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CHANGES IN GENETIC BACKGROUND UNDER SELECTION INFLUENCING THE EXPRESSION OF SELF-INCOMPATIBILITY IN BRASSICA CAMPESTRIS VAR. BROWN SARSON*

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1. INTRODUCTION

In an earlier study of an assessment of divergence among the cultivated forms of *B. campestris* var. brown *sarson*, indications on the role of disruptive selection for flowering time in nature as a major cause for the appearance of SC (self-compatible) forms in otherwise SI (self-incompatible) material were available (Murty, Mathur and Arunachalam, 1965). An experimental verification of the above role of disruptive selection in giving rise to several gradations of self-compatibility from SI forms of brown *sarson* was made, confirming that disruptive selection for a major component of fitness like flowering time would alter the genetic background substantially and consequently change the expression of *S locus* and the incompatibility reaction (Murty, 1965). Subsequent studies on the variability generated by disruptive selection was found to be due to improved recombination, breakage of linkages, release of latent variability making it available for selection and rapidity of divergence coupled with wider adaptation of the material so generated (Ram, Murty and Doloi, 1969). A detailed analysis revealed the more important role of past history of selection than incompatibility reaction in the nature and magnitude of response to selection for flowering time (Murty *et al.*, 1972). The response to selection was found to be higher under disruptive selection than under directional selection.

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Since the intensity, duration and nature of selection will determine the relative changes in the residual genetic background, it is likely that the above material from disruptive selection experiments may provide a further clue whether selection for flowering time can substantially alter the expression of self-incompatibility and the pattern of variation for the measures employed to estimate incompatibility. Such a study will supplement the evidence on the limited but significant correlated changes in self-incompatibility observed and reported earlier by Murty (1965). The present report deals with investigations comparing directional and disruptive selection on the variability for self-incompatibility as measured by fruit set and seed set under controlled pollination.

2. MATERIAL AND METHODS

There were two sets of material in this study. Set I comprised 90 populations derived from the five base populations (bulks) namely, Kanpur Lotni-17 (SI), K. Lotni-27 (SI), Kanpur Tora 5905 (SC), K. Tora 5907 (SC) and GBS II (Inter.) which responded to disruptive selection for flowering time. Out of 85 progenies so generated, 41 were early and 44 late cultures. Similarly 213 populations including the five bulks namely Kanpur Tora 5907 (SC), IARI 117(SC), Assam Local (SI), Pusa BST 2(SI) and GBS I (SI) which responded to two-directional selection for flowering time constituted the materials for set II.

The same material after five cycles of selection in both sets were grown in a randomised block design with two replications for two years during autumn/winter, 1967-68 and 1968-69. The plot size consisted of a single row of 3 metres length, 90 cm apart. The intra- row distance between plants was 15-20 cm. The two characters measuring self-incompatibility, namely percentages of fruit set and seed set under both open and controlled pollinations were recorded in each culture and the base population separately in each set.

These characters were found to be adequate to detect differences in self-incompatibility.

Standard analysis was carried out on an electronic computer IBM 1620 Model II. The percentages of fruit set and seed set under controlled pollination were transformed into arc-sine values before analysis.

3. RESULTS

The proportion of fruit set and seed set under controlled pollination was compared to that under open pollination in both the sets. The comparisons between and within populations and/or selections were also attempted.

Disruptive selection: There was no difference between the base populations and the selections for any of the measures of self-incompatibility (Table 1 and 2a). However, there were significant differences between early and late selections for fruit set under selfing and seed set under open-pollination. The late cultures had larger means than the early cultures. Therefore, self-incompatibility appeared to have more pronounced expression during the early part of the season.

The differences among SC bulks, among SC early selections and among late SC selections were significant for fruit set under selfing. However, there were no differences among SI bulks or among early or among late SI selections. The differences were more pronounced between the SC earlies and the SI earlies. Similar was the situation with lates i.e. SC vs SI late selections where differences were pronounced for fruit set and seed set under selfing only. Therefore, the differences between the two groups of self-incompatibility i.e. SC and SI persisted even after disruptive selection and became more pronounced among early selections. This confirmed that self-incompatibility was the most effective during the early part of the season, in addition to the genotypic differences.

The partitioning of the sums of squares within each population revealed that in one of the two SI populations (K. Lotni-17) and in both the SC populations the differences between early and late selections for fruit set under selfing were significant (Table 2b). However, these differences were not felt on the other characters. Therefore, the effect of disruptive selection towards earliness magnified the differences between the two incompatibility groups and hence the divergence. It was not effective in the late direction.

The intermediate incompatible population, GBS II had lower fruit and seed set under selfing in early selections than in late selections. The means were also intermediate between self-compatible and self-incompatible populations. This supports the earlier finding that incompatibility was intensified for earliness under disruptive selection.

Two-directional selection: There was no difference between bulks and selections for any of the characters except fruit set under selfing for one of the two years only (Tables 3 and 4). During that year, the mean of the selections averaged over all the populations was smaller than that for bulks. When the means for fruit set pooled over years for each population were examined, the bulks had higher means than the selections. However, the situation was reversed in Assam Local and Pusa BST 2, both SI populations.

The differences between early and late selections, were not conspicuous either under open or controlled pollination except in SC populations during 1967-68. However, the differences between and within earlies and lates within each population with different incompatibility specificities were variable and significant in both SC and SI groups of populations.

The differences between SI bulks and SI selections were not significant under selfing. But in the case of SC types they were significant for fruit set only for one year. The differences between SC and SI selections were large for each of the characters, the fruit set and seed set being higher for the SC selections than for the SI selections.

Disruptive vs two-directional selection: Although in both sets many cultures with weak self-incompatibility in otherwise strong self-incompatible populations could be recovered, the frequency was not more under disruptive selection relative to that under two-directional selection. A comparison of their effects on self-incompatibility indicated that disruptive selection altered the degree of self-incompatibility much more than two-way selection (Fig. 1 and 2). The degree was more pronounced in early cultures than in late cultures. The differences between early and late selections under two-directional selection were consistent but marginal and not significant. Therefore, selection forces considerably changed the genetic background of the base populations influencing the expression of self-incompatibility.

4. DISCUSSION

Substantial changes in character association due to changes of genetic background were brought about under disruptive and two-directional selection for flowering time - a vital trait conferring immediate fitness and having a major effect on the breeding system involving *S* locus in brown *sarson*.

Changes in genetic background under selection and breakdown of self-incompatibility:

The proportion of fruit set and seed set under inbreeding in several early and late lines in SI populations revealed that the expression of *S* locus has been considerably modified by changes in residual genetic background under selection. Self-compatibility in an otherwise self-incompatible brown *sarson* could not be accounted by the mutation at S locus alone but could be interpretted on the basis of selection of modifiers to permit week expression of self-incompatibility when threatened by extinction. The breakdown of self-incompatibility under intense selection for morphological and physiological characters in diverse genetic backgrounds has also been reported in *B. oleracea*, *Secale cereale* and *Trifolium hybridum* (Lundqvist, 1960; Thompson and Taylor, 1966; Townsend, 1969). The variable expression of self-incompatibility in cultures within the same population in this study (see Figs. 1 & 2) confirmed the importance of genetic environment. As pointed out by Nasrallah and Wallace (1968), such variable expression of S alleles under inbreeding indicated that genetic mechanisms other than S locus influence the perfection of incompatibility specificities.

According to Lundqvist (1960), the origin of highly self-fertile offspring from self-incompatible parents may be ~~imagined~~ considered along two lines: (i) segregation of new specific combination of modifier genes which act in the offspring plant to impair the pistil reaction to the self-pollen, or (ii) introduction by parental self-gametes of new factors conferring self-compatibility. The latter change might result from (a) mutation of S locus to Sf condition, as also reported by Pandey (1970) in *Nicotiana* or (b) from recombination. Since there was continuous variation for self-compatibility in this study, mutation of S locus could be of no consequence. Moreover, mating preference was developed among early and among late cultures owing to temporal isolation, to a certain extent, during later cycles of selection. This could obviously decrease the degree of heterozygosity. Hence a process affecting recombination will become rarer with decrease of heterozygosity as stated by Lundqvist (l.c.). In addition to modifier genes influencing the expression of S alleles, epistatic genes could also exist in crucifers as reported by Thompson (1967).

Mather (1943) pointed out that a major modifier or switch gene such as S gene could operate in conjugation with the polygenic system. According to him, a change in genetic background could reduce the efficiency of S alleles by a modification of co-adapted polygenic background. While supporting Mather's contention, Denward (1963) stated that if the self-incompatibility reaction was not influenced by modifying genes, an all or none effect should be obtained instead of the continuous variation from complete self-incompatibility to essentially complete self-compatibility. This appears to be true in brown sarson also. As stated by Nasrallah and Wallace (1968), modifier genes may exert their influence through controlling a multitude of factors such as rate of germination and growth of pollen tubes, longevity of ovule function, length of style and rate and duration of synthesis of incompatibility substances. By conditioning these and other responses, modifiers may serve to intensify the activity of the S alleles or to reduce their penetrance. This has been substantiated by pollen tube growth in selfed styles of various categories of F1's representing SC x SC, SC x SI, SI x SI and SI x SC etc. followed by seed set under selfing (Sharma, 1970).

Recently, Pandey (1974) indicated that compatibility can be produced in the SI pollen (but not in SC pollen) by X-radiation also in Nicotiana. However, as stated by Sheppard (1958), a change from outbreeding to inbreeding would usually evolve gradually from a balanced polygenic system adjusted to heterozygosity to atleast partial homozygosity. Recombination - suppressor mechanism, as pointed out by Rajan (1958) could be another cause to overcome long-term disadvantages of shift to inbreeding. Actually, such a chromosomal inversion is closely linked with genes favouring self-pollination in yellow sarson. The possible presence of inversion in SC forms of brown sarson needs to be examined in SC x SI crosses. In a number of such crosses, the seeds per siliqua under open pollination were lower than both the parents indicating the possibility of such a recombination suppressor mechanism. However, this does not appear to be universal since substantial heterosis for seed set was also observed in some SC x SI crosses (Sharma, 1970). Therefore, the nature of differentiation between SC and SI forms of brown sarson does not appear to be so perfect that can completely prevent recombination or cause breakdown of co-adapted gene-complexes as observed in some inter-racial crosses of Drosophila (Wallace and Vetukhiv, 1955).

Factors influencing weakening of incompatibility expression:

The proportion of fruit set and seed set under selfing may not be the true expression of the level of self-compatibility. Substantial influence of weather and seasonal fluctuations was also evident in this study as observed by Leffel (1963) and Townsend (1965) in Trifolium species and by Swamy Rao (1967) in brown sarson. Moreover, the uniform and favourable weather conditions during early part and relatively fluctuating environmental conditions during later part of the crop season to which early and late cultures respectively were subjected could considerably affect the fruit and seed set under controlled conditions. The weakening of the plants with increase in inbreeding might also account for the decrease in the rate of 'High' self-offspring since the self seed set is the product of pollen production and female efficiency (Lundqvist, 1962). As pointed out by Watt (1965), the past history of selection could likely be a more potent factor for inbreeding depression which has equally strong effect on the expression of self-incompatibility. Therefore, appearance of self-compatible plants from otherwise self-incompatible plants of brown sarson or breakdown of self-incompatibility might vary with the past history of the parental population, stringency of selection pressure and seasonal fluctuations.

Consequences of breakdown of incompatibility in breeding of brown sarson

Changes from self-incompatibility to self-compatibility does not appear to be disadvantageous in brown *sarson* under cultivation. As pointed out by Swamy Rao (1967), SI forms might be at advantage under natural conditions and competition. However, in the absence of effective activity of bees and monocropping, SC forms are definitely superior. Owing to their capacity for retaining sufficient heterozygosity due to substantial outcrossing (Cook, 1962; Baker, 1966), SC forms enjoy the advantage of both inbreeders and outbreeders. Self-compatibility also would appear to confer advantage on the populations in disturbed habitats (Stebbins, 1958). This mechanism would prevent gene-flow from neighbouring populations and permit the selection of genotypes favoured by the environment as observed by Grant (1966) in *Gilia*. The advantage of heterozygotes over homozygotes in nature would be reduced under domestication. It would appear that homozygotes might have an advantage depending upon the magnitude of inbreeding depression and spread of genes favouring inbreeding. The net result of the above forces would be a substantial change in the genetic architecture of the populations. ~~followed by the evolution of new races.~~ The diversity within SC and SI forms in the Indian varieties of cultivated brown *sarson* within a limited geographical region of Indo-Gangatic belt confirmed the above conclusions.

5. SUMMARY

Effect of disruptive and two-directional selection for flowering time on the proportions of fruit set and seed set under controlled pollination relative to that under open pollination measuring self-incompatibility was examined in 90 and 213 populations respectively derived each from five different base populations in B. campestris var. brown sarson.

Several cultures with weak incompatibility in otherwise intense self-incompatible populations were recovered under both types of selection practices. However, the frequency was more under disruptive than under two-directional selection. Self-incompatibility appeared to have more pronounced expression in the early cultures than in the late ones. Thus the selection forces considerably modified the residual genetic background of the base populations influencing the expression of S alleles. The variable expression of self-incompatibility in cultures within the same population confirmed the importance of modifier complexes constituting diverse genetic environments.

The probable causes for the breakdown of self-incompatibility or the origin of highly self-fertile offsprings from self-incompatible parents have been elaborated in view of ceadapted polygenic background, epistatic genes, consequent recombination under selection and weather and seasonal fluctuations influencing the perfection of incompatibility specificities. The consequences of such changes from SI to SC forms in brown sarson have also been discussed.

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Table 1. Mean performance of progenies for some traits measuring self-incompatibility under disruptive selection in BRASSICA.

Population	1967-68		1968-69		Pooled over years		
	Early	Late	Early	Late	Early	Late	Bulk
Seeds/siliqua under open pollination							
Kanpur Lotni-17(SI)	21.1	25.5	23.1	22.8	22.1	24.2	22.6
Kanpur Lotni-27(SI)	25.7	28.5	21.8	22.1	23.7	25.3	23.0
Average (SI)	23.4	27.0	22.5	22.5	23.0	24.7	22.8
Kanpur Tora 5905(SC)	19.1	23.0	22.1	22.0	20.6	22.5	19.4
Kanpur Tora 5907(SC)	20.9	19.4	19.9	20.8	20.4	20.1	21.9
Average (SC)	20.0	21.2	21.0	21.4	20.5	21.3	20.7
GBS II (Inter.)	23.8	26.2	22.2	21.2	23.0	23.7	22.9
%Fruit set under open pollination							
K. Lotni-17 (SI)	97.6	98.1	84.2	92.7	90.9	95.4	90.0
K.Lotni-27 (SI)	95.2	97.3	91.0	87.0	93.1	92.1	91.0
Average (SI)	96.4	97.7	87.6	89.8	92.0	93.7	90.5
K. Tora 5905 (SC)	94.5	96.9	89.1	88.3	91.8	92.6	93.0
K. Tora 5907 (SC)	92.6	94.0	89.6	96.3	91.1	95.2	99.0
Average (SC)	93.5	95.5	89.4	92.3	91.4	93.9	96.0

Contd.....

Table 1 (Contd.)

Population	1967-68		1968-69		Pooled over years		
	Early	Late	Early	Late	Early	Late	Bulk
% Fruit set under controlled pollination							
K. Lotni-17 (SI)	6.6	22.3	4.4	21.3	5.5	21.8	9.9
K. Lotni-27 (SI)	7.5	17.3	8.1	16.6	7.8	16.9	5.9
Average (SI)	7.1	19.8	6.3	19.0	6.7	19.4	7.9
K. Tora 5905 (SC)	19.8	33.9	19.6	41.4	19.7	37.6	29.6
K. Tora 5907 (SC)	40.9	75.7	52.2	60.1	41.5	67.4	61.7
Average (SC)	30.9	54.8	36.9	50.8	33.9	52.8	45.7
GBS II (Inter.)	13.8	20.1	19.8	26.1	16.8	23.1	23.2
% Seeds/siliqua under controlled pollination							
K. Lotni-17 (SI)	25.2	37.7	18.5	34.5	21.8	36.1	0.8
K. Lotni-27 (SI)	18.6	26.7	21.2	27.8	19.9	27.7	0.8
Average (SI)	21.9	32.2	19.8	31.2	20.8	31.7	0.8
K. Tora 5905 (SC)	35.2	41.5	34.1	52.1	34.6	46.8	54.8
K. Tora 5907 (SC)	56.7	52.8	64.1	62.4	60.4	57.6	47.7
Average (SC)	46.2	47.2	50.0	57.3	48.1	52.2	51.3
GBS II (Inter.)	29.5	41.5	38.1	45.7	33.8	43.8	10.7

SC - Self-compatible; SI - Self-incompatible; Inter-Partial compatible

Table 2a. ANOVA for some traits measuring self-incompatibility under disruptive selection in BRASSICA.

Sources of variation	DF	Open Pollination				Controlled Pollination			
		Seeds/siliqua		% Fruit set		% Fruit set		Seeds/siliqua	
		1967-68	1968-69	1967-68	1968-69	1967-68	1968-69	1967-68	1968-69
Among treatments	89	13.9	5.5	43.2	141.5	598.5**	600.2**	480.0	605.8
Among bulks	4	12.4	4.5	20.6	25.6	1029.3**	1131.2**	[illegible]*	1582.7* $<$275.0
Between SC bulks	1	9.6	6.2	49.0	36.0	1046.5**	852.6	630.0	1317.7
Between SI bulks	2	0.6	0.1	16.7	14.0	381.5	312.5	104.0	626.3
SC vs SI bulks	1	38.7	11.4	0.0	38.4	2307.6**	3047.4**	262.1	3760.4**
Among selections	84	14.1	5.6	44.8	147.0	584.6**	579.2**	490.8	557.7
Sel. between populations	4	74.4	31.9	105.1	108.2	6674.7**	6506.3**	3066.2*	5052.2**
Sel. within populations	80	11.1	4.3	41.8	148.9	280.0	282.8	362.0	332.9
Among SC selections	32	15.5	6.4	55.9	122.2	547.3**	499.2*	327.3	394.1
Among SI selections	51	11.4	4.3	33.6	162.7	264.2	282.0	456.1	423.5
SC vs SI selections	1	110.1**	46.1*	258.4*	139.0	18117.3**	18300.0**	7491.5**	12634.3**
Bulk vs selections	1	0.3	0.1	2.3	147.2	45.4	236.4	399.1	745.7
Among early selections	40	14.8	5.2	41.0	141.3	341.9	524.0*	572.7	585.3
Among SC early	16	9.9	5.3	46.5	121.7	225.5	532.2*	284.7	428.5
Among SI early	23	13.5	3.7	27.9	160.4	125.6	161.9	500.2	400.2
SC vs SI early	1	125.3**	39.9*	253.8*	13.8	7179.8**	8722.8**	6849.6**	7350.2**
Among late selections	43	12.5	6.1	48.8	153.4	696.7**	568.7**	393.9	504.0
Among SC late	15	17.3	7.8	65.5	121.3	648.7**	366.3	393.7	344.2
Among SI late	27	9.8	4.9	39.8	170.0	291.2	314.2	340.8	394.1
SC vs SI late	1	9.9	10.6	42.4	186.6	12367.1**	10474.2**	1830.9	5868.4**
Early vs late selections	1	56.6*	0.5	25.4	98.2	5466.7**	3238.9**	1377.5	1758.9
SC early vs late	1	78.3**	3.8	62.4	144.4	4174.3**	1963.2*	12.5	591.6
SI early vs late	1	2.5	1.2	0.8	15.1	2722.1**	2172.6**	2554.1*	1751.7
Error	89	11.5	7.3	44.4	114.0	252.2	303.4	489.4	533.1

SC - Self-compatible; SI - Self-incompatible; * and ** - $P < .05$ and $P < .01$ respectively

Table 2b. Within population variances for some traits measuring self-incompatibility under disruptive selection in BRASSICA.

Sources	DF@	K.Lotni-17(SI)		K.Lotni-27(SI)		K.Tora 5905(SC)		K.Tora 5907(SC)		GBS II (Inter)	
		1967-68	1968-69	1967-68	1968-69	1967-68	1968-69	1967-68	1968-69	1967-68	1968-69
Seeds/siliqua under open pollination											
Among earlies	7	13.2	2.9	10.7	2.5	8.3	4.4	7.1	1.4	7.4	4.5
Among lates	7	4.9	3.7	18.1	0.6	3.8	8.3	32.6*	6.6	2.6	9.0
Early vs late	1	0.1	0.9	0.5	0.9	14.9	0.1	69.4*	7.3	14.3	8.0
Error	89	11.5	7.3								
% Fruit set under open pollination											
Among earlies	7	9.7	184.3	50.0	155.9	27.4	202.0	65.1	66.6	18.8	122.3
Among lates	7	17.1	95.3	37.0	246.1*	15.1	170.7	115.4	16.1	72.5	186.8
Early vs late	1	2.1	697.0*	36.1	98.0	45.1	5.3	16.6	386.4	112.5	156.5
Error	89	44.4	114.0								
% Fruit set under controlled pollination											
Among earlies	7	169.6	104.4	116.5	107.7	66.5	356.6	97.8	57.5	44.1	61.2
Among lates	7	527.8*	412.1	118.5	227.7	357.8	323.9	119.3	303.0	126.1	226.4
Early vs late	1	1831.5**	1936.9*	633.7	456.8	502.1	2765.8**	4170.5**	190.2	449.3	309.4
Error	89	252.2	303.4								
% Seeds/siliqua under controlled pollination											
Among earlies	7	712.8	488.5	39.7	308.2	278.5	302.4	59.0	44.2	419.9	134.7
Among lates	7	442.9	388.2	205.6	165.8	344.5	172.8	418.2	511.3	193.0	486.3
Early vs late	1	1220.9	1687.5	410.4	282.6	205.5	1708.2	48.5	14.1	942.9	327.7
Error	89	489.4	533.1								

@ Degree of freedom for "Among earlies" in K.Tora 5907 is 8 while that for "Among lates" in K.Lotni 17 is 11.

* and ** - $P < .05$ and $P < .01$ respectively; SC - Self-compatible; SI - Self-incompatible

Inter - Partial compatible

Table 3. Means for some traits measuring self-incompatibility of progenies under two-directional selection in BRASSICA.

Populations	1967-68		1968-69		Pooled over years		
	Early	Late	Early	Late	Early	Late	Bulk
<u>Seeds/siliqua under open pollination</u>							
Kanpur Tora 5907(SC)	18.2	16.0	18.3	19.9	18.2	18.0	18.2
IARI 117 (SC)	-	17.6	-	18.0	-	17.8	15.6
Average (SC)	18.2	16.8	18.3	19.0	18.2	17.9	16.9
Assam Local (SI)	15.4	13.7	16.1	15.1	15.7	14.4	16.6
Pusa BST 2(SI)	10.5	10.2	15.4	18.7	13.0	14.5	15.6
GBS1 (SI)	18.7	20.3	16.4	16.6	17.5	18.5	20.4
Average (SI)	14.9	14.7	16.0	16.8	15.5	15.7	17.4
<u>% Fruit set under open pollination</u>							
Kanpur Tora 5907 (SC)	95.4	96.6	92.7	94.2	94.1	95.4	95.5
IARI 117 (SC)	-	95.1	-	94.7	-	94.9	93.9
Average (SC)	95.4	95.9	92.7	94.4	94.1	95.2	94.7
Assam Local (SI)	97.9	98.5	91.4	94.4	94.6	96.4	94.5
Pusa BST 2(SI)	98.3	96.5	96.0	96.4	97.2	96.5	98.5
GBS1 (SI)	96.9	98.6	96.7	94.6	96.8	96.6	99.0
Average (SI)	97.7	97.9	94.7	95.1	96.2	96.5	97.3

Contd.....

Table 3 (Contd.)

Populations	1967-68		1968-69		Pooled over years		
	Early	Late	Early	Late	Early	Late	Bulk
% Fruit set under controlled pollination							
Kanpur Tora 5907 (SC)	41.3	61.0	46.2	59.3	43.7	60.2	67.2
IARI 117 (SC)	-	52.0	-	47.3	-	49.6	72.8
Average (SC)	41.3	56.5	46.2	56.3	43.7	56.4	69.9
Assam Local (SI)	4.9	7.0	10.7	11.8	7.8	9.4	4.1
Pusa BST2 (SI)	13.6	15.2	18.3	18.8	15.9	17.0	9.8
GBS1 (SI)	6.2	10.2	14.5	15.8	10.4	13.0	28.5
Average (SI)	8.3	10.8	14.5	15.5	11.4	13.2	14.1
% Seed/siliqua under controlled pollination							
Kanpur Tora 5907 (SC)	52.8	42.1	60.2	59.6	56.5	50.8	49.4
IARI 117 (SC)	-	47.3	-	48.5	-	47.9	54.9
Average (SC)	52.8	44.7	60.2	54.0	56.5	49.3	52.1
Assam Local (SI)	16.4	19.1	29.4	31.2	22.9	25.2	0.1
Pusa BST2 (SI)	26.9	31.7	37.8	37.7	32.4	34.7	27.9
GBS1 (SI)	16.6	27.3	36.4	44.3	25.5	35.8	7.9
Average (SI)	20.0	26.1	34.5	37.7	27.2	31.9	11.9

SC - Self-compatible; SI - Self-incompatible

Table 4. ANOVA for some traits measuring self-incompatibility of progenies under two-directional selection in BRASSICA.

Sources of variation	DF	Open Pollination				Controlled Pollination			
		Seeds/siliqua		% Fruit set		% Fruit set		Seeds/siliqua	
		1967-68	1968-69	1967-68	1968-69	1967-68	1968-69	1967-68	1968-69
Among treatments	212	38.2**	32.2**	43.0**	84.6**	921.6	731.2**	749.9**	659.7**
Among bulks	4	48.2*	8.6	45.5	34.6	1176.5**	2041.7**	1668.2**	158.8
Between SC bulks	1	13.3	2.2	11.2	0.0	29.7	31.4	29.7	41.0
Between SI bulks	2	86.6**	8.2	80.7*	4.7	330.0	326.8**	1911.7**	274.0
SC vs SI bulks	1	6.2	16.0	9.5	129.1*	4016.4**	7481.7**	2819.5**	46.5
Among selections	207	38.1**	32.8**	43.2**	85.9**	921.1**	704.8**	735.3**	671.9**
Between SC sel.	63	17.7	28.2**	45.7**	111.3**	765.3**	548.6**	515.4**	301.1
Between SI sel.	143	41.3**	31.3**	38.9**	75.1**	269.7**	363.3**	580.3**	699.5**
SC vs SI sel.	1	852.7**	527.8**	497.4**	28.4	103889.2**	59374.4**	36761.8**	20073.0**
Bulk vs selections	1	31.5	1.9	0.1	9.2	3.3	958.4**	102.2	135.9
SC bulk vs SC sel.	1	1.4	30.3*	29.7	35.8	7.9	2519.5**	364.9	513.9
SI bulk vs SI sel.	1	26.1	29.2*	14.9	81.7	161.5	117.0	104.1	4.3
Between SC early sel.	15	21.8	31.2**	71.0**	233.9**	743.0**	585.4**	620.9**	224.6
Between SC late sel.	47	16.1	27.8**	38.5**	72.8**	732.1**	544.8**	484.1*	316.9
SC early vs SC late sel.	1	32.2	3.0	1.3	81.6	2665.9**	174.6	400.8	707.9
Between SI early sel.	79	39.0**	33.6**	21.4	70.9**	253.1**	373.0**	588.2**	605.5**
Between SI late sel.	63	44.8**	28.7**	61.4**	81.9**	291.6**	356.9**	565.5**	827.9**
SI early vs SI late sel.	1	9.8	17.6	2.9	27.9	201.4	0.4	885.8	42.6
Error	212	17.0	6.2	20.4	33.1	110.2	59.5	303.9	317.8

SC - Self-compatibility; SI - Self-incompatibility; *,** - $P < .05$ and $P < .01$ respectively

Table 5. General combining ability effects for fruit set and seed set under selfing of ten parents of a 10 x 10 diallel in *Brassica*.

PARENTS		% Fruit set		% Seeds/siliqua	
		1967-68	1968-69	1967-68	1968-69
DS 17M	(SC)	11.30	10.70	3.40	8.50
K.Tora 5905	(SC)	-1.90	-0.06	0.90	0.80
Assam Local	(SI)	-1.50	-1.95	0.50	-5.00
GBS 1	(SI)	-2.90	-0.90	-9.50	0.50
S 472	(SC)	4.20	5.10	2.40	2.50
BS 55-B	(SC)	-0.40	1.90	-1.10	0.10
BS 91-1	(SC)	5.80	1.10	7.10	2.60
GBS II	(Inter)	-4.00	-5.90	2.70	-7.30
K.Lotni-17	(SI)	-4.90	-4.40	-0.10	0.20
K.Lotni-27	(SI)	-6.00	-5.50	-6.30	-2.90

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

INTRODUCTION

Several criteria for measuring the degree of self-incompatibility have been used by various workers in different crop plants, such as, average number of seeds per siliqua, average individual seed weight and total seed weight per pollination in Leavenworthia (Lloyd, 1968); browning of stigma due to oxidation reaction two days after a compatible pollination in Brassica oleracea (Thompson, 1965) and rapidity of transference of cytoplasm in pollen tubes by self-compatible pollen in grasses (Lundqvist, 1961). Equally important as the above measures, is the biochemical analysis of differences in the reproductive organs in contrasting types of self-incompatibility with essentially similar genetic background. Among the chemical constituents which influence the growth of pollen tube, amino acids are important (Tupy, 1961; Kumar and Hecht, 1967) since some of them may be precursors to the enzymes and harmones related to growth phenamenon. Therefore, chromatographic analysis supplemented by precise chemical estimation might help in understanding the major metabolic differences between SC and SI types to plan more detailed biochemical analyses.

The dominance relationship in F1's within and between SC and SI types, might vary with the criteria used. No single criterion may be adequate for determining the extent of self-incompatibility. Therefore, four different measures of self-incompatibility, viz. fruit set and seed set under controlled pollination as compared to that under open pollination, pollen tube growth in the selfed styles of the above F1's and chemical analysis of styles and anthers in two contrasting forms of self-incompatibility have been used in this study. The chemical analysis had to be restricted to only two types due to limitation of time and facility and hence the results may be considered exploratory only.

MATERIAL AND METHODS

The materials for the present study comprised a 10 x 10 diallel (without reciprocals). Five of the parents (DS 17M, Kanpur Tora 5905, S 472, BS 55-B and BS 91-1) were self-compatible (SC), four of them (Assam Local, GBS 1, Kanpur Lotni-17 and K.Lotni-27) self-incompatible (SI) and one (GBS II) with intermediate compatibility (Inter) based on the morphological features described by Singh (1958) and confirmed by pod set under bagging. All the ten parents along with their 45 hybrids were grown in a randomised complete block design with two replications. The plot size was a single row of 3 metres length, 75 cm apart. The distance between plants within rows was 15 cm. The experiment was repeated for two successive years (1967-68 and 1968-69).

Observations on percentage fruit set and seed set under controlled and open pollination were recorded as follows during both years:

Siliquae setting: A total of 150 to 200 buds in each plot were tagged (20 to 25 flower buds/plant) after removing immature buds. Half of them were bagged before anthesis and half left for open pollination. The number of siliquae with atleast three seeds in each were considered as successful and the percentage of fruit set was based on them.

Seeds per siliqua: The number of seeds per successful siliqua, both under bagging and open pollination were recorded. The average number of seeds per siliqua under bagging was expressed as a percentage of those under open pollination. Arc-sine transformation was used for converting the percentages before statistical analysis.

Pollen tube growth in selfed style: A number of buds were selfed 3-4 hours before anthesis in each plot. The styles were collected 48 hours after selfing and fixed in 3:1 acetic-alcohol and transferred 24 hours later to 70 per cent alcohol for preservation. Squashing and staining of styles were done as described by Baker (1963). The length of pollen tubes in the style and length of the style from stigmatic surface to the first ovule in the ovary in atleast ten samples per plot were measured using camera lucida drawings at 50X magnification. The ratio of pollen tube length to style length was determined as follows:

$$LR = \frac{\text{Av. length of pollen tubes}}{\text{Av. length of styles}}$$

Chemical analysis: In addition to the above, a qualitative analysis using one-dimensional paper chromatography (with *n*-butanol-acetic acid and water) for free and total amino acids in the styles and anthers at the time of anthesis was done in two contrasting parents, DS 17M (SC) and GBS 1 (SI). Tryptophan was analysed quantitatively following the colorimetric analysis of Spies and Chamber (1949).

Statistical analysis: Routine analysis of variance for estimating differences among SC and SI populations and Griffing's model (1956) for combining ability effects were used in this study.

RESULTS

The degree of self-incompatibility in the parents and hybrids of the 10 x 10 diallel was assessed by fruit set and seed set under controlled pollination relative to that under open pollination and by pollen tube growth in selfed styles. Chromatographic analysis for total and free amino acids was also carried out in the reproductive organs of DS 17M(SC) and GBS 1(SI) populations at the time of anthesis.

(i) <u>Nature of variation for fruit set and seed set under selfing:</u>

The differences between open and controlled pollinations in the number of fruit set were considerable. However, there were no significant differences between parents and hybrids for these measures of self-incompatibility during two years.

The differences among parents were significant for all the four characters except seeds per siliqua under open pollination (Table 2). These differences among parents were mostly accounted for by the single degree of freedom comparison, SC vs SI for both fruit and seed set under selfing but not under open pollination. The differences among SI lines were not significant for fruit set and seed set under bagging. Similar results were also obtained among SC parents except for fruit set under both open and controlled pollination in one season. Therefore, the differences among parents could not directly be related to the differences between two groups of self-incompatibility although the means were larger for SC group under selfing.

The absence of differences between parents and hybrids indicated that hybridity had no advantage for any of the measures of incompatibility except for fruit set under open-pollination. Among the hybrids, the differences were significant only for seed set under selfing in crosses involving SI parents as females having lower means than crosses involving SC parents as females.

(ii) <u>Pollen tube growth in selfed styles:</u>

The data on pollen tube growth expressed as the ratio of pollen tube length to the style length (LR) in the five SC parents, four SI parents and one with intermediate self- compatibility and in their hybrids have been presented in Table 3. LR greater than 1.0 indicates that the tubes penetrated into the ovary, LR $<$ 1.0 means growth arrested in the stylar tissues and LR = 1.0 shows that the pollen tubes grew to the base of the style but failed to enter the ovary.

Differences were found among the three groups of parents in the degree of pollen tube growth. The tubes in the SC parents invariably showed LR $>$ 1.0 ranging from 1.44 to 2.40 on an average (LR = 1.60 to 3.65 for the longest pollen tube). The intermediate parent also showed LR $>$ 1.0 (i.e. 1.35 for average and 2.70 for the longest tube). While among SI parents, the pollen grains either did not germinate (as in Assam Local and Lotni types) or if germinated, the growth was inhibited in the style (LR = 0.68). These results confirmed the adequacy of grouping the parents among the three incompatibility groups (SC, SI and inter) as made in this study.

The differences in the growth of pollen tubes were substantial among hybrids also. In the F1's of SC x SC or SC x SI type, the value of LR was much larger than 1.0. Therefore, SC types as females permitted good growth of pollen tubes which were frequently seen in the ovary. However, SI x SC crosses gave variable results. In these crosses, the LR values were considerably greater than 1.0 indicating the penetration of tubes in the ovary except in the crosses Assam Local x BS 91-1 where the growth of the pollen tube was arrested in the stylar region (LR $<$ 1.0). In SI x Inter or SC x Inter combinations also the pollen tubes reached the ovary except in the cross Assam Local x GBS II. However, in the SI x SI crosses such as Assam Local x GBS 1, Assam Local x Kanpur Lotni and GBS 1 x K. Lotni types, either the pollen grains failed to germinate or the tube growth was inhibited early in the stylar tissues. Therefore, there would appear to be some specificity of self-incompatibility even among SI parents as evident from the unique behaviour of crosses involving Assam Local, a highly SI type.

The behaviour of BS 55-B (SC) was interesting. Its pollen tube growth was good and the LR $>$ 1.0 even in crosses with highly SI parents like Assam Local and GBS 1 as female parents. Therefore, some specificity prevailed in SC types also in the fertilization of SI types. Some SI types like Assam Local showed strong incompatibility reaction in their F1's whether used as female or male parent. However, a majority of SI types did not show self-incompatibility in their F1's if they were used as pollinators. This pattern of growth of the pollen tubes in selfed styles of different F1's indicated that considerable self-compatibility was exhibited within hybrids involving SC parents either as pollen source or otherwise with some exceptions. However, the crosses involving SI types both as male and female parents exhibited high self-incompatibility.

(iii) Pattern of amino acids distribution in reproductive organs of SC and SI types:

One-dimensional descending paper chromatography was employed after oven-drying the styles and anthers at $60^{\circ} \pm 1^{\circ}C$ temperature. Tryptophan was analysed quantitatively as well.

a) Qualitative analysis: The chromatographic analysis of free and total amino acids did not reveal qualitative differences between anthers and styles of SC and SI parents. Nine amino acids namely cysteine, lysine, histidine, serine, glycine, aspartic acid, glutamic acid, $\mathcal{L}$-alanine and tryptophan were present in free form in all the four samples. In addition, four more amino acids viz. arginine, methionine, tyrosine and phenylanine were also present in bound form in both the groups of plants. Therefore, no qualitative differences between samples could be detected for the composition of free and total amino acids in samples.

(b) Quantitative analysis of tryptophan: The analysis of tryptophan on the basis of dry samples revealed distinct differences among SC and SI samples (see below).

Sample	Reproductive organ	% Transmittance		Optical Distance		% Tryptophan
		Sample	Blank	Sample	Blank	
GBS 1 (SI)	Styles	20	27	.699	.584	.095
DS 17M (SC)	"	18	25	.745	.602	.120
GBS 1 (SI)	Anthers	32	43	.495	.387	.101
DS 17M (SC)	"	31	42	.509	.377	.110

DS 17M, a self-compatible variety had relatively larger amount of tryptophan in both the styles and the anthers than GBS 1, a highly self-incompatible variety. However, the tryptophan content was higher in the style as compared to the anthers in DS 17M. It was just the reverse in GBS 1.

DISCUSSION

Among the mechanisms permitting retention of variability under simple genetic control, self-incompatibility system has extensively been investigated (Lewis, 1949; Lundquist, 1962; Grant, 1966; Thompson, 1967).

Out of the measures of self-incompatibility, fruit set and seed set have commonly been used. Screening a large number of collections on the basis of these two criteria appeared to be adequate provided these measures are relative to those under open pollination in the same material. This was broadly confirmed by the pollen tube growth in the varieties and hybrids in this study. A biochemical basis to demarcate the two extremes of self-incompatibility was attempted in this study. In spite of broad classification into three major groups of self-incompatibility there was considerable variation within each category. There was some specificity of interaction in the measures of self-incompatibility also in some genotypes in each category in their behaviour in crosses with the members of the other categories or even with the members of the same category. This indicated the significant role of the residual genetic background in modifying the expression of the S. locus. This was substantiated by the considerable magnitude of g.c.a. effects in the SC types as compared to the SI types as discussed on following pages and the absence of significant differences between parents and hybrids indicating lack of any heterozygote advantage.

Dominance relationship in F1's between SC and SI types:

The dominance relationship in F1's between parents of contrasting incompatible types would be expected to alter the seed set under conditions not favourable to outbreeding. If the allele for self-incompatibility was dominant over the allele for self-compatibility, the F1's might be wiped out in the absence of suitable pollinating agencies and a diversity of genotypes in the neighbourhood. On the other hand, if variable levels of dominance were found, natural selection could preserve diversity of forms. Self-incompatibility was found to be completely or partially dominant over self-compatibility in SC x SI or SI x SC crosses in the present study, contrary to the findings of Shaw (1936) but similar to Ockendon (1974) (see Table 4). However, there was some specificity in both SC and SI types with reference to the level of dominance as also observed by Pandey (1973) in Nicotiana. Kanpur Tora 5905 and BS 91-1 among SC types and GBS 1 and Assam Local among SI types were exceptions to other parents. Some SC x SC crosses such as

K. Tora 5905 x BS 91-1 and BS 55-B x BS 91-1 tended to be intermediate for fruit set and seed set under selfing while some SI x Inter hybrids, viz. Assam Local x GBS II tended to be more self-compatible. This would indicate that the present distinction between SC and SI types was not so simple as controlled by one or two loci (Lewis, 1949; Lundqvist, 1962) but involved a more complex system of gene regulation including position effect and changes in genetic background as pointed out by Darlington and Mather (1949), Lewis (1963), Nasrallah and Wallace (1968) and Townsend (1969).

The dominance relationships in crosses with GBS 1, a self-incompatible type, were highly variable depending upon the crosses. Its crosses with some of the SC types, viz. DS 17M, K. Tora 5905 and BS 91-1 were self-compatible while rest of the crosses were self-incompatible. Therefore, it may be useful to investigate the mechanism of self-incompatibility in this material. A similar situation was observed in Assam Local (SI) also.

<u>Biochemical and other measures of self-incompatibility</u>: Among the several criteria used for measuring the degree of self-incompatibility, no single criterion was found to be sufficient. However, a consideration of both fruit set and seed set under controlled pollination relative to that under open pollination was found to be adequate for determining the extent of self-incompatibility in brown <u>sarson</u> in the present investigation.

Study of pollen tubes growth in selfed styles has, by and large, supplemented this fact. The growth of pollen tube might be influenced by the cuticle of stigma (Christ in Linskens, 1965) and concentration of the substance responsible for incompatibility reaction in stigmatic layer as observed by Thompson (1965) in <u>B. oleracea</u>. The synthesis of growth promoting auxins like indole-acetic acid (IAA) could also influence the rate of pollen tube growth in compatible and incompatible matings (Konar, 1958). This should be reflected in the biochemical composition of the styles. Among the amino acids participating in the incompatibility reaction in pollen and style (Tupy, 1961) only tryptophan is of prime importance since it serves as the precursor of IAA (Clark and Mann, 1957; Wilkins, 1969). The larger quantity of tryptophan and its relative distribution in reproductive organs of SC types relative to SI types in the present investigation indicated the synthesis of more IAA in the former, thereby promoting faster cell-elongation as suggested by Konar (l.c.) in SC styles than in SI styles. Therefore, the incompatibility reaction of these populations could be due to metabolic blocks of protein synthesis in the styles as pointed out by Kumar and Hecht (1967) in _Oenothera organensis_. Since these results are based on a limited material, generalization is not possible.

In the SC types, the g.c.a. (general combining ability) effects for fruit set and seed set under controlled pollination were the maximum in the positive direction and negative in the SI types. The differences were more pronounced for fruit set which must be useful in a rapid assessment of self-incompatibility (see Table 5).

Thus, the adequacy of fruit set and seed set under selfing as measures of self-incompatibility was confirmed. However, these characters are likely to be influenced by the weather conditions and size of the sample which should be considered while drawing conclusions. Therefore, a large sample of individuals and a sufficient number of flowers on each plant throughout the flowering period is essential for the study of a population for self-incompatibility to avoid errors due to changes in incompatibility with season or phase of growth as indicated by Cook (1962).

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Table 1. Mean performance of parents and hybrids belonging to different incompatibility groups for seeds and fruit set in *Brassica*.

Cross combinations or parents	Frequency	Open pollination				Controlled pollination			
		Seeds/siliqua		% Fruit set		% Fruit set		% Seeds/siliqua	
		1967-68	1968-69	1967-68	1968-69	1967-68	1968-69	1967-68	1968-69
SC selfed	5	16.2	21.9	95.9	93.1	35.5	39.4	40.8	50.3
SI selfed	4	19.4	20.7	91.9	95.2	7.8	9.6	15.8	22.5
Inter selfed	1	15.8	23.2	100.0	100.0	12.0	13.0	5.5	6.6
Parents	10	17.1	21.9	95.9	96.1	18.4	20.7	20.7	26.3
SC x SC	10	16.0	22.0	95.8	96.0	30.3	38.6	44.1	39.4
SC x SI	14	16.3	22.5	98.3	96.5	14.0	18.9	38.1	38.4
SC x Inter	5	15.5	22.7	98.2	96.1	17.2	14.6	42.2	35.5
SI x SI	6	18.2	22.9	99.0	98.3	13.6	21.5	19.4	25.0
SI x SC	6	18.5	21.6	98.3	96.0	23.9	29.6	34.4	26.0
SI x Inter	2	16.2	22.2	96.4	98.0	26.0	28.5	58.5	32.1
Inter x SI	2	21.9	25.2	99.5	93.3	15.0	17.8	59.4	20.5
Hybrids	45	17.5	22.7	98.0	96.3	20.0	24.2	42.3	31.0

SC - Self-compatible; SI - Self-incompatible; Inter - Intermediate compatible

Table 2. ANOVA for traits measuring self-incompatibility in a 10 x 10 diallel in Brassica.

Sources of variation	d.f.	Open pollination				Controlled pollination			
		Seeds/siliqua		% Fruit set		% Fruit set		% Seeds/siliqua	
		1967-68	1968-69	1967-68	1968-69	1967-68	1968-69	1967-68	1968-69
Among entries	54	25.4	15.5	48.1**	23.8	310.2	289.6*	853.6**	732.5**
Among Parents	9	26.0	9.1	149.2**	39.6	523.5*	671.2**	1058.7**	1035.8**
Among SC parents	4	14.0	11.6	131.1**	32.5	277.0	484.0*	39.3	209.5
Among SI parents	4	36.6	8.2	197.5**	44.4	40.3	65.7	54.1	235.2
SC vs SI parents	1	31.2	2.3	28.8	48.7	3442.7**	3842.0**	8954.9**	7543.3**
Among Hybrids	44	25.8	16.9	25.4	20.0	278.1	240.7	815.3**	899.0**
Parents vs hybrids	1	3.9	11.9	138.6*	47.6	2.1	0.6	694.7	0.3
Error	54	19.4	12.1	25.6	25.5	216.8	175.9	344.3	302.5

* and ** - $P < .05$ and $P < .01$ respectively

SC - Self-compatible, SI - Self-incompatible

Inter parents were pooled with SI parents in this analysis.

Table 3. L.R. (length ratio) of pollen tube to style after 48 hours of pollination in selfed styles of parents and their hybrids in *Brassica*.

PARENTS	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	Mean
P1 - DS 17M (Self-compatible)	2.40 (3.10)	2.00 (3.40)	.80 (1.20)	1.20 (1.80)	NR	NR	E	1.90 (2.00)	1.30 (1.92)	*	1.44 (2.06)
P2 - K.Tora 5905 (Self-compatible)		1.94 (3.65)	.91 (1.27)	1.29 (1.73)	1.84 (2.15)	NR	*	1.95 (2.50)	NR	1.50 (1.83)	1.58 (2.15)
P3 - Assam Local (Self-incompatible)			NG	NG	.59 (.82)	1.75 (2.53)	.84 (1.20)	.90 (.90)	.54 (.58)	.68 (.82)	.85 (1.17)
P4 - GBS 1 (Self-incompatible)				.68 (.68)	1.02 (1.44)	2.37 (3.35)	2.76 (3.85)	3.43 (4.51)	NR	NG	2.01 (2.78)
P5 - S472 (Self-compatible)					NR	1.17 (1.25)	NR	1.36 (1.62)	NR	2.26 (2.26)	1.37 (1.60)
P6 - BS 55-B (Self-compatible)						1.44 (1.60)	NR	NR	NG	1.42 (1.78)	1.70 (2.23)
P7 - BS 91-1 (Self-compatible)							NR	1.50 (1.92)	2.03 (2.59)	1.43 (1.57)	1.71 (2.23)
P8 - GBS II (Intermediate compatible)								1.35 (2.70)	NR	NG	1.84 (2.24)
P9 - K.Lotni-17 (Self-incompatible)									NG	NR	1.29 (1.69)
P10- K.Lotni-27 (Self-incompatible)										NG	1.46 (1.65)

NG - No germination; * - germination occurred but tubes failed to break stigmatic surface.

E - Empty pollen grains i.e. no germination; NR - Data could not be recorded

Figures in brackets are the maximum L.R. values recorded.

Table 4. Dominance relationship in crosses between SC and SI types in *Brassica*.

PARENTS		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
P1 - DS 17M	(SC)	SC	SC	SI	SC	SC	SC	SC	Inter	Inter	SI
P2 - K.Tora 5905	(SC)		SC	SC	SC	SC	Inter	SC	Inter	Inter	SI
P3 - Assam Local	(SI)			SI	Inter	SC	Inter	SC	SC	SI	SI
P4 - GBS 1	(SI)				SI	Inter	Inter	SC	Inter	Inter	SI
P5 - S 472	(SC)					SC	SC	SC	Inter	Inter	Inter
P6 - BS 55-B	(SC)						SC	Inter	Inter	Inter	SI
P7 - BS 91-1	(SC)							SC	Inter	Inter	Inter
P8 - GBS II	(Inter)								Inter	Inter	SI
P9 - K.Lotni-17	(SI)									SI	SI
P10- K.Lotni-27	(SI)										SI

SC - Self-compatible; SI - Self-incompatible; Inter - Intermediate compatible