

EFFECTS OF DISRUPTIVE SELECTION FOR FLOWERING TIME IN *BRASSICA CAMPESTRIS* VAR. BROWN SARSON

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1. INTRODUCTION

DURING an investigation of the effect of disruptive selection for flowering time on the magnitude of divergence in some populations of *Brassica campestris* variety brown sarson, qualitative and quantitative differential response to such selection was observed depending upon the base population (Murty, 1965). The divergence for flowering time was so substantial after six cycles of selection that it was not possible in some cases to mate the early with the late group as required under disruptive selection. It was felt that a comparison of the progress of response over years under selection in these populations at this stage would be appropriate and was, therefore, attempted. The relative response to disruptive selection as compared to two-directional selection was also examined in one of these populations for a detailed study. A few selections from this material were found to be highly productive under diverse ecological conditions ranging from Punjab to Assam and were found to be superior to the best available strains. Therefore, the nature of their wide adaptation was also examined and reported in this paper.

2. MATERIAL AND METHODS

The material consisted of five populations of *Brassica campestris* var. brown sarson. Two of them were self-compatible and two self-incompatible while one had intermediate degree of self-incompatibility as measured by pollen tube growth and pod and seed set under selfing. Brown sarson is analogous to rape seed of Europe and is grown in India for its edible oil. The crop is grown in the Indo-Gangetic and Brahamaputra plains and adjacent parts of Western and Central India. The investigation was carried out for six seasons from 1961 to 1968. The crop season was delayed due to unusual weather during the year 1965. Therefore, the data of that year were not considered for the analysis. The data on adaptation were based on tests conducted all over India for three seasons from 1966 to 1968.

Sowing was done during the second half of October and harvest completed by the end of March. The plot size was four rows of 15 feet each. The spacings were 24 inches and 4 inches between and within rows respectively. The seedlings were thinned within 2 weeks after sowing to maintain the above spacing within rows. The crop received a fertiliser doze of 80 lb. N + 40 lb. P_2O_5 + 40 lb. K_2O per acre.

The material was grown in a randomised complete block design with two replicates except during the first year when it was grown in four replicates.

The number of days from sowing to first anthesis in each plant formed the basis for selection. The days from the date of sowing to the date when

50 per cent. of the plants in each progeny completed the opening of the first flower was recorded as 50 per cent. flowering time. Other ancillary data on height of the plants (cm.), number of primary branches, number of secondary branches, number of siliquae on main axis, seeds per siliqua and seed yield per plot (g.) were also recorded. Height was measured in centimetres from the base of the plant to the tip of the growing point of the axis at the completion of flowering.

A random sample of 400 plants was chosen from each variety. Disruptive selection was practised only for flowering time selecting 10 early (E) and 10 late (L) plants. The proportion selected was thus 5 per cent. The cross-pollinated nature of the crop automatically permitted the matings among E's and among L's; matings $E \times L$ and $L \times E$ were made possible by bagging together the selected early and the late plants. The scheme was analogous to that of an experiment on *Drosophila* (Thoday, 1959) except that the matings $E \times L$ and $L \times E$ were also included in this study. In the case of directional selection, no mating was permitted between the early and the late plants, but the progenies of the extremes were carried forward. The variability in the progenies within each variety was so substantial that a sample of 400 plants could again be taken and 10 early and 10 late plants could be selected.

The difference between the means of the early group consisting of the selected early plants and that of the late group consisting of the selected late plants in the progeny populations was taken as a measure of divergence which could also be considered to measure the response to selection.

3. RESULTS

The progress under disruptive selection for flowering time was considerable in all the five populations although differences between populations were observed both in the magnitude and asymmetry of response measured as deviation from the base population (table 1). There was some influence of season on the means. However, the divergence between the early and late groups was consistent. There was a consistent increase in the divergence as time advanced in all the cultures although the rates of response differed (fig. 1). The maximum divergence was observed in Kanpur Lotni-17. The divergence between the earliest and the latest was essentially similar in the populations Kanpur Tora 5905, Kanpur Tora 5907 and GBS II. The divergence at the end of the experiment was not found to be related to that in the first cycle. The maximum divergence between the early and the late groups was found in the populations which were consistent and gradual in their response. As observed during the early years (Murty, 1965), the asymmetry of response was opposite to the previous history of selection of the base populations. However, the degree of divergence was not related to the incompatibility reaction of the parental population. The results confirmed the conclusion of Thoday (1959) that disruptive selection would cause rapid divergence.

The extent of variation among the early and the late groups within each population is given in table 2. Considerable uniformity was observed for flowering time among the early cultures of each population and a limited degree of heterogeneity among the latest within the populations. The magnitude of divergence could not be related to the degree of homogeneity

TABLE 1
Changes in number of days to 50 per cent. flowering under disruptive selection in Brassica

Population	Selection	1961-62	1962-63	1963-64	1964-65	1966-67	1967-68	1968-69
Kanpur Lotni-17 (SI)	Early	—	46.7 ± 2.620	43.3 ± 0.974	44.7 ± 1.557	41.0 ± 0.790	42.0 ± 0.000	36.3 ± 2.149
	Late	—	50.0 ± 2.142	63.1 ± 1.483	68.0 ± 2.159	65.6 ± 0.265	77.3 ± 0.771	77.2 ± 0.736
	Difference	—	3.3	19.8	23.3	24.6	35.3	40.9
	Bulk	49.6	48.9	54.8	50.0	51.0	50.0	51.0
Kanpur Lotni-27 (SI)	Early	—	46.1 ± 1.100	42.0 ± 0.614	44.3 ± 0.514	44.1 ± 0.208	43.0 ± 0.845	37.3 ± 1.209
	Late	—	48.8 ± 1.737	52.3 ± 0.180	58.3 ± 2.765	62.4 ± 2.400	65.6 ± 2.234	66.0 ± 2.351
	Difference	—	2.7	10.3	14.0	18.3	22.6	28.7
	Bulk	48.5	48.7	49.8	49.0	50.0	49.0	48.0
Kanpur Tora 5905 (SC)	Early	—	56.0 ± 2.759	43.2 ± 2.252	49.0 ± 0.840	52.0 ± 1.451	42.6 ± 0.848	37.9 ± 2.758
	Late	—	58.6 ± 5.062	65.0 ± 0.487	61.2 ± 1.478	63.9 ± 1.942	61.8 ± 1.602	63.4 ± 1.355
	Difference	—	2.6	11.8	12.2	11.9	19.2	25.5
	Bulk	58.3	58.3	57.6	58.0	61.0	60.0	57.0
Kanpur Tora 5907 (SC)	Early	—	55.7 ± 1.537	55.9 ± 1.966	54.6 ± 1.533	55.6 ± 0.885	48.0 ± 0.755	44.1 ± 1.196
	Late	—	60.5 ± 2.189	66.1 ± 1.407	65.1 ± 3.055	67.1 ± 2.353	70.5 ± 1.821	70.4 ± 2.265
	Difference	—	4.8	10.2	10.5	11.5	22.5	26.3
	Bulk	60.1	56.1	59.9	60.1	60.0	61.0	60.0
GBS II (Intermediate)	Early	—	55.3 ± 2.191	42.3 ± 0.855	43.3 ± 1.181	44.6 ± 1.006	42.4 ± 0.490	37.4 ± 0.704
	Late	—	59.6 ± 2.439	66.2 ± 2.610	62.4 ± 2.547	63.6 ± 2.547	63.6 ± 0.986	65.4 ± 0.913
	Difference	—	4.3	13.9	19.1	19.0	23.0	28.4
	Bulk	57.5	55.3	51.3	52.2	55.0	54.0	53.5

SI = Self-incompatible; SC = Self-compatible; Intermediate = Intermediate incompatible.

observed both within early and within late groups in populations, Kanpur Lotni-17 and Kanpur Tora 5905 which represented the two extremes of divergence. This effect of disruptive selection in maximising divergence between early and late groups was also confirmed by the very high proportion (varying from 98.6 to 99.9 per cent.) of the treatment sums of squares accounted by the comparison having single degrees of freedom, *i.e.* early *vs.* late (table 2).

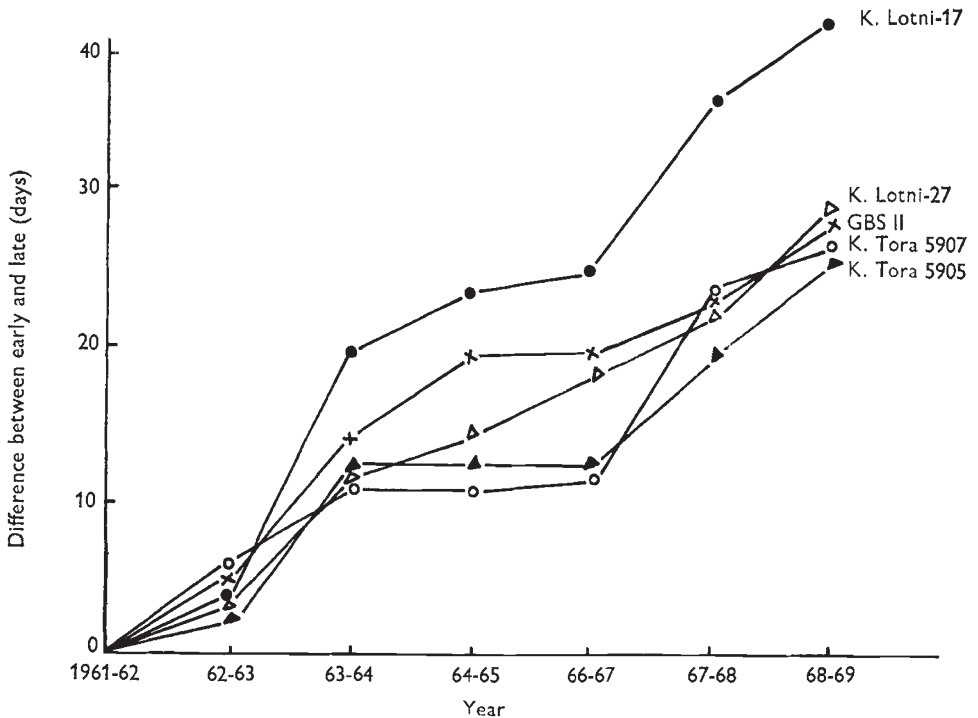


Fig. 1.—Rate of divergence between early and late cultures in five populations of brown *Sarson* under disruptive selection.

The effect of disruptive selection for flowering time was also felt on other characters for which no selection was practised. This correlated response was as large as for flowering time between the early and the late groups (table 3). The magnitude of difference between the early and the late groups for all the traits was almost similar in all the populations. This could be due to the limited difference between the base populations for these traits. In the case of primary branches, the differences were high in Kanpur Lotni-17 and Kanpur Lotni-27 only. Considerable divergence was found for all the populations for secondary branches, siliquae on main axis and seeds per siliqua. These correlated responses could not be directly related to the magnitudes of response obtained for flowering time.

A comparison of the relative changes in the divergence for flowering time under disruptive and two-directional selection had indicated that there was greater response under disruptive selection for flowering time (table 4). The difference for flowering time between early and late groups was nearly 25 per cent. more under disruptive selection as compared to the two-

TABLE 2
*Divergence among and within early and late groups at the end of six cycles
of disruptive selection in five populations of Brassica*

Sources of variation	d.f.	Kanpur Lotni-17	Kanpur Lotni-27	Kanpur Tora 5905	Kanpur Tora 5907	GBS II
Mean sum of squares						
Among earlies	7	36.991	11.714	60.919	12.930†	3.964
Among lates	7	6.496**	44.285	14.705	47.107	4.571
Early vs. late	1	16,252.500* (99.7%)	6612.500* (99.2%)	5151.124* (98.6%)	5867.690* (99.0%)	6441.125* (99.9%)
Error	89	35.997	35.997	35.997	35.997	35.997

† Based on 8 d.f.

* Significant at 1% level.

** Based on 11 d.f.

directional selection (table 4). The difference in the means for other characters between the earlies and the lates was also larger under disruptive selection than under directional selection.

It was observed that the yield of lines obtained from disruptive selection was also better than that from two-directional selection (table 4). Due to the desirable plant type and productivity of some of the early maturing lines from disruptive selection, a co-ordinated trial to compare them with the best local improved type was conducted at 15 locations from Assam to Punjab during 1966-68. The stability parameters (refer Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) for seed yield and days to 50 per cent. flowering for each of the lines is given in table 5. The lines from disruptive selection had regression coefficients ranging from 0.774 to 1.241 for seed yield indicating a linear response of the strains to changing environments; however, DS 17M had average stability with consistently better performance under all the agro-climatic conditions. Similarly these strains were considerably stable (b ranging from 0.894 to 1.152) for flowering time also. Such a diversity in maturity coupled with high yield and consistency of performance over a wide range of ecological conditions would indicate the potential for adaptation of the material generated by disruptive selection.

4. DISCUSSION

The results of the present investigation have provided direct experimental evidence on the useful role of disruptive selection in the improvement of cultivated populations as indicated by Doggett (1965). It has also provided, for the first time, the magnitude of divergence under disruptive selection in quantitative terms. The degree of genetic variability available under selection and the magnitude of divergence in this programme were much higher than those under directional selection (see table 4). Such a release of variability could be due to the exchange of genes and consequent recombination in each cycle of disruptive selection as suggested by Thoday from his work on *Drosophila* (Thoday, 1960; Thoday *et al.*, 1964). The wide adaptation of disruptive selection lines under diverse ecological conditions confirmed that disruptive selection would increase the genetic flexibility of

TABLE 3
Relative changes in the mean performance of some metric traits in five populations of Brassica under disruptive selection for flowering time

	Kanpur Lotni-17		Kanpur Lotni-27		Kanpur Tora 5905		Kanpur Tora 5907		GBS II	
	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late
Plant height (cm.)	1961-62	109.4	104.5	101.8	105.0	116.6	105.0	124.1	116.6	100.0
	1964-65	69.9	109.4	86.9	123.7	82.0	115.8	90.8	124.1	76.6
	1966-67	104.3	150.0	100.8	148.8	104.2	138.5	87.5	141.0	111.4
	1967-68	112.6	131.4	113.2	139.0	124.0	128.4	99.9	124.0	121.9
Primary branches	1961-62	7.3	6.5	7.8	7.6	7.4	6.8	6.1	7.9	6.2
	1964-65	5.6	7.7	5.7	6.8	6.4	10.3	5.2	10.8	6.3
	1966-67	5.0	11.3	5.1	12.2	5.3	10.8	5.2	10.8	6.3
	1967-68	5.7	8.3	5.8	9.4	7.4	7.5	6.6	7.8	7.3
Secondary branches	1961-62	14.2	12.0	22.8	14.3	13.0	12.5	9.6	15.8	12.0
	1964-65	8.6	19.6	8.4	10.7	11.4	18.6	9.0	17.4	15.4
	1966-67	12.3	20.0	10.2	14.6	10.0	19.3	9.0	13.7	14.6
	1967-68	16.1	15.7	13.5	24.8	11.3	16.3	9.8	13.7	14.6
Siliquae on main axis	1961-62	38.3	25.7	34.5	18.1	31.1	36.3	15.7	25.1	20.4
	1964-65	29.8	49.2	22.5	49.5	30.7	51.4	18.0	32.1	27.8
	1966-67	31.3	65.3	23.6	53.3	24.5	50.0	21.3	28.6	36.7
	1967-68	37.6	43.4	32.9	44.4	38.1	37.3	14.1	14.1	17.0
Seeds per siliqua	1961-62	19.1	16.7	21.7	14.1	11.0	16.6	11.8	14.1	11.0
	1964-65	14.0	15.7	12.4	16.1	9.7	12.2	11.8	17.1	14.0
	1966-67	9.5	19.0	12.3	18.5	12.1	18.5	11.8	17.1	14.0
	1967-68	11.6	15.8	11.2	15.1	14.8	14.3	12.4	13.9	14.9

TABLE 4

Relative changes in flowering time and other related traits under disruptive and two-directional selection for flowering time in Kanpur Tora 5907 of Brassica

Year	Selection	Days to 50% flowering		Height (cm.)		Primary branch		Secondary branch	
		DIS	DIR	DIS	DIR	DIS	DIR	DIS	DIR
1961-62	Base	60.1		105.1		7.6		14.3	
1966-67	Early	55.6	59.0	87.5	106.0	5.2	6.1	9.0	7.3
	Late	67.1	68.0	141.0	134.5	10.8	7.1	17.4	9.8
1967-68	Early	48.0	49.0	99.0	109.0	6.6	6.8	13.7	15.4
	Late	60.5	67.0	124.0	138.3	7.8	7.2	9.8	18.5

Year	Selection	Siliquae on main axis		Seed per siliqua		Average yield/plot	
		DIS	DIR	DIS	DIR	DIS	DIR
1961-62	Base	18.1		14.1		182.5	
1966-67	Early	18.0	33.0	11.8	16.4	336.0	221.3
	Late	32.1	42.7	17.1	14.7	394.0	233.8
1967-68	Early	21.3	27.8	12.4	20.2	335.9	203.8
	Late	28.6	39.4	13.9	15.2	393.9	276.2

DIS = Disruptive selection; DIR = Two-directional selection.

TABLE 5

Stability parameters of some strains derived from disruptive selection in Brassica for seed yield and days to 50 per cent. flowering

Strains	Seed yield per plot (g.)			Days to 50% flowering		
	$\hat{\mu}$	\hat{b}	$\hat{\sigma}_s^2$	$\hat{\mu}$	\hat{b}	$\hat{\sigma}_s^2$
DS ₁	0.814	1.111	0.061	48.600	1.023	2.856
DS ₂	0.711	0.923	0.026	48.946	0.894	1.237
DS 17 M	0.804	0.938	0.017	49.446	0.912	2.804
DS 17 T	0.903	1.241	0.020	46.400	1.152	7.281
DST ₃	0.722	1.014	0.013	47.426	1.119	1.863
DST ₄	0.599	0.774	0.014	48.820	0.901	2.176
Experimental Mean	0.759	1.000	0.000	48.106	1.000	0.000

$\hat{\mu}$ = Varietal average over locations.

\hat{b} = Regression coefficient representing response of the variety to changing environments.

$\hat{\sigma}_s^2$ = Squared deviation from linearity.

the population as indicated by Thoday (1959) as compared to the existing strains developed mainly by directional selection.

Selection, in general, has been directional in several crop plants with little or no gene flow between the two extremes of the population. Hutchinson (1965) and Doggett (1965) postulated that disruptive selection programmes using cultivated, wild and semi-wild forms could be of great use in crop improvement. In fact, substantial variability for seed yield could also be generated by disruptive selection for flowering time alone in this crop (Ram, Murty and Doloi, 1969). Reports from Taiwan also indicated that considerable increase in yield and stability of performance were achieved in soybean by subjecting the hybrid populations to disruptive

selection (Tsai *et al.*, 1967). The variability lost under selection in general is replenished under disruptive selection by the mating system which provides new alleles from the other extreme groups in each cycle. This could be the cause for the better response as compared to that under directional selection. Recombination could add to this response still further.

There is considerable controversy concerning the possibility that disruptive selection may sometime lead to isolation (Thoday and Gibson, 1962; Scharloo *et al.*, 1967; Thoday, 1967). While it would be difficult to establish sexual isolation in the type of experiment undertaken in this study, the quantitative measurement of divergence using multivariate analysis had provided adequate proof of the extent and rapidity of divergence under disruptive selection than under directional selection. Difficulty was encountered in continuing this experiment because it became impossible to cross the early and late selections after six cycles because of the wide divergence in their flowering period. This showed that temporal isolation which gave rise to discrete populations in a disruptive selection experiment in which negative assortative mating was not enforced could be established, as also suggested by Thoday and Gibson (1970). The experiments of Scharloo *et al.* (*loc. cit.*) provided no evidence that isolation played a role under disruptive selection for bristle number in *Drosophila*. However, selection for a character like flowering time which is a major component of fitness under natural as well as human selection (as in this study) could rapidly result in divergence between populations.

As pointed out by Thoday (1959), the release of the latent variability by disruptive selection could be considered to be an important phenomenon for breeding work.

5. SUMMARY

1. The effect of disruptive selection in five base populations of *Brassica campestris* variety brown sarson representing different degrees of self-incompatibility and maturity was examined.

2. As a result of six cycles of rigorous selection pressure, rapid divergence could be obtained between two groups of individuals within the same population even when there was a high rate of gene flow. The rapidity of divergence was so great that, in certain circumstances, it could constitute a base for isolation since temporal isolation for flowering for which selection was exercised, could itself be substantial.

3. The response to selection was found to be skewed and asymmetric since the magnitude of difference between the high and the low groups for flowering time varied with the parental populations having different maturity periods indicating the important role of past history of selection for further response.

4. The relative changes in the means of some traits in the populations have been compared under disruptive and two-directional selection for flowering time.

5. The correlated response observed for several other developmental traits related to flowering time was striking.

6. The heterogeneity between the early and the late groups could not be related with the type of incompatibility reaction.

7. The release of latent variability under disruptive selection has been discussed.

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