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# THE NATURE OF DIVERGENCE IN RELATION TO BREEDING SYSTEM IN SOME CROP PLANTS

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THE availability of statistical tools to quantitatively measure the genetic divergence between two or more populations and the relative contribution of individual characters to the total divergence in such comparisons have permitted the tracing of evolutionary patterns in some organisms such as rice, Nicotiana and man and in choosing parents for hybridization in crop plants (Blackith, 1960; Morishima and Oka, 1960; Murty et al., 1962; Rao, 1958). At present the breeding methods adopted in crop improvement are broadly divided into those for self-, cross- and oftencross-pollinated and vegetatively propagated groups. While it is possible that under natural selection, the nature of divergence between populations is influenced by the breeding structure of the population, the situation could be considerably modified under human selection for productivity where certain genotypes, which would have become extinct in nature are preserved and usually favoured in some cases. While genetic diversity and stability are simply related, the relationship between productivity and genetic diversity is complex (Allard, 1961). Since adaptability under human cultivation is dependent on stability and consistency of performance over seasons, its relationship to the breeding system of the cultivated crops is of interest. The available evidence on the homeostatic mechanisms indicate that homeostasis is not a direct function of heterozygosity but is a product of long natural selection and is not simply related to the breeding system (Mather, 1960; Thoday, 1955). Therefore, a comparison of the relative importance of some characters in intra-specific divergence in cultivated crops belonging to different pollinating categories, their relationship to fitness and the nature of gene action for these characters are examined in this paper.



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# MATERIALS AND METHODS

The crops that have been chosen are Brassica campestris var. brown sarson [self-compatible (SC) and self-incompatible (SI) supposedly with one-locus control of outbreeding], linseed and wheat which are self-pollinating, Nicotiana rustica and Sorghum which are variable in their outbreeding. The divergence was assessed using Mahalanobis  $D^2$  statistic and the relative contribution of each character to the divergence was estimated according to the procedure

outlined by Rao (1952). Canonical analysis was done as discussed by Anderson (1959). The material was grown during the years 1961-64 at the Indian Agricultural Research Institute, New Delhi.

The characters chosen were the major factors influencing yield, namely, flowering time, height, number of primary branches or tillers, number of secondary branches, number of fruits on main axis and number of seeds per capsule or number of spikelets depending on the crop in the grain crops and leaf size, leaf number and height in  $\mathcal{N}$ . rustica where leaf is the consumable product.

#### RESULTS

Considerable genetic variability was observed for each of the characters in the crops examined. On the basis of the relative contribution of individual characters to the divergence between all the possible pairs of comparisons it was not possible to directly relate the genetic divergence to geographical distribution in any of the crops under consideration. A summary of individual characters contributing maximum to divergence in each crop is presented in Tables 1–3.

# TABLE 1

Percentage contribution of various characters to genetic divergence

(Based on D<sup>2</sup>-statistic)

	No. of	No. of	No. of	No. of
Flow		~~~~~	aamaulaa	aaada

Crops		ering time	Height	mary branches	dary branches	on main axis	per capsule
Brassica	SI SC	$53 \cdot 4 \\ 12 \cdot 6$	$17 \cdot 4$ $32 \cdot 8$	$4 \cdot 7$ 12 \cdot 8	11·1 7·7	$\begin{array}{c} 8 \cdot 3 \\ 11 \cdot 4 \end{array}$	5 · 1 22 · 7
Linseed*		$5 \cdot 8$	$9 \cdot 5$	78.4	2.6	0.5	10.0
		Flow- ering time	Height	No. of tillers	No. of grains per ear	Grain density	1000 grain weight
Wheat		36.9	<b>27</b> .5	5.6	7.5	13.1	9•4
	•	Flow- ering time	Growth rate	Pani- cle length	Distance between whorls	Spikelet num- ber	
Sorghum*		4.0	2.6	6.4	10.4	68.5	
		Height upto panicle	Height	Leaf size	No. of leaves		
Tobacco		24.8	<b>21 ·</b> 0	50•4	3.8		

\*Percentage contribution of other characters studied are not presented.

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# TABLE 2

Relative values of the coefficients in the first two canonical vectors in some crops

Cr	rops	Flow- ering time	Height	No. of pri- mary bran- ches	No. of secon- dary bran- ches	No. of cap- sules on main axis	No. of seed per cap- sule
Brassica	SI						
	$\mathbf{Z}_{\mathbf{I}}$	0.7593	0.5399	-0.2984	0.1866	-0.0800	0.0422
	$\mathbf{Z}_{2}^{T}$	0.1429	-0.2092	0.3615	0.6803	-0.1410	-0.5681
Brassica	SC						
	$\mathbf{Z}_{r}$	0.4351	0.6959	0.2491	-0.2310	-0.0074	0.4604
	$Z_2$	-0.0392	0.4895	-0.0311	0.1458	0.6029	-0.6112
Linseed							
	$\mathbf{Z}_{r}$	0.1408	-0.0544	0.9251	-0.3390	0.0548	-0.0553
	$Z_2$	0.3552	0.6766	-0.1775	-0.4032	-0.0321	0.0873
		Flow- ering time	Height	No. of tillers	No. of grains per ear	Grain density	1000 grain weight
Wheat	_						0.0050

0.2034 0.1074 -0.3191 -0.2972 $\mathbf{Z}_{\mathbf{r}}$ 0.63900.5907

	$Z_2$	0.1511	0.3664	-0.1035	0.1652	0.8850	0.1474
		Flow- ering time	Height	Growth rate	Pani- cle length	Leaf length	
Sorghum							
	$\mathbf{Z}_{\mathbf{I}}$	0.0777	0.0663	0.0219	0.9470	0.3032	
	$Z_2$	0.7138	0.6806	0.0784	-0.1351	0.0493	
		Height up to panicle	Height	Leaf size	No. of leaves		
Tobacco							
	$\mathbf{Z}_{r}$	-0.0158	0.1303	0.9911	0.0063		
	$Z_2$	0.7052	0.6186	-0.0763	0.3372		

In Brassica, it can be seen that flowering time, height and no. of secondary branches and no. of seeds per capsule contributed the maximum to divergence in 87 per cent of the total comparisons in SI types and  $75 \cdot 8$  per cent in SC types. The average  $D^2$  per comparison was 6.99 and 5.12 in SI and SC groups respectively indicating considerable genetic diversity in each category. While height

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#### TABLE 3

## Canonical roots and their percentage contribution to total variation in some crops

	Crops		λı	λ2	Rest	Total	Total No. of roots
Brassica	SI	V	264.9	61.0	68.0	393.9	6
		Р	67·3	15.5	17.2	$100 \cdot 0$	
Brassica	$\mathbf{SC}$	···· V	-137.0	99.5	102.8	339 <b>·</b> 3	6
		Р	40.4	29.3	$30 \cdot 3$	100.0	
Linseed		V	3706.5	917.5	126.2	4750 <b>·2</b>	7
		Р	<b>78</b> .0	19.3	2.7	$100 \cdot 0$	
Sorghum		$\mathbf{V}$	$93565 \cdot 0$	370.6	$239 \cdot 1$	94174 <b>·7</b>	5
8		Р	99.4	$0 \cdot 4$	0.2	100.0	
Wheat		$\mathbf{V}$	$1035 \cdot 0$	731.2	437.8	$2204 \cdot 0$	6
		Р	$47 \cdot 0$	$33 \cdot 2$	19.8	100.0	
Tobacco		V	$50 \cdot 1$	24.9	6.0	81.0	4
		Ρ	61.9	30.7	7.4	100.0	

V-Value of roots; P-Percentage contribution to total variation.

and seeds per siliqua followed by flowering time and primary branches were important in the SC types, flowering time, height and no. of branches contributed the maximum in SI types. However, intraand inter-cluster divergences in both these groups would point to the predominant role of flowering time and height in the intra-specific differentiation in this crop. The importance of seeds per capsule in SC types is expected since, under forced inbreeding, selection for this attribute is important for survival. In the canonical analysis, the coefficients of the first and second vectors have confirmed the above observation. The relative importance of the characters was also substantiated in the canonical analysis as can be seen from the size of the coefficients in Z<sub>1</sub> in SC and SI brown sarson. In the SI types, the coefficient of seeds per siliqua was large in the second vector only as compared to its important role in both the vectors in the SC types. The sign for this character was negative in the second vector in both the types. The estimates for heritability (proportion of additive component) in Brassica var. brown sarson were 0.56, 0.75 and 0.45 for flowering time, height and primary branches respectively indicating predominantly additive gene action for these characters. In linseed also, height, flowering time, number of tillers and number of seeds per capsule were potent forces for divergence. Among them height and number of tillers were the most important (Table 2). This situation was also reflected in the coefficients of the canonical vectors. Additive gene action was predominant for

flowering time, height and number of tillers and non-additive for the rest of the characters. In the case of wheat also, flowering time and plant height along with grain density were the highest contributors. However, grain density and 1,000 grain weight are indirectly influenced by tiller number and grains per ear. The canonical analysis again confirmed the importance of flowering time and plant height.

In the case of sorghum, spikelet number, distance between whorls, panicle length and days to flower contributed to nearly 89 per cent to the total divergence. In the canonical analysis, the coefficient for panicle length was the largest in the first vector. In the second vector, days to flower and plant height were the most important.

In the case of *Nicotiana rustica*, leaf size and height upto panicle which is an indirect measure of flowering time were important in that order. In the first canonical vector, the coefficient for leaf size was the largest. In the second vector, height upto panicle and total height were important. The selection for the vegetative part in this crop might be responsible for the above results. The heritability estimates were  $62 \cdot 5$  per cent for flowering time and  $21 \cdot 1$  per cent for leaf number. In flue-cured tobacco also, flowering time and height were reported to be mostly of additive nature with additive  $\times$  additive interactions in some cases.

The proportion of variation contributed by the first two canonical roots varied from 80.2 per cent to 99.8 per cent in all the crops, the exception being SC *Brassica* in which  $\lambda_1$ ,  $\lambda_2$  and  $\lambda_3$  contributed 40.4 per cent, 29.3 per cent and 12.6 per cent respectively. Moreover, the second root was also quite substantial in all the crops except sorghum.

#### DISCUSSION

The D<sup>2</sup> analysis, canonical vectors and the size of canonical roots have revealed parallel features in the mechanism of genetic diversity in all the crops examined in spite of their contrasting breeding systems. A two dimensional representation of the relative positions of the varieties with regard to divergence using the first two canonical variates as co-ordinate axes was found to be adequate in all the cases (Table 3). Flowering time, height and primary branches or tiller number were, in general, the greatest contributors to divergence in the grain crops. The causes for such a similarity needs to be examined to reassess the present breeding procedures which have been divided into those for self-, cross- and vegetatively-propagated crops separately. While the choice of genetically diverse parents in breeding programmes is recognized, genetic diversity is not quantitatively assessed and is taken as synonymous with phenotypic or even geographical diversity. Moll *et al.* (1962) could not find any direct relationship between geographical distribution and genetic diversity as reflected in heterosis between crosses in maize. Timothy (1963) observed considerable phenotypic divergence between Mexican, Brazillian and Andean maize collection but little genetic diversity between them as measured by the performance of the crosses between them. Geographical distribution and genetic diversity could not be directly related in any of the crops examined in this study also. Genetic drift and selection in different environments could cause greater diversity than geographical distance. However, geographical isolation could be important in the alteration in breeding structure as pointed out by Wallace (1963). Isolation which prevents gene exchange in outbreeders might confirm the advantage of genotypes which can stand inbreeding and more so in disturbed habits as pointed out by Stebbins (1958) who producd evidence that selfers at the diploid level were more restricted in area of distribution than the outcrossing relatives while it was just the reverse at the polyploid level. Any advantage of heterozygotes over homozygotes would also appear to be reduced under cultivation by man. An adequate explanation for this is yet to be obtained. Although most of the crop plants are polyploids, diploidization has occurred for most of the loci in selfas well as cross-pollinated crops. Wright (1940) has pointed out that while the partial isolation of local populations is important for rapid differentiation from other populations, local differentiation within a species based on non-adaptive inbreeding effect or local conditions of selection could permit a very effective process of selection. Therefore, genetic diversity and its relationship to productivity under human selection appears to be quite complex and needs critical investigation. In all the cases examined in this study, the most potent factors for divergence are also those important for fitness under natural conditions, while those selected by man such as seed size have only limited influence. Further, selection by man is for stability with respect to environments. However, heterozygosity or homozygosity cannot be related to stability (Thoday, 1955; Mather, 1960; Beardmore, 1960) but stability is specific for a particular character in each cross and is related to the genotype of the individual as observed by Matzinger (1963). Mather (1960) considers that "heterozygotes appear to be superior in outbreeding species not because of any inherent advantage of their heterozygosity but because they have been adjusted by natural selection while homozygotes are not. " Griffing and Langridge (1963) have also pointed out that self- and cross-fertilized plants are essentially similar in their homeostatic responses. Moreover, variation in inbreeders can be as large as in outbreeders as pointed out by Morley (1959). Therefore, under human conditions, the genetic architecture resulting from the long processes of natural selection is more important than the pollinating system. As pointed

by Wright (1950) many components of fitness have averages near their optimum and variance of fitness for genetic fluctuations of such characters is largely epistatic. However, selection of such components away from their optima could change the epistatic nature of such fluctuations with respect to fitness into that of additive nature. Therefore, components of fitness are more important to the diversity than other characters selected solely by man and have limited relation to the breeding system particularly under cultivation by man.

The nature of gene action in the above characters influencing divergence is summarized below :

Crops	Proportion of additive component to total phenotypic variation							
Crops	Flowering time	Height	Primary branches	Remarks				
Brassica	0.56	0.75	0.49 to $0.58$	Murty, Mather and Arunacha- lam (1965)				
Linseed	0.72	0.75	0.31 to $0.42$	Murty and Anand, 1966				
Wheat	$\begin{array}{l} \text{Additive} \times \\ \text{additive} \\ \text{interaction} \end{array}$	Additive	Additive and additive $\times$ additive interaction					
Sorghum	0.45	0.92	0 <b>·79</b>	N. G. P. Rao, unpublished				
Nicotiana tabacum	Mostly additive	Mostly additive		Matzinger et al., 1962				
Nicotiana rustica	Mostly additive	54.9		(I.A.R.I. unpubli- shed data)				
Pennisetum typhoides	0.72	0.79	0.53					

It is evident that all the above characters are mostly additive or additive and complementary epistatic, although the crops belong to different breeding systems.

Dempster (1963) has also concluded that selection in cross-bred populations is expected to act chiefly on additive variance. The available evidence indicates that additive genetic variance is most important for factors influencing yield such as flowering time, height and no. of tillers in cross- as well as self-pollinated crops. There are very few reliable estimates about the role of epistasis and the dominance variances were biased due to linkage bias (Gardner, 1963). Genotype-environment interactions are found to be important in self- as well as cross-pollinated crops. In conclusion, a direct relationship of the breeding system of crops could not be established with genetic diversity, characters contributing to genetic diversity and their mode of gene action. On the other hand, components of fitness under natural forces have not only contributed maximum to the genetic diversity as assessed quantitatively but were mostly additive in gene action irrespective of the pollinating mechanism. Where human selection was against natural selection such as seed size, dominance and non-allelic interactions of unfixable nature are found to operate. Therefore, it is proposed that the possibilities to formulate common breeding procedures for the group of characters contributing to divergence in both self- and cross-pollinated crops may be explored.

#### SUMMARY

The nature of genetic divergence as assessed by statistical distance and canonical analysis and its relationship to the components of genetic variation in outbreeding populations as in *Brassica*, selfpollinated crops like linseed, wheat and *Nicotiana*, and material with variable degree of outbreeding like sorghum was examined for some components of yield and characters related to fitness.

In general, height, flowering time, tiller number and number of seeds were the largest contributors to genetic diversity in all the above-mentioned crops. The nature of gene action for the above three characters, which contribute substantially to the fitness under natural and human selection, was mostly additive, as compared to the other characters favoured only by man, which were mostly nonadditive. In sorghum also, spikelet number, number of whorls and panicle length were the predominant factors for intra-specific divergence. However, in Nicotiana tabacum, in which selection by man is for the vegetative parts, the degree of heterosis and non-additive components of genetic variance could be related to the divergence. The canonical analysis confirmed the important role of height, flowering time, and tiller number in all the above crops which have different breeding systems. Moreover, neither the proportion of the first two canonical roots to the total nor the coefficients in the canonical vectors could be related to the mode of the natural breeding system.

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The nature of genetic mechanisms influencing the components of fitness in relation to the breeding systems is discussed in relation to the formulation of breeding methods for improving specific characters.

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#### DISCUSSION

S. S. RAJAN : If characters concerned with genetic divergence are the same both in selfpollinated and cross-pollinated crops, does it mean that breeding procedures need not be based on the mating system? Should you not be more concerned with whether the direction of natural selection and human selection are unidirectional or are opposing each other?

For the information of the group, it may be stated that self-compatibility can arise out of self-incompatibility not only by disruptive selection but also by other mechanisms. For instance, characters concerned with pollination are linked and are probably involved in an inversion which restricts recombination.

B. R. MURTY : (1) Breeding procedures are based on the extent and nature of genetic variability which is influenced by the breeding system. The data presented by me has indicated that additive genetic variance was predominant for components of fitness under natural selection, in both self- and cross-pollinated crops examined. If human and natural selection are in the same direction, the above statement still holds good. Where they work in opposite directions, non-additive components play a dominant role in both self- and cross-pollinated crops. The similarity of the results in canonical analysis and D<sup>2</sup> analysis in the three groups of plants studied confirms the parallel features of genetic variation for components of fitness, irrespective of the breeding structure.

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(2) Evidence that disruptive selection for flowering time is one of the major mechanisms for self-compatibility was obtained in our experiments. Other mechanisms are not ruled out.

G. B. DEODIKAR : You indicated lack of overlapping in self- and cross-incompatibles. Do you think that recent trends in the use of male steriles goes against these general trends in natural populations?

B. R. MURTY : I have indicated that the method is potent enough to clearly delineate the self-incompatible and self-compatible categories and even the sub-groups in each category. The role of changes in residual genetic background, under selection, in the changes in the compatibility has been emphasized in our experiments. Use of male steriles by man for exploiting heterosis in crops does modify both the above-mentioned phenomena.

G. B. DEODIKAR : If we are dealing with a genotype adapted to wider range of habitats, does it mean it has more than one canonical vector for channelling the homeostasis process?

B. R. MURTY: The canonical vectors are linear compounds of the characters under study with suitable transformations. The number of canonical roots is the same as the number of characters used in the study. Information on relationship with homeostasis is not available.

K. L. MEHRA : Methods of discriminant analysis and D<sup>2</sup> statistic require mathematical analysis which, at times, are difficult to work with and especially for those workers who are not trained in mathematics. Dr. E. Anderson has presented simple, precise and dependable procedure in metroglyph analysis which has recently been improved by Hatheway. Associated characters could be studied by using simple pictorialized seatter diagram and hybrid index method.

B. R. MURTY : As I pointed out earlier, the choice of the characters which are potent forces of divergence is important in any method of analysis. D<sup>2</sup> analysis has provided a quantitative measure of divergence and the relative contribution of each character to the total divergence between pairs of populations, which is not possible in the method developed by Anderson. Actually, Hatheway has shown that canonical analysis has considerably improved upon the precision and conclusions obtained by metroglyph analysis.

DEVENDRA SHARMA: Previous work has shown that homeostatic mechanism in the populations is a function of heterozygosity rather than polymorphism of the population. Do you think polymorphism in the populations would control homeostatic mechanism in the populations?

B. R. MURTY: Heterozygote superiority is one of the causes of polymorphism in populations and need not be related to the homeostatic mechanisms. Our data in *Brassica campestris* var. brown *sarson* has confirmed the previous findings of Thoday, Beardmore and Harrison on *Drosophila* and mice, that homeostasis is not necessarily directly related to heterozygosity but is a function of the genetic architecture of the individuals and populations, which is a product of long natural selection.

V. L. ASNANI : In your genetic divergence studies, you have studied the components of yield only and have not reported the results on yield as a character. Is it so because, you also think, as Dr. Grafius thinks, that yield as such is not a character and only components of yield are important?

B. R. MURTY : The characters chosen were those influencing yield and some of them also happen to be yield components. My emphasis is on the role of these characters in genetic

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diversity rather than yield itself. I do not wish to comment here about the ideas of Grafius. But I do feel that information on the relative contribution of yield components is also as important as that on the final yield.

A. K. ROYCHOUDHURY : I would like to ask you what are the differences between Fisher's 'discriminant function', Mahalanabis's D<sup>2</sup> statistic and canonical analysis in measuring genetic divergence. If there are differences, then what are the relative advantages and disadvantages of these methods?

B. R. MURTY: In discriminant function, the relative importance of each character used in the function is decided by the breeder and need not be related to the genetic variability for the character. Discriminant function is a linear compound of the first degree. D<sup>2</sup> statistic is a second degree statistic with automatic weightage for each character depending on the second degree statistics of the group of characters concerned. Canonical analysis is another method of multivariate analysis, using the approach of vector analysis.