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EFFECT OF ENVIRONMENT ON THE GENETIC DIVERGENCE AMONG SOME POPULATIONS OF LINSEED

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Selection for rust resistance in Indian Exotic hybrids and for some desirable characters such as high tiller number, large seed size and earliness in crosses between Indo-Gangetic and Peninsular types did not result in anticipated genetic advance in spite of their diverse geographical origin. Reports on similar selection studies indicated that the residual genetic background could substantially alter the degree of association between characters (Jeswani, 1962; Pfahler, 1965). It was felt desirable, therefore, to study the nature of genetic divergence among some lines of linseed and their exotic and indigenous parents and to examine the nature of differentiation between the Peninsular and Indo-Gangetic types belonging to diverse agro-climatic regions. The results of such a study conducted over two seasons are reported in this paper.

Materials and Methods

Seventeen Indian varieties of which seven were of Peninsular (P), ten of Indo-Gangetic (G) and three of exotic origin (E) were grown in two rows of 3m length in four replications during 1961–62 and 1962–63 at the Indian Agricultural Research Institute, New Delhi. The spacings between and within rows were 30 and 10 cms respectively. Observations were recorded on a random sample of 40 plants in each variety on characters related to yield, namely, height, height at branching, number of tillers per plant, number of fruit-bearing branches, number of seeds per capsule in 1961–62 and flowering time along-with these characters in 1962–63. Height was measured from the ground to the tip of the main axis. The height at which branching started was measured as the distance from the ground to the point where the fruit-bearing secondaries started on the main tiller. Only those tillers which had a minimum of five capsules were included for observations on tiller number. The number of branches which bore capsules were counted as fruit-bearing branches. The material was classified into groups on the basis of genetic divergence measured by D^2 statistic, as described in Rao (1952).

Results

A study of varietal means (Table 1) indicated that the variance for the height at branching was more than that for total height. A major portion of this variance for height at branching is contributed by the exotic parents. In the variety Afghanistan-2, the differences between these two heights were minimum in 1961–62 which was confirmed by the flowering pattern also. In this variety, tillering was highly non-synchronous with a majority of the tillers being produced late in the season resulting in poor capsule set and development.

INTER- AND INTRA-GROUP ANALYSIS

The differences among the varieties were significant for all the characters in both the years (Table 2). The variation between the groups, P, G and E was significant for all he characters except number of tillers per plant and number of fruit-bearing branches for 1962–63 (Tables 1 and 2). The variation within each of the three groups was also considerable for practically all the characters.

TABLE 1

Mean values for six characters for 20 *populations of linseed* (1961–62 *and* 1962–63)

Name of Variety			A	B	C	D	E	F	K
N.P. 11	P	I	44·5	23·0	6·1	26·6	65·1	6·1	—
		II	48·2	26·3	7·3	37·7	98·0	8·2	86·9
N.P. 12	G	I	49·5	31·2	5·1	28·4	86·9	7·0	—
		II	54·8	32·6	9·6	65·5	156·8	8·8	97·1
N.P. 122	G	I	53·6	28·2	4·0	26·3	81·8	7·1	—
		II	57·6	34·3	6·8	31·9	116·2	8·7	92·2
N.P. 124	G	I	46·8	30·6	5·9	43·2	124·3	7·1	—
		II	52·1	32·7	9·1	61·1	149·5	8·5	97·0
T. 1193	G	I	59·1	32·3	5·0	39·2	86·6	7·0	—
		II	62·2	38·6	5·9	51·4	115·7	8·2	86·8
H 614–1–11	G	I	59·1	33·0	3·3	21·2	71·5	7·4	—
		II	59·3	35·4	4·5	30·3	95·3	8·5	82·4
N. 55	P	I	51·1	25·5	6·3	35·0	67·6	6·3	—
		II	53·9	30·8	8·0	48·4	95·0	8·3	85·3
X 4–29	P	I	49·0	26·9	4·4	29·3	60·2	7·1	—
		II	54·5	31·0	7·7	50·0	119·6	8·6	89·7
M 10	P	I	48·9	22·8	6·9	40·1	95·2	5·8	—
		II	52·4	26·8	7·8	48·1	105·8	7·6	79·6
Mayurbhung	G	I	53·1	26·1	4·9	29·8	72·2	8·1	—
		II	58·2	30·0	6·8	39·3	126·1	8·6	84·5
Afghanistan-2	E	I	95·8	90·8	7·7	48·3	58·5	8·6	—
		II	99·7	71·0	7·6	61·1	128·7	8·6	121·4
Wada	E	I	100·0	61·2	2·9	20·6	53·3	8·3	—
		II	108·7	71·6	4·2	28·7	64·5	8·6	89·1
A 17–1–1	E	I	73·6	46·8	4·4	36·2	52·3	7·6	—
		II	79·3	52·0	7·8	69·5	132·8	8·4	103·8
NP (RR) 9	G	I	59·2	34·1	4·9	30·8	76·4	6·5	—
		II	65·7	38·6	6·7	48·0	121·7	8·4	91·1
NP (RR) 37	G	I	48·4	27·1	5·4	32·1	75·0	7·1	—
		II	53·0	30·2	7·8	58·7	145·9	8·6	88·6
NP (RR) 38	G	I	46·3	26·2	4·8	29·4	66·2	6·2	—
		II	49·2	29·6	6·4	36·2	86·4	8·3	87·2
NP (RR) 45	G	I	51·2	27·3	6·0	31·8	80·4	7·0	—
		II	59·8	34·7	8·2	62·5	149·4	8·1	91·7

TABLE 1 (Contd.)

Name of Variety			A	B	C	D	E	F	K
NP (RR) 204	P	I	46·8	24·8	3·4	25·4	61·7	6·0	—
		II	53·9	30·9	5·1	45·9	109·8	8·2	81·7
NP (RR) 267	P	I	51·9	31·7	4·7	25·5	53·1	6·1	—
		II	58·9	36·8	6·4	45·6	96·5	8·4	92·0
Mohaba	P	I	53·7	25·9	4·9	20·5	42·9	7·1	—
Local		II	62·8	33·4	6·0	42·7	113·5	8·4	83·7
	P	I	49·4	25·8	5·2	28·9	63·7	6·4	
		II	55·0	30·8	6·9	46·9	105·5	8·3	
	G	I	52·3	29·6	4·9	31·2	82·1	7·1	
		II	57·2	33·7	7·2	50·1	126·3	8·5	
	E	I	89·8	66·3	4·9	35·0	54·7	8·2	
		II	95·9	64·9	6·6	53·1	108·7	8·6	

A—Height (cm.); B—Height at branching (cm.); C—No. of tillers; D—No. of fruit-bearing branches; E—No. of capsules per plant; F—No. of seeds per capsule; K—Flowering time (days); I—1961–62; II—1962–63; P—Peninsular types; G—Indo-gangetic types; E—Exotic types.

The mean values of P, G and E revealed that the exotic types were taller with a large number of fruit-bearing branches and seeds per capsule and approximately equal number of effective tillers (Table 1). Among Indian accessions, Gangetic types were significantly taller and had more number of capsules per plant and seeds per capsule than the Peninsular types. F. Wada, a flax type, was found, as expected, to possess less number of tillers per plant, fruit-bearing branches and capsules per plant than the other exotic types.

A major portion of the variation among populations for all characters except tiller number and number of fruit-bearing branches was accounted for by the inter-group comparison although considerable differences could be observed within groups also in both the years. This was particularly true among the exotics where the variation was much pronounced. The number of productive tillers was of the same order in Peninsular and Indo-Gangetic types under a favourable environment (as in this investigation) indicating that the alleles for high tiller number were not lost in the Peninsular types.

The intra-group analysis revealed greater homogeneity for flowering time in the Peninsular types (range of 7 days) than in the Indo-Gangetic (range of 14 days) and the exotic (range of 23 days) types.

The range of variation for tiller number in the Indo-Gangetic types was more than twice that in the Peninsular types. This pattern was, however, not reflected in yield due to the non-synchronous tillering of Indo-Gangetic types.

WILKS'S Λ AND D^2 ANALYSIS

The differences among the varieties for the aggregate of six characters

TABLE 2

Analysis of variance of means for some characters in linseed

Source	d.f.		Mean sum of squares A†	B	C	D	E	F	K
Varieties	19	I	949·70**	1038·07**	5·70**	226·29**	1339·84**	236·85**	—
		II	1017·60**	658·79**	7·80**	488·33**	2238·86**	7·02**	345·46**
Between P, G, E	2	I	7695·26**	7583·76**	0·77	160·25**	4802·38**	1345·70**	—
		II	8055·15**	5410·93**	1·98	181·89	3992·75**	13·44**	1570·62**
Within P, G. E	17	I	156·10**	267·99**	6·28**	234·06**	932·48**	106·40**	—
		II	189·65**	99·71**	8·49**	524·38**	2032·52**	6·27**	201·53**
Among P	6	I	38·97**	36·12	6·09**	175·00**	1044·65**	119·77**	—
		II	87·30**	52·66**	4·86**	21·98	352·31	9·21**	76·56**
Among G	9	I	88·78**	35·33	2·59**	154·10**	1054·99**	100·31**	—
		II	98·94**	42·80**	9·18**	563·80**	2299·69**	5·51	96·02**
Among E	2	I	810·41**	2010·57**	23·44**	771·03**	44·67	93·68**	—
		II	904·95**	494·95**	16·26**	1854·20**	5870·89	0·85	1049·52**
Error	57	I	7·18	24·60	0·48	40·16	366·74	25·81	—
		II	9·70	5·49	0·80	96·56	466·46	3·18	6·90

I—1961–62; II—1962–63; *—Significant at 5% level; **—Significant at 1% level; †As in Table 1.

TABLE 3

Cluster means for six characters in linseed (1961–62 *and* 1962–63)

Cluster	A*		B		C		D		E		F	
	I	II	I	II	I	II	I	II	I	II	I	II
I	48·2	51·5	23·8	28·0	6·4	7·7	33·9	48·1	76·0	99·6	60·7	40·3
II	48·5	53·9	28·2	31·8	5·3	8·1	32·4	55·7	82·2	134·6	69·3	42·5
III	55·0	59·6	30·7	35·8	4·2	5·9	28·1	42·2	71·8	109·2	67·0	42·1
IV	53·4	60·5	26·0	31·7	4·9	6·4	25·2	44·0	57·6	119·8	76·0	42·9
V	73·6	79·3	46·8	52·0	4·4	7·8	36·2	69·5	52·3	132·8	76·1	42·3
VI	95·8	99·7	90·8	71·0	7·7	7·6	48·3	61·1	58·5	128·7	85·5	43·1
VII	100·0	108·7	61·2	71·6	2·9	4·2	20·6	28·7	53·3	64·5	82·8	43·1

*As in Table 1.

tested by Wilks' Λ criterion revealed highly significant differences among the populations for both the years.

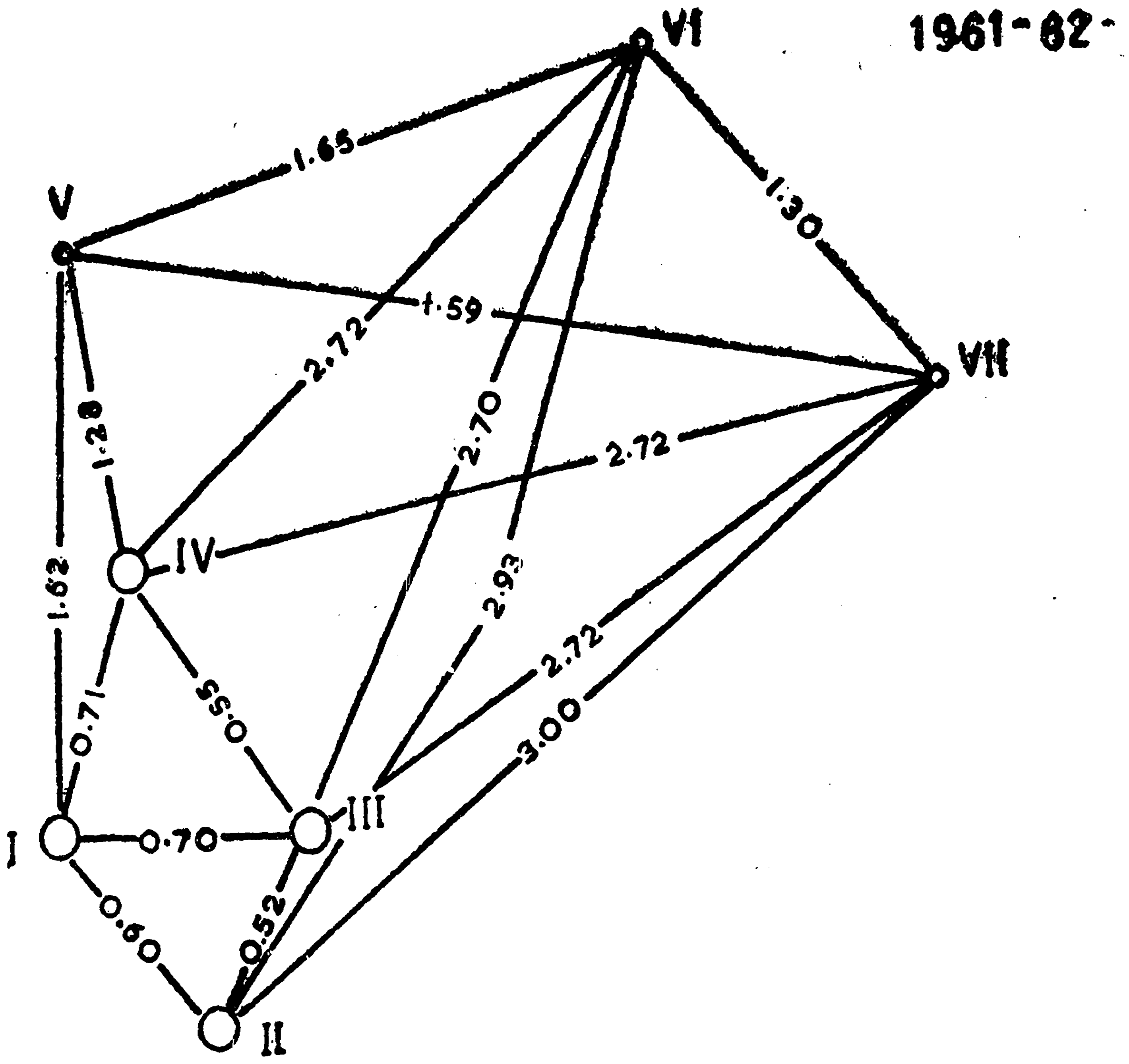
The individual D^2 values were obtained for all the possible pairwise combinations of the varieties for both the years and on this basis, the twenty populations could be formed into seven clusters.

It was interesting to observe that the number and composition of the clusters remained the same in both the years, though the year 1962–63 was found to be better for crop growth than 1961–62. For the same reason, the divergence of the exotic types from others was magnified in 1961–62.

The three exotic types formed three distinct and widely divergent clusters situated in approximately the same positions from each other in both the years. The cluster means have also brought out the differences between exotic and Indian types for all the characters (Table 3). The pattern of the disposition of the clusters was parallel in both the years (Fig. 1 and Table 4). The first cluster contained only Peninsular types while the second had two Gangetic types, three types derived from Gangetic × Exotic crosses and one from Peninsular × Exotic cross. The third cluster had three Gangetic types of which, namely, T. 1193 and H 614-1-11 were exotic derivatives. Two varieties in this cluster were derived from Peninsular × Exotic crosses. Among the two varieties in the fourth cluster, one was a Peninsular type from Malwa tract. The other member (Mayurbhung) of this cluster was considered so far as a Gangetic type. However, it is grown in a region overlapping both the Peninsular and Indo-Gangetic tracts with considerable variability in the agro-ecological conditions due to hills, valleys and forests. It is appropriate, therefore, to consider this variety as an intermediate form between the Peninsular and Indo-Gangetic types. This suggestion is confirmed by its phenotypic appearance as well.

Among the three last clusters, VI and VII were the most divergent from the rest of the clusters. Afghanistan-2 (Cluster VI) and F. Wada (Cluster VII) were close to each other as compard to A 17-1-1 (Cluster V). Although Afghanistan-2 was from a region closer to the Indo-Gangetic area, it was more divergent from the Indian varieties than A 17-1-1. It had also the features of the flax type such as tall habit, late maturity, limited period from flowering to maturity, small capsules and seeds and low oil content. It was highly non-synchronous in tillering characteristic of winter types, which was certainly a disadvantage for oil types. F. Wada, being a flax type, was distinctly different from the rest as expected. One of the reasons for the divergence between Afghanistan-2 and F. Wada could be due to the fact that the former was from a secondary centre of origin while the latter was an introduction from Australia.

The disposition of the first five clusters revealed that cluster V containing an exotic type was distinct from the cluster I, II, III and IV respectievly in 1961–62 and I, II, IV and III in 1962–63 in this order, the relative distances being in the descending order of magnitude.



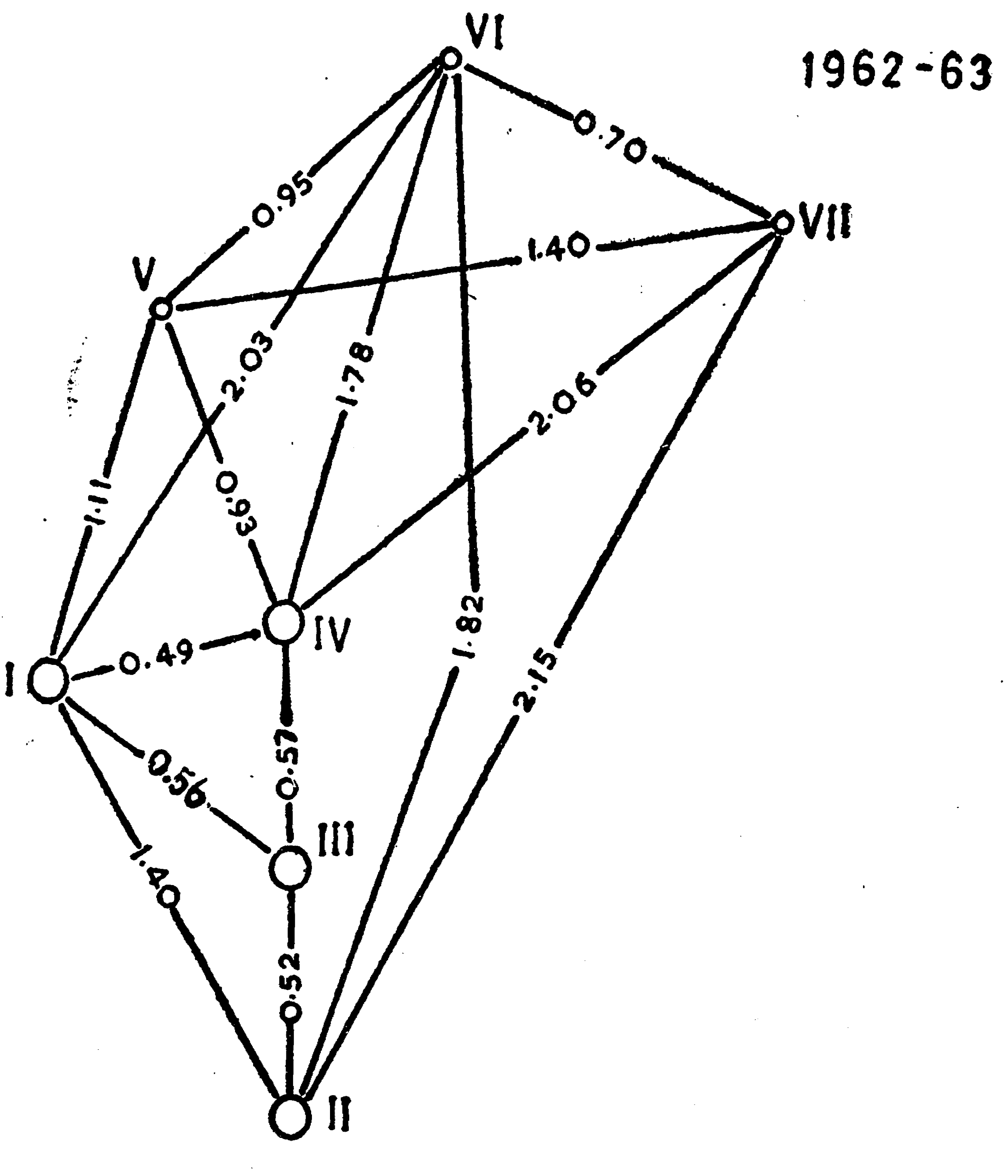


Fig. 1. Group constellations of 20 varieties of linseed on the basis of genetic divergence. I. 1–N.P. 11 (P); 7–N. 55 (P); 9–M. 10 (P); II. 2–N.P. 12 (G); 3–N.P. 122 (G); 4–N.P. 124 (G); 5–T. 1193 (G); 8–X–4–29 (P); 15–N.P. (RR) 37 (G); 17–N.P. (RR) 45 (G); 18–N.P. (RR) 204 (P); III. 6–H–614–1–11 (G); 14–N.P. (RR) 9 (G); 16–N.P. (RR) 38 (G); 19–N.P. (RR) 267 (P); IV. 10–Mayurbhung (G); 20–Mohaba Local (P); V. 13–A–17–1–1 (E); VI. 11–Afghanistan–2 (E); VII. 12–F. Wada (E). P–Peninsular, G–Gangetic, E–Exotic.

TABLE 4

Intra-and Inter-cluster D^2 values in linseed (1961–62 *and* 1962–63)

Cluster	I	II	III	IV	V	VI	VII
I	7·78 6·54	16·11	29·84	28·17	145·07	497·02	542·09
II	14·38	9·48 9·14	19·69	20·74	134·68	493·97	526·55
III	32·20	23·25	14·38 10·69	16·34	83·15	409·82	408·91
IV	29·18	24·25	13·94	9·60 5·25	80·68	397·57	399·20
V	121·65	100·25	60·57	83·27	—	152·39	140·12
VI	408·50	356·75	264·98	307·67	90·89	—	98·18
VII	576·92	498·76	393·32	423·11	202·71	51·21	—

Above diagonal—1961–62; Below diagonal—1962–63

The third cluster closest to cluster V containing A 17-1-1 consisted of one culture, NP(RR) 9 derived from a cross between A 17-1-1 (Cluster V) and NP 124 (cluster II) which occupied an intermediate position between clusters II and V as expected. NP(RR) 267 also belonging to cluster III was a derivative of a cross between NP 11 (cluster I), a Peninsular type and A-2-1 considered to be related to A 17-1-1 (cluster V). The fourth culture in the third cluster was H 614–1-11, a hybrid derivative between an unknown exotic type and a Gangetic type developed in Uttar Pradesh. Its parentage was, however, not available.

The second cluster also contained four (out of the six) varieties derived either from A 17-1-1 or its relatives in crosses with Indian types. It had also two Indo-Gangetic types which were unrelated to any of the exotic types. NP 12 and NP 124 were closely related, the latter being a mutant from the former.

The fourth cluster was surprisingly as close to cluster V as cluster III was, although it had no variety related in any way to A 17-1-1 (Cluster V).

The above results held good and the clustering pattern based on genetic divergence remained stable for both the years.

CANONICAL ANALYSIS

Canonical analysis of the data for both the years broadly confirmed the grouping obtained by D^2-analysis. The diversity of the three exotics from the rest and the relative positions of the members within a culster were clearly brought out. The proportion of variation accounted for by the first two canonical roots were 93·7% and 93·2% respectively in 1961–62 and 1962–63

TABLE 5

Values of the coefficients of the first two canonical vectors Z_1 and Z_2 in Linseed

Year		A*	B	C	D	E	F
1961–62	Z_1	0·7881	0·4019	–0·3239	–0·3294	0·0601	–0·0079
	Z_2	0·1221	0·5798	0·7232	0·2708	–0·1372	–0·1813
1962–63	Z_1	0·8397	0·1909	–0·1373	–0·1714	0·4432	0·1171
	Z_2	–0·0181	0·5087	0·8304	0·0203	0·1290	–0·1349

*As in Table 1.

which were similar in both the years. A comparision of the two canonical vectors (Table 5) brought out the important role of height and the minor role of seeds per capsule for primary and the number of tillers and height at which branching started for secondary differentiation in both the years.

DISCUSSION

The present investigation which was undertaken to study the nature of differentiation of the varieties of linseed grown in two major ecological zones in India-Peninsular region and Indo-Gangetic alluvium and to examine the degree of diversity of new varieties derived by hybridisation between the exotic and indigenous types has shown some interesting results.

It was found that the amount of genetic divergence between any two clusters was not related to the distance between the geographical areas from which they came. One of the reasons could be the arbitrary formation of zones involving national boundaries without an understanding of the selection forces in operation in those areas which would not result in any consistent relation between genetic and geographical diversity as evident in the study of Timothy (1963) and Edwards and Leng (1965) in maize. Actually, Timothy considered the degree of heterosis in crosses between populations as a measure of genetic diversity which is not sound. This is because heterosis is sensitive to any change in the allelic frequencies of the loci controlling the character as a result of sub-division, amount of gene flow, genetic drift and variation in ecological conditions (Dobzhansky, 1963).

The results of this study have also revealed that the inter-varietal divergence was greater in the Peninsular than in the Gangetic types. This could be attributed mainly to the differences in the regions and environments in which they were grown in India. The soil type in the Peninsular tract varies from red laterite to deep clays in the valleys with considerable alluvium also. Consequent retention of moisture during the crop growth could be an important force of natural selection. Further the ranges of day and night temperature are wide in the different regions of the same Peninsular tract, providing diverse ecological conditions for crop growth. The Indo-Gangetic alluvium, on the other hand, has a limited range of latitude, variability in soil, temperature and rainfall.

The peninsular rust-resistant types occurred alongwith the rust resistant Gangetic types in clusters II and III. An examination of the history of this material revealed that screening and selection in the early generations for rust resistance was made only in Delhi and after substantial uniformity is achieved, the material was tested for their performance in different areas. This would normally prove disastrous for recommending material for peninsular tract which has a wide ecological variation. However, this did not happen due to the highly synchronous tillering, early vigour, few secondary branches and larger seed size found in A 17-1-1, the rust resistant donor. These characteristics are also observed in the Peninsular types due, probably, to entirely different constellation of genes. Subsequent selection for rust resistance in the derivatives of (Peninsular types ×A 17-1-1) crosses could be responsible for the resemblance of most of the existing rust-resistant types with the Indian parents.

It was interesting to observe that NP (RR) 9 performs well both in Peninsular and Gangetic tracts. This variety appears to be an intermediate form between Gangetic and Exotic types judged from its phenotypic appearance. Since the exotic rust resistant donors are well adapted to both Peninsular and Gangetic tracts, it is likely that NP(RR) 9 has inherited this characteristic from them. Moreover, it is large-seeded and synchronous in tillering with a few secondary branches like the peninsular types. It appears to have some residual genetic variability which might permit greater homeostasis in variable environments. It is to be examined whether any cytological mechanism in involved for the preservation of this cryptic variability.

Finally, the results of this study suggest that classification of a number of genetic stocks using D^2 statistic provides not only a set of groups from which parents can be chosen for further breeding programmes but indicates that such grouping remains stable over environments. This points to the potency of the method of grouping. It is also worth pointing out that the characters included should be related to the fitness of the population to obtain stability of grouping over environments.

Summary

The nature of differentiation between 20 varieties of linseed of diverse origin was examined over two seasons utilizing multivariate analysis.

The material could be grouped into seven clusters, the three exotics forming three distinct individual clusters. The number and composition of the clusters remained the same in both the years in spite of considerable seasonal differences. The stability of the grouping was confirmed by the canonical

analysis also indicating the utility of multivariate analysis in analysing intra-specific differentiation.

Considerable diversity among the peninsular types was observed which could be related to the diverse ecological conditions within this region. The seven derived types which are rust resistant revealed an irregular pattern of distribution among the clusters but could be related to the region of their adaptation.

The results of the investigation were discussed with particular reference to the breeding programme for linseed improvement in India.

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