

Combining Ability and Maternal Effects in *Brassica campestris* **L. var. 'Yellow Sarson'**

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Summary. A diallel analysis of combining ability, including maternal effects, genotype X environment interaction and the progress under selection, is reported in three selected crosses of *Brassica campestris* L. var. 'yellow sarson', involving 15 types, including 10 four-valved and 5 two-valved types from different parts of India. Twelve characters, including oil content, were studied in the F_1 generation.

The investigation has revealed only marginal superiority of F_1 's over the parents for most of the characters related to yield. There was no relation between heterozygosity and stability of performance over environments for yield or its components or for oil content. Substantial maternal effects were observed which also interacted with environments. Creation of variation for primary and secondary branches would be essential for changing yield level in 'yellow sarson'. The presence of limited additive variation available for selection for yield components should be augmented by biparental mating the early segregating generations to break linkages, and was demonstrated by the recombinants obtained when this method was adopted.

The magnitude of genotype $-$ environment interactions in this study, as compared with the total genetic components for yield, oil content, number of siliquae on main axis and presence of large reciprocal variances in relation to general and specific combining ability variances for practically all characters, and the large interaction of $\hat{\sigma}^2$ rl, narrowed down the expected effectiveness of selection.

Biparental mating in the three best crosses yielded three new recombinants outyielding the best check T 10 by the margins of 14%, 39% and 15%, respectively, in the yield trial. These recombinants had more primary branches and secondary branches, larger main axes and more siliquae with an increased number of seeds per siliqua, than any of the F_1 's in this study.

Key words: 'Yellow sarson' - Oleiferous *Brassica* - Biparental mating $-$ Combining ability $-$ Reciprocal effects - Maternal effects - Genotype-environment interactions

Introduction

Of the three sub-species of Oleiferous *Brassica campes* $tris$ L., i.e. 'toria' 'brown sarson' (analogous to rape seed) and 'yellow sarson', the last is considered to be the most drought-tolerant and to have the best oil quality. It is self-compatible, bold-seeded and has two-valved and four-valved types. The increase in the number of valves gives the impression of being associated with improved yield although no experimental evidence is available on this aspect. The distribution of 'yellow sarson' in India is localised in large areas of Eastern India, such as Bihar, with good rainfall during the monsoon, and in Western India (Rajasthan) and adjoining provinces with limited rainfall. Although this crop is grown in both these major regions during October-March, after the end of the monsoon, the types from the two regions are distinctly different in many characters related to branching, height and maturity and are adapted to different ecological conditions. This study attempts to examine the general and specific combining abilities (sca) and reciprocal effects, the corresponding interactions over locations and the outcome of selection in the progenies of some of the crosses.

Materials and Methods

The material under study consisted of 15 varieties of *Brassica campestris* L. var. 'yellow sarson' selected on the basis of geographical origin and productivity. Ten parents were four-valved, namely I.B. 1063, 1077, 43, 23, 1026, 11, 1054, 1078, 1062, 113, and five were two-valved varieties from Uttar Pradesh, i.e. Y.S. 51,

T 151, C4, T 42 and T 10. These were crossed in all possible combinations, including reciprocals. The 15 parents and 210 F , 's were grown at two locations, Delhi $(77^\circ 17'$ E, longitude and 28° $38'$ N latitude), and Pusa, (Bihar) (86 $^{\circ}$ 3' E longitude, 26 $^{\circ}$ 15' N latitude) in a randomized complete block design with three replications during October-March in 1970-71. The subsequent seven generations were grown in Delhi. The two locations, separated by 1400 kms., are in contrast, showing major differences in the fertility of the Indo-Gangetic alluvium, distribution and extent of rainfall, proximity to Himalayan ranges, farming systems followed and growing season. The latter is more fertile, more prone to floods, warmer during the latter period of crop growth and more fertile with silt. In addition, there are differences of latitude and longitude. The latter is a predominant area of 'yellow sarson' while Delhi is the area of the overlapping distribution of both 'campestris' and 'juncea' groups. Each plot consisted of a single row of three metre length for the F_1 's and of duplicate rows of F_2 's. The advanced generations of biparental progenies from F_2 's (BIP¹'s as per Mather, 1971) were grown in four row plots three-metres long. The distance between and within rows was 75 cm. and 10 cm., respectively. Fertilizer was applied at the concentration of 60 kg. $N + 40$ kg $P_2O_5 + 30$ kg. K₂ O/hectare. Sowing was done in the first week of October at both locations. Observations were recorded on twelve characters related to yield and oil content on the F_1 's, six of them on a single plant basis on five plants chosen at random, while six other characters were scored on a row basis. Oil estimation was done on samples from row bulks, two replications from both locations, using a Nuclear Magnetic Resonance Spectrometer supplied by the Joseph Stephan Institute, Llujbjana, Yugoslavia. Combining ability analysis was carried out according to Model I, Method I, as outlined by Griffing (1956). Pooled estimates of general combining ability (gca) and specific combining ability (sca) variances were made as suggested by Daljit Singh (1973).

Results

The analysis of variance pooled over two locations (Table 1) based on individual plant data revealed large and significant differences between entries, between locations and between location x entries interaction for all the twelve characters. Analysis was also carried out on row means and will be mentioned where necessary. The differences among the parents, among the F_1 's and between the reciprocals were also highly significant for most of the characters. Interaction between parents and locations were not significant except for seed size and days to flower.

The hybrids were taller than the parents and also significantly superior to them in number of primary branches, length of main axis and length of siliqua, but similar to the parents in the number of secondary branches and seed per siliqua, indicating heterosis in the desired direction for some yield components.

The parents as a group and hybrids as a group showed significant interactions with environments for ten of the twelve characters. Thus, hybrids were no more stable than the parents over environments for any of the characters, contrary to findings for maize (Matzinger et al. 1959). Reciprocal effects had also shown significant interaction with environments for all the characters. The influence of locations on the difference between parents vs hybrids was reflected in the large interactions for all the characters, except for number of primary branches, length of main axis and length of siliqua.

The analysis of variance of the six characters based on row means (Table 1) also indicated the presence of significant differences among the parents, among the hybrids and between the reciprocals, for all the characters except 50 percent flowering and seed size in the reciprocals, with significant superiority of the hybrids over the parents.

These results would suggest that the magnitude of heterosis and reciprocal effects have environmental specificity, even for characters like flowering time for which the parents did not show interaction.

Combining Abilities

Pooled analysis of combining ability over locations revealed significant differences in the general combining ability (gca) effects of the parents for all the characters, with large interaction effects of gca, sca and reciprocals with locations (Tables 2, 3).

A comparison of the relative sizes of genetic variance $(\hat{\sigma}_{\rho}^2 + \hat{\sigma}_{\rho}^2 + \hat{\sigma}_{\rho}^2)$ with those of interaction variances $(\hat{\sigma}_{\rho}^2 + \hat{\sigma}_{\rho}^2)$ $\hat{\sigma}_{\rm sl}^2$ + $\hat{\sigma}_{\rm rl}^2$) has been made. The error variance was large when compared with genetic and genotype \times environment variances for primary branches, secondary branches, length of main axis, length of siliqua, days to maturity, seed size, yield and oil content, indicating large sampling errors. In such cases, inferences should be based on single plant data rather than row means. The genetic variance is almost equal to the interaction variance for length of main axis, seeds per siliqua, seed size, weight per unit volume and oil percent. It was much smaller than the interaction variance for primary branches, secondary branches, siliquae on main axis, length of siliqua and yield. Gene action was predominantly non-additive although an additive component was also substantial for five characters, including oil content and 50 percent flowering.

The heritability estimates revealed that selection would be easy for length of main axis, days to flower and maturity, seeds per siliqua and yield. The estimate of heritability for oil content was 11 percent only, which is probably explained by the limited range $(41\% - 44\%)$ among the parents for this character.

¹ BIP's are progenies of crosses between radom pairs of $F₂$ plants

Error d.f. is 448 only for oil percent

Error d.f. is 5400 for the first six characters related to yield on a single plant basis c Error d.f. is 448 only for oil percent
Error d.f. is 5400 for the first six characters related to yield on a single plant basis
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Table 2. Analysis of variance of combining ability and genotype-environment interactions Table 2. Analysis of variance of combining ability and genotype-environment interactions

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a and b significant at 5% and 1% level, respectively a and $\frac{1}{2}$ significant at 5% and 1% level, respectively

General Combining Ability

The pooled estimates of gca effects of the 15 parents for the six characters based on single plant data considered together with the parental means has shown that desirable alleles for different characters are dispersed among the parents (Table 3). The gca effects for the other six characters had also revealed a similar situation.

The combining ability studies indicated that the parents I.B. 1026, I.B. 1054, C 4 and T 10 were the best combiners for both developmental traits and yield components. Therefore, biparental mating was resorted to in the F_2 's of the three best crosses involving the above parents, viz. I.B. 1054 \times T 10, C4 \times I.B. 1026 and T 10 \times T 42, in order to isolate new recombinants by breaking adverse linkages and releasing variability. Thirty BIP's from each cross were carried forward for five more generations, corresponding to the $F₇$ generation by the year 1976 (Table 4). The performance of twelve advanced progenies in 1976 is given in Table 5. Three of them were derived from the cross I.B. $1054 \times T$ 10. They uniformly and significantly outyielded the best check T 10 by 14%, 39% and 15%, respectively. These lines are also superior in plant type to the existing cultivars (Table 4). They have larger numbers of primary branches, larger main axes and more siliquae, compared with the performance of their corresponding F_1 . In addition, these lines have more secondary branches and an increased number of seeds per siliqua, not recorded in any of the F_1 's in this study, and are evidently recombinant products recovered after the breakage of adverse association under biparental mating. The latest data from the All India Trials in 1978-79 has confirmed the wide adaptability of entry No. 11 from I.B. $1054 \times T$ 10 (Table 5).

As the material contained both two- and four-valved types, a comparison of these two groups was made to see if higher valve number would be more productive. The difference between the two-valved and four-valved types were negligible for number of primary branches, length of main axis, siliqua size and seeds/siliqua (Table 4). The F_1 's between the two groups were not superior to those within the respective groups. The situation was similar for seed size and oil content (42-43% in both cases). However, the two-valved types were later by a week and yielded more than the four-valved types. Thus, yield increase **is** not necessarily directly related to the number of valves. This was also reflected in the performance of the crosses between the two groups.

Discussion

The information gathered in this investigation has shown that the F_1 's as a group were equal or only marginally superior to the parents as a group in their means for practically all the characters. Moreover, the F_1 's were not bet-

S.no.		Cross combination			Yield kg/ha generation 790	S.no.	Cross combination C 4 \times 1.B. 1026 BIP-5			Corres- ponding generation F,	Yield kg/ha 811
1.	T 10 \times I.B. 1054 (Check)			F_{s}		8.					
2.	I.B. $1054 \times T$ 10 BIP-5			F_{7}	816	9.	22 $, \,$	$, \,$		F,	750
3.	, ,	, ,	\rightarrow	F,	822	10.	I.B. $1054 \times T10$		Selection 1 $BIP-5$	F_{α}	792
$\overline{4}$.	$, \,$	$, \,$	\bullet	F_{η}	1081	11.	$, \,$, ,	Selection 2 $BIP-5$	F_{σ}	1296c
5.	\rightarrow 3	$, \, \cdot$	$, \cdot$	F_{7}	963	12.	, ,	$, \, \cdot$	Selection 3 BIP ₅	F_{α}	686
6.	$C4 \times I.B. 1026$, ,	F_{7}	699	13.	$\bullet\bullet$, 1	Selection 4 $BIP-5$	F,	1097c
7.	5.5 $, \,$, ,	F,	953	14.	$T10$ (check)				946

Table 5. Replicated yield trial of BIP entries during the year 1976 (four rows, each plot of $10' \times 2'$ rows in three replications)

The first BIP generation corresponds to F_3 *Note:* Crop growth affected in 1976 due to aberrant weather

Presentation of breeding steps followed

In 1977 the best family yielded 23.6 quintal/hectare

a includes progenies of four selected single plants

b 30 BIPs/cross combinations

ter than the parents in their stability over environments for yield or its components and oil content as revealed by the magnitude of the corresponding genotype \times environment interaction. Therefore, heterozygosity per se would not seem to confer stability of yield or its components in this material. The study revealed significant maternal effects and their interactions with the environment. The heritability estimates for yield (20 percent) were higher than those of the major direct components, such as the number of primary and secondary branches, siliqua on main axis and seed size. The exceptions were the seeds per siliqua and length of main axis. This could be attributed to the limited potential for primary branches and the major contribution of main axis and seeds per siliqua to yield in this crop. Therefore, creation of variation for the number of primary and secondary branches would seem essential to improve yield and this was confirmed by the performance of the selected lines (Table 5).

The pattern of variation within and between crosses in the F_1 's and F_2 's revealed only limited additive components available for selection in the F_2 's and intermating in the early segregating generations might be useful to release any concealed variability due to linkage.

The magnitude of genotype-environment interactions, and the significant reciprocal differences in this study for yield, oil content and other attributes influencing yield, could limit the progress of selection in this material if a suitable maternal parent was not chosen.

Reports vary regarding the stability of $\hat{\sigma}_{g}^{2}$ over locations compared with that of $\hat{\sigma}_{s}^{2}$ (Rojas and Sprague 1952; Matzinger et al. 1959). In the present study, the magnitude of $\hat{\sigma}_{\text{sl}}^2$ was larger than $\hat{\sigma}_{\text{sl}}^2$ for several characters. The ratio of $\hat{\sigma}_{\rm s}^2 / \hat{\sigma}_{\rm cl}^2$ could be compared to the ratio of $\hat{\sigma}_{\rm s}^2 / \hat{\sigma}_{\rm sl}^2$. On this basis also, the former is relatively small. Rojas and Sprague (1952) suggested that a large interaction component $\hat{\sigma}_{\rm sl}^2$ would involve considerable instability to the variances and would limit selection. Schutz and Bernard (1967) also observed large $\hat{\sigma}_{\text{sl}}^2$ in soybean. They felt that most of the $g \times e$ interaction could be attributed more to differences in the correlation of one environment with the other environment than to other differences. On the other hand, Sprague and Tatum (1942) observed that variances

of sca is larger in highly selected material. The limited diversity in the elite material of 'yellow sarson' in this study could be responsible for the high non-additive component for most of the characters studied, similar to that reported by Sprague and Talum (1942) rather than interenvironmental correlation.

In the serial analysis of combining ability in another oilseed, linseed, (Anand and Murty 1969) postulated that the presence of maternal effects would cause a bias of estimate in combining ability. The presence of large maternal effects for several characters in this study, could also have affected the estimates for other components of genetic variation.

Genotype x Environment Interaction

Assessment of genotype-environment interactions would be useful for identifying material with wide adaptation and acceptable yield level (Comstock and Moll 1963; Eberhart and Russell 1966; Perkins and Jinks 1973; Wright 1976). Wright (1976) cautioned that improvement of stability is associated with increased performance in the poor, at the expense of good, environments. Therefore, in a rainfed crop like 'yellow sarson', it would be useful to supplement variance component analysis with stability analysis. Also, diverse environmental effects could be substantial in epistatic components, as in barley (Jana, 1975). Such a situation was evident in the present study too and was confirmed by large epistatic components, which would limit the effectiveness of selection based on one environment. The present study indicated significant maternal effects for most of the characters except oil content, seeds per siliqua and days to flower. Differences between reciprocal crosses were also considerably influenced by environment for four important characters, namely, siliquae on main axis, days to flower, days to maturity and yield. It is interesting that there were no differences in the overall means of F_1 versus reciprocal F_1 's for days to flower but their interaction with environments was significant. Therefore, choice of specific cross combinations for selection should take into account these interactions. Actually the pronounced maternal effects in oilseeds and their relation to the period available for oil synthesis in the seed needs more investigation, as evident from several such reports in oilseeds, e.g., Craig (1961) in rape, Hemingway et al. (1962) in *Brassica juncea* (coss), Canvin (1965) in sun-flower, and Gross and Stefansson (1966) in rape and turnip rape. Westerman (1971) observed that plants which flower later interact more with the environment than those flowering early. The productivity of selected lines in this study (Table 5) did not show such a relationship. In fact, there would appear to be several situations where the magnitude of interactions cannot be related to any specific category of genetic effects (Mather 1971; Perkins and Jinks 1971). A comparison of early and late parents for yield and oil content has shown very few differences in the period from flowering to maturity. However, the yield differences were large between these two groups. Therefore, earliness for flowering and maturity may be less important for yield than the period available from flowering to maturity. A comparison of the two best F_1 's for yield and two poorest F_1 's has indicated that F_1 performance was not reflected in the F_2 in this study. However, two of the 10 best crosses for yield have shown

ary branches. The presence of maternal effects in sunflower reported by Fick (1975) for oil content was interpreted by him as the effect of mitochondria and chloroplasts in the cytoplasm involved in oil synthesis.

comparable performances in both the F_1 and F_2 generations (Table 5). The oil content of these best crosses varied between 40 to 45 percent while days to flowering varied from 53 to 61 days in contrast to 47 to 48 in the F1 's poor in yield. There was also very limited variation in these crosses for the number of primary branches and seeds per siliqua. Variations was also present for second-

The present study showed that oil formation is influenced by the maternal parent as in crosses with IB 1054. These results were similar to those of Yermanos and Knowles (1962) in flax, Brim et al. (1968) in soybean, Knowles and Hill (1964) in safflower, Jellum (1966) in corn embryo and Kanno et al. (1965) in rape seed. It would be useful to carry out enzymatic studies in oil synthesis and the role of the maternal genotype, as was done in soybean (Singh and Hadley 1968). The selection of an appropriate female in a crossing programme and the study of its biochemical activity for oil synthesis are essential for improving oil content and quality in *Brassiea.*

Crosses between groups representing different constellations of characters should be explored by promoting recombination to alter the adverse associations between oil content maturity and yield. Such a programme using biparental mating has already resulted in the creation of an array of plant types in this study. Some of them with the altered plant frame combined high productivity, oil content earliness (compared to the best available cultivars) and have a good potential for cultivation in the major areas of 'yellow sarson' in this country.

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