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Differentiation among barley landrace populations from the Near East

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Summary

The structure of variation in 67 barley landraces from Syria and Jordan was investigated by using various morphological and developmental traits measured on spike progenies from the landraces grown in a favorable environment in Syria. Factor analysis was used to identify trait complexes that accounted for major proportions of the total variation among landrace populations.

Subsequently, the landraces were clustered into nine distinct groups based on their similarity for all traits. Each group showed a close association to specific geographic or environmental factors, indicating that adaptive processes also are operating in current agricultural systems. These results show the usefulness of thoroughly describing the locations where germplasm accessions originate.

Finally, I investigated what proportion of the quantitative variation among landraces was due to differences in plant type. Populations were grouped according to their similarity for qualitatively inherited morphological traits. Subsequent analyses of variance on quantitatively inherited traits showed that this type of classification was as effective as geographic grouping in distributing the variance among and within groups. This result suggests that germplasm collections can be arranged according to either geographic information or morphologic similarity. Practical implications for agronomic evaluation and utilization of germplasm collections are discussed.

Introduction

The dissimilarities between populations of a plant species that originate from diverse environments reveal insight into the processes involved in adaptation and species differentiation (Briggs & Walters, 1984). Studies of adaptive traits of plants make the assumption that each plant population has been reproducing under environmental conditions within a geographical location long enough for selective processes to be effective.

However, this assumption cannot be made for agricultural crops in areas where transportation is readily available. Examining this situation in Syria revealed that farmers are generally very concerned about seed quality and prefer to buy seed from neighbors recognized for their farming skills if their own supplies are insufficient. Another factor con-

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tributing to the localized distribution of specific plant types is that farmers consider certain varieties more desirable for certain growing conditions and uses. Therefore, the primary objective of this study was to describe traits and groups of traits that differentiated landrace populations, and the second objective was to determine whether phenotypically similar populations originated from environments that were geographically, climatically, or edaphically similar.

The existence of such associations would help additional germplasm collection missions (Marshall & Brown, 1975) and in assembling representative samples of large germplasm collections (Brown, 1987). These smaller but representative samples of the total collection could be used to develop the core of a collection (Brown, 1987) to facilitate exploratory evaluation of complex traits and enhance utilization of germplasm collections. The development of such a core is based on the assumption that genetic variation in crop plants is structured along axes of geographic variation and degree of genetic relationship. Thus, a third objective was to examine whether phenotypic similarity for qualitative descriptor traits had predictive value for the variance distribution of quantitatively inherited and productivity-related traits among and within groups of landrace populations. The material used is particularly suited for such investigations because barley is a very old crop in Syria and Jordan, and the landraces have been evaluated under growing conditions resembling those at their sites of collection.

Materials and methods

Landrace Collection. Landraces of barley were collected in Syria and Jordan during harvest season 1981 by using methods developed by Marshall & Brown (1975). The 70 sampling sites were separated by at least 10 km, and 100 random spikes were collected at each site. Distance between sampling sites for individual spikes was ca. 1.5 m. The spikes collected at one site make up a population. Geographical locations of population sites and their groupings according to growing regions are shown in Fig. 1. Growing regions had ranges of mean annual rainfall between 160–550 mm, mean annual temperatures between 15.5 and 19.0° C, and variation in types of management practices (Table 1). The geographical coordinates for sampling sites and seed samples are available from the Genetic Resources Unit at the International Center for Agricultural Research for Dry Areas (ICARDA), Aleppo, Syria, and from the Bundesforschungsanstalt für Landwirtschaft (FAL), Braunschweig, Federal Republic of Germany (FRG).

Landrace evaluation. The barley accessions were grown in 1981/82 at ICARDA center at Tel Hadia, Syria, where the predominant soil type is a calcic luvisol. Planting was done during the week of 7–14 December in a field that had been fallowed in the two previous seasons. The rainfall of 338 mm approximated the long-term average of 342 mm (ICARDA, 1984). Temperatures were below average during the January-March growing season. Weeds were controlled by hoeing.

From each of 67 populations, 100 single-spike progenies were sown. For 34 populations, all spikes provided enough seed to plant 1-m rows, spaced 50 cm apart. For the remaining 33 populations, only 3–5 seeds per spike were available, so they were sown in hill plots spaced 50 cm apart in perpendicular directions. Every eleventh plot was sown to one of the two check cultivars, either ‘Badia’, an improved six-row cultivar used in ICARDA breeding nurseries or ‘Arabic abied’, a landrace population used as a Syrian national check. During the growing season, 12 traits were recorded on a plot basis (Table 2).

Analysis of variance. The analyses of variance, based on plot values, were computed on each trait by using the PROC NESTED procedure of SAS (1985), according to the linear model:

$$x_{ijk} = \mu + r_i + p_{ij} + e_{ijk}, \text{ where}$$

x_{ijk} : single plot observation
μ : overall mean
r_i : effect of the i^{th} group
p_{ij} : effect of the j^{th} population within the i^{th} group

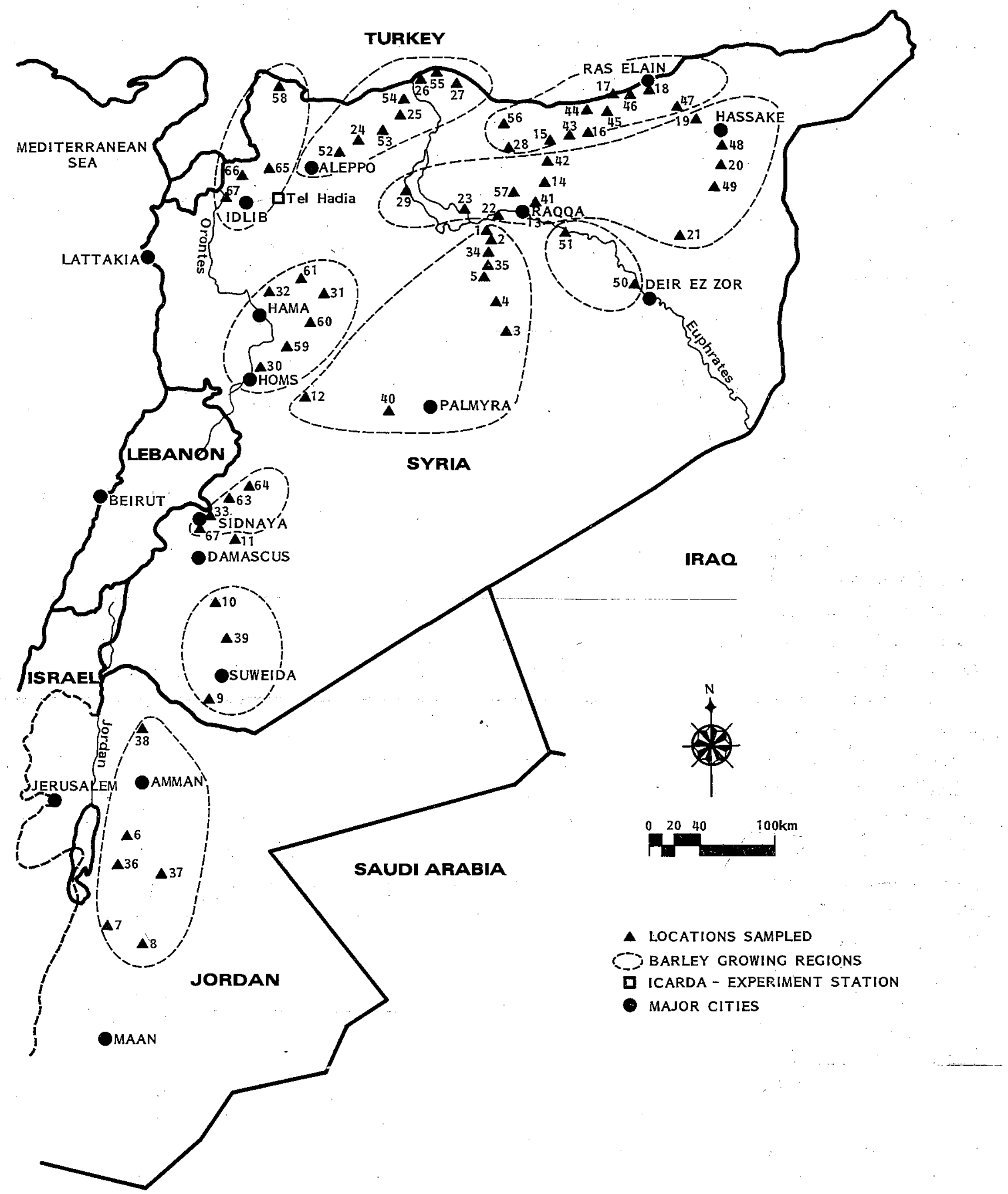

Fig. 1. Geographical origin of 67 barley landrace populations collected in Syria and Jordan and their grouping according to similarity in climate, soil, and crop husbandry.

e_{ijk} : deviation of single progeny value from population mean

Populations were grouped on the basis of their geographical origin, as well as by the results of the cluster analyses.

Cluster analysis. Cluster analyses were computed by using population means for all quantitative traits. For qualitative traits, the percentages of lines within a population that expressed certain character states were used. As a similarity measure, I used the correlation between populations calculated on the transposed data matrix after arcsin transformation was performed to make all values positive. Population means were clustered by the unweighted pair group method using arithmetic averages (UPGMA) as described by Sneath & Sokal (1973).

Table 1. Characterization of 10 barley-growing regions in Syria and Jordan; data collected from Brichaumbaut & Wallen (1963), Walter & Lieth (1961), FAO & UNESCO (1974), Keatinge et al. (1986) and ICARDA (1984)

Region	Mean annual rainfall (mm)	Mean temperature (°C)	Elevation above sea level (m)	Soil type, management practices
Jordan	160–400	19	800–900	Calcic Xerosols/calcic Luvisols, frequently late planting
Suweida	300–400	15.5	800–900	Vertic Cambisols, in rotation with wheat
Sidnaya	250–300	–	1300–1400	Chromic Luvisols, shallow, rocky soils; large variation in planting dates
Hama	250–350	16.5	400–500	Chromic Vertisol, in diverse rotations, high yield expectations
Idlib	450–550	17.2	500–750	Chromic Luvisol, in complex rotations, intense management
Aleppo	270–330	17.4	400–550	Calcic Livisol/Vertisol; in rotation with wheat and food legumes
Ras el Ain	230–330	18.5	300–420	Calcic Xerosol, gypsic Xerosols, barley monoculture, or in rotations with fallow
Raqqa	180–230	–	250–320	Calcic Xerosol, monoculture, frequent green stage and mature crop grazing
Palmyra	< 180	19.0	250–550	Gypsic Yermosol, frequent late season mature crop grazing
Deir ez Zor	120 + Irrig.	18.0	200	Gypsic Fluvisols, saline, irrigated

Table 2. Abbreviations, units of measurement, and scoring systems for traits on spike progeny rows from 67 barley landrace populations

Trait	Unit of measurement	Explanation
Growth habit (GH)	score	1 = erect (GHE), 2 = semi-erect (GHS), 3 = prostrate
Early growth vigor (EGV)	score	1 = much more vigorous than adjacent check cultivars 9 = much less vigorous than adjacent check cultivars
Days to heading (HD)	d	days after sowing
Mildew infestation (MIS)	score	1 = no symptoms observed 9 = heavy sporulation observed on the head and flag leaf (only on 33 populations)
Culm length (CL)	cm	rounded to the nearest 5 cm, average height from soil to head peduncle
Flag leaf width (FLW)	mm	measured on the widest part of the leaf of one random plant in 50 randomly chosen head rows per population
Width of penultimale leaf (PLW)	mm	measured on the widest part of the leaf on the same 50 rows that were measured for flag leaf width
Awn length (AL)	cm	measured on one randomly chosen plant in the same head row as the previous traits
Awn barbing (AB)	score	1 = smooth (ABS), 2 = semi-smooth (ABSS), 3 = rough
Seed color (SC)	score	1 = white (WS), 2 = non-white
Lodging susceptibility (LS)	score	1 = plot completely upright (90°) 9 = plot lying on ground (0°)
Kernel row number (R)	score	2 = 2-rowed (2R), 6 = 6-rowed

Factor analysis. Factor analyses were conducted on the correlation matrix. Diagonal elements were replaced by the squared multiple correlations of each trait with all other traits. The first three axes were rotated by applying the Varimax-option in the PROC FACTOR procedure of SAS (1985).

Results and discussion

Structure of the combined variation of all traits. Few of the correlations among the 13 traits measured on two-rowed spike progenies were significant, and even the significant ones rarely exceeded 0.60 (Table 3). The highest correlations occurred between the widths of the flag and penultimate leaves, the percentages of progenies with erect and semiprostrate growth habits, and plant height and lodging score.

The factor analysis showed that the first three factors accounted for 54, 28, and 10%, respectively, of the total variation among traits in the barley landrace populations. Because the fourth vector represented only 6% of the total variation, only the first three were used for further analyses.

The Varimax rotation of the three axes showed that the first factor was highly correlated with width of flag and penultimate leaves and all qualitative morphological traits (Table 4). A landrace with a high score for this factor had wide leaves and high frequencies of plants with erect growth habit at tillering, semismooth long awns, and white seeds. A high score for the second factor was highly correlated with tall plants, lodging susceptibility, earliness, and short awns. The importance of plant height and lodging score to this factor suggests that it is related to plant size. However, that days to heading is negatively correlated with the second factor suggests that this factor really is associated with a high rate of development rather than total plant size. The only trait significantly correlated with the third factor is early growth vigor: Thus, early growth vigor largely is independent of the other traits measured.

That the total variation and covariation among the 65 two-rowed barley landraces for 13 traits

Table 3. Phenotypic correlations among 13 traits measured on 65 two-rowed barley landrace populations from Syria and Jordan. On the diagonal are the squared multiple correlations of one trait with all other traits

	FLW[1]	PLW	HD	CL	LS	AL	EGV	% WS	% 2R	% ABS	% ABS	% GHE	% GHS
FLW	0.95	0.94**	–0.01	–0.20	–0.23	0.54**	–0.23	0.56**	–0.04	–0.58**	0.68**	0.67**	–0.70**
PLW		0.93	0.11	–0.21	–0.30	0.48**	–0.11**	0.45**	–0.00	–0.48**	0.59**	0.62**	–0.65**
HD			0.74	–0.64**	–0.73**	0.37**	0.45**	0.02	0.02	0.29	–0.24	0.07	–0.11
CL				0.73	0.75**	–0.61**	0.19	–0.49	–0.01	–0.10	–0.01	–0.39*	0.29
LS					0.81	–0.62**	–0.18	–0.38*	–0.04	–0.29	0.05	–0.32	0.28
AL						0.73	0.00	0.63**	0.07	–0.13	0.42**	0.45**	–0.46**
EGV							0.56	–0.27	–0.05	0.12	–0.27	0.09	–0.15
% SCW								0.74	–0.05	–0.36*	0.48**	0.62**	–0.51**
% 2R									0.16	0.03	0.18	–0.14	0.11
% ABS										0.66	–0.54**	–0.33*	0.43**
% ABSS											0.63	0.45**	–0.44**
% GHE												0.85	–0.86**
% GHS													0.81

[1] Abbreviations of traits are explained in Table 1.

* Significant at $P = 0.01$.

** Significant at $P = 0.001$.

could be reduced to three factors suggested several interesting features of these materials. Initially, note that the first factor was composed primarily of qualitative traits (Table 4), which are commonly used to describe barley plant types. Because factor 1 accounts for 54% of the total variation among the barley landraces, it has strong discriminatory power for these populations. My results confirm that these morphological and developmental traits are good descriptors for differentiating barley germplasm accessions, a conclusion that contradicts the results from Murphy & Witcombe (1981), who studied barley accessions from the Himalayan region. In their large study of a group of highly variable barley accessions, qualitative traits, including those I observed, contributed little to the first axis of origination, which is comparable to my first factor. Perhaps this discrepancy owes to the fact that Murphy & Witcombe (1981) studied many more quantitative traits than I did. Herein, nearly 40% of the generalized variance was contributed by qualitative traits.

The first factor also had significant positive contributions from leaf widths and awn length (Table 4). These traits are similar to qualitative traits in

Table 4. Correlations for various barley traits with the first three factors after Varimax-rotation. Traits were measured on 65 two-rowed barley landraces from Syria and Jordan

Trait	Factor 1	Factor 2	Factor 3
Flag leaf width	0.94*	−0.10	−0.08
Width of penultimale leaf	0.85*	−0.17	0.03
% Erect growth types	0.78*	−0.27	0.27
% Semi smooth awns	0.72*	0.10	−0.29
% White seeds	0.64*	−0.37	−0.34
% Smooth awns	−0.66*	−0.32	0.01
% Semiprostrate growth types	−0.80*	0.21	−0.29
Lodging score	−0.10	0.91*	0.00
Plant height	−0.16	0.84*	0.01
Awn length	0.49*	−0.64*	−0.22
Days to heading	−0.14	−0.78*	0.28
Early growth vigor	−0.17	−0.25	0.65*
% Two-rowed heads	−0.05	−0.04	−0.20

* Value greater than the root mean square of all the values in the matrix.

that they tend to have high heritabilities and, therefore, fit the concept that this factor denotes plant type. These three traits also can be interpreted as physiologic inasmuch as they are the major source of photosynthate during grain filling (Evans et al., 1975). In dry regions, they also are a major part of the transpirational surface area controlling water loss during this period of growth. The importance of this physiological complex for differentiating barley landraces also was found by Murphy & Witcombe (1981) for Himalayan barleys. In their study, the flag and penultimate leaf widths, spike and grain weights, and length were major contributions to the first axis of origination. Similarly, Spagnoletti-Zeuli & Qualset (1987) found that a combination of awn length, kernel number and weight per spike, and number of nodes per spike contributed greatly to differentiating among 26 groups of durum wheat accessions from the World Germplasm Collection. These results indicate that size and weight of the reproductive organs of the main shoot and the vegetative organs supporting them contribute substantially to the variation among germplasm accessions of small grains. In this study these differences appear to be closely associated with certain plant types.

Associations between plant types and geographical factors. The cluster analysis based on all traits revealed clear groupings of the 67 barley populations. Using a similarity value of 0.6 as the minimum requirement for cluster membership resulted in nine clusters.

Cluster 1 contained all landraces from Jordan and three populations from southern Syria (Fig. 1 and Table 5). Except for population 60, the locations where cluster 1 landraces were collected had high winter temperatures, high levels of irradiation, and highly variable planting dates in common. The landraces in this cluster were early and had large culms, long awns, high scores for early vigor, wide flag and penultimate leaves, white seeds, predominantly smooth awns, and erect growth habit at tillering (Table 5).

Cluster 2 had only two landraces, both of which originated from the Hauran region in southern Syrias. This region is climatically similar to Jordan,

Table 5. Composition of nine clusters formed on the basis of all traits, and their mean values for all plant traits

Cluster number	Predominant area of origin	Population numbers (Fig. 1)	FLW*	PLW	HD	CL	LS	AL	EGV	% WS	% 2R	% ABS	% ABS	% GHE	% GHS
I	Jordan, S. Syria	6, 7, 8, 36, 37, 38, 39, 60, 62	10.7	13.3	130.7	50.5	6.0	15.0	4.4	96.6	99.8	25.2	47.2	78.3	20.2
II	S. Syria	9, 10	10.8	14.2	132.8	45.4	5.4	14.9	3.6	93.3	100.0	42.2	49.7	44.8	50.1
III	Anti-Lebanon	11, 33, 63	9.8	12.8	135.2	43.6	4.8	14.5	4.9	99.3	100.0	27.4	3.1	67.0	31.6
IV	Northwestern Syria	30, 31, 32, 58, 59, 61, 64, 65, 66, 67	8.6	11.4	134.8	44.7	4.4	15.2	4.6	93.0	99.9	78.7	17.2	58.6	39.9
V	Northeastern Syria	13, 14, 16, 17, 20, 21, 23, 24, 25, 26, 27, 29	9.0	12.3	135.3	45.3	5.0	14.7	5.1	28.0	100.0	67.5	13.5	47.8	40.9
VI	Northeastern Syria	2, 15, 19, 28, 34, 35, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 52, 53, 54, 55, 56, 57	8.1	10.9	131.1	53.3	6.3	13.8	4.6	26.7	100.0	61.7	13.2	33.0	52.3
VII	Northeastern Syria	12, 18, 22	9.0	12.1	133.8	47.8	5.4	14.6	4.6	28.7	100.0	63.8	10.8	23.0	54.5
VIII	Euphrates River banks	50, 51	11.7	14.3	134.1	67.6	7.3	13.5	3.8	80.1	0.0	0.0	0.5	16.6	57.6
IX	Central Syrian Steppe	1, 3, 4, 5	9.0	12.2	133.9	50.0	5.6	13.7	5.1	18.5	99.2	71.3	5.9	58.2	31.8

* Abbreviations for traits are explained in Table 2.

but it has high soil fertility and adequate rainfall for high yields. The landraces in cluster 2 differ from those in cluster 1 in that their mean heading date was two days later, and they had shorter culms, better early growth vigor, and a higher percentage of smooth awns (Table 5).

In cluster 3, two populations from the Anti-Lebanon mountains north of Damascus were grouped together with a population from the foothills of these mountains. This region has cool temperatures throughout the growing season, winter snowfalls, shallow and rocky soils, and both fall and spring planting. The landraces had short culms, late heading dates, and a high percentage of rough awns.

Cluster 4 contained populations from west-central and northwestern Syria where barley is grown in marginally productive fields but with plentiful moisture. These barley populations had short culms, long awns, good lodging resistance, narrow leaves, and a high percentage of plants with smooth awns and erect growth habit.

Clusters 5 and 6, which contained the largest numbers of landraces, both covered the same broad area of northern and northeastern Syria, which is the major barley-growing area of this country. It has a complex land ownership system, and barley is grown in monoculture or in rotation with fallow and is grazed during early growth. Frequently, the mature crop is grazed by sheep if the plants are too short and the yields too low for mechanical harvest (Nordbloom, 1983). These two clusters of barley populations had higher than average percentages of dark seeds, smooth awns, and plants with prostrate growth habit, narrow leaves, ~~short awns, and average early growth~~ vigor. The clusters differed significantly in culm length, days to heading, and lodging resistance.

Cluster 7 had three populations that also originated in northern Syria. As would be expected, their characteristics were similar but intermediate to the landraces in clusters 5 and 6 for expression of the traits for which the previous two groups differ. They do have a lower percentage of plants with erect growth habit than populations in clusters 5 and 6.

Cluster 8 contained two populations that originated from the irrigated banks of the Euphrates River. They differed substantially from all other landraces. They were later in flowering, much taller, shorter awned, highly susceptible to lodging, and had six-rowed heads, good early growth vigor, rough awns, and mostly semiprostrate growth habit.

Cluster 9 contained populations that originated from the Syrian Steppe, where barley cultivation is infrequent and occurs in areas where rainwater collects. These landraces had long culms, short awns, narrow leaves, lodging subceptibility, and higher than average percentages of dark seeds and smooth awns.

These associations of clusters of similar barley populations with certain geographic regions that have dominating environmental factors support the view that 'geographic axis' of variation exist for indigenous plant materials (Brown, 1987). However, within the broad and somewhat variable area of northeastern Syria where barley is dominant, no clear associations of barley landraces with specific environmental factors were found. Several reasons could account for this lack of association. First, barley has been cultivated for a relatively short time in this area (Wirth, 1971). Second, frequently the seed produced there is of poor quality, so farmers import seed from neighboring areas or countries to sow next year's crop. Also, the complex land ownership system may discourage using locally produced seed.

The distribution of the nine clusters was examined graphically by plotting the landraces according to scores for factors 1 and 2 from the factor analysis (Fig. 2). Cluster 8, which contained the six-rowed populations from the Euphrates River bank, was excluded from this analysis. The populations from Jordan and southern Syria were clearly separated from other landraces by high scores for factor 1 (Fig. 2). These populations had a wide range of scores for factors 2, however. Clusters 4, 5, and 6, each of which contained many landraces, formed homogeneous groups with some overlap. Each of these clusters represented a narrow range of the total variation depicted when compared with the clusters from the south. Clusters 7 and 9 formed a link between clusters 5 and 6.

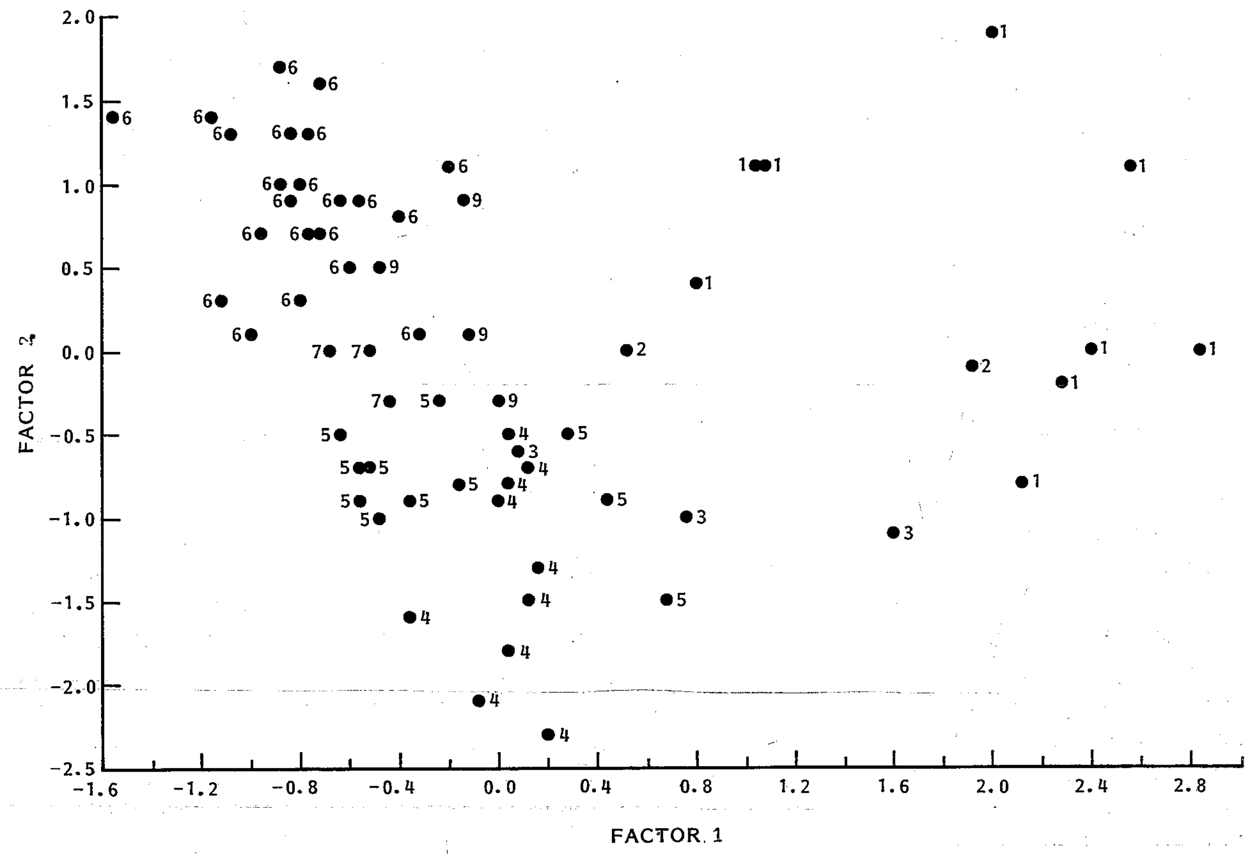

Fig. 2. Plot of the rotated (Varimax) factor-scores for 65 two-rowed barley landrace populations labeled with the number of the cluster they belong to; the clustering was based on all traits recorded (Table 4).

Therefore, it seems that these large clusters of populations from northeastern and eastern Syria form a continuous spectrum of variation along the second axis of variation, with predominantly low scores for factor 1. This suggests that factor 1, which represents differences in plant type, differentiates between landraces from northern and southern regions, whereas factor 2 differentiates between populations from eastern and western regions.

Phenotypic similarity and variance distribution. To examine the effect of grouping landrace populations based on morphological similarities (i.e., descriptor traits) on the distribution of the variance between and within groups for quantitatively inherited, productivity-related traits, I performed a second cluster analysis based solely on the qualitative traits (SC, AB, R, GH) and leaf widths (Table 2). It gave 10 groups of populations (Fig. 3) with correlations of r = 0.8, indicating a high level of homogeneity within each cluster.

When the clusters from this analysis were compared with those formed on the basis of all traits, the groups formed for the populations from Jordan and western Syria are very similar (Table 5 and Fig. 3). Populations from northwestern Syria were split in two groups by the second analysis, but they were closely related. Populations from the Euphrates River again formed a distinct group. The remaining populations from the northeastern parts of Syria were placed into five clusters by the second analysis, but there were no evident geographical associations for these clusters.

The grouping by the second analysis was used to examine the impact of this clustering on the varia-

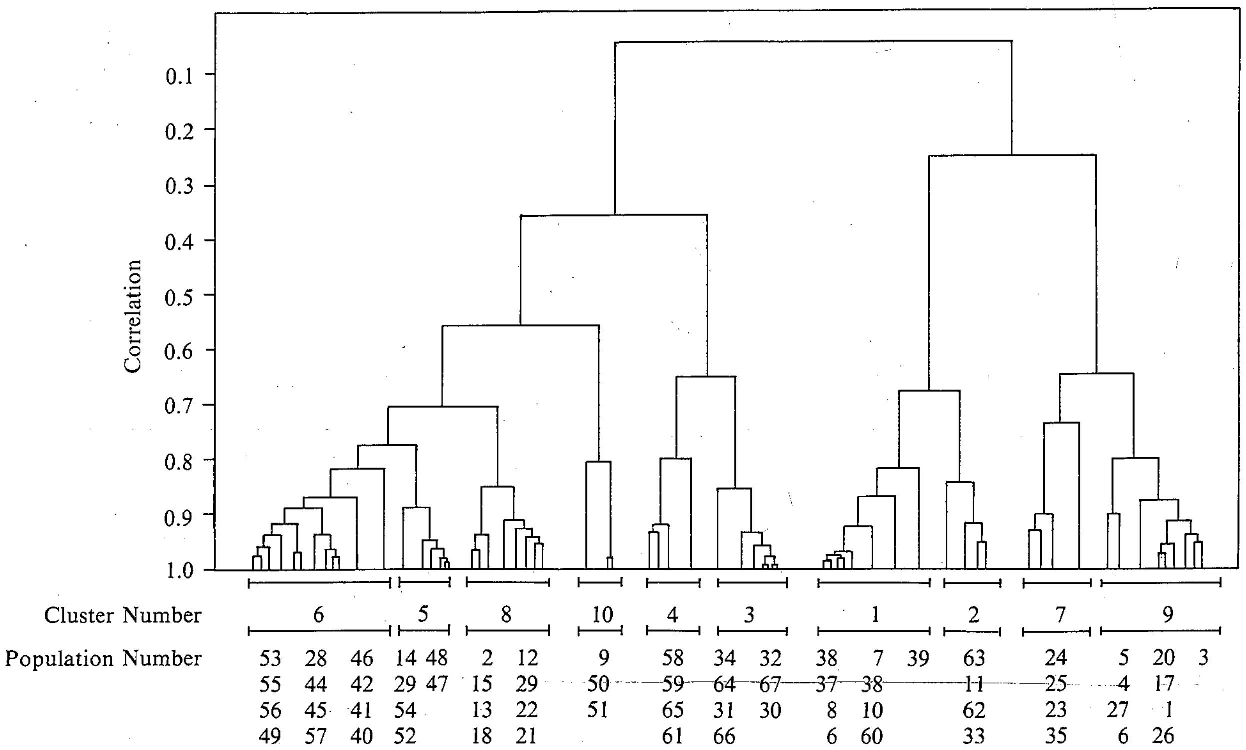

Fig. 3. Dendrogram of the similarities of 67 barley landrace populations, based on correlations using all qualitative traits, as well as the leaf widths

nce distribution of the remaining traits. The clustering based on morphological traits was as effective as the grouping solely by geographic regions (Table 6), when comparing traits not used for clustering (HD, CL, LS, AL, EGV) (Fig. 1). In both cases, about one-third of the variation among populations was assignable to differences among the groups.

Both approaches to grouping landraces (i.e., geographical similarity of the collection sites and morphological similarity of the landraces) appeared to structure the variation of quantitatively inherited traits and could, therefore, be used for choosing accessions to form a core sample. Evidently, the clustering based on the similarity of all traits and representing all three axes of variation was still more effective in structuring the phenotypic variation (Table 6). The various methods for grouping were tested further for how they distributed the variance of the mildew infestation score (MIS), which was not used in the multivariate analysis. Using overall similarity gave better differentiation for the mildew reaction trait than did the clustering based on morphological traits, which represented only the first axis of variation. However, the grouping based solely on geographical origins of populations gave the best differentiation among groups for the mildew reaction trait. These comparisons demonstrate the importance of compiling good geographical descriptions of areas where germplasm accessions are collected. Additionally, descriptive traits are useful for subclassifying accessions within a germplasm collection. My results suggest that the grouping of populations gives the best differentiation when it is based on traits that represent more than one major axis of variation for a collection.

Table 6. Distribution of quantitative variation among and within groups of populations formed by different criteria, in percent of the total variation among populations

Traits	Total variance among populations	Grouping based on geographic information		Grouping based on cluster analysis of morphological traits		Grouping based on cluster analysis of all traits	
		among	within	among	within	among	within
FLW	1.28	40.7	59.3	82.9	17.1	82.82	17.18
PLW	1.45	38.0	62.0	81.9	18.1	73.92	20.63
HD	4.96	15.6	84.4	26.7	73.3	66.75	26.08
CL	28.36	38.0	62.0	36.7	63.1	79.37	24.20
LS	0.74	22.0	78.0	48.3	51.7	75.80	33.25
AL	0.55	50.0	50.0	40.5	59.5	62.52	37.48
EGV	0.35	11.1	88.9	13.8	86.2	23.69	76.31
MIS	0.61	79.8	20.2	55.4	44.6	70.91	29.09

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