Adaptive Responses and Genetic Divergence in a World Germplasm Collection of Chick Pea *(Cicer arietinum L.)*

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Summary. A world germplasm collection of 5477 lines of chick pea were evaluated for eight characters related to fitness and yield at two locations in India. Multivariate analyses as Mahalanobis D^2 statistic, canonical analysis, and factor analysis were used for the classification of this material and to assess the genetic divergence between them.

On $D²$ analysis and grouping the whole collection fell into six clusters with substantial genetic divergence between them. Despite the overall parallelism between genetic diversity and geographical distance stringent natural and human selection or geographical barriers preventing gene flow were found to have played a significant role in the genetic divergence of this material.

Plant type was reflected as the most important character operating in the genetic divergence between geographical groups, followed by seed colour and flower colour. Significant negative correlations were found between I00 seed weight and number of seeds per pod and seed colour.

Further independent classification using canonical analysis confirmed the results obtained from the D^2 analysis. Factor analysis was used to resolve the intercorrelations between the eight variables into fewermeaningful factors which could explain the major forces in intraspecific differentiation. The loadings in the first factor reflected the importance of characters related to the reproductive capacity of the individual. Inclusion of flowering time and seed maturity time in the second factor which has an equal contribution suggests the importance of these characters in the competitive ability of the plant under natural and human selection.

Introduction

Chick pea (*Cicer arietinum* L.) being one of the five major cultivated pulse crops has an extensive geographical distribution. No attempt has so far been made to study the genetic divergence in this crop through an effective quantitative approach, and very little is known about the role of quantitative characters for subspecific differentiation. Adaptation in plant populations is a complex response affected by several interacting individual and population functions. It is unlikely that adaptive traits could be attributed to a single gene or to a small number of genes (Bennett 1970). Multivariate analysis provides a useful statistical method for analysing the various causative factors and their interrelationships operating on and within plant populations under natural and human selection. It has been successfully used to classify biological populations and to identify factors influencing their genetic divergence (Anderson 1958; Majumdar and Rao 1958; Nair and Mukherjee 1960 and Murty et al., 1965).

The evaluation of the Chick pea germplasm was done at the Indian Agricultural Research Institute, New Delhi, India, during 1966-70.

In the present study a set of quantitative characters related to fitness and yield was used to assess the nature of genetic divergence in aworldgermplasm collection of chickpea using D^2 statistic of Mahalanobis (1936), canonical analysis and factor analysis. The results are presented in this communication.

Materials and Methods

The material comprised of 5477 varieties of chick pea from seventeen countries. The complete collection was grown at two locations in India in augmented randomised block designs with the major cultivars as controls. Eight plant characters were selected for the present analysis. The mean value for each character from the two locations was used for the analysis. The characters were scored as follows:

1. Plant type: Spreading-1, Semi-spreading-2, E rect- 3 .

2. Flower colour: White-1, Pink-2, Violet-3.

3. Days to flower: Number of days from the date of sowing till 50 % of the plants in a line had flowered. (Each line had not less than 30 plants of a variety.)

4. Days to seed maturity: Number of days from the date of sowing till the seeds have matured in 50 % of the plants in a line.

5. Pod size: Small-l, Medium-2, Large-3.

6. Number of seeds per pod: The average of 50 pods selected at random from a line.

7. Weight of 100 seeds: Recorded in grams.

8. Seed colour : Pink or light pink- I, light-Brown-2, Brown-3, Yellow-4, Light green or green-5, Black-6.

The total collection was grouped into 11 populations¹ as shown in Table 1. Countries contributing fewer than three varieties were grouped with geographically adjacent countries.

From the residual matrix, four successive vectors and roots were calculated (see Rao 1952, 1964, Arunachalam 1967). Group constellations of the 11 populations were diagrammatically represented in the $\lambda_1 - \lambda_2$ chart.

Table 1. Geographical origin of the eleven populations of Chick pea

Population	Geographical origin	No. of varieties included
	Origin unknown	27
2	Afghanistan	6
3	Algeria, Morocco	29
4	Burma, India	1579
5	Iran, Iraq, Israel	3761
6	Mexico	12
7	Nigeria, Sierra Leone, Tanganyka	6
8	Pakistan	34
9	United Arab Republic	8
10	United States of America	8
11	U.S.S.R.	7

Table 2. Means for the eight characters of Chick pea

Statistical Analysis

A random sample of I00 varieties representing the 11 populations was chosen for variance analysis to ascertain whether significant differences existed for the means of the eight characters studied.

D^2 Analysis

The calculation of the D^2 values involved the following steps. (a) The uncorrelated linear combinations $(y's)$ were obtained by pivotal condensation of the common dispersion matrix, of the correlated variables $(x's)$ (Rao 1952). (b) The mean values for the eight characters for different populations were transformed into the mean values of a set of uncorrelated linear combinations (Y's). (c) The D $\,$ between the ith and the jth populations for k characters was calculated as follows
 D^2 ij = \sum (Yit – Yjt)². The D² for k characters are calculated separately and added up to give D^2 ij.

(d) The D-squares for each character for eachcombination were ranked in the descending order of magnitude and the rank totals were obtained for each character for all combinations (see Murty and Arunachalam 1967). The clustering of populations was by the method suggested by Rao (1952). After clustering, the intra and intercluster relationships were studied and the distances represented diagramatically using D values.

Canonical Analysis

Canonical analysis in most cases permits the representation of the populations in a two dimensional chart depending on the proportion of variation accounted for by the first two roots. The between product sum matrix (A-matrix) is computed using the mean values of the uncorrelated linear combinations for all the characters for all the varieties. From the fourth power of the Amatrix, canonical vector 1 is retrievedby repeated iterations on a trial vector. After standardising the first canonical vector the first canonical root is extracted.

Factor Analysis

Among the several methods of factor analysis available the centroid method is popular and relatively simple. The centroid method outlined by Holzinger and Harman

¹ The word population is used here in a wider sense. It means a group of varieties arbitrarily pooled on the basis of geographical origin, see Table 1.

(1941) was used in this analysis. The model assumes that a set of p correlated variables and their inter-correlations could be adequately described by k factors $(k < p)$ which are linear and additive (Maxwell, 1961). The extraction of factors involved successive iterations. The magnitude of the coefficients of each character (factor loadings) are used to understand the relative importance of those characters in each factor. In the centroid method, the estimation of the factor loadings is done through the quantities known as communalities. Cattel (1965) has defined communality as the portion of a variance of a variate which is due to k common factors. The estimates of communalities are obtained by an iterative procedure, starting with a trial vector (see Arunachalam 1967; Murty et al. 1970).

 $D²$, canonical and factor analyses were programmed on an IBM computer for the present analysis.

Results

The means and the variance-covariance matrix for the eight characters are given in Tables 2 and 3 respectively. Variance analysis of 100 varietes representing the eleven populations showed significant differences among the means for each of the eight characters studied.

1.
$$
D^2
$$
 Analysis

The coefficients of the uncorrelated linear functions of y's are given in Table 4. Based on this, the 11 populations formed six clusters (Fig. 1). The inter and intra cluster average D^2 values are given in Table 5. The maximum inter cluster divergence was observed between clusters III and IV $(D = 2.91)$. Clusters I, II, IV and V were nearer to each other and within this group, clusters II and IV ($D = 1.48$) and IV and V ($D =$

Pod size		No. of seeds/pod		100 seed weight		Seed colour	
x_{5}	${\tt Y}^{}_{\tt S}$	x_{β}	${\rm Y}^{}_6$	x_7	Y ₇	$x_{\rm R}$	Y ₈
2.378	5.506	1.300	-0.866	18.533	-1.224	3.080	2.318
2.333	5.276	1.233	-0.811	16.117	-1.759	1.833	1.511
2.372	5.472	1.358	-0.325	18,495	-1.195	2.895	2.748
2.149	4.898	1.498	-0.260	14.845	-1.388	2.979	1.621
2.296	5.303	1,417	-0.322	18.128	-1.312	2.839	2.535
2.400	5.574	1.613	0.245	17.763	-0.667	3.063	1,930
2.375	5.328	1.276	-0.591	26.475	-0.932	2.500	2.813
2.091	4.842	1.448	-0.538	17.455	-1.077	2.750	1.555
2.075	4.504	1.225	-1.280	13,800	-2.376	3.250	2.177
2.225	5.121	1.463	-0.343	13.988	-1.903	2.688	1.572
2.314	5.352	1.429	-0.422	16.571	-1.206	4.289	3.077

 $x's = actual means$ y's = transformed uncorrelated means

Cluster	- 1	$\scriptstyle\rm II$	Ш	IV	v	VI
Ι. П $_{\rm III}$	0.57 (0.76)	3.04 (1.74) 0.90 (0.95)	7.63 (2.76) 4.07 (2.02)	3.16 (1.78) 2.20 (1, 48)	2.51 (1.58) 3.11 (1,76)	1.79 (1, 34) 1.52 (1.23)
Ш IV				8.46 (2.91)	5.06 (2.25) 2.21	4.71 (2.17) 1.83
V					(1.49)	(1, 35) 1.18
VI						(1.09)

Table 5. Inter and intracluster average D^2 values

The D values are given in parenthesis.

Fig. 1. Clusters and their inter-relationships

Intercluster distances are shown in D values, and intracluster distances as D^2 (Table 5)

1.49) showed very little divergence between them. Cluster VI which is of unknown origin has small but approximately equal distances to clusters I, II, IV and V. Moreover it appears to be heterogeneous in itself. This might suggest that the 27 lines in this cluster have different geographical origins but are closely related to the material from Asia and the Near East. Clusters I and II have average intra cluster D values of 0.755 and 0.950 respectively, suggesting substantial genetic diversity within themselves.

The mean values for the eight characters for each cluster are given in Table 6. Clusters I, II and VI com-

Fig.2. Group constellations of 11 populations of chick pea (*Cicer arietinum*) in λ ¹ - λ ² chart

prised largely of spreading to semi-spreading plants, whereas clusters If, IV and V contained semi-spreading and erect types. Mean 100 seed weight was maximum in clusters I and VI (18.78), intermediate in clusters II, IV and V (16.64) and low in cluster III (13.80). Cluster IV showed the highest value for the average number of seeds per pod (1.61) followed by clusters I, If, V and VI having intermediate values (1.37) and cluster Ill having the lowest value (1.23).

The order of contribution to total divergence was plant type, seed colour, 100 seed weight, and number of seeds per pod. Plant type (28.1% of the total pair-

Cluster	Plant type	Flower colour	Days to flowering	Days to mature	Pod size	No. of seeds per pod	100 seed weight	Seed colour
\bf{I}	1.580	1.550	107.970	179.80	2.35	1.35	19.03	2.75
$_{\rm II}$	1.952	2.330	104.550	177.95	2.20	1.41	15.60	1.57
III	2.400	1.650	103.850	178.68	2.09	1.23	13.80	3.25
IV	2.025	2.025	104.230	177.28	2.40	1.61	17.76	3.06
V	2.130	2,000	104,040	175.23	2.31	1.43	16.57	4.28
VI	1,950	1.956	106.530	180.57	2.38	1.30	18.53	3,08

Table 6. The cluster means for the eight characters

Table 7. The canonical vectors

C. vector	Plant type	Flower colour	Days to flower	Days to mature	Pod size	Seeds per pod	100 seed weight	Seed colour
Z1	-0.6524	0.0755	0.0089	-0.0092	0.3365	0.2858	0.4672	0.3940
Z ₂	0.1926	0.4953	0.0146	-0.0434	0.0928	0.4475	0.3627	-0.6124
Z3	0.6674	0.2607	0.0638	-0.0087	0.0712	0.0481	0.2746	0.6322

The sum of all canonical roots $= 27.597$

 y^4 = 19.931 y^3 = 3.390 y^3 = 2.40 Contribution of $\lambda_1 = 71.88$ % $\lambda_2 = 12.28$ % $\lambda_3 = 8.69$ %

wise comparisons) have contributed to the maximum intercluster divergence, followed by seed colour (23.01 %) , 100 seed weight (16.26 %) and the number of seeds per pod $(9.64 %)$. The contribution of each character was parellel in intra and intercluster D^2 suggesting the influence of similar factors at both the levels of differentiation.

2. Canonical Analysis

Clusters were independently derived by canonical analysis to verify the grouping obtained by D^2 statistic. Canonical vectors are given in Table 7. The sum of the six canonical roots is 27.597 of which λ_1 is 19.837, λ_2 3.390, λ_3 2.40, and the rest 1.97. Since 84.16 % of the total variation is explained by the first two canonical roots a two dimensional representation of the relative positions of the varieties is considered adequate Fig.2. Although the first vector alone accounted for more than 71.87 % of the total variation, the second and third vectors together accounted for 20.97 $*$. Therefore the predominant axis of variation essentially remains the first vector, second and third vectors playing a considerable role in further divergence.

The absolute magnitude in the coefficients of canonical vectors would indicate the relative role of characters in primary and secondary differentiations. The importance of plant type, I00 seed weight, seed colour, and pod size in the primary differentiations between populations is reflected in the corresponding coefficients of the first canonical vector. Similarly, seed colour, flower colour, seeds per pod and 100 seed weight are reflected in their corresponding coefficients in the second and third canonical vectors indicating their relative importance in secondary differentiations. Plant type appears to be important in canonical vectors I and 3, although the directions in the vectors are changed. The change in sign between vectors could imply a balancing effect for an intermediate optimum between different plant types. A similar situation is observed for seed colour, although of a lesser magnitude with change of sign in vectors 2 and 3. Hundred seedweight is important in all the four vectors and appears to have played an important role in the divergence between populations.

3. Factor Analysis

The total correlation matrix is given in Table 8 andthe factor loadings and communalities in Table 9. Two factors were found to be adequate to account for more than 84 $%$ of the total communality. Although each of the eight variables is represented by a coefficient in each factor the magnitude of these coefficients deter-

	Plant	Flower	Days to	Days to	Pod	No. of seeds	100 seed	Seed
	type	colour	flower	mature	size	per pod	weight	colour
	x1	х2	х3	х4	x5	х6	х7	х8
x1 x2 x3 x4 x5 x6 x7		0.2839	-0.1879 -0.1790	-0.0957 -0.0861 0.1033	0.0654 -0.1813 -0.1325 0.1127	0.1182 0.2422 0.2021 0.1444 -0.3275	-0.1100 -0.3361 0.2008 0.1973 0.2628 $-0.4533*$	0.2298 $0.6149**$ 0.0066 0.1688 $-0.4687*$ 0.3967 $-0.5482**$

Table 8. Total correlation matrix for eight characters in Chick pea

Significant at 5 % level

** Significant at 1 % level.

The diagonal values being unity are omitted

Plant characters		Factor coefficients	Communalities		
		2.	Original	Calculated	
1. Plant type	0.361	-0.219	0.284	0.179	
2. Flower colour	0.598	-0.504	0.615	0.612	
3. Days to flowering	0.132	0.396	0.202	0.174	
4. Days to maturity	0.249	0.505	0.197	0.317	
5. Pod size	-0.250	0.176	0.263	0.093	
6. No. of seeds/pod	0.442	-0.109	0.397	0.207	
7. 100 seed weight	-0.322	0.402	0.263	0.266	
8. Seed colour	0.416	-0.647	0.615	0.592	
Total			2.835	3.346	

Table 9. Factor loadings and communalities in the centroid factor analysis

Contribution of factors $1¹$ ₁²₃²₃

As % of the total original communality 36.9 47.2

mines the relative importance of the different variables in intra-specific differentiation. The first factor contributed 38.9 % of the total communality and the factor loadings were significant, for flower colour, number of seeds per pod and seed colour. P lant type and hundred seed weight are also implicated although to a lesser degree. The loadings in the second factor were in favour of seed colour, flower colour, I00 seed weight, days to flowering and days to seed maturity.

Discussion

Adaptive response and evolution of ecotypes is a function of the population as a whole rather than of individuals. Plant populations restricted to limited geographical area or subjected to identical environmental pressures evolve adaptive gene complexes which are conserved by genetic linkage or stringent natural or human selection. Such co-adaptive adjustment of the genotypes is polygenic in nature. Evaluation of subspecific differentiation and adaptive processes should therefore be done using population parameters drawing upon the full resources of the genetic variability offered by that population. As pointed out by Stebbins (1965) the action of natural selection was dependent to alarge extent on the relationships between genes and their ultimate effects on morphological features, because natural selection would operate on the frequency of phenotypes. The genetic architecture of a population is also controlled by the breeding behaviour of the individuals. Changes in the breeding systems have accelerated the genetic divergence in natural populations (Stebbins 1957). Chick pea is an inbreeding crop and no information is available suggesting a change in its breeding behaviour under varied environmental conditions.

From Figure 1 and Table 5 it would be seen that geographically adjacent countries group together into clusters I and If. However, clusters I (intracluster

 $D = 0.755$) and II ($D = 0.95$) comprise substantial genetic divergence within themselves and cover large geographical area. A further analysis based on Tocher' s classification (Rao loc.cit.) will be attempted to examine the intra geographical divergence in these populations. According to Vavilov (1951) the Indian center and the Central Asiatic center are the primary centres of origin (diversity) of cultivated chick pea. The Near Eastern centre is suggested to be a secondary centre.

The inclusion of the eight varieties from the United States in cluster II suggests the possible introduction of these varieties from Asia in the recent past. Cluster IV comprises varieties from Mexico. Chick pea is not indigeneous to the Mexican centre. Its introduction to Mexico by Spaniards dates back to the early post-Columbina era. Despite the close relatedness of cluster IV to clusters I, II and V, human and natural selection under totally different agro-climatic conditions has resulted in the genetic divergence of the Mexican varieties into a separate cluster. Depending upon the breeding system, selection pressure and the extent of genetic isolation the differentiation of a species into distinct ecotypes may be slow or very rapid (Bennett 1965, Gregor 1938, 1939). Examples of such rapidgenetic differentiation under intense selection pressures in new habitats are already reported in *Piswn* inSouth America (Harland 1948), cultivated potatoes in India (Swaminathan 1968) and pigeon peas (Cajanus cajan) in Mexico (Swaminathan 1970).

The maximum intercluster divergence of cluster III from the rest cannot be explained on the basis of geographical distances alone. Geographical barriers preventing gene flow or else intense natural and human selection for diverse adaptive gene complexes must be responsible for this genetic divergence. Bennett (1970) has referred to rapid ecotype differentiation even in the absence of reproductive isolation in outbreeding species. Similar genetic divergence is reported by Murty et al. (1965) in *Brassica*, Timothy (1963) in maize, and Vairavan et al. (1973) in *Oryza.* The close relationship between clusters I, II, V and VI suggests homogeneity in ecotypic differentiation. Such homogeneity could suggest geographical proximity to the centres of origin of a particular species. It could also suggest similarities of natural and human selection operating on these varieties. However, in chick pea, the geographical distribution of clusters I, II, V and

VI overlaps the primary and secondary centres of origin suggested by Vavilov.

The primary characters contributing to genetic divergence have variously been reported in different cultivated crops. Days to 50 % flowering, plant height, and tiller number are reported to be important in the divergence of grain crops (Vairavan et al., loc.cit. ; Murty and Tiwari 1967 ; Jawahar Ram and Panwar 1970). In chick pea however, plant type was the most important ingredient for primary differentiation. Chick pea is extensively grown in tropical and sub tropical regions with varying daylength and intensity of sunshine. In northern India for example it is cultivated as a winter crop with suboptimal availability of sunshine, where a spreading plant type becomes specially advantageous for efficient photosynthesis. In tropical regions however an erect and bushy plant type prevents excess transpiration enabling the plant to survive under semiarid conditions. Human selection on seed weight, number of seeds per pod and seed colour could have acted as causes of secondary differentiation. Table 8 shows significant negative correlations between I00 seed weight and number of seeds per pod. Similar negative correlations are also observed between seed weight and seed colour. The large seeded 'Kabuli' type grown extensively in the Middle east, India, Afghanistan and other Mediterranean regions is light coloured. It is likely that a conscious selection for seed-weight has resulted in an unconscious selection for seed colour as indicated by the negative correlations.

Further independent classification of these populations by canonical analysis confirms the classification derived by D^2 analysis, Fig. 2. The magnitudes of plant type, 100 seed weight, seed colour and pod size in the first canonical vector, reflects the relative importance of these characters in the primary differentiation of this species. Similarly seed colour, flower colour, seeds per pod and I00 seed weight important in the secondary differentiation is reflected in the second and third canonical vectors. The changes in the signs of the coefficients of plant type and seed colour between vectors indicate a balancing effect for an intermediate optimum under diverse influences of natural and human selection.

Factor analysis is useful to provide a meaningful assessment of the major forces responsible for the inter and intraspecific differentiation. Murtyet al. (1970) examined the genetic divergence in the populations of

five cultivated crops using centroid method of factor analysis. From their analysis it was found that the number of factors and the factor loadings were influenced by the past history of selection on a particular crop. This was attributed to the changes in the genetic association between the characters under stringent selection. They also found that the first factor which contributed substantially to the total communality was concerned with the reproductive capacity of the species and to those characters related to the components of fitness under natural and human selection. A similar situation is observed in chick pea where 38.9 % of the total communality was contributed by the first factor. Flower colour, number of seeds per pod and seed colour, have important loadings in the first factor. The inclusion of flowering time and seed maturity time as important, in the second factor suggests the significant contribution of these characters for the competitive ability of these varieties under natural selection.

trast to the modern cultivars of cereals which are products of intense directional selection for yield and uniformity, these varieties contain substantial genetic variability. Chick pea is important as a major source of vegetable protein in the predominantly cereal diet of developing nations like India. Despite the significant role of this crop in maintaining an optimum proteincalorie ratio (Sukhatme 1970)in the everyday diet of large masses of people, very little effort was made for its genetic improvement till recently. Most of the present day varieties are primitive cultivars. In con-

Modern breeding programmes aim at the maximisation of yield and phenotypic uniformity tailored to suit artificial environments created by advanced agricultural practices, the major components of which are strictly controlled. This trend towards increasing uniformity erodes the genetic variability in the cultivated crops. Reduction in the genetic variability has often resulted in the poor adaptive responses of crop varieties to diverse environmental pressures.

The present evaluation of the chick pea germplasm collection has revealed substantial genetic variability comprised in these primitive varieties collected from all over the world. The multivariate analysis of factors influencing adaptive responses and genetic divergence in these primitive cultivars has shown significant interrelations of genetic traits in the evolution of co-adaptive gene complexes and ecotypes. The recent

implementation of advanced breeding practices for the improvement of this crop will soon replace the primitive cultivars with high yielding varieties with phenotypic uniformity and reduced genetic variability. As Frankel (1950) has rightly remarked "the success or failure depends on the adaptability in the crop, that is upon the recombinational variability". Despite the great technological advancements in chemical and physical mutagenesis it is increasingly evident during the last three decades, that adaptive genetic variability useful for crop improvement are more readily found in the primitive cultivars and their wild relatives. This emphasises the urgent need for large scale exploration and conservation of these varieties to enrich the breeding stocks for future crop improvement.

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R. K. J. Narayan and A. J. Macefield: Genetic Divergence in aWorld Germplasm Collection of Chick Pea 187

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