

The emergence of new centres of diversity: evidence from barley

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Summary. Statistical analyses of data from a large barley germplasm collection of worldwide origins revealed that material from the USA now contains more variability in toto than material from any other country. In addition trends of overall diversity for other countries suggest that there is little association between high overall variability and what are considered as traditional “centres of origin” or “centres of diversity” for this crop. The five countries of highest overall diversity worldwide were found to be (in descending order): USA, Turkey, Japan, USSR and China. Cluster analyses revealed that relatedness of germplasm was by far strongest between certain European countries, which were also in general of a more intermediate diversity level. The data presented here suggests that the variability present in gene pools still varies substantially by country but according to patterns which appear different from those described previously.

Key words: Germplasm – Variability – Gene pools – Countries

Introduction

A long standing concept concerning crop plants is that genetic diversity is more prevalent in certain countries or geographical centres than in others. This concept became fully established through the work of Vavilov (1926). The concept of “centres of origin” and more particularly of “centres of diversity” has helped stimulate concern about genetic erosion since it was felt that diversity was being lost fastest in the countries in which it was most abundant (Harlan and Martini 1936; Harlan 1975). However, concern for these losses has not been limited to those countries rich in native diversity. It was felt that the

adoption worldwide by farmers of modern cultivars, which are genetically more uniform than traditional landraces, was having devastating effects to reduce diversity not only in developing but in developed countries as well (NAS 1972).

While there is clear evidence that, at the species level, there has been a dramatic increase in the rates of extinction (Myers 1979; Frankel and Soule 1981), the global picture for the major crops is far from being as clear-cut. Recent evidence suggests that the overall levels of variation within some countries have increased (Cox et al. 1986). This was confirmed by two recent surveys of breeders which, in addition, showed that breeders often find most of the required variability within advanced breeding lines (Duvick 1984; Peeters and Galwey 1988). These results suggest that major changes may have taken place in the past few decades in the reserves of variability available to breeders worldwide.

The cause of these changes is simple to define. Perhaps due primarily to the stimulating effects of the concepts proposed by Vavilov, germplasm has since been extensively collected and exchanged worldwide, and at an accelerating pace (Plucknett et al. 1983). Since these exchanges are generally associated with breeding efforts, but also that efforts have varied in intensity between individual countries, gradual shifts in world patterns of diversity are not difficult to forecast and the formation of new “centres” out of the old ones can be postulated. This explains perhaps why the Vavilovian concepts have constantly been modified and have led Harlan to conclude in 1971: “I am prepared to question even the fundamental concept of ‘centers’ as a universal phenomenon”.

A global reassessment of the situation would presently be useful. Particularly it would be important to determine what the levels of variability worldwide by country now are and to determine what the implications are for

the future. These are the aims of this paper which compares the overall distribution of variability presently existing by country gene pool for one of the major crops. It is based on barley evaluation data which were assembled over 20 years on approximately 5,000 accessions of worldwide origins.

Materials and methods

The data of the barley germplasm collection of the AFRC at the Institute of Plant Science Research (formerly the Plant Breeding Institute or PBI), Cambridge, UK were selected for the analysis. The collection had its origins in the 1930s as a working collection which was gradually increased in size over the years. It includes material from vastly different sources such as germplasm from some of the recent collecting missions. The available data on the samples represented field and laboratory evaluation work for entries of the collection which was carried out at the Institute from 1966–1986. Each datum represented the average of observations taken over three years.

The question of origin

For the purpose of these analyses, all entries whose origin was unknown were deleted. Origin was defined as country where bred and/or first released in the case of hybrids or country where collected in the case of landraces. A large proportion of hybrids in this collection were known to have been developed within given countries and were obtained from institutes of that country. Old cultivars were generally classified as landraces. Since material was usually obtained from different sources within a country "origin" was taken in its widest sense and represented a sample of the gene pool available to breeders of that country. This gene pool was composed in part or in full of landraces, breeders' lines and commercial cultivars. Because of the scale of the analyses, no attempt was made here to exploit further than at the country level the data on origin.

Statistical procedures

The statistical analyses, which were all done on the Cambridge University 3084 Q IBM mainframe, were mainly based on programmes written in GENSTAT, although ALGOL 68, BCPL, FORTRAN and SPSSX were also used. The following protocol was used.

In order to avoid any bias in the analyses from redundant entries, possible duplicates were first identified by exact matching of ratings across all evaluated traits and any potential duplicate was deleted. The reduced matrix, with entries with uniquely different ratings, contained over 100,000 observations each averaged over 3 years. Twelve qualitative and 18 quantitative traits were selected for the analyses.

Since not all entries were evaluated for the same characters, the proportion of entries evaluated per country across all characters was calculated and found to be similar. This confirmed the fact that entries were not evaluated in any particular order and that comparative analyses could be done between material on a country basis. Analyses requiring strictly comparative ratings were done by first generating matrices in which each entry had been fully evaluated for all the selected traits.

Tests were subsequently made to determine whether country of origin was the most appropriate separator for groups of entries. Both multivariate techniques and simple tests, such as ANOVA, or differences in Spearman's rank correlations (r_s) of quantitative traits between the total sample of neighbouring countries were used.

To assess overall country variability, the Shannon-Weaver Index or $H' = -\sum p_i \log(p_i)$ was chosen to describe variation for qualitative traits (p_i is the proportion of the total number of entries in the i^{th} class) (Shannon and Weaver 1949). For computations of H' zeros, when present, were replaced by 0.001 which was found to have little weight in the calculations. Standard deviations were taken to assess the level of variation present for quantitative traits. The appropriate parameter was then calculated for each trait and in each country. Subsequently, overall country means over all traits were calculated for both parameters and these in turn were used to calculate average country ranks. Rank, therefore, was a relative measure of total country diversity.

Another approach was used to assess the variability of the germplasm by country. The number of unique classes of observations (or character combinations) found in a randomly drawn sample of accessions can be calculated and it can be determined how this number changes as entries are added to the sample. When this is done on a country basis, the resulting curves allow a comparison of how rapidly overall variation initially increases with sample size and at what level it starts levelling off. Hence, not only can the total level of variation be estimated by country sample but a comparison is possible on which particular sample generates the fastest a given level of variation.

Approximately one half of the collection (2,472 entries) was analysed by cluster analysis (centroid method). The purpose of this analysis was to assess precisely the degree of relatedness between individual entries and ultimately between and within countries. In order to make the analyses feasible in terms of computing, a program was first written to separate entries in random groups on the basis of origin and such that only entries which had been evaluated for exactly the same traits were pooled together. As a result, 27 individual cluster analyses were done and were summarized by counting, according to their origin, the number of highly related pairs of entries ($\geq 95\%$ similarity).

Distances between countries overall were estimated by Canonical Variate Analysis which, in this case, was done on a matrix of 2,423 accessions originating from 32 countries and all evaluated for a selected group of 10 quantitative traits. Results were plotted in a three-dimensional stereoscopic plot, calculated from the country means of the first three canonical variates.

Results

Partition of variation by country of origin

Spearman's rank correlations for quantitative characters by country of origin showed that country samples were uniquely different. Individual correlations were calculated across all 18 quantitative characters for the overall matrix (all countries) as well as in the gene pools of 11 countries represented by at least 100 accessions. The strongest associations which were found per trait and per country in these 12 individual analyses are summarized in Table 1. Very different and sometimes fully opposite correlations were found. Large differences were also found even between neighbouring countries with a similar proportion of hybrid material. Because of this, correlations between two given traits overall (across all countries) were in general much weaker than within any given country. The strongest association was found in Spanish

Table 1. Strongest associations for quantitative characters including disease resistances overall and for selected countries^a

Character	Identifier	Correlation	Country	N	r_s	r_s overall
Ear droop	1	1 × 4	Japan	130	0.5699*	0.1770*
Flag droop at ear emergence	2	2 × 13	USA	239	0.5845*	0.0497*
Juvenile erectness	3	3 × 12	Overall	901	0.5349*	0.5349*
Thousand grain weight	4	4 × 7	Japan	132	0.6624*	0.3592*
Seed length	5	5 × 4	Japan	117	0.6526*	0.3642*
Ears per plant	6	6 × 12	USA	36	0.5586*	0.2970*
Nodes per ear	7	7 × 4	Afghanistan	58	0.6761*	0.3592*
Ear density	8	8 × 7	Ethiopia	468	0.6333*	0.4787*
Awn length	9	9 × 4	Afghanistan	91	0.6792*	0.3357*
Peduncle-length	10	10 × 4	Afghanistan	43	0.6062*	0.0085*
Straw length	11	11 × 7	S. Africa	195	0.5663*	-0.1420*
Frost susceptibility	12	12 × 13	Overall	825	-0.5702*	-0.5702*
Lodging susceptibility	13	13 × 1	W. Germany	115	-0.5130*	-0.2297*
<i>Erysiphe graminis</i> resis.	14	14 × 2	Afghanistan	43	-0.5345*	0.1332*
<i>Puccinia hordei</i> resis.	15	15 × 16	Spain	116	0.6866*	0.3271*
<i>Puccinia striiformis</i> resis.	16	16 × 7	Ethiopia	44	0.5631*	-0.1807*
<i>Rhynchosporium secalis</i> resis.	17	17 × 3	Netherlands	56	0.6443*	0.3282*
Alpha amylase activity	18					
All correlations < ±0.5000						

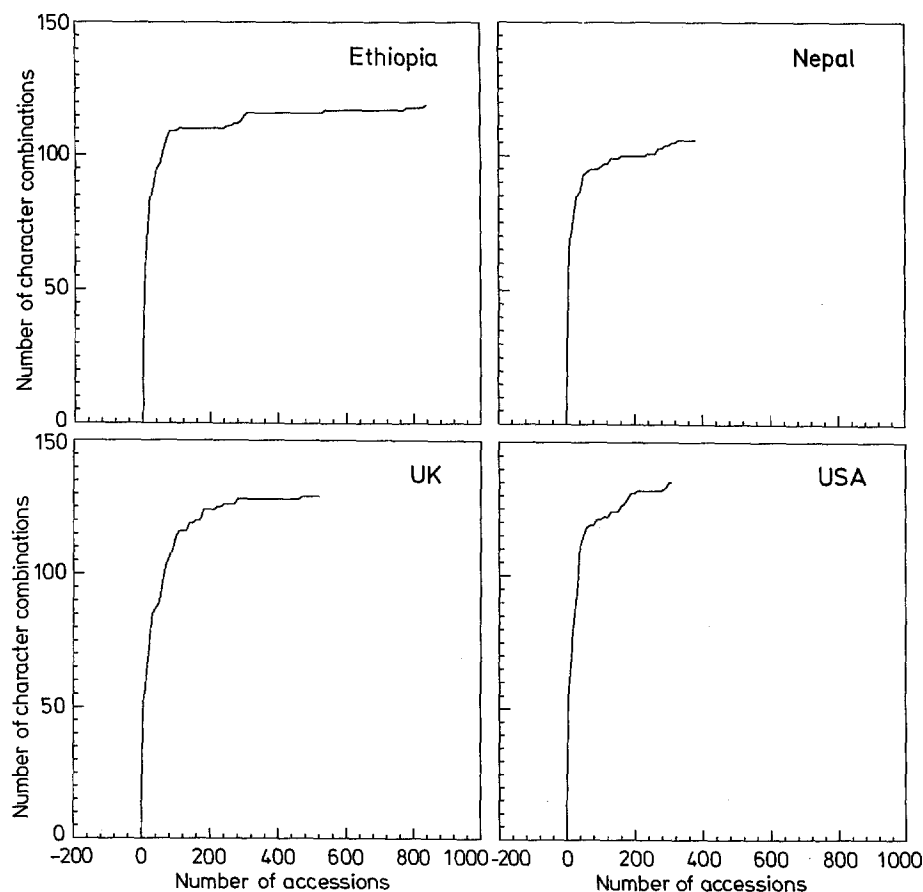
^a On the basis of Spearman's rank correlations and with $N \geq 30$ * $P < 0.001$ **Fig. 1.** Increase in new character combinations with sample size for accessions from four different countries (calculated for increments of 10 randomly selected accessions)

Table 2. Countries sorted by decreasing mean diversity of their germplasm across all characters^a

Country	N	Per-centage evalu-ated ^b	Aver-age rank ^c	Status ^d		
				% UN	% LA	% HY
USA	306	84	2.5	21	1	42
Turkey	63	86	5.5	27	67	5
Japan	140	84	6.0	32	9	52
USSR	90	81	6.5	43	39	14
China	29	86	9.0	90	7	0
West Germany	128	84	9.0	25	6	67
France	85	76	9.5	16	1	76
Yugoslavia	17	88	10.0	76	6	18
Belgium	20	85	11.0	55	0	35
Italy	13	85	11.5	100	0	0
India	23	78	13.5	61	17	9
Poland	11	91	14.0	45	0	36
UK	520	76	14.0	14	7	63
Argentina	13	92	15.5	46	15	0
Israel	12	92	16.0	17	42	25
Afghanistan	104	84	18.5	0	100	0
Canada	70	86	18.5	7	0	53
Ethiopia	837	70	18.5	0	100	0
Tibet	46	87	18.5	0	100	0
Hungary	12	92	20.0	58	8	25
Iran	22	77	23.0	82	18	0
Sweden	79	82	23.0	15	5	62
Korea Republic	17	88	24.5	53	29	18
Pakistan	417	50	24.5	3	97	0
Austria	20	85	26.5	40	10	25
Finland	12	92	26.5	17	0	75
Netherlands	109	80	26.5	18	2	73
Denmark	60	82	31.5	13	2	60
Nepal	375	78	32.5	0	100	0
Norway	15	87	35.0	27	27	40
South Africa	205	81	36.0	5	0	87
Australia	19	79	36.5	11	16	63
Czechoslovakia	12	92	36.5	17	8	67
Morocco	18	89	45.5	39	61	0
Spain	116	85	45.5	1	99	0

^a For observations taken on 30 characters (18 quantitative and 12 qualitative with $N \geq 10$)

^b Per entry and across all 30 individual characters

^c Over 62 countries (for calculation method see text)

^d Status:

% UN = proportion of germplasm of unknown origin

% LA = proportion of germplasm of landrace origin

% HY = proportion of germplasm of hybrid origin

(remaining % = special stocks such as mutants, etc.)

germplasm between resistance to *Puccinia hordei* and *Puccinia striiformis* ($r_s = 0.6866$). The fact that variation was strongly partitioned by origin was confirmed by an ANOVA (not shown) and by multivariate statistics (see below).

Variability by country gene pool

Results assessing total variability by country gene pool based on both qualitative and quantitative characters are

presented in Table 2. In the process of carrying out these analyses, it was noted that the mean diversities both for qualitative and quantitative traits were substantially lower overall than on a per trait basis and that, if the diversity index was maximal for a given trait in the material from a given country, it was often minimal for another trait in the same material. Hence, it appeared that high variability is difficult to achieve across all characters, whatever the origin of the germplasm. Yet clear differences between countries were found and the results showed that total variation present in the gene pool of the US was in fact the highest among all the countries investigated. Furthermore some of the countries which had been described either as putative "centres of origin" (e.g. Israel or Iran; Nevo et al. 1986) or "centres of diversity" (e.g. Ethiopia; Qualset 1975) had in fact lower levels of overall diversity than was observed in material from the USA.

The number of character combinations per randomly drawn sample and by origin were calculated for four countries which perhaps have been most often described in the analyses of barley samples. Results are shown in Fig. 1. This figure shows that substantially less variation is obtained from drawing for example a random sample from Nepal than from the USA, whether at the asymptote or below. A precise comparison is provided in Table 3 which mainly confirms the results obtained in Table 2. Table 3 shows that a breeder is most likely to find a needed character in material originating from the USA gene pool.

These assessments show that countries like the USA and the USSR have accumulated a very diverse germplasm base. This country diversity was not associated either with a high proportion of landrace or hybrid material in the collection and was substantially different by country of origin although variability was often high. In this collection the US material, which originated from different sources within the country, is composed of at least 40% of varieties or breeders' stocks. The proportion of hybrid material for some of the countries is indicated in Table 2.

Results from multivariate tests

Distances between countries were estimated by Canonical Variate Analysis (Pielou 1977). Results (in a three-dimensional stereoscopic plot) are shown in Fig. 2, and show a prominent grouping of European countries (for country codes see Table 4) in particular between the UK, Netherlands, France, West Germany, Sweden, Denmark and Hungary. Other groupings appear to fall mainly according to similar climatological zoning but the results show an extremely close overall proximity between the germplasm of the USSR and the USA (overlapping points).

Table 3. Number of unique character combinations observed in the germplasm from different countries and in comparison with material from the USA^a

Country	Total	Unique observations	Proportion of the overall variation	Proportion of the USA variation ^b
USA	306	135	0.94	1.00
USSR	90	118	0.82	0.97
West Germany	128	118	0.82	0.95
U.K.	520	129	0.90	0.94
Turkey	63	110	0.76	0.93
Japan	140	115	0.80	0.93
France	85	111	0.77	0.92
Afghanistan	104	111	0.77	0.92
Canada	70	105	0.73	0.88
Netherlands	109	105	0.73	0.86
Ethiopia	837	119	0.83	0.85
Sweden	79	101	0.70	0.85
Tibet	46	94	0.65	0.83
Denmark	60	98	0.68	0.83
Nepal	375	106	0.74	0.77
Pakistan	417	96	0.67	0.70
South Africa	205	88	0.61	0.67
Spain	116	81	0.56	0.66
Overall	4,304	144	1.00	

^a For $N \geq 40$ accessions

^b Calculated for the total number of entries of each country and by comparison with the same number of randomly sampled entries from the USA; for countries with a total number of entries larger than the number of entries from the USA, 300 randomly sampled entries of the two countries were taken and compared

Results from the cluster analyses are summarized in Table 4. This table shows that extremely high relatedness between country material occurs only between some European countries in particular between the Netherlands and the UK. Table 2 also shows that these countries were of a more intermediate diversity level. Such relatedness, which is well established in European germplasm (Linde-Laursen et al. 1987), is bound to have been the result of extensive exchanges of the same advanced lines between European breeders and here the results show that, at a very high level of relatedness between individual entries, not a single bond was found between the germplasm of the USSR and the USA. Table 4 also shows that entries of some countries are highly related with each other (for example South Africa) and therefore it is not surprising that the germplasm of such countries is also of a lower overall level of diversity (Tables 2 and 3). Other countries in which the diversity was exceptionally low were Spain, Australia and Morocco, although the latter was recently claimed to be another "centre of domestication" for barley (Molina-Cano et al. 1987). Israel and Morocco were also recently reported to be of low diversity for wheat, although in a smaller analysis, but which also confirmed the overall relatedness between the germplasm of the USA and USSR (Spagnoletti Zeuli and Qualset 1987).

Discussion

Collecting missions and subsequent exchanges of germplasm have had profound effects on the distribution of

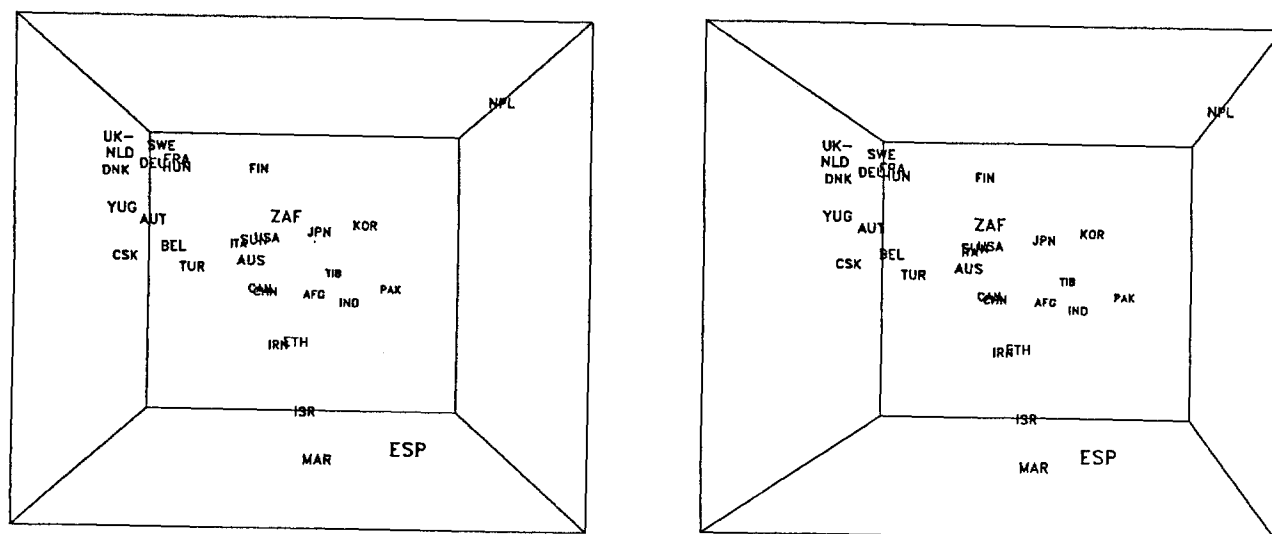


Fig. 2. Three dimensional stereoscopic plot of country positions

Table 4. Observed bondings between highly related accessions by geographical origin in 27 cluster analyses representing 2,472 entries (centroid method)

Country	Code	Total entries	Number of country bondings ^a
Afghanistan	AFG	48	AFG (6); IRN (1); TUR (1)
Argentina	ARG	10	ZAF (1)
Australia	AUS	8	AUS (1)
Austria	AUT	16	AUT (2); HUN (2); NOR (2); USA (1)
Belgium	BEL	8	BEL (1); SWE (1); UK (2); USA (3)
Bulgaria	BGR	6	POL (1)
Bolivia	BOL	1	
Canada	CAN	34	CAN (1); TUR (1)
Chile	CHL	1	
China	CHN	17	CHN (1); KOR (1); TIB (1)
Colombia	COL	1	
Crete	CRT	4	
Czechoslovakia	CSK	8	DDR (1); DNK (1); FRA (2); NLD (2); SWE (2); UK (3); USA (1); YUG (1)
East Germany	DDR	8	DDR (1); FRA (10); NLD (11); SWE (2); UK (43); YUG (2)
West Germany	DEU	52	DEU (4); ITA (1); NLD (1); SUN (1); SWE (1); UK (5)
Denmark	DNK	38	DDR (1); DNK (6); FRA (1); JPN (1); NLD (6); SWE (2); UK (11); USA (1)
Algeria	DZA	2	
Egypt	EGY	5	
Spain	ESP	97	ESP (23)
Ethiopia	ETH	510	EGY (6); ETH (289)
Finland	FIN	9	
France	FRA	43	FRA (7); NLD (15); SWE (2); UK (67); YUG (1)
United Kingdom	UK-	308	NLD (82); SWE (18); UK (172); USA (3); YUG (3); ZAF (2)
Greece	GRC	4	
Hungary	HUN	10	IRL (1); NOR (1); POL (1)
India	IND	14	IND (3)
Ireland (Eire)	IRL	4	
Iran	IRN	12	IRN (1); POL (1); TUR (1)
Iceland	ISL	2	TUR (1)
Israel	ISR	8	
Italy	ITA	10	
Jordan	JOR	1	
Japan	JPN	102	JPN (22); KOR (1); NLD (1); TUR (1)
Korea Republic	KOR	11	
Libya	LBY	1	
Manchuria	MAN	2	USA (1)
Morocco	MAR	14	MAR (4); ZAF (3)
Mexico	MEX	6	
Nigeria	NGA	1	
Netherlands	NLD	67	NLD (27); SWE (7); YUG (1)
Norway	NOR	11	NOR (2)
Nepal	NPL	215	NPL (119)
New Zealand	NZL	1	
Pakistan	PAK	222	PAK (288)
Peru	PER	2	
Poland	POL	6	
Portugal	PRT	3	
Romania	ROM	4	
Saudi Arabia	SAU	1	
Sudan	SDN	1	
USSR	SUN	36	SUN (1)
Sweden	SWE	53	SWE (3); USA (3); YUG (1)
Tibet	TIB	22	
Turkey	TUR	31	TUR (6)
Uruguay	URY	2	ZAF (1)
USA	USA	171	USA (14)
Yugoslavia	YUG	7	
South Africa	ZAF	181	ZAF (346)

^a Single pairs or multiple bondings within or between countries and with similarity $\geq 95\%$ (all pair bondings indicated only once, e.g. AFG-IRN noted only under Afghanistan)

variation by country. New “centres of diversity” have been created. These are the gene pools of given countries which are composed of breeders’ lines and cultivars developed within the country. Despite the exchanges of germplasm which have taken place worldwide, variation in these pools has remained highly partitioned by geographical origin and the degrees of overall variation by country have remained substantially different. Large countries, in particular the USA and the USSR, have accumulated an extremely diverse overall germplasm base. For example 94% of the total observed variation of the whole collection (in terms of unique characters combinations) was found in only 306 accessions from the USA (Table 3). The origin of this variability is probably best accounted for by the germplasm introductions which took place in the US from substantially different ecological and geographical sources (Harlan 1984). A similar historical basis of germplasm introductions, together with the needs to breed for ecologically variable conditions, could also explain the extremely high overall diversity levels found in material from the USSR, Japan and China. The very high level of diversity present in these countries generally appears to have been overlooked.

Core collections of variability

Since degrees of variation were found to change substantially from one country to the other and simultaneously that correlations between characters were also found to have remained strongly divided by geographical origin, a distinction between variability per se and quality of the variation is needed. Countries of very low variation nevertheless contain combinations of characters not prevalent elsewhere. An example is germplasm from Spain which was found to be among the least variable but also contained some of the strongest correlations between characters (Tables 1–3). These results confirm the importance of passport data in the management of diversity from germplasm collections (Peeters and Williams 1984).

Passport data should be particularly useful in assembling sub-collections which contain a representative sample of the diversity of the whole collection. These subsets or “core” collections were first proposed by Frankel (1984) and would have clear advantages in future work with germplasm collections. They would enable curators of gene banks to provide breeders with a representative sample of the available diversity of their collections in which the chances of finding a needed trait would be optimized. In this study it was found that large numbers were not required to achieve this end. Recently Brown (1988) has suggested core samples size of 3,000 entries on the basis of sampling theory. This number was found here to be a realistic one. For the reasons given above, sampling for such cores should be done primarily on the basis of origin.

Conclusions

Despite extensive collecting of germplasm and its subsequent exchange between countries, combinations of characters have remained substantially different in germplasm by country gene pool. Therefore, the best strategy for conservation purposes as well as breeding is to continue to keep material from as many different geographical sources as possible. Germplasm introduction programs have been highly successful in broadening the germplasm basis of a number of countries at and beyond the levels of variation present in any other single country previously known to have very high levels of native variability. Since a large number of gene banks have now been created and that these have further stimulated exchange programmes and the distribution of germplasm (Plucknett et al. 1987), the overall variability basis in cereals worldwide may become even wider in the future.

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