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Morocco as a possible domestication center for barley: biochemical and agromorphological evidence

J. L. Molina-Cano [1], P. Fra-Mon [2], G. Salcedo [2], C. Aragoncillo [2], F. Roca de Togores [1] and F. García-Olmedo [2]

[1] Department of Barley Breeding, La Cruz del Campo, S.A., Malting and Brewing Company, P.O. Box 53, E-41080 Sevilla, Spain
[2] Department of Biochemistry, Escuela Tecnica Superior de Ingenieros Agronomos, Universidad Politecnica, E-28040 Madrid, Spain

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Summary. The distribution of genetic variants of a group of low molecular weight, chloroform-methanol soluble proteins (CM proteins), among Moroccan and non-Moroccan accessions of *Hordeum spontaneum* and among selections from several Moroccan landraces of *H. vulgare* and cultivars of the same species with widespread European origin, suggests that domestication of barley might have taken place in Morocco. An agromorphological characterization of the *H. spontaneum* accessions further supports this hypothesis. The possible Moroccan origin of the French cultivar 'Hatif de Grignon' and of several Spanish 6-rowed barleys is also presented.

Key words: Wild barley – Hordeum – Domestication – Center of Origin

Introduction

Cultivated barley (*Hordeum vulgare* L.) has been considered, on the basis of its evolutionary pattern, as an oligocentric crop; this means that barley has a definable center of origin, the Fertile Crescent, and one or more centers of diversity, for instance Ethiopia (Harlan 1975).

The center of origin of a crop may be defined as the region where domestication took place and can be recognised because there the wild ancestor survives together with its derived crop. The wild species is usually living in a wild status in the core of its range and, sometimes, survives as a weed at the periphery of it (Zohary 1964). The discovery of *H. spontaneum* C. Koch as a weed of barley in Morocco (Molina-Cano and Conde 1980; Molina-Cano et al. 1982) enlarged the know western limits of the area of distribution of the wild ancestor of cultivated barley, which were previously thought to be Cyrenaica, in the east of Libya (Harlan and Zohary 1966; Harlan 1979). At about the same time, Chinese workers reported the occurrence of *H. spontaneum* in the Qinghai-Xizang plateau of China (Xu 1982). Today, therefore, both the eastern and western limits of the area of distribution of wild barley have been considerably enlarged and, consequently, the Fertile Crescent can be called into question as the only center of origin of barley. More recently, Bekele (1983) has argued for the possibility of a multiple origin of cultivated barley.

Giles and von Bothmer (1985) argued that it is very difficult to state whether Morocco and China are true centers of origin of barley or should rather be considered as secondary centers.

Molina-Cano et al. (1982) put forward the following 2 alternative hypotheses to explain the occurrence of *H. spontaneum* in Morocco: i) It was formerly wild there and has survived after becoming a weed. ii) It was introduced there in historical times, presumably as an admixture with barley seeds coming from elsewhere, possibly from the Near East.

For making the correct choice among the two former hypotheses it is necessary to study the genetic relationships among the Moroccan weed barleys and their counterparts from other regions of its range, particularly from the core of the Fertile Crescent, i.e., Israel, Iraq, Syria, Iran, etc., but also from other peripheral regions such as Libya and Afghanistan. As suggested by Harlan (1980, personal communication) Libya is indeed a very critical region in this context. Genetical differences between the Moroccan and the other wild barley populations would tend to exclude the second hypothesis, that of the introduction of *H. spontaneum* into Morocco from elsewhere, and would support the first hypothesis, that of a domestication carried out in situ. Giles and Lefkovitch (1984, 1985) found clear differences among Moroccan and Iranian accessions of *H. spontaneum*, both in germination pattern and in agromorphology.

In addition, the study of the genetical relationships among Moroccan weed barleys, Moroccan cultivated barleys, and southern European cultivated barleys should also offer some insights into the origin of the latter.

In our survey, we have investigated the genetic variability of the CM-proteins, which are the main components of the A-hordeins (Salcedo et al. 1980, 1982). The A-hordeins are less variable both in the cultivated and in the wild species than the B-, C- and

D-hordeins (Doll and Brown 1979; Shewry et al. 1979, 1983) and are, therefore, more suitable biochemical markers in phylogenetical studies. Wheat CM-proteins were among those used by Johnson and coworkers in their extensive studies on the origin and evolution of *Aegilops-Triticum* species (Johnson 1972, 1975: Johnson and Hall 1965). Our survey has been complemented with an agromorphological study of the *H. spontaneum* accessions.

Materials and methods

We present in Table 1, the name, origin, source of seed and pedigree, where known, of all the cultivars and accessions studied. The 8 accessions of *H. spontaneum* from Morocco are all the available material collected in the 2 expeditions reported by Molina-Cano and Conde (1980) and Molina-Cano et al. (1982). Each of the 8 populations of weed barley was collected as a group of about 15–20 single spikes; they were not yet completely mature and therefore unthreshed. These populations have since been conserved in isolation as single-spike progenies. The composite of Moroccan landraces of cultivated barley was formed by bulking together grain from single spikes of the 9 original populations. This bulk was sampled afterwards on the basis of the agromorphological appearance of its individual component plants. The accessions from Cyrenaica (Libya) were kindly sent us by Dr. K. Hammer (Zentralinstitut für Genetik und Kulturpflanzenforschung, German Democratic Republic). The remaining accessions of *H. spontaneum* from some of the relevant regions of its range of distribution, were kindly supplied by Dr. J. C. Craddock (USDA World Barley Collection).

The cultivated barleys sampled could be divided into 4 groups: i) Landraces from Morocco; ii) primitive cultivars of Spanish and French origin that were, in turn, derived from landraces; iii) modern French cultivars; iv) European cultivars of non-Mediterranean origin.

Biochemical methods

The extraction and 2-dimensional fractionation of barley CM-proteins was carried out essentially as described by Salcedo et al. (1984), on single kernels from the progenies of individual spikes of each population studied.

Delipidated kernels were extracted twice with chloroform: methanol 2 : 1 (v/v) and the solvent vacuum-evaporated. The extracts were fractionated by 2-dimensional gel electrophoresis: the first dimension was a pH-gradient electrophoresis on preformed pH gradients (ampholines 5–8), and the second one, a starch-gel electrophoresis (pH 3.2). Gels were stained with 0.05% nigrosine, in methanol-water-acetic acid (5 : 5 : 1 by vol). To ascertain the relative positions of different protein variants in the 2-dimensional maps, electrophoresis of mixtures of the appropriate samples was carried out.

Agromorphological studies

The characters studied were mainly chosen to give a picture, as complete as possible, of the differences among the accessions of *H. spontaneum*. From the set of 28 characters studied, only 8 of them, listed in Table 2, gave significant differences among accessions, when analyses of variance were carried out.

Results

Variation in CM-proteins (A-hordeins)

The CM-proteins were analyzed by 2-dimensional electrophoresis in all the *H. spontaneum* and *H. vulgare* samples listed in Table 1. Figure 1 is a composite diagram where the relative positions of all the variants are shown in the 2-dimensional map. The CM-proteins are low molecular weight, salt-soluble hydrophobic polypeptides that are selectively extracted from barley endosperm with chloroform : methanol 2 : 1 (v/v) (Salcedo et al. 1980). The standard phenotype, that of 'Zephyr' barley, consists of 5 components: CMa-1, CMb-1, CMc-1, CMd-1 and CMe-1 (Fig. 1, black spots). Variants for these proteins were identified on the basis of their alternative appearance in the survey and, in the case of the more frequent ones, by studying their inheritance in appropriate crosses (Salcedo et al., 1984). Results are summarized in Table 3.

The variant proteins CMe-2,2′ were found in 7 out of 8 *H. spontaneum* accessions from Morocco; in 12 out of 14 *H. vulgare* (6-rowed) accessions also from Morocco and, finally, in the French cultivar 'Hatif de Grignon' and its derivatives 'Precoce Lepeuple', 'Monlon', 'Astrix', and 'Hop', all of the 6-row type.

These variants seem thus to be restricted to Moroccan weed and cultivated barleys and, also, to some French cultivars. Two line-selections ('Anezal' nos. 2 and 4) from the same Moroccan landrace carried CMe-1 and CMe-2,2′, respectively, indicating that the original population was segregating at the *CMe* locus. This landrace was not included in the bulk that originated accessions A-L. Several single plants from this landrace

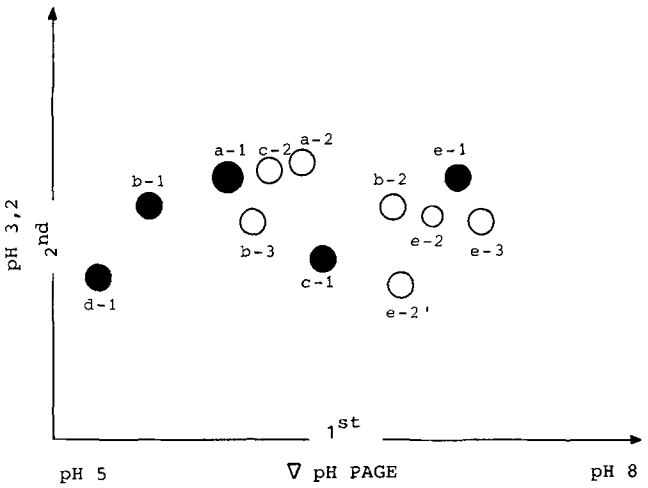

Fig. 1. Composite diagram showing relative positions in the 2-dimensional map and designations of all observed variants (black spots correspond to proteins found in the "standard phenotype" of *Hordeum vulgare*, cv. 'Zephyr')

Table 1. Description of barley material used (cultivars or accessions)

Species	No. of rows	Code or name	Pedigree	Origin	Source of the seed
Hordeum spontaneum C. Koch	2	No. 1 – No. 8	Weed races	Morocco	Collection of La Cruz del Campo, S.A.
Hordeum spontaneum C. Koch	2	No. 9 (PI 253573)	Wild race	Israel	USDA World Collection
Hordeum spontaneum C. Koch	2	No. 11 (PI 282581)	Wild race	Israel	USDA World Collection
Hordeum spontaneum C. Koch	2	No. 13 (PI 254894)	Wild race	Iraq	USDA World Collection
Hordeum spontaneum C. Koch	2	No. 14 (PI 219921)	Wild race	Afghanistan	USDA World Collection
Hordeum spontaneum C. Koch	2	No. 15 (PI 211041)	Wild race	Afghanistan	USDA World Collection
Hordeum spontaneum C. Koch	2	No. 16 (PI 212305)	Wild race	Afghanistan	USDA World Collection
Hordeum spontaneum C. Koch	2	No. 18 (AHOR 9719/82)	Wild race	Libya	Gatersleben (DDR)
Hordeum spontaneum C. Koch	2	No. 19 (AHOR 9721/82)	Wild race	Libya	Gatersleben (DDR)
Hordeum vulgare L.	6	A–L	Selections in a composite of landraces	Morocco	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	Selection 'Anezal' No. 2 and No. 4	Selection in a population from Anezal	Morocco	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Almunia'	Selection in a Spanish landrace	Spain	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Albacete'	Selection in a Spanish landrace	Spain	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Berta'	Selection in a Spanish landrace	Spain	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Cerro'	Selection in a Spanish landrace	Spain	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Lupe'	Selection in a Spanish landrace	Spain	INIA (Spain)
Hordeum vulgare L.	2	'Porthos'	'Lignee 207' × 'Emir'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Hatif de Grignon'	'Selection in a landrace from 'Ile de Ré'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Precoce Lepeuple'	'Mob 575' × 'Hatif de Grignon'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Monlon'	'Breustedt Schladener' × 'Hatif de Grignon'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Astrix'	'Weih 259-711' × 'Ares' × 'Hatif de Grignon'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	6	'Hop'	('Gembloux 456' × 'Feebar') × 'Hatif de Grignon'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Beka'	'Bethge XIII' × 'Kneifel'	France	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Troubadour'	61229 × 6271	Netherlands	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Zephyr'	'Heine 2149' × 'Carlsberg'	Netherlands	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Printa'	'Menelick' × 'Balder'	Netherlands	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Spratt Archer'	'Archer' × 'Spratt'	Ireland	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Logra'	'Vada' × 'Zephyr'	Great Britain	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Karri'	'Carlsberg' × 'Rigel'	Finland	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Donaria'	'Isaria' × 'Kneifel'	Germany	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Rika'	'Kenia' × 'Isaria'	Sweden	Collection of La Cruz del Campo, S.A.
Hordeum vulgare L.	2	'Ingrid'	'Balder' × ('Binder × Opal')	Sweden	Dr. A. Hagberg
Hordeum vulgare L.	2	'Bomi'	'Bonus' × 'Minerva'	Denmark	Dr. A. Hagberg

Table 2. Agromorphological characterisation of *Hordeum spontaneum* accessions[a]

Characters[b]	Morocco									Israel			Iraq	Afghanistan				Libya			Morocco		All other origins	
	1	2	3	4	5	6	7	8	$\bar{x}$	9	11	$\bar{x}$	13	14	15	16	$\bar{x}$	18	19	$\bar{x}$	$\bar{x}$	SD	$\bar{x}$	SD
1	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	0	0	0	2	0	0.75	0.5
2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	0	0	0.3	0	0	0	2	0	0.50	0.5
3	76.8	71.8	74.0	57.4	70.2	68.2	71.2	64.0	69.2	76.4	74.2	75.3	61.6	78.0	81.6	78.8	79.5	63.8	77.6	70.7	69.2	6.1	74.0	7.3
4	3.1	3.9	4.7	4.4	4.4	4.7	4.6	4.2	4.3	3.8	4.2	4.0	3.8	2.9	3.0	3.1	3.0	3.5	4.0	3.7	4.3*	0.5	3.5	0.5
5	29.6	29.0	22.8	24.2	15.0	27.6	22.4	15.6	23.3	27.2	15.6	21.4	23.0	22.0	24.6	19.2	21.9	19.2	12.0	15.6	23.3	5.6	20.4	4.9
6	27.0	28.4	31.2	30.4	26.8	29.2	25.4	23.4	27.7	22.6	25.6	24.1	23.6	19.8	25.0	28.0	24.3	26.0	23.0	24.5	27.7**	2.6	24.2	2.5
7	59.0	55.0	54.0	52.0	53.0	49.0	54.0	51.0	53.4	45.0	26.0	35.5	37.0	31.0	36.0	36.0	34.3	41.0	40.0	40.5	53.4***	3.0	36.5	5.9
8	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	1	1.5	0	0	1	0

[a] Significant differences in analysis of variance for a certain character between accessions from Morocco and those from other origins are reported (*$P \leqq 0.05$; **$P \leqq 0.01$; ***$P \leqq 0.001$)

[b] List of characters: *1.* Leafiness at heading stage. Codes, 0: Low foliage development; 1: medium; 2: strong. *2.* Plant habit at heading stage. Codes, 0: prostrate; 1: semi-prostrate; 2: erect. *3.* Plant height (cm). *4.* Stem diameter (mm). *5.* No. spikes per plant. *6.* No. kernels per spike. *7.* 1,000 kernels weight (g). *8.* Spike density. Codes, 0: compact; 1: intermediate; 2: lax

Table 3. Phenotypes observed in the electrophoretic analysis of CM proteins in *Hordeum spontaneum* and *H. vulgare*[a]

Species	Accession code or name and origin	CMa		CMb			CMc		CMd	CMe		
		a-1	a-2	b-1	b-2	b-3	c-1	c-2	d-1	e-1	e-2,2′	e-3
H. spontaneum	1, 2, 4, 5, 6, 7 (Morocco)	+	–	+	–	–	+	–	+	–	+	–
H. spontaneum	3 (Morocco)	+	–	–	–	+	+	–	+	+	–	–
H. spontaneum	8 (Morocco)	+	–	–	+	–	+	–	+	–	+	–
H. spontaneum	9, 11 (Israel)	+	–	+	–	–	+	–	+	–	–	+
H. spontaneum	13 (Iraq); 14, 15 (Afghanistan)	–	+	+	–	–	+	–	+	+	–	–
H. spontaneum	16 (Afghanistan); 18 (Libya)	+	–	+	–	–	+	–	+	+	–	–
H. spontaneum	19 (Libya)	+	–	+	–	–	–	+	+	+	–	–
H. vulgare	A, B, C, D, E, G, H, K, L (Morocco)	+	–	+	–	–	+	–	+	–	+	–
H. vulgare	F (Morocco)	+	–	–	–	+	+	–	+	+	–	–
H. vulgare	I, J (Morocco)	+	–	–	–	+	+	–	+	–	+	–
H. vulgare	Selection Anezal no. 2 (Morocco)	+	–	+	–	–	+	–	+	+	–	–
H. vulgare	Selection Anezal no. 4 (Morocco)	+	–	+	–	–	+	–	+	–	+	–
H. vulgare	'Almunia', 'Albacete', 'Berta' and 'Cerro' (Spain) and 'Porthos' (France)	+	–	–	+	–	+	–	+	+	–	–
H. vulgare	'Hatif de Grignon', 'Precoce Lepeuple' (France)	+	–	–	+	–	+	–	+	–	+	–
H. vulgare	'Monlon', 'Astrix' and 'Hop' (France)	+	–	+	–	–	+	–	+	–	+	–
H. vulgare	'Zephyr', 'Printa' and 'Troubadour' (Netherlands); 'Lupe' (Spain); 'Beka' (France); 'Spratt Archer' (Ireland); 'Logra' (England); 'Karri' (Finland); 'Bomi' (Denmark); 'Donaria' (Germany); 'Ingrid' and 'Rika' (Sweden)	+	–	+	–	–	+	–	+	+	–	–

[a] + = present; – = absent

were collected by Molina-Cano, Gomez-Campo and Conde during their 1980 trip, near the village of Anezal, in the surroundings of the Djebel Siroua, in a thin stand of barley cultivated in an isolated field. The selections were made on the basis of agromorphological appearance.

The variant CMb-3 was found only in Moroccan material, both cultivated of the 6-row type and weed.

The allele CMb-2 has been found in Moroccan *H. spontaneum,* in 4 out of 5 Spanish 6-rowed cultivars, and in the 6-rowed French cultivars 'Hatif de Grignon' and its derivative 'Precoce Lepeuple', and in the 2-rowed 'Porthos'.

Some protein variants were found only in wild barleys outside Morocco: CMa-2 in *H. spontaneum* from Iraq and Afghanistan, CMc-2 from Libya, and CMe-3 from Israel.

Protein CMd-1 was found to be invariant among all the studied material.

Variation in agromorphological characters

The relevant results are presented in Table 2. The accessions of *H. spontaneum* from Morocco have a high foliar development and an erect habit at heading, as well as tillers that are significantly shorter and thicker than those of the accessions from other origins. Moreover, their yielding ability is much higher for they have a significantly higher thousand-kernel weight and number of grains per spike and, also, a higher tillering capacity – number of spikes per plant. Besides, the Moroccan weed barley has a spike denser than that of *H. spontaneum* from the other origins. All these observations indicate that the former is much closer to the cultivated species than the other wild barleys studied.

If we examine in Table 2, the similarities of *H. spontaneum,* Morocco, versus *H. spontaneum* Israel, Iraq, Afghanistan, and Libya, we can conclude that they are very slight. And this is true even when we compare accessions from Morocco and Libya, that are neighbouring countries.

Discussion

Both the biochemical and the agromorphological data seem to indicate that Moroccan weed barleys are clearly different from those from elsewhere, although we should allow for the limited number of non-Moroccan accessions studied. These results are in good agreement with those by Giles and Lefkovitch (1984, 1985). Even the Libyan accessions are very dissimilar from the Moroccan ones. This implies a long period of isolation of the latter.

The striking phenotypic similarity between *H. vulgare* and *H. spontaneum* from Morocco, as well as the distribution of the less frequent protein variant, CMb-3, could be explained in terms of introgression. However, the prevalence of CMe-2,2′ in both types of Moroccan barleys is not easily explained by introgression – this allele probably originated there – and suggests that a domestication process might have occurred in Morocco, a situation which would be similar to those postulated for China (Xu 1982) and Ethiopia (Bekele 1983), regions well apart from the Fertile Crescent.

We could thus conceive the domestication of barley as a process carried out over a continuum of very different environments, i.e., as a noncentric crop, "sensu" Harlan (1975).

The situation in Morocco could be explained as follows: (i) The real wild types would disappear at an undetermined moment after domestication had taken place. This situation might be explained because of the progressive desertization of the Sahara from the 3rd millennium BC onwards (Harlan 1975). Under those drier conditions, the only suitable land for wild barley was restricted to the more humid and favorable environment of cultivated barley fields, where soil moisture was conserved by ploughing. Away from those fields, on the very dry and hard *Artemisia* steppe, only xerophytes could live. (ii) *H. spontaneum* was adapted to survive as a weed in cultivated barley fields, then introgression started that led it to its present level of similarity with its cultivated companion. A similar situation is described for Libya by Hammer et al. (1985).

In conclusion, the evidence presented here supports the hypothesis that Morocco is a center of origin of barley, providing we allow for the limited evidence based on: i) the restricted number of populations analysed, and ii) the small number of protein systems used.

The French cultivar 'Hatif de Grignon' and all its derivatives share with most of the Moroccan weed and cultivated barleys proteins CMe-2,2′, which suggests the possible African origin of this variety, which is, in turn, a selection within an old French landrace from Ile de Re. This possible Moroccan origin of 'Hatif de Grignon' is in agreement with its known good adaptation to arid regions, particularly in Spain. Four out of five Spanish varieties share with 'Hatif de Grignon', 'Precoce Lepeuple' and 'Porthos', all of French origin, the allele CMb-2, which is also carried by the Moroccan *H. spontaneum* no. 8. This evidence favours the suggestion of the presumed Moroccan origin of 'Hatif de Grignon' and further supports the North African origin of the Spanish 6-rowed barleys (Wiebe 1968).

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