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Geographical trends within a diverse spring barley collection as identified by agro/morphological and electrophoretic data

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Abstract For ex-situ germplasm conservation purposes, the concept of genetic diversity being concentrated in certain geographic regions is useful for the conscious selection of diverse forms. Numerous studies of barley and other major corp species often confirm the concentration of simply-inherited, phenotypically-obvious markers within the Vavilovian centres of diversity/origin. However, more recent studies of electrophoretic patterns and or more complexly-inherited traits do not always confirm the same geographic patterns. Unfortunately, few studies of world germplasm collections have screened a range of agro/morphological/electrophoretic patterns using the same germplasm collection as a consistent base for evaluation purposes, making precise genetic estimates of diverse geographic areas difficult. A diverse collection of 1 118 spring-sown barley cultivars was, therefore, evaluated for both agro/morphological and biochemical genetic markers in an effort to identify appropriate criteria for the construction of a comprehensive ex-situ germplasm collection. On the basis of both agro/morphological and biochemical data, countries whose cultivated barley germplasm was identified as diverse and genetically distinct were Algeria, Afghanistan, Argentina, Ethiopia, India, Peru and Turkey. However, within broad limits, separate cluster analyses of the agro-morphological and electrophoretic patterns identified dissimilar groups of countries, which demonstrated that a collection strategy based solely on country of origin is inappropriate.

Key words Hordein · Esterase · Morphology · Barley · Genetic resources · Geographical distribution

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Introduction

Vavilovian concepts of conspicuous, highly-heritable characters being concentrated in certain geographic regions of the world are firmly entrenched in disciplines such as field-crop conservation biology. However, as world collections are evaluated for more complexly-inherited characters, it has become apparent that quantitative characters may not follow the same geographic patterns of diversity as for qualitative characters. These divergent studies have been reported across many crop genera including barley (Negassa 1985; Peeters 1988), bread and durum wheat (Bogyo et al. 1980; Spagnoletti-Zeuli and Qualset 1987), maize (Doebley et al. 1988), okra (Martin et al. 1981), and lentil (Erskine et al. 1989). However, few studies of world collections use the same germplasm collection as a consistent base for evaluation purposes, and may distort true underlying relationships of geographic patterns of diversity between quantitative and qualitative characters. The current study used a world collection of 1 118 spring-sown barley cultivars to detect trends of geographic diversity between 21 agro/morphological and six biochemical genetic markers.

Materials and methods

The plant material used in this study was the spring-sown barley (*Hordeum vulgare* L.) collection of the Crop & Food Research Institute for which geographical data was known. Details of field plot management, choice of the 21 agro/morphological, biochemical descriptors and their associated characters states have been reported previously (Cross 1992). Because many individual countries were represented by few accessions, neighbour or near neighbouring countries with few accessions were pooled to form a reduced set of 25 country groupings (Table 1). This reduced set was the basis of all multivariate comparisons. Because the agro/morphological variables were sometimes correlated (Cross 1992), the Mahalanobis distance was chosen over the Euclidean distance (e.g. Jardat et al. 1987), and for the biochemical data, heterogeneity estimates (Nei and Roychoudhury 1974) and Nei's genetic distance (Nei 1972) were between all paired country comparisons. Both the agro/morphologi-

Table 1 Frequency of barley accessions by country of origin

Country groupings	Number of accessions	Frequency (%)
Afghanistan (AFG), Iran	15	1.3
Algeria (DZA), Libya, Tunisia, Egypt	25	2.2
Argentina(ARG)	14	1.3
Australia (AUS), South Africa	104	9.3
Austria (AUT), Switzerland	21	1.9
Canada (CAN)	40	3.6
China (CHN)	22	2.0
Czechslovakia (CSK), Hungary	14	1.3
Denmark (DNK)	44	3.9
Ethiopia (ETH)	242	21.6
France (FRA)	31	2.8
Germany (DEU), Belgium	84	7.5
India (IND)	17	1.5
Italy (ITA), Greece, Yugoslavia	11	1.0
Japan (JPN), Korea	19	1.7
Morocco (MAR), Portugal, Spain	20	1.8
Nepal (NPL), Pakistan	10	0.9
Netherlands (NLD)	36	3.2
New Zealand (NZL)	18	1.6
Peru (PER), Bolivia, Chile	16	1.4
Sweden (SWE), Finland, Norway	38	3.4
Turkey (TUR), Cyprus, Syria, Jordan	18	1.6
Ukraine (UKR)	29	2.6
United Kingdom (GBR), Ireland	51	4.6
United States of America (USA)	179	16.0
Total	1118	100.0

cal (Mahalanobis distance) and biochemical (Nei's genetic distance) comparisons were subjected to cluster analysis using the average linkage (UPGMA) clustering strategy and associated dendrogram (Belbin 1989).

Results

Agro/morphological descriptors

Geographical distribution of the 21 agro/morphological descriptors and their associated character states are given in Table 2, from which several general trends were noted. Firstly, no individual country had an inverse phenotypic contrast among any of the 21 descriptors. Secondly, simply-inherited phenotypically-obvious descriptors (Cross 1992) were "concentrated" only in part in countries of the "Fertile Crescent" (AFG, NPL, TUR)[1] and, on average, were not dissimilar from the remaining countries. Thirdly, an Oriental/Occidental geographic cline was noted for some specific character states, with the short-awn character largely confined to countries of East Asia (Hoodedness descriptor-character state #3), and hooded varieties (either sessile or elevated hoods) confined to Nepal (Hoodedness descriptor-character states #1,2). There was an abnormally-high proportion of short-haired rachilla varieties in Ethiopia, whereas most of the naked forms of barley were found in the Orient and the converse with covered barleys in the Occidental regions. For kernel-row number, there was a general geographic distribution of 6-row

Table 2 Geographic distribution (%) of 21 agro/morphological descriptors and their associated character states (refer Cross 1992 for descriptor-character state descriptions)

Country of origin	Growth class			Height score			Heading			Kernel row number			Spike density			Spikelet group			Hoodedness score				
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	4	5
AFG	7	–	93	53	47	–	67	13	20	53	47	7	7	80	13	53	40	7	–	–	–	100	–
ARG	–	7	93	29	21	80	71	21	8	93	7	–	21	79	–	64	36	–	–	–	–	100	–
AUS	1	6	93	34	42	24	71	27	2	62	34	5	27	52	21	53	31	16	2	–	–	98	–
AUT	–	24	76	10	33	57	38	57	5	62	33	5	10	71	19	29	38	33	–	–	–	100	–
CAN	–	15	85	10	33	58	23	75	3	68	32	–	20	40	40	10	70	20	5	3	3	91	–
CHN	–	5	95	18	36	46	68	27	5	91	9	–	23	50	27	55	41	5	–	–	14	86	–
CSK	–	–	100	14	50	36	36	64	–	14	64	21	14	57	29	7	64	29	–	–	–	100	–
DEU	1	21	78	4	55	41	49	48	3	38	55	7	22	51	27	5	43	52	1	1	1	97	–
DNK	–	48	52	9	59	32	7	93	–	16	77	7	21	52	27	5	46	50	2	2	–	96	–
DZA	–	8	92	12	32	56	32	60	8	80	20	–	8	72	20	36	56	8	–	–	–	100	–
ETH	–	10	90	9	56	35	28	57	15	58	24	18	28	56	16	21	75	4	1	–	–	99	–
FRA	3	29	68	7	61	32	26	71	3	23	65	13	23	64	13	16	39	45	–	–	–	100	–
IND	–	6	94	71	11	18	88	6	6	59	29	12	6	59	35	47	53	–	–	–	–	100	–
ITA	–	–	100	27	73	–	73	27	–	91	9	–	18	46	36	64	36	36	–	–	–	100	–
JPN	–	16	84	37	37	26	63	37	–	53	47	–	16	37	47	42	37	21	–	–	5	95	–
MAR	–	–	100	50	30	20	80	20	–	80	20	–	50	20	30	55	40	5	–	–	–	100	–
NLD	–	19	81	–	75	25	6	94	–	3	84	14	11	61	25	3	53	44	–	–	–	100	–
NZL	–	28	72	17	61	22	17	78	6	11	89	–	6	83	11	11	56	33	–	–	–	100	–
NPL	–	–	100	30	60	10	90	–	10	80	10	10	20	30	50	30	70	–	30	20	–	50	–
PER	–	6	94	6	44	50	69	31	–	88	13	–	50	44	6	81	23	6	–	–	–	100	–
SWE	–	61	39	5	34	61	8	84	8	11	82	8	8	53	40	5	37	58	–	3	–	97	–
TUR	–	11	89	44	33	22	67	33	–	67	33	–	11	67	22	67	17	16	–	–	–	100	–
UKR	3	7	90	10	55	45	52	38	10	45	55	–	28	38	34	21	62	17	–	–	–	100	–
GBR	–	51	49	20	47	33	26	71	4	6	86	8	10	49	41	14	43	43	–	–	–	100	–
USA	1	6	93	18	48	34	72	27	1	82	15	3	18	56	26	54	39	7	6	1	1	91	–

Table 2 (Continued)

Country of origin	Awn roughness		Rachilla hair		Kernel covering		Lemma colour		Grain colour			Growth habit			Awn colour					Glume colour			
	1	2	1	2	1	2	1	2	1	2	3	1	2	3	1	3	5	7	9	1	3	5	7
AFG	7	93	33	67	20	80	93	7	54	49	7	100	–	–	27	73	–	–	–	40	33	27	–
ARG	–	100	79	21	–	100	79	21	29	64	7	93	7	–	7	71	14	–	7	7	50	36	7
AUS	7	93	66	34	1	99	90	10	27	71	2	98	2	–	14	76	9	–	1	30	30	40	1
AUT	5	95	67	33	–	100	91	9	43	48	9	95	5	–	10	67	19	–	5	14	43	33	10
CAN	53	47	53	47	5	95	95	5	58	40	2	98	2	–	30	55	15	–	–	30	38	32	–
CHN	18	82	53	27	5	95	100	–	55	45	–	96	4	–	27	73	–	–	–	23	50	27	–
CSK	–	100	29	71	7	93	93	7	50	43	7	100	–	–	21	64	7	–	7	21	29	43	7
DEU	7	93	35	65	7	93	95	5	47	51	2	98	2	–	12	65	21	–	2	24	18	55	2
DNK	5	95	32	68	5	95	98	2	48	52	–	98	2	–	14	71	14	–	2	16	30	55	–
DZA	4	96	64	36	4	96	96	4	64	32	4	92	8	–	24	68	8	–	–	20	64	16	–
ETH	2	98	80	20	15	85	62	38	32	42	27	85	15	–	32	48	12	–	8	33	28	25	14
FRA	3	97	26	74	7	83	97	3	61	39	–	97	3	–	10	58	32	–	–	13	19	68	–
IND	6	94	47	53	23	77	47	53	18	53	29	94	6	–	29	29	35	–	6	6	18	71	6
ITA	–	100	82	18	18	82	100	–	64	36	–	100	–	–	36	55	9	–	–	18	46	36	–
JPN	5	95	63	37	37	63	90	10	58	37	5	100	–	–	21	57	11	–	11	11	21	58	11
MAR	–	100	30	70	10	90	95	5	30	70	–	100	–	–	35	65	–	–	–	25	35	40	–
NLD	3	97	25	75	3	97	94	6	33	61	6	100	–	–	8	69	22	–	–	33	11	50	6
NZL	–	100	33	67	6	94	100	–	33	67	–	100	–	–	–	83	17	–	–	17	17	66	–
NPL	50	50	40	60	60	40	90	10	70	20	10	100	–	–	50	40	10	–	–	30	20	40	10
PER	6	94	88	12	–	100	81	19	6	94	–	100	–	–	31	63	6	–	–	6	50	44	–
SWE	8	92	42	58	3	97	100	–	53	47	–	92	8	–	5	71	34	–	–	34	13	53	–
TUR	17	83	56	44	6	94	89	11	39	61	–	100	–	–	11	72	17	–	–	11	56	33	–
UKR	3	97	52	48	17	83	93	7	45	48	7	90	10	0	17	62	14	–	7	28	21	45	7
GBR	2	98	59	41	6	94	100	–	59	41	–	96	4	–	8	73	20	–	–	35	16	49	–
USA	31	69	69	31	11	89	84	16	47	44	10	99	1	–	26	64	6	–	4	13	48	31	7

Country of origin	Stem colour		Head shape		1 000 seed weight					Test weight				Brown rust				Purple auricle		
	1	4	1	2	1	2	3	4	5	1	2	3	4	1	2	3	4	0	1	2
AFG	100	–	100	–	7	7	20	33	33	47	20	13	20	7	47	40	7	67	33	–
ARG	93	7	93	7	–	14	14	7	65	71	21	7	–	29	43	28	–	43	29	29
AUS	96	4	81	19	5	11	10	24	51	37	26	29	9	13	42	39	6	42	31	27
AUT	86	14	90	10	14	19	10	38	19	43	19	29	10	–	14	67	19	29	38	33
CAN	98	2	58	42	33	10	18	25	15	43	28	25	5	15	28	55	3	28	33	40
CHN	100	–	77	23	41	14	14	9	23	68	23	5	5	9	27	46	18	68	9	23
CSK	86	14	93	7	–	–	29	29	42	–	21	71	7	7	21	64	7	14	29	57
DEU	88	12	89	11	5	1	36	40	18	7	14	66	12	7	24	70	2	17	1	12
DNK	93	7	91	9	7	–	32	39	23	9	16	66	9	2	30	66	2	9	9	82
DZA	100	–	80	20	4	16	–	16	64	52	36	12	–	8	44	48	–	44	16	40
ETH	90	10	84	16	31	11	8	19	31	47	26	24	3	9	29	59	3	81	9	10
FRA	81	19	97	3	3	3	26	58	10	7	17	68	10	10	23	67	–	10	23	67
IND	71	29	77	23	6	6	35	35	18	24	35	29	12	6	35	29	29	35	53	12
ITA	100	–	82	18	18	–	46	–	–	36	46	9	9	9	36	36	18	46	36	18
JPN	90	10	79	21	26	–	32	21	21	16	32	42	11	–	37	47	16	58	16	26
MAR	100	–	70	30	35	10	10	25	20	75	10	15	–	20	15	65	–	50	45	5
NLD	83	17	94	6	3	8	14	61	14	6	6	72	17	11	17	72	–	11	8	81
NZL	94	6	89	11	–	–	17	61	22	17	11	50	22	28	44	28	11	–	22	67
NPL	90	10	50	50	50	–	10	10	30	40	–	60	–	10	20	70	–	70	20	10
PER	100	–	94	6	–	–	–	19	81	50	44	6	–	44	25	31	–	69	19	13
SWE	95	5	79	21	8	3	29	47	13	11	3	74	13	3	8	84	5	13	18	68
TUR	100	–	78	22	–	6	17	22	56	56	1	28	6	11	33	50	6	56	33	11
UKR	100	–	93	7	17	–	14	31	38	28	17	31	24	10	21	62	7	35	41	24
GBR	94	6	90	10	–	4	28	31	37	6	6	75	14	6	24	71	–	24	4	72
USA	94	6	86	14	18	15	7	12	48	51	32	13	2	9	35	49	7	45	39	16

spikes (character state #1), whereas 2-row barleys were prevalent not only in West European countries but also in areas of the Mediterranean, Middle and Near East, Americas and the Pacific. The *deficiens* type of 2-row barley was not confined to any particular country or region. Fourthly, diversity of the quantitative traits (height, heading, seed weight, test weight, brown rust susceptibility) were neither concentrated in countries of the "Fertile Crescent" nor in any Occidental-Oriental pattern. There were, however, high proportions of both the light-test-weight and the small-seed-weight phenotypes found in Canada, China, Ethiopia, Morocco and Nepal. New Zealand was similar to Europe for most quantitative traits, whereas Australia was similar to countries of the Mediterranean and North African region.

Biochemical allelic frequencies

The geographic distribution of the two most-frequent alleles for each of the six biochemical descriptors is given in Table 3, although all alleles and their associated frequencies (Cross 1992) were included in the calculation of heterogeneity estimates (Table 4).

Distribution of *hordein* alleles at the *Hor*1, *Hor*2 or *Hor*3 loci (Johansen and Shewry 1986) showed no clear Vavilovian pattern. Turkey, India and Nepal were characterised by slight diversity at the *Hor*1 locus, although *Hor*1:*Pr* was consistently the second- or third-most-frequent allele. Elsewhere, the *Hor*1 locus was characterised by moderate-to-high proportions of *Hor*1:*Pr* for most countries; the European region and Ethiopia were relatively high, the Mediterranean and Near Eastern countries were slightly below the world average, and the Middle East was low in proportion. Generally, there was neither a consistent proportion nor a geographic concentration of the second-most-frequent *Hor*1 allele. For the *Hor*2 locus, alleles *Ar*, *La*, *An* were in similar proportion to each other for all geographic regions, although West European countries tended toward combinations of *Hor*2:*Rf*, *Ca*, *Pr* while Mediterramean and Middle Eastern countries had higher proportions of *Hor*2:*Je*, *Gl*, *So*. The *Hor*3 locus was characterised by an exceptionally-high proportion of *Hor*3:*Cb*. India and Ethiopia were the only exceptions to this worldwide trend, with very-high proportions of the alternative allele (*Hor*3:*Ni*).

As observed for the *hordein* alleles, the distribution of the *esterase* alleles at the *Est*2, *Est*4 or *Est*5 (Hvid and Nielson 1977; Nielsen and Johansen 1986) also showed no clear Vavilovian (nor Occidental-Oriental) pattern.

Worldwide, the *Est*2 locus had an equal proportion (40% each) of the alleles *Fr* and *Dr*, and was consistent for most countries except for Peru (75% *Est*2:*Dr*) and Nepal (50% *Est*2:*Un*). Compared to *Est*2, alleles at the *Est*4 locus had a different but inconsistent geographic distribution where, for example, Canada, Algeria, India, Nepal and the United States of America (CAN, DZA, IND, NPL, USA) had a very high (> 80%) proportion of *Est*4:*At*, compared with the worldwide average (69%) for this allele. The *Est*5 locus also showed no geographic pattern and was characterised by a consistently-high proportion of the *Est*5:*Pi* allele for all countries. Further, there was no consistent pattern in the residual proportions of either *Est*5:*Mi* or *Est*5:*Me*.

Average heterogeneity

Heterogeneity estimates (Table 4) on average showed the *Hor*1, *Hor*2 and *Est*2 as the most, and *Hor*3 and *Est*5 as the least, heterogeneous among the six biochemical loci. Average heterogeneity for each country was similar,

Table 3 Geographic distribution and allelic proportion (in brackets) of the two most frequent alleles for six biochemical descriptors

Country of origin	*Hor1*		*Hor2*		*Hor3*		*Est2*		*Est4*		*Est5*	
AFG	Br(.47)	Pr(.27)	Gl(.27)	La(.20)	Cb(.93)	Ni(.07)	Dr(.40)	Fr(.33)	At(.60)	Su(.40)	Pi(1.0)	–
ARG	Ha(.36)	Al(.21)	La(.21)	Ar(.93)	Cb(.93)	Ni(.07)	Pr(.43)	Dr(.60)	At(.79)	Su(.21)	Pi(.93)	Mi(.07)
AUS	Pr(.57)	Fr(.16)	Wk(.22)	Ar(.10)	Cb(.93)	Ni(.07)	Fr(.47)	Dr(.42)	At(.62)	Su(.38)	Pi(.85)	Me(.10)
AUT	Pr(.57)	Fr(.14)	Ca(.24)	Ar(.14)	Cb(.95)	Ni(.05)	Dr(.52)	Fr(.29)	At(.71)	Su(.29)	Pi(.95)	Mi(.05)
CAN	Pr(.40)	Ha(.18)	Ar(.18)	La(.18)	Cb(.95)	Ni(.05)	Dr(.68)	Fr(.25)	At(.85)	Su(.15)	Pi(.15)	Mi(.08)
CHN	Pr(.55)	Fr(.14)	An(.23)	Ar(.14)	Cb(.96)	Ni(.04)	Dr(.64)	Un(.23)	At(.64)	Su(.36)	Pi(.82)	Mi(.13)
CSK	Pr(.71)	Fo(.14)	Ca(.29)	Rf(.14)	Cb(1.0)	–	Fr(.57)	Dr(.36)	At(.71)	Su(.29)	Pi(.86)	Me(.07)
DEU	Pr(.55)	Fo(.14)	Ca(.16)	Rf(.14)	Cb(.90)	Ni(.10)	Pr(.57)	Dr(.35)	At(.65)	Su(.35)	Pi(.85)	Me(.14)
DNK	Pr(.75)	Ha(0.7)	Pr(.30)	Ca(.27)	Cb(.27)	–	Dr(.66)	Fr(.27)	At(.75)	Su(.25)	Pi(.82)	Me(.14)
DZA	Pr(.36)	Al(.28)	La(.28)	Ar(.20)	Cb(1.0)	–	Fr(.44)	Dr(.40)	At(.84)	Su(.16)	Pi(.80)	mI(.16)
ETH	Pr(.73)	Al(.28)	La(.29)	Ar(.20)	Cb(.12)	Ni(.88)	Fr(.53)	Dr(.16)	At(.78)	Su(.22)	Pi(.84)	Me(.15)
FRA	Pr(.68)	Ar(.16)	Ar(.29)	Ca(.26)	Cb(.97)	Ni(.03)	Dr(.55)	Fr(.36)	Su(.52)	At(.48)	Pi(.71)	Mi(.26)
IND	Cl(.29)	Kw(.24)	Ro(.18)	Je(.18)	Ni(.77)	Cb(.23)	Fr(.65)	Pn(.18)	At(.88)	Su(.12)	Pi(.70)	Me(.18)
ITA	Pr(.36)	Fr(.27)	So(.46)	La(.18)	Cb(1.0)	–	Pn(.46)	Fr(.36)	At(.73)	Su(.27)	Pi(1.0)	–
JPN	Pr(.32)	Cl(.32)	Ar(.26)	Ca(.16)	Cb(.90)	Ni(.10)	Fr(.47)	Dr(.37)	At(.79)	Su(.21)	Pi(.95)	Mi(.05)
MAR	Pr(.70)	Kw(.20)	Ar(.30)	Je(.20)	Cb(1.0)	–	Dr(.55)	Fr(.25)	At(.70)	Su(.30)	Pi(.85)	Mi(.15)
NLD	Pr(.58)	Ar(.17)	Ca(.22)	Pr(.19)	Cb(.94)	Ni(.06)	Dr(.57)	Fr(.42)	At(.58)	Su(.42)	Pi(.97)	Me(.03)
NZL	Pr(.89)	Ar(.06)	Ca(.28)	Pr(.22)	Cb(1.0)	–	Dr(.61)	Fr(.33)	At(.61)	Su(.39)	Pi(.39)	–
NPL	Al(.50)	Pr(.30)	La(.50)	Gl(.20)	Cb(.20)	Ni(.20)	Un(.50)	Fr(.40)	At(.80)	Su(.20)	Pi(.90)	Me(.10)
PER	Pr(.75)	Kw(.06)	Ar(.69)	La(.06)	Cb(1.0)	–	Dr(.75)	Fr(.19)	At(.75)	Su(.25)	Pi(.25)	Me(.06)
SWE	Pr(.63)	Ha(.16)	Ca(.16)	Pr(.21)	Cb(.97)	Ni(.03)	Dr(.47)	Fr(.45)	At(.63)	Su(.37)	Pi(.76)	Me(.21)
TUR	Ar(.50)	Ha(.22)	Cl(.17)	Ar(.11)	Cb(.94)	Ni(.06)	Dr(.33)	Fr(.33)	At(.56)	Su(.44)	Pi(.72)	Mi(.22)
UKR	Pr(.62)	Fr(.17)	La(.21)	Ar(.14)	Cb(.97)	Ni(.03)	Dr(.48)	Fr(.45)	At(.52)	Su(.48)	Pi(.86)	Mi(.07)
GBR	Pr(.49)	Ha(.22)	Cr(.18)	Rf(.16)	Cb(1.0)	–	Dr(.57)	Fr(.41)	At(.55)	Su(.45)	Pi(.78)	Me(.18)
USA	Pr(.42)	Fr(.20)	Ar(.26)	La(.15)	Cb(.93)	Ni(.07)	Dr(.43)	At(.37)	At(.85)	Su(.15)	Pi(.86)	Mi(.12)

Table 4 Heterogeneity estimates of six biochemical descriptors among 25 countries

Country	*Hor1*	*Hor2*	*Hor3*	*Est2*	*Est4*	*Est5*	Mean ± SE
AFG	0.69	0.84	0.13	0.71	0.50	0.00	0.48 ± 0.14
ARG	0.81	0.91	0.14	0.67	0.35	0.14	0.50 ± 0.11
AUS	0.64	0.90	0.13	0.59	0.48	0.27	0.50 ± 0.11
AUT	0.65	0.88	0.09	0.64	0.42	0.09	0.46 ± 0.13
CAN	0.79	0.88	0.10	0.49	0.26	0.23	0.46 ± 0.13
CHN	0.68	0.89	0.09	0.54	0.47	0.32	0.50 ± 0.11
CSK	0.48	0.87	0.00	0.56	0.42	0.27	0.43 ± 0.12
DEU	0.63	0.91	0.19	0.56	0.50	0.27	0.51 ± 0.11
DNK	0.43	0.83	0.00	0.49	0.38	0.31	0.41 ± 0.11
DZA	0.78	0.85	0.00	0.64	0.27	0.34	0.48 ± 0.14
ETH	0.45	0.84	0.22	0.65	0.34	0.27	0.46 ± 0.10
FRA	0.52	0.81	0.06	0.58	0.51	0.44	0.49 ± 0.10
IND	0.83	0.89	0.37	0.55	0.21	0.47	0.55 ± 0.11
ITA	0.76	0.76	0.00	0.66	0.42	0.00	0.43 ± 0.15
JPN	0.76	0.88	0.19	0.63	0.34	0.10	0.49 ± 0.13
MAR	0.54	0.87	0.00	0.63	0.43	0.26	0.46 ± 0.12
NLD	0.63	0.86	0.11	0.52	0.49	0.06	0.44 ± 0.13
NZL	0.21	0.85	0.00	0.53	0.49	0.00	0.35 ± 0.14
NPL	0.65	0.72	0.34	0.61	0.34	0.19	0.47 ± 0.09
PER	0.44	0.52	0.00	0.41	0.39	0.12	0.31 ± 0.08
SWE	0.58	0.85	0.05	0.58	0.47	0.38	0.49 ± 0.11
TUR	0.67	0.92	0.11	0.74	0.51	0.44	0.56 ± 0.14
UKR	0.59	0.90	0.07	0.57	0.51	0.25	0.48 ± 0.12
GBR	0.70	0.89	0.00	0.51	0.50	0.36	0.50 ± 0.13
USA	0.77	0.88	0.13	0.66	0.26	0.26	0.49 ± 0.13
Mean:	0.63	0.85	0.02	0.59	0.41	0.23	0.47
± SE	0.03	0.02	0.02	0.02	0.02	0.03	0.01

with standard errors of each country's mean spanning most of the total range. The most variable countries ($H > 0.5$) were Argentina, Australia, China, India, Turkey and the United Kingdom. Ethiopia ($H = 0.46$) and Nepal ($H = 0.47$) were not among the most variable countries. New Zealand and Peru were the least variable for average heterogeneity among the *Hor* and *Est* loci.

Cluster analysis

Results of cluster analysis are expressed as dendrograms for the agro/morphological (Fig. 1) and biochemical (Fig. 2) descriptors, with each data set partitioning different sets of country groupings. The most "significantly-different" grouping (i.e., the first nodal point or "branch" in the dendrogram) identified Nepal (Fig. 1, group VI) and the country-grouping Ethiopia + India (Fig. 2, group VI) based on agro/morphological and biochemical data respectively. At the second nodal point, Algeria + Argentina + Peru + Nepal (Fig. 1, groups V + VI) and Italy + Nepal + Ethiopia + India (Fig. 2, Groups V + VI) were the most different from the remaining countries based on agro/morphological and biochemical evidence respectively. Differences in country groupings were demonstrated up to the fifth nodal point for both agro/morphological and biochemical descriptors (Figs. 1 and 2).

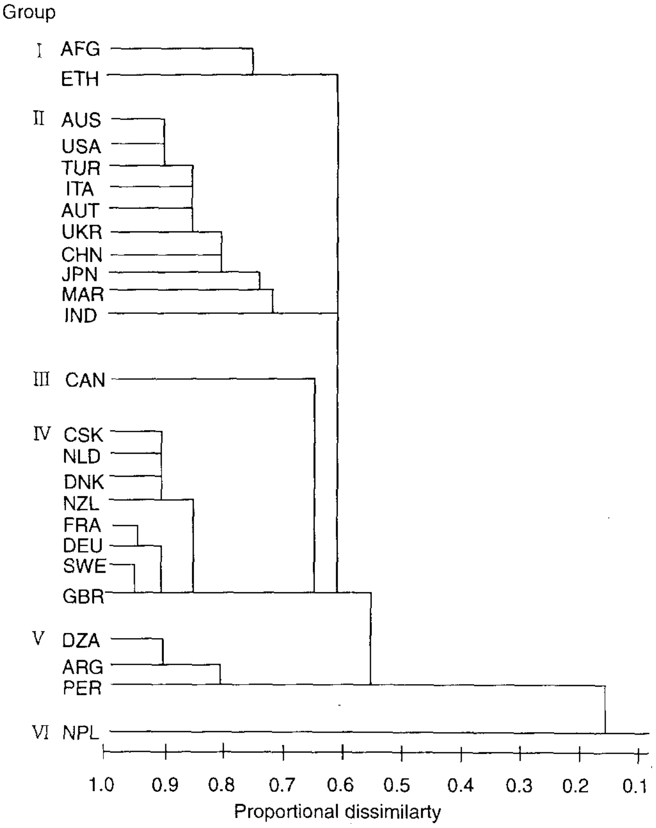

Fig. 1 Dendrogram of Mahalanobis distances using average linkage cluster analysis of 21 agro/morphological descriptors among 25 countries

Discussion

There are few world surveys with descriptors in common with the current study. Despite the small number of barley varieties used in this study, the Crop & Food Research world barley collection is similar to other studies in character-state distribution for most agro/morphological (Tolbert et al. 1979; Takahaski et al. 1983; Somaroo et al. 1986) and esterase (Kahler and Allard 1970) data and, within broad limits, is therefore representative of other world holdings. Unfortunately, there has been no published world survey for hordein variation but, based on European surveys (Linde-Laursen et al. 1982), the disproportionate and consistently high frequency of the *Hor2*: *Ca*, *Pr*, *Ar*, *Rf* and *La* alleles are typical of that region, and are most likely a result of the extensive use of the high-malting-quality cultivar "Carlsberg II" and linkage between these *Hor2* alleles and *Ml-a*, powdery mildew resistance (Jensen et al. 1980; Linde-Laursen et al. 1982).

The current study demonstrated that differing patterns of geographical variation are dependent upon the type of evaluation data. The agro/morphological data highlighted Nepal as most distinct from the remaining countries, whereas the biochemical data identified both Ethiopia and India as most distinct. Other combina-

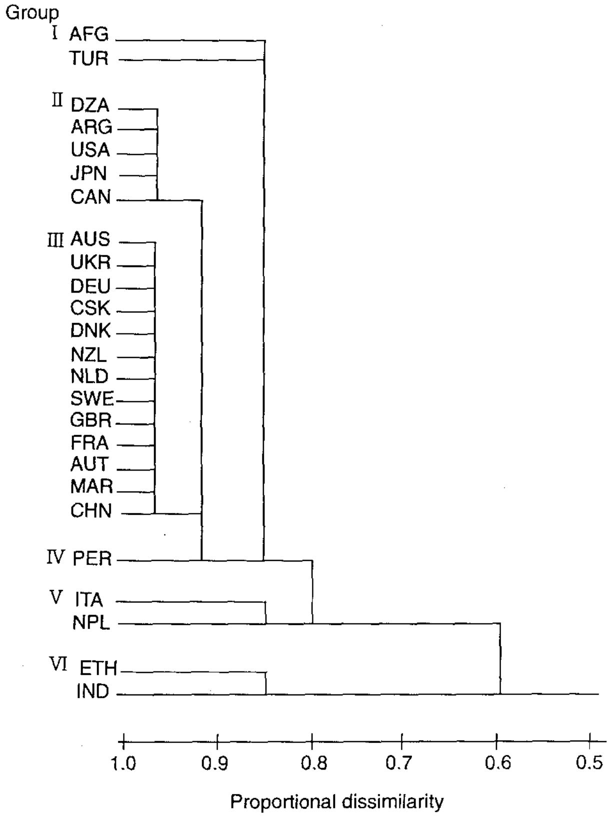

Fig. 2 Dendrogram of Nei's Genetic Distances using average linkage cluster analysis of six polymorphic biochemical descriptors among 25 countries

tions of countries were included in this "distinctly-different" set with progressive fusion points within the cluster analyses (Figs. 1 and 2), but at no level of dissimilarity did the "set of most distinct" countries match according to both agro/morphological and biochemical data. Thus, neither of these parameters can be used as individual descriptors for the establishment of comprehensive collections. Further, variability *per se* is not an adequate strategy for collection as demonstrated by the various combinations of heterogeneity estimates of Table 4. For example, an overall similar (non-significant) mean heterogeneity over six biochemical loci was observed for Nepal (NPL) and Morocco (MAR), despite this overall estimate being composed of highly-contrasting heterogeneity values at the *Hor*2 and *Hor*3 loci.

The lack of agreement between the agro/morphological and biochemical data sets has been discussed in an earlier paper (Cross et al. 1992). The consequences of this lack of agreement in determining the most "significantly-different" countries has serious consequences in the search for novel forms of germplasm. Furthermore, collection strategies based on "a diversity of forms" is also suspect, as the biochemical heterogeneity data demonstrate that overall heterogeneity estimates can be composed of highly-contrasting variability at differing loci. The problem remains, therefore, as to the most appropriate collection strategy that will sample the range of natural diversity within a species.

The present study adds to an increasing volume of evidence that collection strategies based exclusively on Vavilovian concepts (Williams 1988) are restrictive in sampling a species' total diversity. These studies demonstrate significant, and sometimes continuous, variation beyond the Vavilovian "centres of origin" and have been reviewed earlier (Cross et al. 1992; Porceddu and Damania 1992). Both reviews emphasise eco-geographic features as being important determinants in sampling crop diversity.

In recent years, there is clear evidence that at the intra-species level there has been a dramatic increase in the rate of extinction of their endemic variation (Frankel 1975; Harlan 1975). Shifts in geographical patterns of diversity have also been observed through, for example, the activities of international trade in plant varieties and germplasm exchange associated with breeding and selection (Peeters 1988). Despite these trends, and the continuing absence of alternative collection strategies, geographic patterns of variation will continue to provide some information and a basis for understanding the germplasm of modern-day crops (e.g., Harlan 1971; Hua et al. 1988; Hinata 1988; Konishi 1988), and for formulating appropriate collection strategies for crop species whose endemic populations are still abundant (e.g., Ehrman and Maxted 1990). However, an appropriate strategy for the comprehensive collection of genetically-eroded endemic crop species remains unsolved.

A recent study, detailing significant diversity and the detection of numerous novel forms of storage glutenin protein in wheat (Cross and Guo 1993), highlighted the usefulness of pre-1935 landrace collections of worldwide origin. Based on this study, and given that this wheat example can be extended to include barley, then the "landrace" component of a crop species diversity should be a significant factor in the formulation of comprehensive barley germplasm collections.

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