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IBPGR morphological descriptors – their relevance in determining patterns within a diverse spring barley germplasm collection

R. J. Cross[1], A. G. Fautrier[2], and D. L. McNeil[2]

[1] Curator and Project Leader, N.Z. Crop Germplasm Centre, DSIR Crop Research, Private Bag, Christchurch, New Zealand
[2] Plant Science Department, Lincoln University, Canterbury, New Zealand

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Summary. The International Board for Plant Genetic Resources (IBPGR) promotes a minimum set of morphological characters thought satisfactory for the custodial management of crop germplasm collections. The purpose of such conserved germplasm is as a genetic resource for future plant breeding programmes. Because future plant breeding requirements are not always known, the curator's strategy in maintaining an adequate germplasm resource is to conserve as wide a range of genetic diversity as possible. How is diversity measured to ensure a wide range of conserved germplasm? The IBPGR minimum descriptors detail genetic diversity at particular points in a genome corresponding to the observed characters. The purpose of the present study was to investigate whether diversity as identified by the IBPGR minimum set of descriptors could yield satisfactory measures of diversity in a contrasting set of genomic markers. A diverse spring-sown barley collection of 1379 cultivars was evaluated for the 12 IBPGR minimum taxonomic characters. An additional nine phenotypic characters and six biochemical markers were evaluated to enable diversity comparisons. Cluster analysis of the various sets of data revealed groups of accessions for each of the three data sets. A poor level of agreement (congruence) between data sets was observed in all comparisons indicating that, for cultivated barley at least, diverse collections according to the IBPGR minimum descriptors is not necessarily related to equivalent levels of diversity in other genetic characters. Implications of the relevance of the IBPGR descriptor list and appropriate collection strategies are discussed.

Correspondence to: R. J. Cross

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Introduction

There is little doubt over the concept of genetic diversity being concentrated in certain geographical locations. However, the problem of locating the most appropriate and diverse geographical areas for particular genetic traits remains. The pioneering work of Vavilov clearly showed that variation of simply inherited, phenotypically obvious traits was confined to a relatively few restricted areas and led to the concept of centres of diversity being nominated as the place of origin of cultivated plants (Vavilov 1949–50; Zohary 1970). The International Board for Plant Genetic Resources (IBPGR) priorities (Williams 1988) for the collection of economically important food crops are firmly based on these Vavilovian concepts, and plant collection has concentrated on those geographical areas exhibiting high levels of diversity of simply inherited, phenotypically obvious traits.

However, using a wider range of both simply and complexly inherited traits, several systematic studies of world germplasm collections have cast doubt over the 'traditional' or Vavilovian concepts of clearly defined centres of diversity. Surveys of world germplasm collections and herbaria records have shown that not all centres of diversity represent centres of origin (e.g., Harlan 1971; Jones 1983). Generally, multiple centres of diversity for a particular crop species may arise through (1) human migration dispersing the cultivated crop species away from its centre of origin, as is the case with *Phaseolus vulgaris* dispersed among the Americas

(Gepts et al. 1988) and ranging from South America to Europe and East Africa (Martin and Wayne-Adams 1987a, b; Gepts and Bliss 1988), with new diverse forms arising through hybridisation (Martin and Wayne-Adams 1987b). *Triticum durum* provides a comparable case involving hybridisation (Asins and Carbonell 1989), (2) mutation (e.g., *Phytolacca dodecandra*: Adams et al. 1989), and/or (3) introgression with wild species (e.g., cassava: Nassar 1978) followed by selection for locally adapted types (Harlan 1961; Harlan and Zohary 1966; Martin and Wayne-Adams 1987b).

The IBPGR promotes the collection and description of plant germplasm; therefore, recommendations made on plant description should also reflect the range of natural diversity within the species. Currently, the IBPGR provide internationally recognised descriptor lists (Erskine and Williams 1980) which cover most of the important crop genera. These descriptor lists follow a similar pattern (Chapman 1989; Cross 1990). For each descriptor list, custodians of collections are encouraged to score the 'characterization and preliminary evaluation' sections as the minimum description for any given germplasm accession. Therefore, the problem for any set of germplasm accessions is whether the 'minimum' evaluation reflects a similar level of diversity in other genetic characters.

The objective of this study was to establish the level of agreement between the morphological and biochemical patterns of diversity using cultivated barley as the experimental organism. All experiments were conducted on the same group of individuals (the DSIR Crop Research world barley collection) and, therefore, the common denominator to both the morphological and biochemical evaluations was the individual accession. As a working hypothesis, it was assumed that, because the genetics of the individual has not changed, the systematic evaluation of genetically determined characters from the morphological and biochemical studies would ultimately agree. Congruence between the morphological and biochemical studies would then indicate that the underlying pattern of species diversity has been identified. Lack of agreement between the two studies would indicate either that the theoretical (e.g., characters chosen were under poor genetic control), the existence of procedural (e.g., sampling error) problems in one or both of the analyses, or else that additional data was needed to resolve the true underlying relationship between individuals. As an alternative to this working hypothesis, there may be no relationship between the groups of characters used in the comparison.

Materials and methods

Three sets of evaluations were scored on 1379 individual genebank accessions from the DSIR Crop Research world cultivated barley collection. The first comprised the 12 phenotypic markers recommended by the IBPGR (IBPGR 1982) as the 'minimum' required for the description of an individual cultivated barley genebank accession. The second evaluation set included an 'additional' nine morphological characters, and the third set was composed of six seed-storage protein (hordein) and leaf esterase isozyme 'biochemical' markers. These 27 descriptors are summarised in Table 1; details of the character states within each descriptor have been published previously (IBPGR 1982; Cross 1990, 1992).

Table 1. IBPGR 'minimum' (1.1–1.12), 'additional' (2.1–2.9) and 'biochemical' (3.1–3.6) descriptors used in the discrimination between individual genebank accessions

1.1 Growth class	1.10 Kernel covering	2.7 Test weight
1.2 Plant height	1.11 Lemma colour	2.8 Brown rust resistance
1.3 Heading	1.12 Grain colour	2.9 Purple auricle
1.4 Row number	2.1 Growth habit	3.1 Hor 1
1.5 Spike density	2.2 Awn colour	3.2 Hor 2
1.6 Spikelet number	2.3 Glume colour	3.3 Hor 3
1.7 Hoodedness	2.4 Stem colour	3.4 Est 2
1.8 Awn roughness	2.5 Head Shape	3.5 Est 4
1.9 Rachilla hairs	2.6 Seed weight	3.6 Est 5

The level of agreement between the three data sets was based on a comparison of the placement of individual genebank accessions to various groupings following cluster analysis. Comparisons were made at the 20-cluster level. This level was chosen because subsequent higher-order clusters were being partitioned at a level of sensitivity greater than the range of categorical character states within individual descriptors (Cross 1990). Cluster analysis for the three data sets was calculated using the multivariate statistical package PATN (Belbin 1989). Differences between pairs of individual accessions was an overall dissimilarity measure (Canberra metric) based on the presence/absence of character states across all descriptors. These dissimilarity indices, calculated between all possible pairs of accessions, were subjected to an agglomerative fusion of groups using the group average linkage (UPGMA) fusion strategy (Belbin 1989; Peeters and Martinelli 1989).

Congruence between clusters was measured by the level of agreement between individual clusters identified by the IBPGR minimum data set and clusters identified by the biochemical data set. The common demoninator to all clusters was the accession number and, therefore, the level of agreement between the two data sets was achieved by identifying the highest proportion of accession numbers held in common between clusters. Because interest was in the ability of the IBPGR minimum data set to predict pattern in alternative evaluations (e.g., biochemical), the calculation of the proportion of accessions in common between the two data sets was expressed as a percentage of the IBPGR minimum data set.

Results

The proportion of accessions in common between cluster comparisons is given in Tables 2, 3 and 4 for the 'IBPGR minimum-IBPGR minimum plus additional', 'IBPGR minimum-biochemical', and 'IBPGR minimum plus additional-biochemical' data-set comparisons respectively.

Table 2. Congruence of clusters – proportion of accessions in common between the 'IBPGR minimum' and 'IBPGR minimum plus additional' clusters, expressed as a percentage of the total number of accessions within each IBPGR minimum cluster

Minimum plus additional clusters (%)	IBPGR minimum clusters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	42.9	28.0	.	.	5.6	0.9	1.6	.	23.1	.	.	.	.	.	.	.	.	.	.	.
2	21.4	64.0	.	.	.	0.9	.	.	9.4	.	.	.	.	.	.	.	.	.	.	.
3	35.7	8.0	100.0	100.0	94.4	.	0.3	.	31.9	.	.	.	.	.	.	.	.	.	.	.
4	.	.	.	.	.	37.5	1.4	1.7	1.8	.	.	.	.	.	.	.	.	.	.	.
5	.	.	.	.	.	8.0	1.1	0.6	18.2	.	.	.	.	.	.	.	.	.	.	.
6	.	.	.	.	.	46.4	9.3	5.8	4.6	.	.	.	.	14.3	1.9	.	.	.	.	.
7	.	.	.	.	.	.	.	.	5.2	.	.	.	.	.	.	.	.	.	.	.
8	.	.	.	.	.	.	.	15.0	3.0	.	.	.	.	.	.	.	.	.	.	.
9	.	.	.	.	.	.	0.8	21.4	0.6	.	.	.	.	.	.	.	.	.	.	.
10	.	.	.	.	.	.	0.3	13.9	.	.	.	.	.	.	.	.	.	.	.	.
11	.	.	.	.	.	.	.	12.7	.	.	.	.	.	.	1.9	2.0	.	.	.	.
12	.	.	.	.	.	.	8.2	0.6	.	.	.	15.4	13.0	.	5.6	.	.	.	13.6	6.2
13	.	.	.	.	.	.	5.5	.	.	.	.	20.5	26.1	35.7	5.6	21.6	40.0	33.3	.	.
14	.	.	.	.	.	0.9	7.4	5.2	.	.	.	18.0	21.7	43.0	63.0	66.7	55.0	44.4	.	.
15	.	.	.	.	.	.	3.8	1.2	0.3	.	.	23.1	.	.	.	.	.	.	.	50.0
16	.	.	.	.	.	0.9	14.2	8.1	.	.	.	7.7	17.4	7.1	22.2	5.9	5.0	22.2	.	6.3
17	.	.	.	.	.	0.9	10.6	0.6	.	6.1	.	.	21.7	.	.	.	.	.	.	.
18	.	.	.	.	.	0.9	11.4	1.7	1.8	93.9	100.0	15.4	.	.	.	3.9	.	.	86.4	37.5
19	.	.	.	.	.	1.8	14.2	4.6	.	.	.	.	.	.	.	.	.	.	.	.
20	.	.	.	.	.	0.9	10.1	6.9	.	.	.	.	.	.	.	.	.	.	.	.

Table 3. Congruence of clusters – proportion of accessions in common between the 'IBPGR minimum' and 'Biochemical' clusters, expressed as a percentage of the total number of accessions within each biochemical cluster

Biochemical clusters (%)	IBPGR minimum clusters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	7.1	16.0	9.1	.	5.6	0.9	0.3	.	3.6	.	.	.	.	.	.	.	.	.	.	.
2	.	4.0	.	13.2	.	1.8	0.5	.	3.0	.	.	2.6	.	.	.	.	.	.	4.5	.
3	7.1	.	.	6.7	.	23.2	18.5	50.9	8.8	15.2	16.0	12.8	4.3	.	7.4	9.8	5.0	5.6	9.1	12.5
4	21.5	20.0	9.1	6.7	5.6	11.6	10.1	4.5	15.5	18.2	20.0	12.8	8.8	.	3.7	7.8	.	5.6	9.1	18.7
5	14.3	8.0	27.3	6.7	11.0	7.1	27.2	16.2	15.5	18.2	20.0	12.8	39.1	42.9	24.1	29.4	15.0	22.2	4.5	18.7
6	.	.	.	.	.	0.9	1.6	.	.	.	8.0	.	.	.	.	.	.	.	4.5	.
7	.	8.0	.	.	.	12.5	12.8	8.1	11.6	9.1	12.0	15.4	17.4	28.7	22.2	21.6	25.0	16.7	22.7	6.3
8	.	.	.	.	.	.	0.8	.	.	.	.	7.7	8.8	7.1	.	.	.	11.1	.	.
9	7.1	.	9.1	.	5.6	0.9	2.5	0.6	0.7	6.0	.	2.6	.	.	7.4	.	.	.	.	.
10	14.3	8.0	.	13.2	16.7	0.9	0.8	0.6	5.2	.	.	2.6	.	.	.	.	.	.	.	.
11	21.5	8.0	27.3	26.7	16.7	33.0	15.3	11.6	14.6	18.2	12.0	7.7	13.0	7.1	16.7	21.6	30.0	11.1	27.3	43.8
12	7.1	4.0	.	6.7	11.0	.	0.3	.	0.7	.	.	2.6	.	.	3.7	.	5.0	.	.	.
13	.	.	.	.	5.6	1.8	0.5	.	.	.	.	.	4.3	.	7.4	.	.	5.6	4.5	.
14	.	8.0	.	.	.	.	0.3	0.6	1.5	.	.	2.6	.	7.1	.	2.0	5.0	5.6	.	.
15	.	8.0	9.1	6.7	5.6	0.9	0.3	0.6	2.1	.	.	.	.	.	.	.	.	.	.	.
16	.	.	.	.	.	0.9	1.6	.	.	3.1	.	7.7	4.3	.	.	3.9	5.0	11.1	.	.
17	.	.	.	.	.	.	1.4	4.5	0.9	.	.	2.6	.	.	.	.	.	.	9.1	.
18	.	.	9.1	6.7	11.0	2.7	0.8	.	5.8	.	.	.	.	.	3.7	.	5.0	.	.	.
19	.	4.0	.	6.7	5.6	.	1.4	0.6	6.5	6.0	8.0	.	.	.	.	.	.	5.6	4.5	.
20	.	4.0	.	.	.	0.9	3.0	1.2	4.0	6.0	4.0	7.7	.	7.1	3.7	3.9	5.0	.	.	.

For the 'IBPGR minimum-IBPGR minimum plus additional' data-set comparison (Table 2), there was no consistent trend of accession numbers belonging to individual clusters in the IBPGR minimum data set in common with accessions of individual clusters in the IBPGR minimum plus additional data set. On average, 80% of the accessions belonging to an individual IBPGR minimum cluster were spread over three clusters in the IBPGR minimum plus additional data set. The most 'diffuse' intersection between data-set clusters was among

Table 4. Congruence of clusters – proportion of accessions in common between the 'IBPGR minimum plus additional' and 'Biochemical' clusters, expressed as a percentage of the total number of accessions within each IBPGR minimum cluster

Biochemical clusters (%)	IBPGR minimum plus additional clusters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	7.2	9.8	1.9	5.3	4.1	.	.	.	.	.	.	.	.	.	.	.	.	.	1.6	.
2	3.1	.	5.1	.	4.1	1.8	.	.	.	.	.	2.1	1.5	.	.	.	.	0.7	.	.
3	5.2	.	1.9	28.6	8.0	22.8	29.4	52.8	76.2	60.0	8.3	21.3	3.0	7.0	23.5	16.7	6.3	17.0	14.5	64.0
4	13.4	19.6	9.6	1.8	9.5	19.3	58.8	11.1	4.8	4.0	4.2	2.1	1.5	10.6	17.6	3.1	14.6	17.0	4.8	8.0
5	16.5	17.6	14.7	8.9	16.2	11.4	.	8.3	11.8	4.0	37.5	17.0	20.9	22.5	23.5	33.3	39.6	17.7	43.5	12.0
6	.	.	.	.	1.4	0.9	.	.	.	.	.	.	7.5	.	.	.	2.1	2.1	.	.
7	11.4	3.9	7.7	14.3	18.9	12.3	.	11.1	2.4	4.0	25.0	17.0	16.4	23.2	5.9	12.5	20.8	12.1	9.7	.
8	.	.	.	.	.	.	.	.	.	.	.	2.1	11.8	0.7	.	1.0	.	.	.	.
9	1.0	.	1.9	.	1.4	.	.	.	.	.	.	6.3	3.0	1.4	2.9	2.1	4.2	2.1	4.8	.
10	7.2	5.9	10.9	3.6	.	1.8	.	.	.	.	.	.	.	0.7	.	.	.	.	.	.
11	22.7	17.6	14.1	37.5	16.2	21.1	.	11.1	4.8	4.0	20.8	12.8	14.9	18.3	14.7	19.8	8.3	18.4	14.5	12.0
12	1.0	2.0	3.3	.	.	.	.	.	.	.	.	4.3	.	1.4	.	1.0	.	.	.	.
13	.	.	0.6	.	.	1.8	.	.	.	.	.	.	4.5	2.1	.	1.0	2.1	0.7	.	.
14	.	.	2.6	.	4.1	0.9	.	.	.	.	.	.	4.5	0.7	2.9	.	.	0.7	.	.
15	1.0	3.9	4.5	.	4.1	.	.	2.8	.	.	.	.	.	.	.	.	.	.	1.6	.
16	.	.	.	.	.	.	.	.	.	.	.	6.4	3.0	4.2	.	3.1	.	2.1	.	.
17	1.0	.	.	.	.	.	11.8	.	.	24.0	.	.	.	.	2.9	4.2	.	2.8	.	2.0
18	3.1	2.0	10.3	.	8.0	1.8	.	.	.	.	.	2.1	.	1.4	2.9	.	.	.	.	.
19	5.2	2.0	9.6	.	2.7	1.8	.	2.8	.	.	.	.	1.5	.	.	.	.	4.3	4.8	.
20	1.0	15.7	1.3	.	1.4	2.6	.	.	.	.	4.2	6.4	6.0	5.6	2.9	2.1	2.1	2.1	.	2.0

IBPGR minimum cluster numbers 6, 7, 8 and 9 which were spread over 11, 16, 15 and 11 clusters respectively of the IBPGR minimum plus additional data set.

Congruence between 'IBPGR minimum and biochemical' data sets was very poor (Table 3). Accession numbers within an individual cluster as identified by the IBPGR minimum data set were in all cases spread over many clusters of the biochemical data set. On average, 80% of the accessions identified in an individual IBPGR minimum cluster were spread over six clusters in the biochemical data set. The most extreme example of lack of congruence was with 'IBPGR minimum cluster number 7', where the accession numbers identified by that cluster were spread over the entire range of biochemical clusters.

A modest 'improvement' of congruence between morphological and biochemical clusters was achieved with the 'IBPGR minimum plus additional-biochemical' data-set comparison (Table 4). On average, 80% of the accessions identified in an individual 'IBPGR minimum plus additional' cluster were spread over five biochemical clusters.

Discussion

For germplasm collections the impartial description of the genome is important in ensuring that the sampling of individuals represents the range of a species' natural diversity. The IBPGR minimum descriptors are just one particular set of genetic markers among numerous possible alternative genome descriptions, representing a consensus arrived at by a crop-specific panel of experts convened by the IBPGR. The descriptor lists are a collection of phenotypically obvious genetic markers that are characterized by factors of low cost of evaluation, ease of scoring, and relatively simple inheritance. It is likely, therefore, that the IBPGR minimum descriptors are designed as the first step in discriminating among individuals and, by implication, provide a method of establishing comprehensive germplasm collections. A major objective of the current study was to test if the IBPGR minimum descriptor pattern of diversity could predict clusters of accessions useful for other genetic characteristics.

If the IBPGR minimum data set could detect the true species pattern of diversity, then the IBPGR minimum descriptors pattern of diversity would not be significantly altered by the addition of more data, involving either (1) data of 'similar' type (the nine additional morphological descriptors, Table 2) or (2) data of relatively dissimilar type (biochemical descriptors, Table 3). The current study showed that the pattern of diversity according to the IBPGR minimum data set had little resemblance to either option. A third cluster contrast, between the 'IBPGR minimum plus additional' and 'biochemical' data sets also confirmed the lack of congruence between data sets (Table 4).

Lack of congruence could only have arisen from either (1) theoretical problems (2) procedural problems or (3) more data being required to resolve the underlying relationship of species pattern. 'Theoretical problems'

with the lack of congruence between clusters should have been minimal since all characters used in the current study were formally recognised genetic markers under relatively simple genetic control. However, pleiotropic effects are possible between some of the descriptors. For example, pleiotropy between some of the morphological and esterase markers would have, to some extent, distorted the independence among character states and, therefore, biased the distribution of pattern within the data-set comparisons. However, the correlation between variables was not great (Cross 1990) and thus lack of congruence due to poor choice of appropriate descriptors is unlikely. 'Procedural' problems, such as sampling error, is also an unlikely explanation for the lack of congruence between data sets because all experiments were based on the same group of individual accessions, and results from the individual experiments were highly repeatable (Cross 1990). The possibility of 'not enough data' being responsible for the lack of congruence seems unlikely too as the DSIR collection contained 1379 accessions which according to the various descriptors used, included a large proportion of unique phenotypes (Cross 1992). Each of the 1379 accessions was scored for 29 descriptors, yielding 40,000 data points for the various statistical analyses. Therefore, on the basis of a large proportion of unique phenotypes and a large number of data points, the detection of trends within the data-set comparisons should have been possible.

Even so, the lack of congruence remains. It may be unreasonable to consider diversity in terms of a few (12 IPBGR, 21 'IPBGR plus additional') genetic markers. From a conceptual point of view, the diversity of one set of genetic probes across the genome (e.g., morphological) was considered to sample a similar pattern of diversity compared to an alternative set of probes (e.g., biochemical). These sets of genetic markers are known to be located in different parts of the genome (Cross 1990) and, because evolutionary forces act differently on particular sections of the genome, the different sets of markers should reflect different patterns of diversity. Therefore, lack of congruence between the morphological, quantitative and biochemical patterns of diversity could be due to differing diversity patterns within the genome itself. Thus, is unreasonable to expect the IBPGR minimum barley descriptor list, or any minor modification of it, to be used as a basis for the formulation of comprehensive collections.

Other studies

The lack of congruence observed in the current study has also been noted in other surveys of world crop collections. For example:

(1) A distinct altitudal cline was observed among 27 morphological characters in teosinte (Smith et al. 1981), among seven morphological characters in cultivated Ethiopian barleys (Negassa 1985), and among eight quantitative spike characters in wheat (Bogyo et al. 1980).

(2) A distinct latitudinal cline was observed among eight physiological growth stages in bilberry (Vanninen et al. 1988), and among 23 isozyme loci between Northern Flint and Southern Dent races of maize grown in the USA (Doebley et al. 1988).

(3) Major geographical differences have been observed outside the traditional Vavilovian centres of origin. For example, major differences were detected between world regions and continents among 29 phenotypic characters of okra (Martin et al. 1981), among eight quantitative spike characters in durum wheat (Spagnoletti-Zeuli and Qualset, 1987), and among 19 isozyme loci in *Cucumis sativus* (Knerr et al. 1989). Peeters (1988) found a distinct geographical trend among 19 quantitative characters in cultivated barley, which was in contrast to Tolbert et al. (1979) who observed only negligible geographical differences between world regions in a study of five morphological characters in a world collection of that same species.

(4) Cultural practices are also known to have significant effects on the observed pattern of a species diversity, such as the flooding tolerance of East Asian barley (Takeda and Fukuyama 1989), of characters relating to reproductive fitness and heading time (e.g., durum wheat: Spagnoletti-Zeuli et al. 1985; lentil: Erskine et al. 1989) and of daylength sensitivity incorporated into winter-sown early maturing crops as a mechanism to avoid summer drought (e.g., barley: Ceccarelli 1987).

Only a few authors have considered combinations of qualitative, quantitative and/or biochemical evaluations of world germplasm collections. As with the current study, these surveys failed to confirm similar patterns of diversity according to combinations of these character traits. For example, lack of congruence between qualitative and quantitative evaluation were noted in safflower (Wu and Jain 1977), barley (Jaradat et al. 1987), and in wheat and barley landraces from Nepal and the Yemen Arab Republic (Damania et al. 1985). There was also no congruence of patterns of diversity between quantitative and biochemical evaluations in pearl millet (Tostain and Marchais 1989). However, a variable level of congruence has been observed between patterns of diversity for qualitative and biochemical characters. For example, good agreement between patterns was observed among six isozymes and qualitative (Vavilovian) genetic markers in a world collection of chickpea (Tuwafe et al. 1988), and among six isozymes in 14 commercial cultivars of *Cucurbito pepo* (Decker 1985). Partial agreement between patterns of diversity of ecological, morphological and electrophoretic traits was observed in *Quinua* (Wilson 1988) but there was no agreement between patterns of qualitative and biochemical traits in cucumber (Knerr et al. 1989) or pearl millet (Tostain

and Marchais 1989). Esquinas-Alcazar (1981) noted negligible morphological difference within populations of *Lycosperiscon pimpinellifolium* but these same populations showed a large amount of electrophoretic isozyme variation. Finally, many diseases and insects are location-specific and, through co-evolution, have lead to a diverse range of plant genetic resistances in response to an ever-changing pathogen (Allard 1988, 1990). Therefore, high levels of diversity for resistance to insects and diseases are known to occur in these specific 'hot spot' (Plucknett et al. 1987) locations. For example, numerous diverse forms of genetic resistance to foliar diseases in wheat and barley have been found in Ethiopia (Qualset and Schaller 1969; Qualset 1975; Negassa 1985) and amongst wild barley populations in Israel (Nevo et al. 1979).

The apparent divergence of these systematic surveys when compared to the Vavilovian centres of origin have been discussed extensively by Murphy and Witcome (1981) and Cross (1990). These authors consider that under domestication highly heritable qualitative characters, such as those identified by Vavilov, will be less affected by natural selection than quantitative characters that are linked to survival and productivity. Allard and co-workers studied changes in allelic frequencies within a bulk population over 60 generations, and concurred with the idea that evolutionary processes in genetically variable populations are highly effective in increasing the frequency of alleles conferring environmentally fit genotypes (Allard 1988, 1990). Quite different patterns of allelic diversity would, therefore, be expected to emerge according to the different selective advantages operating on various characters within the genome.

Future direction

Two issues emerge from this study. Firstly, from the numerous divergent surveys of crop diversity it is clear that concentrating on traditional Vavilovian centres of diversity is not an efficient collection strategy. Secondly, no one evaluation method can reliably predict overall species pattern, or indeed pattern according to some other contrasting set of genomic traits. The problem of determining the most efficient collection and characterization strategy remains. Collection could be extended beyond the Vavilovian centres to include a broad range of geographical sites as well as particular ecological niches such as those of disease 'hot spots', a range of daylength environments, and of temperature and/or humidity extremes. Once these geographical and ecological niches are sampled then, for evaluation purposes, sets of accessions ('gene pools': Anon 1988; Singh 1989) could be developed based on ecological similarities, with a sub-classification within each group that may include factors such as geographical origin. A revised IBPGR minimum descriptor list (Cross 1992) could then be applied to detect the relative distribution of clusters of individuals, with identification of 'gaps' and the construction of a comprehensive collection of phenotypic types within each 'ecological germplasm pool'. By having a clearly defined ecological type, breeders may be more willing to screen germplasm collections for useful traits in the knowledge that the accessions under test are already of a nominated type and so give the breeders an increased chance of finding the desired genotype.

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