37			1.46		
Gúdar													
Provenance	9	167.986	9.42	0.00	7.275	6.17	0.00	0.491	1.93	0.09	0.0483	0.61	0.78
Block	3	45.334	2.54	0.08	2.959	2.51	0.08	0.595	2.33	0.10	0.1447	1.82	0.17
Error	27	17.838			1.179			0.255			0.0793		
Mean		38.02			8.94			2.92			0.92		
Navafría													
Provenance	18	288.94	2.27	0.01	5.901	1.16	0.32	1.855	2.74	0.00	0.0567	0.84	0.65
Block	3	4010.74	31.5	0.00	298.102	58.76	0.00	2.998	4.43	0.01	0.2395	3.54	0.02
Error	54	127.23			5.073			0.677			0.0676		
Mean		67.04			12.25			3.86			1.26		
"Pooled" variance	234	82.01			3.84			0.34			0.043		

†d.f. = degrees of freedom; F = variance ratio; P = P-value.

significant in all sites except Gúdar. It was always non-significant for survival.

The highest heteroscedasticity occurs on height. The maximum ratio of variances is 7.5, for estimates of Aragües and Gúdar. On the other traits this maximum ratio does not exceed 5.0. No correcting action is considered necessary for the subsequent analysis.

3.2 Combined Analysis

The combined analysis of variance (Table 4) did show highly significant differences between sites for all variates. There were very significant differences between the average effects of prov-

enances in total height (*H*) and significant in survival (*SUR*). A large part of this significance, particularly in *SUR,* was due to the simple contrast between German and Spanish material. No significant differences appeared in diameter (*D*) and number of branches (*NB*).

Fig. 2 presents the bivariate representation of provenances taking as co-ordinate axes the estimates of *H* and *SUR.* It shows the clear separation between German and Spanish material. German provenances, particularly *D3*, appear of superior growth to the Spanish. Only *SG1, BU* and *CS* get near the height growth of the German material. The southern-most provenance *GR* appears as the slowest growing. Conversely, the comparison on *SUR* shows 4 of the 6 German provenances
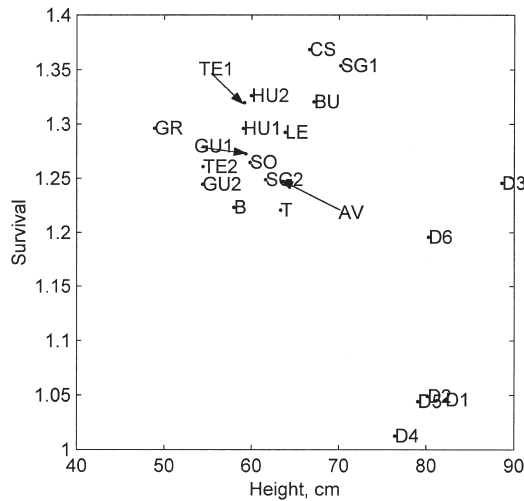
Fig. 2. Joint plot of provenances on *H* (cm) and *SUR* (transformed variate). Coordinates are adjusted means estimated from model (1) with *H* as abscissas and *SUR* as ordinates.

behaving as the worst survivors. Nevertheless, neither the Wolfgang nor the Laufen provenances appear to be significantly outyielded on survival by the Spanish provenances.

This has been verified applying the method of Tukey-Kramer. The provenance from Valsaín, *SG1,* is not confidently outyielded (95% level) in height by *D3* as, using formula (2), the estimate of difference is 18.4±20.4cm. The comparison of *D3* and *BU* gives 21.5±19.7cm indicating the confident superiority of *D3*. The same procedure applied for survival to *SG1* with *D3* gave the interval –0.11±0.31 showing no significant difference. The interval for the difference between *SG1* and *D2* is 0.30±0.29 indicating a barely confident superiority of *SG1*. The above results on height should be read with caution as it is shown below the presence of significant interaction. It implies that the average differences between provenances are not expected to be the same at individual sites. This does not happen

Table 4. Analysis of variance between sites after model (1). All 22 provenances included.

Origin	d.f.†	SS	MS	F	P
H					
Site	4	11107.0	2776.7	67.4	0.00
Provenance	21	6006.3	286.0	6.9	0.00
Country	1	3986.5	3986.5	96.7	0.00
Provenance\Country	20	2019.8	101.0	2.5	0.00
Residual	57	2348.5	41.2		
D					
Site	4	468.13	117.03	53.9	0.00
Provenance	21	47.73	2.27	1.1	0.43
Country	1	0.69	0.69	0.32	0.57
Provenance\Country	20	47.04	2.35	1.08	0.41
Residual	57	123.54	2.17		
NB					
Site	4	16.50	4.12	18.8	0.00
Provenance	21	5.11	0.24	1.1	0.37
Country	1	0.23	0.23	1.0	0.47
Provenance\Country	20	4.89	0.24	1.1	0.38
Residual	57	12.51	0.22		
SUR					
Site	4	1.774	0.444	39.0	0.00
Provenance	21	0.531	0.025	2.2	0.01
Country	1	0.313	0.313	27.5	0.00
Provenance\Country	20	0.217	0.011	1.0	0.47
Residual	57	0.649	0.011		

†d.f.=degrees of freedom; F=variance ratio; P=P-value; SS, MS sums of and mean squares

with survival, as interaction appears not significant.

Estimates of diameter growth averaged across sites were highest for the alpine *D6, SG1* and *HU2.* Four German provenances were the slowest growing in diameter. Provenances *SG1, HU2, SO* appear with the highest values of *NB,* whereas *D1, D4* and *BU* showed the lowest values. Again as interaction appears significant for both traits the comparison of main effects averaged across sites is to be examined with care and inference at specific sites must be preceded by a study of interaction.

3.3 Interpretation of the Interaction

Results of the variance test for interaction with estimates from Tables 3 and 4 were very significant for the first three variates and non-significant for *SUR* (P = *0.52*). We proceed with the description of the interaction only on *H*, the most important variate, and limited to the Spanish provenances.
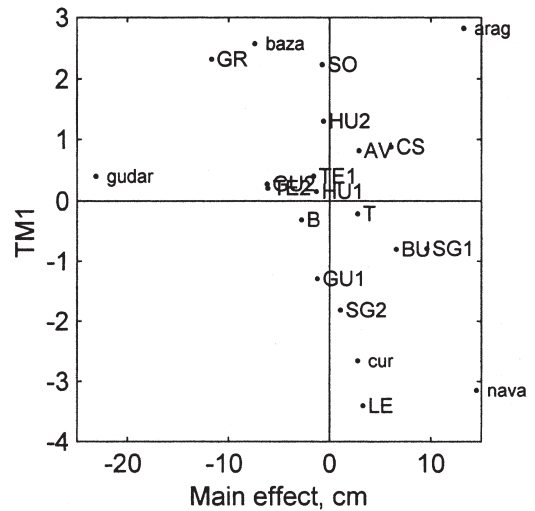
As the average response in growth to environmental variation may be assumed to be linear, the first model used in order to explain the interaction was model (3). However, the regression sum of squares was about 10% of the total interaction sum of squares, so small that it was not even significant.

Factorial regression models were fitted as described in Section 2.2. In all cases the remaining unexplained interaction was very significant. Therefore, a linear relationship of the specific

Fig. 3. Biplot of height after model (4). Percentage of interaction sum of squares explained by the first multiplicative term (TM1) = 50%. The analysis uses data only from the Spanish provenances. Abscissas are the main effects of Provenance or Site and ordinates are $\sqrt{\theta}\gamma_i$ or $\sqrt{\theta}\delta_j$. Provenances labelled in upper case, sites in lower case.

adaptability with the chosen climatic and geographic covariates did not appear supported by the data and/or did not provide a satisfactory interpretation of the interaction.

The fitting of model (4) with only one term reduced the interaction sum of squares by 50% and took the comparison of the residual variance with the "pure error" variance to the border of non-significance (see Table 5). Though the parametric dimension of the first multiplicative term, actually used for testing, may somewhat exceed the correct number of degrees of freedom (Mandel 1971), the P-value was low enough to be reasonably confident on its significance. Moreover, the mean absolute value of the interaction effect recovered by the multiplicative term (2.5 cm) was 62% of that of the provenance main effect (4.02 cm).

We include the biplot as Fig. 3. Provenances and sites are represented taking as abscissas the corresponding main effects and as ordinates the estimates of $\sqrt{\theta}\gamma_i$ and $\sqrt{\theta}\delta_j$, respectively. The better growing provenances and the more produc-

Table 5. Analysis of variance of the multiplicative model (4) of interaction in *H*. Only Spanish provenances. The "pure error" mean square used for tests is the "pooled" variance from Table 3 divided by the number of replicates.

Origin	d.f.	SS	MS	F	P
Interaction *P*L*	51	2046.66	40.13	2.01	0.00
TM1	18	1014.26	56.35	2.75	0.00
Residual	33	1032.40	31.29	1.51	0.05
"Pure error"	234	4797.00	20.50		

Column labels have the same meaning as in Table 4. TM1 means first multiplicative term.

tive sites appear, therefore, on the right of the plot. Provenances and sites with ordinates of the same sign interact positively. In the case of different signs, their interaction is negative. In both cases, the amount of interaction gets larger as the corresponding points are more distant from the X-axis. Thus, fast growing provenances like *SG1, BU, LE* are well adapted to Navafría and Curueño and unadapted to Aragües and Baza. On the contrary, *SO* and *CS* appear better adapted to Aragües and Baza. The Gúdar site appears scarcely interactive in correspondence to its lower productivity.

Provenances close to the trial sites show good specific adaptation. Thus, *LE* appears adapted to Curueño, *GR* to Baza, *SG2* and *SG1* to Navafría, and *HU2* to Aragües. Occasionally, geographically close provenances, such as *SO* and *BU,* show a different response.

In general, provenances from sources under some Mediterranean influence appear to be stable or better adapted to Aragües and Baza than to the interior and more continental sites Navafría and Curueño.

3.4 Clustering

Fig. 4 is the dendrogram resulting from the application of the clustering procedure. It was applied to the means of all variates of the Spanish provenances. The within sites correlation matrix among variates is given in Table 6.

The procedure stopped at the 5% level leaving 4 final groups. Group 1 includes good growing provenances, from the central and more continental mountains, adapted to Navafría-type environments. A representative can be *SG1*. The second group, close to the former, includes two provenances, *BU* and *AV,* rather stable and fast growing. The third group includes average-to-good growing provenances from eastern mountains with some Mediterranean influence. They may be represented by *CS* and can be described as stable but occasionally showing some adaptation to Aragües and Baza. The last group includes slow growing provenances from mountains with Mediterranean influence, specifically adapted to Aragües and Baza. It includes the Nevadensis provenance, *GR.* This fourth group appears as the most separate
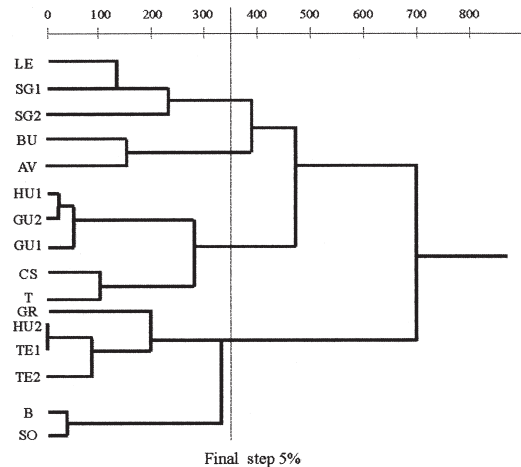
Fig. 4. Dendrogram resulting from multivariate clustering of the Spanish provenances based on the Provenance+Interaction sum of squares. Metric based on the "pooled residual ("pure error") variance-covariance matrix. The horizontal axis is the clustering criterion. The vertical line signals the stopping point at the 5% level.

Table 6. "Pooled" within trial correlation matrix among variates.

	H	*D*	*NB*
D	0.817		
NB	–0.688	–0.679	
SUR	0.238	0.236	–0.222

from the other three. A statistical clustering procedure has always some heuristic character. If the procedure is stopped one step before ($P \approx 0.1$), this fourth group would be split and give place to a fifth group including *B* and *SO*.

4 Discussion and Conclusions

Former work on the species has found that there are small changes of ranking based on height measured at different tree ages between 6 and 58 years, but differences among groups remain stable (Giertych and Oleksyn 1992). Coefficients

of variation of additive and phenotypic effects vary little with time for height and other variates, though diameter is sensitive to changes in competition (Hannrup et al. 1998). Therefore, though measured at a young stage with competition practically non-existent, the traits studied allow some confidence on the validity of conclusions regarding the behaviour of the provenances. Future development should corroborate these early findings.

From an analysis of early trials (Wright et al. 1966, Lines and Mitchell 1964) it was found that the height growth of Spanish populations is lower than that of German material. It is now accepted that the best provenances come from Central Europe including some from Germany (Giertych 1979, Giertych and Oleksyn 1992).

Our results show that the better growing Spanish provenances, though inferior, get near to some of the German ones. This fact suggests breeding possibilities from the tested material and should help to discard the belief that all Spanish provenances are of very low quality (Lines and Mitchell 1964). The worst provenance *GR* represents the real border of the southern range of the species. It is surely under strong selection pressure and should not be taken as representative of the Iberian material.

The different growth rate of German and Spanish provenances is mainly due to different daily rates with little influence of the total length of the growth period (Alía et al. 1998). Differences in survival seem to be related to height growth since on dry years the percentage of shoot mortality is lower for the slower growing plants. The lower number of branches in the German provenances, could be related to the fact that provenances transferred southwards form few and thin branches (Ståhl 1998) in comparison to local provenances. Differences among German provenances were detected when tested on other sites, and their relative height growth in Spain agrees with that previously reported (Stephan and Liesebach 1996).

Height ranking for the Spanish populations agrees with that found in New Zealand (Sweet 1964). No GE interaction was found by Sweet, in contrast with the results of the present study, which includes a greater number of provenances and surely more environmental variability. The detection of interaction contradicts the widely accepted species homogeneity at early ages with respect to growth and phenology (Khalil 1969) and absence of interaction (King 1965). A wide range trial with older material of the species was reported recently showing the presence of interaction (Shutyaev and Giertych 1997).

Interaction confirms the existence of local effects that cause the specific adaptability of provenances. These effects have been previously described (Giertych and Oleksyn 1981, Hurme et al. 1997, Oleksyn et al. 1998). Working with other material, significant interaction between height and temperature has been reported (Mergen et al. 1974). Important clinal effects have also been found on Pinus sylvestris (Ruby 1967, Saatcioglu 1967, Junttila 1986). In our case we were unable to model their influence on the basis of some climatic and geographical features of origins and sites. A multiplicative model with one term provides, however, some sensible interpretation of the interaction. The biplot (Fig. 3) shows not only the adaptability of provenances to the site closest to the source but also the different behaviour of some provenances of close geographic origin. This should be the consequence of small changes in the original environment as was already indicated in the delineation of provenance regions in Spain. This different behaviour has been found in populations with small genetic distance (Prus-Glowacki and Stephan 1994). It may be related to the time of appearance of the species in Spain.

In the above-mentioned study, focusing exclusively on Spanish material, the use of isozymes resulted in most of the variation found at the population level (Gst = 4%). Estimates of variance components from these data (not included) suggest a structure of the variability at a geographical level. More than 70% of the total variation in height, 14% in diameter and 40% in branching is among populations, whereas no differences are detected in survival. This can be explained by natural selection acting on phenotypes and traits related to biomass production (Eriksson 1998).

Prus-Glowacki and Stephan (1994) applied clustering on 7 provenances, based on genetic distances computed from allelic frequencies at 11 enzyme loci. They obtained two groups, with the Nevadensis provenance (*GR*) and one population from the Pyrenees (*HU2*) remaining isolated. The first group included *SG1* and *SO*. It can

be interpreted as a Central Spanish group. In the second there were *T, TE1* and *TE2,* clearly an Eastern Spanish group. From those found by clustering on multivariate interaction, Groups 1 and 2 contain *SG1* together with other provenances not included in their work, but from the same geographical origin. Populations *GU1* and *GU2* are geographically close to provenances in the previous groups but join *HU1* in our Group 3, reflecting the adaptation to different ecological conditions, mainly derived from a longer dry season. Two geographically close sources, *CS* and *T,* are also placed in Group 3. On the other hand, *SO,* genetically close to the Central populations, appears with two populations from the Pyrenees, *HU2* and *B,* in a subgroup that joins *TE1* and *TE2* forming our Group 4. The provenance *GR,* which appeared very distant genetically from the rest, is placed in this group due to its poor growth performance on most sites. In general, the populations follow a geographical pattern of variation, with occasionally large differences among close origins as a result of their isolation and of different ecological conditions. Departures from this pattern may be interpreted as a result of the action of selective processes on populations deriving from the postglacial refugia in the Iberian Peninsula.

The provenance from Valsaín *SG1,* occupies the first rank in growth and is recommended for use in breeding programs for the species in Spain, based on the establishment of clonal seed orchards (Pardos and Gil 1986). The same provenance is presently recommended for afforestation in a large part of the area of distribution of the species.

In conclusion, this study presents some new results concerning the adaptation of marginal and southern populations of Scots pine. Processes are different to those reported in the northern area of the species, with a continuous range and connection among populations.

Acknowledgements

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