Morphological and agronomical diversity patterns in the Spanish barley core collection

J. M. LASA[1], E. IGARTUA[1], F. J. CIUDAD[2], P. CODESAL[2], E. V. GARCÍA[2], M. P. GRACIA[1], B. MEDINA[1], I. ROMAGOSA[3], J. L. MOLINA-CANO[3] and J. L. MONTOYA[2]

[1] *Estación Experimental de Aula Dei (CSIC), Departamento de Genética y Producción Vegetal, Zaragoza, Spain*
[2] *Servicio de Investigación Desarrollo y Tecnología Agraria (SIDTA), Junta de Castilla y León, Valladolid, Spain*
[3] *Centre UdL-IRTA, Lleida, Spain*

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Seven thousand years of barley cultivation under the environmental hardships typical of the Mediterranean climate have generated genetic singularity of the Spanish barleys, consistently reported in the literature. From the Spanish National Collection of 2289 accessions, a core subset with 159 landraces and 16 old varieties was constituted. Twenty-seven characters were evaluated for the core collection, to define the structure of the diversity. Several evaluation trials were carried out in 1999–2000, whereas yield trials were performed in earlier years. Phenotypic diversity was large for most of the characters studied. Comparisons of genetic diversity between the core and the original collections suggested that the core is a good representation of the existing diversity in the BNG. Comparisons with results of studies on Spanish materials from other collections seem to indicate that the Spanish diversity is not well represented in some world collections. Principal component analyses for quantitative and qualitative characters revealed a clear distinction between two- and six-row cultivars, and also between landraces and commercial varieties. Geographical origins of the landraces were correlated with grain yield, heading date, duration of grain filling period, and growth class. In relation to diseases, altitude played an important role on the resistance to powdery mildew and brown rust. For brown rust, all the resistant landraces came from low altitudes. These geographical gradients seemed consistent with prior knowledge about barley adaptation, and would confirm the agreement between passport data and true adaptive origin of these landraces from a geographical point of view.

José M. Lasa, Estación Experimental de Aula Dei (CSIC), Departamento de Genética y Producción Vegetal, P.O. Box 202, 50080 Zaragoza, Spain. E-mail: lasa@eead.csic.es

For the last eight decades, barley breeding in Europe was based on crossbreeding between geographically diverse gene pools (FISCHBECK 1992). Crossbreeding started about 80 years ago, and it currently relies mostly on the successful cultivars produced in the process, and much less on landraces and primitive cultivars, dominant in the beginning. This situation has led to a great concern among barley breeders in Europe about the increasing genetic narrowness of the elite germplasm pool (THOMPSON et al. 1990; MELCHINGER et al. 1994). It is unlikely that the genetic variability present in landraces has been fully exploited, especially in the displaced landraces from peripheral European countries (AHOKAS and POUKKULA 1999). Thus, barley is a good example of a crop which could benefit from a more extensive use of non-conventional germplasm. When properly evaluated, locally adapted germplasm shows many interesting traits that may be used for the improvement of current cultivars (HADJICHRISTODOULOU 1993, 1995).

In some semi-arid areas of Spain, landraces and primitive cultivars (directly selected from local landraces) have not been totally replaced by newly bred varieties. The only reason for this is that farmers still prefer traditional cultivars under certain environmental conditions because they yield more. Barley has been cultivated in Spain for over 7000 years, under the environmental hardships typical of Mediterranean climate. Genetic singularity of Western Mediterranean barleys, including Spanish, has been consistently reported in the literature (TOLBERT et al. 1979; PEETERS 1988). These facts suggest the existence of specific adaptation traits in autochthonous barleys that have not been totally incorporated into modern cultivars. The Spanish National Germplasm Bank (BNG) holds a collection of 2289 barley accessions, from which 1805 are landraces collected in Spain in the first half of the 20th century, before the extensive introduction of modern varieties. The Aula Dei Experimental Station carried out an extensive agronomic and morphologic evaluation of these landraces under semi-arid conditions since 1984. Recently a Spanish core collection was assembled (IGARTUA et al. 1998), based on stratified sampling across agroecological regions defined for barley cultivation. Diversity of accessions within provinces and agroecological regions was maximized by taking into account passport data and agronomic evaluations.

The objectives of this paper are i) to analyse how the core collection represents the existing variability, ii) to find out the structure of the genetic diversity and iii) to assess how the geographical origin and the structure of the diversity are related.

MATERIAL AND METHODS

The Spanish barley core collection is constituted of 159 landraces plus 16 old varieties that have been extensively use in the country (Ager, Albacete, Almunia, Barberousse, Dobla, Hatif de Grignon, Monlon, Pané, Alpha, Beka, Hassan, Kym, Pallas, Union, Wisa, Zaida). The selected landraces were collected from 1931 until 1954, with a most extensive collection in 1944. It was evident during the first evaluations that many accessions were heterogeneous. It was decided, however, that the core collection should be made of inbred lines, to facilitate its maintenance, and to ensure the repeatability of its evaluations. Thus, the dominant type in each accession was selected, and self-pollinated for at least three years. As barley populations consist of sets of highly homozygous plants, it was assumed that the accessions would be close to complete homozygosity after this process. The geographical distribution of the accessions is shown in Fig. 1. Latitude of collection sites varied between 28°39′N (Canary Islands) and 43°04′N; longitudes were from 17°53′E (Canary Islands) to 3°12′E; altitudes spanned from 7 m to 1587 m above sea level. Some provinces could not be

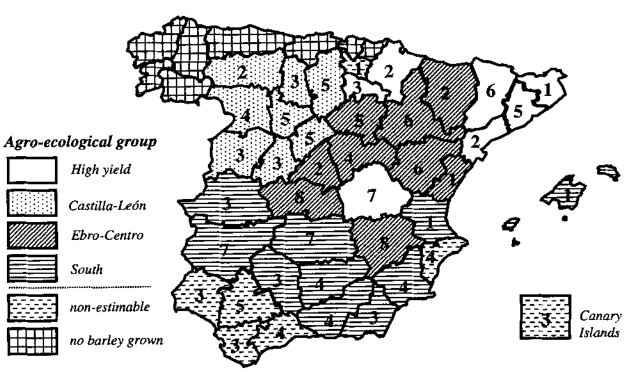

Fig. 1. Division of Spanish provinces in agroecological regions, according to consistency of historical barley grain yields. Also shown, number of six-row entries per province selected for the core collection.

ascribed to agroecological regions because of lack of historic data. In order to include all accessions for some analyses, these provinces were assigned an agroecological group based on geographical vicinity and knowledge of climatic and agricultural characteristics. The accessions from Canary Islands were classified as belonging to a distinct fifth agroecological region, due to their remote origin.

Agronomic evaluation of 1650 entries of the BNG was carried out under semi-arid conditions in the central Ebro valley. Average rainfall was 412 mm per year, ranging between 232.2 and 699.5 mm during the evaluation period of seven seasons, from 1985 to 1991. Evaluation was carried out with sets of variable number of accessions per year. Experimental designs were always un-replicated augmented designs, with check/entry ratios of 0.1 in 1985 and 1986, and 0.25 the rest of the seasons. Plot sizes were 2 rows, 25 cm apart, 1.2 m long in 1985 and 1986, and 4 rows, 25 cm apart, 2.5 m long from 1987 on. Agronomic management was done according to local practices. Sowings were done in autumn, usually during November. The commercial cultivars that belong to the core collection were also part of the accessions held at the BNG, and were thus evaluated with the landraces, a few every year. As the conditions of the field trials varied between years, quantitative trait values between years were not directly comparable. Not all trials were evaluated for the same set of traits. The characters measured for a majority of accessions at these trials were: plant height, grain yield, test weight, row number, spike density, awn roughness, rachilla hairs and kernel covering. Quantitative characters were recorded every year into a discrete scale by splitting the continuous distributions into classes (usually five), one standard deviation wide, centred around the mean.

The core collection was again evaluated for morphological and quantitative traits at new field trials in the 1999–2000 season. One trial was carried out in Valladolid (Castilla-León agroecological region), with one replicate, plot size of 6 rows 25 cm apart, 3 m long. A very late sowing (March) was also done at Valladolid, to provide contrasting environments for phenological development. Growing conditions at this trial were excellent, and was used for morphological characterization. The accessions were also visually evaluated for disease reaction at a disease-prone environments (Girona, in the high-yield agroecological region) in the 1999–2000 season, following natural infection. The list of traits measured or evaluated at these trials is provided in Table 1. For some morphological descriptors, we followed the guidelines of IPGRI (1994), whereas for others we used simplified coding, also shown in Table 1. Some traits

Table 1. *Descriptive statistics of the Spanish barley core collection, for characters determined at the Valladolid 1999–2000 trial*

a) Continuous quantitative characters	Mean	Standard deviation	Minimum	Maximum
Tillers per plant	2.0	1.6	1.0	3.0
Days to heading	106.8	7.2	93.0	127.0
Grain filling period (days)	36.2	3.7	26.0	45.0
Plant height (cm)	123.8	7.0	103.5	146.0
Spike length (cm)	8.6	1.6	4.5	12.9
Spikelet number	24.6	4.2	15.6	37.6
Kernels per spike	70.3	9.6	39.2	97.2
1000 kernel weight (g)	36.5	5.1	23.0	51.3

b) Discrete quantitative characters	States	Relative frequencies 1	2	3	4	5	6	7	8	9
Waxiness	1 = no wax, 9 = max. waxiness	0	0	5	1	17	14	49	14	0
Brown rust reaction	1 = tolerance, 9 = susceptibility	2	2	4	7	3	8	18	30	26
Powdery mildew reaction (Girona)	1 = tolerance, 9 = susceptibility	2	2	5	11	16	24	27	13	0
Photoperiod sensitivity	1 = insensitive, 7 = high sensitivity	23	–	50	–	15	–	12	–	–
Lodging	1 = no lodging, 9 = max. lodging	15	9	18	17	19	13	8	1	0
Spike density	3 = lax, 5 = interm., 7 = dense	–	–	28	–	64	–	8	–	–

c) Qualitative characters	States	Relative frequencies 1	2	3	4	5	6	7
Growth class	1 = winter, 2 = facultative, 3 = spring	13	10	77	–	–	–	–
Growth habit	3 = prostrate, 5 = intermediate, 7 = erect	–	–	30	–	57	–	13
Stem pigmentation	1 = green, 2 = purple	49	51	–	–	–	–	–
Auricle pigmentation	1 = green, 2 = purple	36	64	–	–	–	–	–
Leaf hairiness	1 = presence, 2 = absence	52	48	–	–	–	–	–
Row number	1 = 2-row, 2 = 6-row	11	89	–	–	–	–	–
Kernel covering	1 = naked, 2 = covered or semi-covered	0	100	–	–	–	–	–
Lemma awn barbs	1 = smooth, 2 = rough	6	94	–	–	–	–	–
Glume and glume awn length	1–5 = shorter, as long, longer, twice than kernel, lemma-like	28	58	11	3	0	–	–
Rachilla hairs	1 = short, 2 = long	46	54	–	–	–	–	–
Awn pigmentation	1 = absence, 2 = presence antocyanin	19	81	–	–	–	–	–

were measured on a plot basis: days to heading, grain filling period, 1000 kernel weight, waxiness, brown rust reaction, powdery mildew reaction, photoperiod sensitivity, lodging, growth class, growth habit, stem pigmentation, auricle pigmentation, leaf hairiness and row number. Plant height was averaged for three measurements spread over the plot. Tillers per plant were counted on five plants per plot, before jointing. Spike length, spikelet number, kernels per spike, spike density, kernel covering, lemma awn barbs, glume and glume awn, rachilla hairs and awn pigmentation were determined in the laboratory, on a sample of five main stems per plot. Photoperiod sensitivity was derived from the difference of heading dates between the 'standard' autumn sowing and the 'late' March sowing at Valladolid.

For the measurement and comparisons of phenotypic diversity, we used the Shannon-Weaver information index (H'), normalized as described by TOLBERT et al. (1979), to ensure that it always fluctuates between 0 and 1.

Differences of trait means among agroecological regions were checked by analysis of variance, using the variance of accessions within regions as error. Altitude and latitude effects on trait distributions were assessed by covariance analysis. When more than one of these factors were significant, the best combined models were searched, following a factorial regression approach (VAN EEUWIJK 1995). As latitude and altitude are true geographic entities, and agroecological regions are partially counfounded with them, they were included as covariates in the combined models prior to the introduction of the 'agroecological region' source of variance.

The entries of the core collection were classified using principal component analysis. This was done separately for qualitative and quantitative traits, as in most cases they may represent sets of loci with different selection history. All calculations were performed with PROC GLM and PROC PRINCOMP of SAS (1988).

RESULTS AND DISCUSSION

The distributions of morphological and quantitative traits for the core collection showed a wide range of diversity in most cases (Table 1 a, b, c). The results for quantitative traits from the evaluations carried out in previous years cannot be summarized as a single distribution for low or moderate heritability traits, as genotype-by-environment interaction could be large. For this reason, the results presented in Table 1 correspond just to the 1999–2000 field trials. It can be said, however, that the discrete distribution of grain yield, test weight and plant height for the old field trials presented a sizeable number of accessions at each of the five classes defined. As for the traits in Table 1, only kernel covering showed no variation, because all accessions presented covered kernels. Some quantitative characters (Table 1a), as tillers per plant, grain filling period, spike length, spikelet number, kernels per spike, and 1000 kernel weight, usually suffer large environmental influence and genotype-by-environment interaction. Thus, their mean values have a limited descriptive value, as they represent the behaviour of the entries under a single set of the many possible environmental conditions. The standard deviation and range, however, are valuable indicators of diversity. It is remarkable the huge differences that existed among entries for agronomically important traits as plant height and kernel weight. The last trait is essential to define grain quality, and ranged from unacceptable to optimum values. The phenological responses (as days to heading and photoperiod sensitivity) and other adaptive traits, as growth class and growth habit, also presented wide distributions. It is worth noting the relatively large number of photoperiod sensitive entries found. One could speculate that the mechanism of photoperiod sensitivity may hasten the late development in some accessions, thus helping to avoid the terminal drought stress conditions so frequent in the Mediterranean area.

There was a rather severe attack of at least two diseases in the trial at Girona (brown rust and powdery mildew), and of one at Valladolid (powdery mildew). Only the results for the Girona trial are presented in Table 1, as some entries lacked this evaluation in Valladolid. The disease reactions showed a very wide spectrum, from extremely susceptible to tolerant. These trials were un-replicated, and thus the results might be biased due to uneven natural infection, among other error causes. But powdery mildew was detected at both Valladolid and Girona, providing unplanned replication. And the reactions of the accessions at the two sites were quite consistent ($r = 0.6$), even in inevitable presence of some genotype-by-environment interaction.

Comparisons of genetic diversity

Table 2 presents the normalized Shannon-Weaver (H') values for the Spanish core collection compared to the original Spanish Barley Collection for some common traits, determined at the 1985–1991 trials for the original collection. Only high heritability traits were considered for this comparison, for the same reasons stated above. The rather similar values under the two columns suggest that the core collection is a good representation of the original collection. The most important difference was the presence

Table 2. *Shannon-Weaver normalized index (H') for some traits in common in the original Spanish barley collection (BNG), the Spanish core collection and the USDA World collection (USDA-ARS Information Network)*

Characters	BNG	Core	World
Row number	0.249	0.363	0.903
Spike density	0.848	0.787	0.663
Awn roughness	0.385	0.169	0.342
Rachilla hairs	0.750	1.000	0.712
Kernel covering	0.030	0.000	0.561

of a few naked barleys in the original collection, but none in the core. This is a typical, and unavoidable, situation of loss of rare alleles when creating core subsets.

The "World" column in Table 2 shows the H' values for what we could call a good representation of the world diversity, calculated from the Germplasm Resources Information Network (USDA 2001) data. The comparison with the Spanish material presents differences mainly for row number and kernel covering. Clearly there was a much higher proportion of six-row and covered-kernel materials in the core than in the USDA world collection, which presents larger diversity.

A second comparison was made to determine whether the Spanish diversity present in other studies from world collections actually resembled the existing Spanish diversity. In Table 3 we provide H' values of Spanish landraces included in other studies, such as CROSS (1994), with 20 entries from Morocco, Portugal and Spain, from the New Zealand collection, and TOLBERT et al. (1979) with 63 Spanish landraces from the USDA world collection. The results suggest that the Spanish diversity present in these collections, specially the New Zealand one, may not be a faithful representation of the existing diversity.

Table 3. *Comparison of genetic diversity (H') for traits in common for Spanish landraces from the collections of New Zealand, USDA world, and the Spanish core*

Characters	Core	NZ	USDA
Awn colour	0.701	0.934	
Awn roughness	0.169	0.000	0.220
Growth class	0.640	0.000	0.610
Growth Habit	0.861	0.000	
Kernel covering	0.000	0.469	0.000
Purple auricle	0.951	0.779	
Rachilla hairs	1.000	0.881	
Row number	0.363	0.722	0.530
Spike density	0.787	0.937	
Stem colour	0.999	0.000	

Summarizing these comparisons, we can conclude that the Spanish core collection seems to be a good subset of the National Germplasm Collection, and that the Spanish accessions present in other collections may not represent a good sample of the existing Spanish diversity.

Structure of the genetic diversity

To analyse the structure of the genetic diversity among the set of accessions that constitutes the core collection, we performed principal component analysis on the matrix of accessions by characters, separately for quantitative and qualitative traits. The first two components for the quantitative trait matrix explained 43 % of the variance (Fig. 2). Characters related with spike and yield presented the largest loadings on the first component, and the phenology, like days to heading and grain filling period, for the second component. Some conclusions could be extracted for these materials; first of all is that grain yield, 1000 kernel weight, and lodging were very related, and secondly, that the way to get higher yields in these material is not to increase kernel number per spike, but to get a good grain filling. At the same time early flowering and long filling periods result in a better behaviour of the materials. The placement of grain yield in the graph, in the middle of the six-row landraces cloud, and far from commercial cultivars (other than Albacete and Almunia) supports the hypothesis of the presence of specific adaptation traits in locally adapted genotypes. Similar findings with landraces from different countries were reported by CECCARELLI et al. (1987) and AHOKAS and POUKKULA (1999).

Distinction between six- and two-row landraces was very clear, and also between landraces and commercial varieties. The exceptions were the six-row commercial cultivars Albacete and Almunia, due to their origin in selections from Spanish local populations. Commercial and two-row material occupy the North-East quadrant of the graph, and grain yield is not located close to the commercial material, indicating that the old six-row landraces tend to behave better than commercial varieties under semi-arid conditions. Six-row landraces covered the rest of the quadrants, indicating wide diversity.

The first two first principal components calculated for the qualitative characters were responsible for 39 % of the variance (Fig. 3). Number of rows, as such, was not included in the analyses. Nevertheless, there was again a clear division between spike morphology groups, with the exception of cultivarAlpha (labelled in Fig. 3), a two-row variety that has mostly

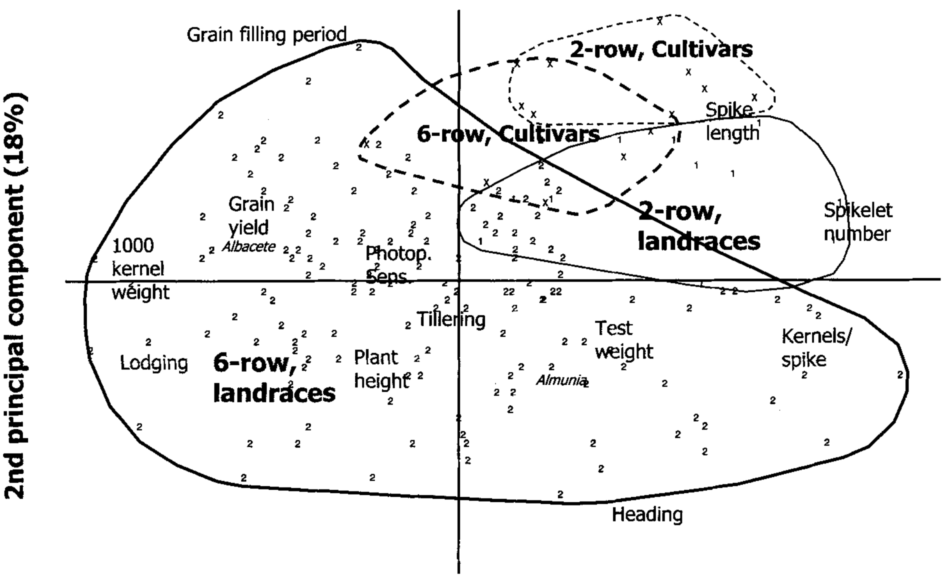

Fig. 2. Biplot of first two principal components for quantitative characters. Symbols for accessions are '1' for two-row landraces, '2' for six-row landraces, and 'x' for commercial cultivars.

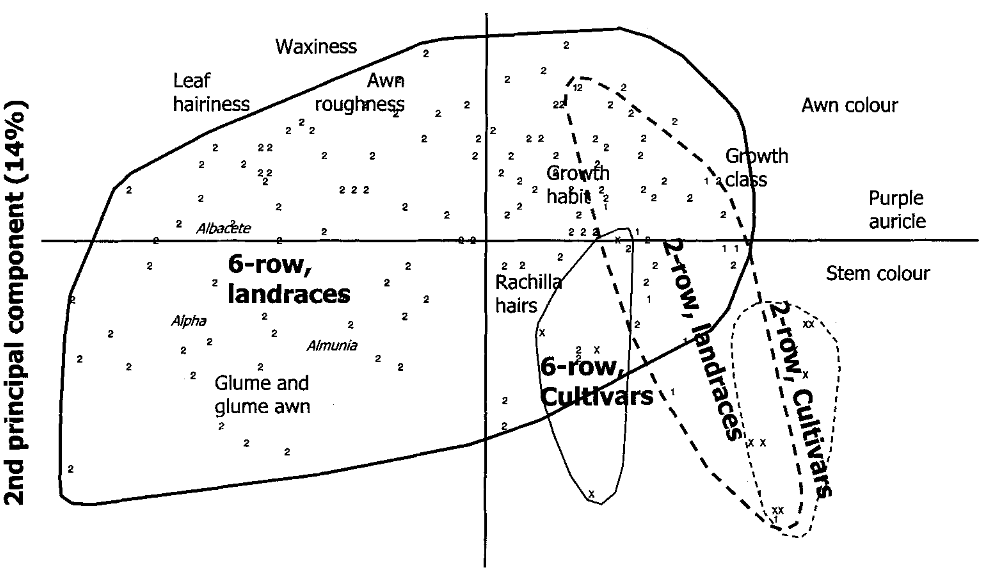

Fig. 3. Biplot of first two principal components for qualitative characters. Symbols as in Fig. 2.

six-row background. Again the two commercial cultivars of Spanish origin fell within the cloud of points of Spanish landraces, rather than with the other commercial materials. Overall, presence of pigmentation seemed to pull in the direction of the two-row material, and the explanation could be either the isolated evolution of the two types of material, or the presence in the same arm of chromosome 2 of pigmentation genes and the gene *vrs1*, main responsible of the number of rows.

Diversity and geographical origin

Only accessions with complete passport data were allowed into the core collection, and thus it was possible to investigate the influence of altitude and latitude on the structure of the diversity found, to-

Table 4. *Coefficients of determination for latitude and altitude as independent variables explaining the variability of the characters measured (at $P < 0.05$), and for agroecological region as source of variation in an analysis of variance (also $P < 0.05$)*

Characters	Single models					Combined models
	Latitude linear	Latitude quadratic	Altitude linear	Altitude quadratic	Agroecological region	
Days to heading	**18.3**[1]	–	2.8[2]	–	15.5	**18.3**
Grain filling period (days)	**13.1**	**3.7**	5.2	–	13.5	**16.8**
Spike length (cm)	–	**3.3**	–	–	–	**3.3**
Spikelet number	**9.6**	**8.8**	–	–	10.4	**18.5**
Kernels per spike	**2.6**	**6.8**	–	–	–	**9.1**
1000 kernel weight (g)	**4.8**	–	**4.8**	–	–	**7.6**
Test weight (kg)	**7.8**	–	–	–	**7.6**	**7.8**
Grain yield	**6.8**	–	2.9	–	**7.9**	**13.1**
Brown rust susceptibility	5.6	–	**25.0**	–	**16.4**	**25.0**
Powdery mildew reaction (Girona)	–	**5.7**	**5.5**	–	**6.9**	**20.6**
Powdery mildew reaction (Lleida)	–	**6.5**	**7.2**	–	**12.2**	**23.5**
Photoperiod sensitivity	**8.7**	–	–	2.5	9.7	**8.7**
Lodging	–	**2.4**	–	–	–	**3.7**
Spike density	**3.1**	–	–	–	–	**3.1**
Growth class	**9.8**	**3.8**	–	–	6.7	**13.6**
Growth habit	3.9	1.5	**5.6**	–	–	**5.6**
Leaf hairiness	–	–	**3.6**	–	**10.4**	**11.3**
Row number	**4.0**	–	–	–	–	**4.1**
Awn pigmentation	–	–	–	–	7.7	**7.7**

[1] Figures in bold mean that the variable in this column was retained in the multiple model.
[2] Figures in smaller font mean that the variable in this column explained a significant amount of the character, but were not retained in the multiple model.

gether with the influence of the agroecological region. For these analyses, all quantitative traits were expressed as discrete variables with five states (as stated above). The characters that showed significant associations with any of these factors are presented in Table 4. Latitude, altitude, and regions were not totally independent. There was a correlation coefficient between latitude and altitude of 0.25. Also, latitude and altitude were different among regions. Therefore, it was impossible to separate completely the influence of the three factors. In Table 4 we present first the results obtained for single models, when only one factor was taken into account (in linear and quadratic form for latitude and altitude). The last column in Table 4 presents the results for the best combined models, always introducing latitude and altitude (in order of their respective importance in each case) prior to the introduction of the agroecological region.

Overall, latitude was the geographical factor that accounted for the larger proportion of variance. For instance, early heading and longer filling period, with a result in a higher grain yield and test weight, were associated with Southern geographical origin of the landraces. Spring types (growth class = 3) were more common in the South, same as photoperiod sensitive types. Altitude played an important role in few, but very relevant cases. Prostrate growth habit frequency increased at higher altitudes, but the most important effects were detected for disease tolerance. Altitude played an important role on the resistance to powdery mildew and, especially, brown rust, with resistant landraces always coming from low altitude origins (Fig. 4). PAPA et al. (1998) also found geography-dependent distribution of growth habit for local barleys in the Mediterranean region (Sardinia), though the adaptive explanation was not evident in their case.

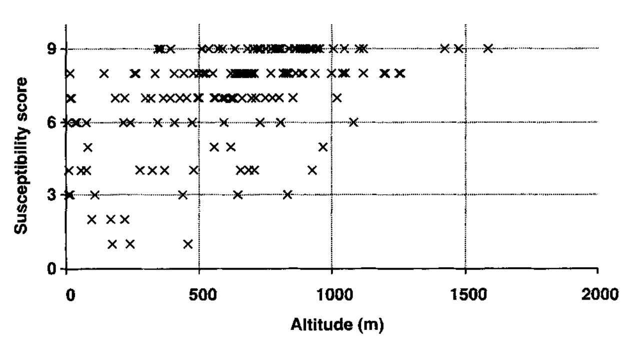

Fig. 4. Plot of altitude of collection site versus brown rust (*Puccinia hordei*) susceptibility.

Table 5. *Yield (kg/ha) and landrace origins compared with historic yield of the Spanish agroecological regions*

Agroecological region	Historic yield	Evaluation (Ebro-Centre), 1986–1991
South	1.086	1.737
Ebro-Centre	1.576	1.498
Castilla-Leon	1.876	1.437
High-yield	2.056	1.737

Though there were twelve characters with different means for agroecological regions, only five remained in the combined models. The variance due to regions was absorbed by latitude or altitude for the other seven characters. There was a significant difference for grain yield among regions that is presented in Table 5. The grain yields presented in this table are means of the grain yield in standard deviation units for the accessions from each agroecological region tested each evaluation year. For better interpretation of the results, the overall grain yield means for each region were converted back into kilograms per hectare. There were several accessions, assumed random, from each region (except Canary Islands) evaluated each year. Thus, the comparison between agroecological regions is rather balanced for years. The behaviour of groups of accessions coming from different origins gave differential responses when tested in the same region, in this case, in Ebro-Centre. It is interesting to note that the entries from the historically lowest yielding area (South), gave higher yields than the entries from the Castilla-León and Ebro-Centre regions, and similar to the High-yield group of entries, all of them coming from historically more favourable regions. As the evaluation sites were quite arid (evident from the average yields), it could be speculated that the adaptive traits present by the Southern entries actually carried an advantage under the harsh evaluation conditions.

In Spain, a more Southern location would generally mean higher temperatures both during winter (less requirement for winter growth habit) and during grain filling (thus with an advantage for early heading types). Also, higher altitudes mean cooler temperatures, for which the prostrate growth habit usually confers increased tolerance. The finding of disease tolerant accessions mostly at low altitudes could be related with the existence of selective pressure towards tolerance only at coastal areas, more humid and better suited for the survival of fungal pathogens. Thus, the observed geographical associations seem consistent with prior knowledge about barley adaptation, and would confirm the real agreement between passport data and true adaptive origin of these landraces, from a geographical point of view. The total proportion of variance explained by the three factors was never large. But taking into account the coarse nature of the analyses, focusing only onto macro-geographical parameters and the inherent large error of unreplicated trials, the results were encouraging.

Current work and use of the core collection

Our work is currently focused on a very thorough agronomic evaluation of the Spanish barley core collection under differential environments, and in studies of diversity patterns based on molecular markers. Finally, we want to stress that the use of these landraces in our breeding programme has produced good results for semi-arid areas. By direct crossing, some varieties like Candela have been obtained, and the male sterile facilitated recombination of some of these landraces has allowed the creation and recurrent selection of populations which show good prospects.

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