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The Inheritance of Partial Self-compatibility in *Brassica oleracea* L. Inbreds Homozygous for Different S-Alleles

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Summary. In a study of partial self-compatibility in *Brassica oleracea*, flower number, seeded siliqua and seed production were recorded on self- and cross-pollinated inflorescences of 32 progenies obtained by inter-crossing and selfing 8 plants homozygous for the incompatibility alleles S_2, S_5, S_{15} and S_{45}.

Progeny differences for both self- and out-cross seed production could be largely attributed to G.C.A. effects which were essentially uncorrelated. For cross-pollinated inflorescences heterosis was also important. Significant differences were found for selfed seed set and its two components, the proportion of flowers producing seeded siliquae and the numbers of seed per seeded siliqua, between parents with the same S-allele which could not be attributed to S-genotype alone. No evidence of increased self-compatibility in particular S-allele heterozygotes (mutual weakening) could be found.

Outcross seed production depended primarily on the numbers of seeds set per seeded siliqua while self seed production was largely determined by the proportion of flowers which produced seeded siliqua. It is suggested that this is a key character for the production of inbred lines with reduced partial self-compatibility.

Key words: *Brassica oleracea* – Partial self-compatibility – Seed production – S-alleles

Introduction

Brassica oleracea has a single locus, multi-allelic, sporophytic self-incompatibility system (Thompson 1957) which is utilised in the production of horticultural and agricultural hybrid cultivars. Unfortunately the incompatibility system often fails to operate with complete efficiency (partial self-compatibility) with the result that inbreds seeds (sibs) are frequently present in hybrid cultivar seed lots.

The degree of partial self-compatibility appears to be controlled by modifier genes (Nasrallah and Wallace 1968; Haruta 1966; Hodgkin 1975) and by the degree of dominance of the incompatibility alleles (S-alleles) present (Thompson and Taylor 1966a). It is also influenced by environmental and physiological factors such as temperature (van Marrewijk and Visser 1975), relative humidity (Carter and McNeilly 1975), age of plant and age of flower (Hodgkin 1976).

Hodgkin (1975, 1978, 1980) studied the mode of action of genes modifying the strength of self-incompatibility and found that the inheritance of self seed production in partially self-compatible plants was complex, but it was possible to identify inbreds which produced fewer selfed seeds because they had a large proportion of flowers with a fully-functional incompatibility system.

In the previous experiments a single recessive or moderately recessive S-allele was used, with the result that no observations were made on the relation between S-allele and the level of partial self-compatibility present, or on the interactions between S-alleles. This paper describes an experiment in which inbred plants homozygous for different S-alleles were intercrossed in order to obtain further information on the inheritance of partial self-compatibility in *B. oleracea* and, in particular, to investigate the effect of different S-alleles on the expression of genes modifying S-allele function.

Materials and Methods

Eight inbred plants (7 Brussels sprout and 1 cabbage) were intercrossed and selfed by bud pollination to give a half diallel with selfs. Of the 36 possible progenies four had insufficient seeds – the selfed progenies of parents 1, 2 and 7 and the crossbred 1-2. The parent plants were homozygous for four different S-alleles; parents 1 and 2 for S_2, parents 3 and 4 for S_5, parents 5 and 6 (the cabbage) for S_{15} and parents 7 and 8 for S_{45}. The dominance relationships of the S-alleles in the parents are as follows (from Thompson and Taylor 1966b; Ockendon 1975; van Hal unpublished):

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S_2 S_5 – S_2 dominant to S_5 in pollen, independant action in stigma
S_2 S_{15} – S_2 dominant to S_{15} in pollen, independant action in stigma
S_2 S_{45} – independant action in pollen, S_{45} dominant to S_2 in stigma
S_5 S_{15} – S_{15} dominant to S_5 in pollen, independant action in stigma
S_5 S_{45} – S_{45} dominant to S_5 in pollen and partially dominant in stigma
S_{15} S_{45} – S_{45} dominant to S_{15} in pollen, independant action in stigma

Mutual weakening between the S-alleles in a number of these combinations has been reported by van Hal (unpublished) and Thompson (1972) and so has partial dominance of S_2 to S_{45} in the stigma. The 32 available progenies were sown into peat blocks and planted to give two blocks in each of which rows of experimental plants alternated with rows of Brussels sprout cultivar used as pollinator (Hodgkin 1978). During the year of flowering (1974) one inflorescence from each of four randomly chosen plants of every progeny in each block was bagged to permit only self pollination. Self and outcross seed set, seeded siliqua production and flower number were recorded from these inflorescences and equivalent unbagged ones as described previously (Hodgkin 1978). The numbers of seeds per flower and its two components, the proportion of flowers giving seeded siliquae and the number of seeds per seeded siliquae were analysed as log transformations using the procedure of Gilbert (1967) which fits additive parental main effects or 'combining abilities' according to the model

$$Y_{ij} = b_i + b_j + \text{interaction}$$

where b_i is the general combining ability (G.C.A.) of the ith parent plus one half of the general mean, b_j that of the jth parent plus one half of the general mean, and the interaction, or specific combining ability (S.C.A.), includes all differences not attributable to parents. Each analysis was performed with and without the selfed progenies included and the analyses of data from bagged inflorescences were done for parents and for S-alleles. Tables of untransformed data are given but the analyses given are based on transformed data. Significance was tested against the pooled within family variance, since block differences were not significant.

Table 1. Means for seed set on unbagged inflorescences of *B. oleracea* half diallel progenies

Progeny	Unbagged inflorescences			Bagged inflorescences		
	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae
3-1	4.78	0.73	6.42	0.83	0.24	2.53
3-2	7.90	0.72	10.98	0.80	0.20	3.24
3-3	3.26	0.64	4.81	2.74	0.47	5.50
4-1	3.82	0.60	5.40	0.83	0.38	2.00
4-2	9.95	0.70	14.23	3.14	0.27	10.67
4-3	5.48	0.77	6.75	4.95	0.59	7.84
4-4	3.87	0.66	5.77	2.07	0.50	3.94
5-1	6.18	0.61	10.30	1.25	0.35	3.19
5-2	11.88	0.75	15.18	1.99	0.32	6.64
5-3	12.03	0.82	14.29	5.89	0.67	8.05
5-4	9.64	0.73	12.87	5.58	0.66	7.87
5-5	2.21	0.32	5.69	1.61	0.37	3.38
6-1	4.90	0.75	6.40	0.41	0.16	2.00
6-2	5.89	0.67	8.21	1.44	0.18	5.53
6-3	6.61	0.68	10.00	1.02	0.24	3.75
6-4	7.14	0.79	9.09	1.06	0.30	4.09
6-5	6.69	0.82	8.21	2.49	0.31	5.91
6-6	0.84	0.28	2.99	0.30	0.09	2.45
7-1	5.77	0.69	9.15	0.35	0.14	1.87
7-2	7.62	0.69	11.49	0.37	0.15	2.81
7-3	7.53	0.74	9.86	0.64	0.19	2.56
7-4	6.46	0.77	8.29	1.06	0.27	3.50
7-5	6.33	0.69	8.83	2.10	0.39	4.03
7-6	5.42	0.63	7.41	0.06	0.04	1.50
8-1	3.92	0.77	5.00	0.44	0.19	2.26
8-2	5.57	0.81	6.93	0.31	0.15	2.11
8-3	6.47	0.77	8.48	0.73	0.26	3.00
8-4	7.07	0.74	9.37	1.07	0.30	3.75
8-5	5.78	0.69	8.57	1.82	0.39	4.06
8-6	5.50	0.63	8.78	0.49	0.18	2.69
8-7	5.40	0.74	7.12	0.74	0.21	3.27
8-8	1.70	0.39	4.20	0.38	0.15	2.64
Mean	6.05	0.68	8.47	1.53	0.29	4.02

Table 2. Analysis of seed production variates (after log transformation) on unbagged inflorescences of *B. oleracea* half diallel progenies

Item	d.f.	Mean squares		
		Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae
G.C.A.	7	3.4746***[a]	1.9432***	1.3828***
S.C.A.	24	2.8790***	1.3693***	0.6520***
Within family variance	199	0.5281	0.3226	0.1681

[a] *** indicates significance at the $P < 0.001$

Results

Seed Production on Unbagged Inflorescences

The number of seeds produced per flower on unbagged inflorescences averaged 6.05 with progeny means of from 0.84 to 12.03 (Table 1). Both G.C.A. and S.C.A. were highly significant ($P < 0.001$, Table 2) in the analysis which included selfed progenies, but the S.C.A. term was not significant when selfs were excluded. This was because substantial heterosis occurred; selfed progenies averaging 2.38 seeds per flower and crossed progenies 7.24.

The G.C.A. constants (Table 3) show a twofold difference between the best and worst arrays. Parents 2, 3 and 5 contributed high seed set levels and parents 1, 6 and 8 contributed low levels; this is reflected by the seed set levels of the available selfed progenies (Tables 1, 3).

Progeny means for the fraction of flowers with seeded siliquae ranged from 0.28 to 0.82 with an experimental mean of 0.68 (Table 1). The analysis with selfed progenies showed significant G.C.A. and S.C.A. variation ($P < 0.001$, Table 2) but neither term was significant when selfs were excluded. It appeared that heterosis (the selfed progeny mean was 0.46 compared with an outcross progeny mean of 0.72), and differences between selfed progenies were the only important sources of between progeny variation for this character.

The mean number of seeds per flower on unbagged inflorescences was 8.47 with progeny means ranging from 2.99 to 15.18 (Table 1). Both G.C.A. and S.C.A. were highly significant ($P < 0.001$, Table 2) when selfs were included and, as before, a major cause of the significant S.C.A. term was heterosis, crossbred progenies giving almost twice as many seeds as selfed ones. However, S.C.A. was significant ($P < 0.01$) in the analysis without self data, suggesting that there were other forms of genetic interaction for the character. In contrast with the other component a highly significant GCA was obtained when selfed progenies were excluded from the analysis. The G.C.A. constants showed that parents 2 and 5 contributed the highest seed set and 1 and 8 the lowest. Crossbred progenies 6-5, 2-8 and 3-4 (Table 1) had fewer seeds than expected because of gene interaction.

The number of seeds per flower was closely correlated with its two components at both genotypic and phenotypic levels (Table 5). The correlation coefficients between the two components were much lower and only the genotypic one was significant (0.43, $P < 0.001$, Table 5).

Table 3. Array constants (twice the Gilbert Constants) for seed production variates on unbagged and bagged inflorescences from a half diallel between *B. oleracea* inbreds

Array	Unbagged inflorescences			Bagged inflorescences		
	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae
1	4.89	0.69	6.30	0.68	0.24	2.31
2	8.14	0.72	11.17	1.34	0.21	5.17
3	7.26	0.75	9.54	2.12	0.34	4.42
4	7.08	0.73	9.42	2.53	0.40	5.67
5	8.36	0.73	11.18	3.02	0.44	5.68
6	6.02	0.71	8.30	0.99	0.20	3.64
7	6.36	0.71	8.88	0.76	0.20	2.73
8	5.67	0.74	7.75	0.80	0.24	3.02

This is probably a reflection of the nature of the variation found for seeded siliqua per flower.

For unbagged inflorescences therefore, seed production was under the control of genes acting in a largely additive or dominant manner on seed number per seeded siliqua. Heterosis was an important feature for both components of seed set, and inbred progenies produced less than one third of the final seed set of crossbred progenies. Gene interaction was present, but was relatively unimportant, for seed number per seeded siliqua.

Seed Production on Bagged Inflorescences

Some plants of all progenies set seed on bagged inflorescences giving an experimental mean of 1.53, higher than that obtained previously (Hodgkin 1978, 1980). Progeny means ranged from 0.06 to 5.89 (Table 1) and analysis showed that only G.C.A. was significant ($P < 0.001$, Table 4). There was evidence of some heterosis for bagged seed set, selfed progenies producing on average 1 seed per flower fewer than crossbred ones.

Both G.C.A. and S.C.A. variation were partitioned into that which could be attributed to S-allele differences and that which was due to differences between progenies or parents with the same S-genotype. G.C.A. variation for both sources was highly significant ($P < 0.001$, Table 4) although it was higher for parents carrying different S-alleles. The array constants show that S_8 (parents 3 and 4) was associated with high seed sets while S_2 (parents 1 and 2) and S_{45} (parents 7 and 8) were associated with low sets. By contrast, parents with S_{15} showed a large degree of independant variation, one giving highly self compatible progenies and the other only moderately self-compatible ones.

The between S-allele interaction term was significant at $P < 0.05$ (Table 4) and the progeny means suggested that this was because the seed set in S_5 S_{45} and S_{15} S_{15} progenies was lower than expected. The former probably reflects the dominance of the low partial self-compatibility of the S_{45} parents and the latter inbreeding depression in two of the S_{15} S_{15} progenies (5-5 and 6-6).

On average bagged flowers produced 0.29 seeded siliquae per flower, less than half that produced by unbagged inflorescences. However, progeny differences were much more marked than for the unbagged character ranging from 0.04 to 0.67 (Table 1) and only G.C.A. effects were significant ($P < 0.001$, Table 4). The partition of the variation showed that both within and between S-allele variation were important, but the latter was the greater. The differences between the constants and their ranking were similar to those for seeds per flower (Table 3) except for a slightly higher value for parents 1 and 2.

The number of seeds per siliqua averaged 4.02 and progeny means ranged from 1.50 to 10.67 (Table 1). Both G.C.A. and S.C.A. terms were significant ($P < 0.001$ and $P < 0.01$ respectively, Table 4) but whilst G.C.A. effects were significant both for between and within S-alleles, S.C.A. effects were significant only for differences between progenies with the same S-alleles.

The G.C.A. constants (Table 3) showed that whilst S_5 parents behaved similarly (as did S_{45} ones) there were significant differences between S_2 and S_{15} parents. The progeny means suggested that the significant S.C.A. term was a reflection of a high seed set for progeny 4-2 and a low seed set for progeny 4-3 (both S_2 S_5). There was no evidence of significant heterosis.

Both components of seed set were closely correlated with bagged seed set per flower, particularly at the genotypic level (Table 5). In contrast to the unbagged data there was also a significant correlation between the two

Table 4. Analysis of seed production variates (after log transformation) on bagged inflorescences of *B. oleracea* half diallel progenies

Item	d.f.	Mean squares		
		Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae
G.C.A.	7	17.0852***	5.6587***	4.1518***
between S-alleles	3	23.9224***	8.9015***	4.5236***
within S-alleles	4	11.9555***	3.2266*	3.8729***
S.C.A.	24	1.4052	0.9340	0.6300**
between S-alleles	5	2.5335*	0.4705	0.5612
within S-alleles	19	1.1083	1.0560	0.6480*
Within family variance		1.0599 (196)	1.1969 (196)	0.3204 (171)

*, **, *** indicate significance at the 0.05, 0.01 and 0.001 levels respectively. The number in parenthesis gives the appropriate degrees of freedom for the within family residual mean square

Table 5. Correlation coefficients for seed set in *B. oleracea*. The upper triangle contains phenotypic correlations (d.f. 194) and the lower triangle genotypic ones (d.f. 30) based on family means

Unbagged seeds per flower	1	–	0.17	0.70***	0.17	0.83***	0.16
Bagged seeds per flower	2	0.16	–	0.05	0.87***	0.20	0.87***
Unbagged seeded siliquae per flower	3	0.79***	0.01	–	0.10	0.24	0.02
Bagged seeded siliquae per flower	4	0.16	0.92***	0.09	–	0.18	0.54**
Unbagged seeds per seeded siliquae	5	0.88***	0.24*	0.43***	0.19	–	0.20
Bagged seeds per seeded siliquae	6	0.17	0.94***	−0.05	0.73***	0.30**	–
		1	2	3	4	5	6

*, **, *** indicate significance at the 0.5, 0.01 and 0.001 levels respectively

components at both the phenotypic (0.54, $P < 0.01$) and genotypic (0.73, $P < 0.001$) level.

The inheritance of seed production on bagged inflorescences was controlled largely by additive genes, with some evidence of dominance for low levels of self-compatibility in the S_{45} parents. Heterosis was slight affecting only the production of seeded siliqua, and gene interaction was virtually absent.

Discussion

Both bagged and unbagged seed production were largely controlled by genes acting additively or showing some dominance and, for unbagged seed set, heterosis was a major feature. However, the G.C.A. constants indicated that the two characters were independantly inherited. Thus, parent 5 had high constants for bagged and unbagged seeds per flower and parent 6 had low ones, whilst parent 2 had a high constant for bagged seed set and a low one for unbagged seed set. Parent 2 with a moderately high constant for unbagged seed set had a low constant for bagged seed set. The results confirm the existance of inbreds with high outcross seed production and low self seed production and suggest that selection for both characteristics may be successful in non-inbred material.

The correlation coefficients between the bagged and unbagged variates of the two components of seeds per flower were not significant, with the exception of that between bagged and unbagged seeds per seeded siliqua at the genotypic level (0.30, $P < 0.05$, Table 5). Much higher correlations between these two variates were found previously (Hodgkin 1978, 1980), but present results support the earlier conclusion that the number of seeds per seeded siliqua on bagged inflorescences is related to that on unbagged inflorescences. The correlations between bagged and unbagged G.C.A. constants show this even more clearly. Neither seeds per flower or seeded siliquae per flower were correlated but there was a significant correlation (0.85, $P < 0.01$) between bagged and unbagged seeds per seeded siliqua.

The results also support the earlier conclusion that the more important component for outcross seed set is seed number per seeded siliquae, while for self seed set it is the proportion of flowers in which partial self-compatibility occurs and which therefore set seed. The numbers of seeds set per siliqua on selfing would appear to be considerably influenced by those fertility factors which determine outcross seed set.

The major objective of this study was to investigate the expression of partial self-compatibility in progenies with different S-genotypes. Of the S-alleles used S_2 and S_{45} are usually classified as moderately recessive (Ockendon 1975) and S_5 and S_{15} as highly recessive. It has been suggested that plants with recessive S-alleles are more likely to be partially self-compatible than plants with dominant ones. Plants with combinations of some of these alleles (S_5 S_{15}) have been found to be highly self-compatible, possibly because of a phenomenon described as mutual weakening (Thompson 1972).

The results suggest that the levels of partial self-compatibility vary considerably, independantly of S-allele status, even for alleles as recessive as S_{15}. Mutual weakening would be expected to induce specific allelic interactions in the progenies but there was no evidence of this as the observed interactions could be attributed to individual progenies or to dominance for reduced partial self-compatability. Mutual weakening cannot therefore be regarded purely as an S-allele specific phenomenon and some background effects must be involved in its expression. It seems not unlikely that low self-compatibility lines can be obtained for any S-allele and that partial self-compatibility is controlled by genes acting largely independantly of the S-locus. The association between partial self-compatibility and recessive S-alleles may have occurred because the breeding of better open pollinated cultivars has resulted in

an increasingly narrow genetic base with an unconscious preference for the commoner recessive S-alleles together with a degree of inbreeding.

In three previous studies (Hodgkin 1975, 1978, 1980) considerable gene interaction was found as well as additive and dominant gene action. In contrast, these results show that gene interaction does not always occur and that selection of inbred lines with reduced partial self-compatibility may not be as difficult as was previously suggested. While breeders may prefer to retain plants with dominant S-alleles, the results suggest that agronomically superior plants with recessive S-alleles should not be discarded before their self-compatibility level has been tested. The test used to assess self-compatibility will depend on the breeder's facilities and preferences but all my experiments suggest that it is sufficient to record the proportion of flowers in which partial self-compatibility occurs, because a successful reduction in self seed set has always depended on this.

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Literature

Carter, A.L.; McNeilly, T. (1975): Effects of increased humidity on pollen tube growth and seed set following self pollination in Brussels sprouts (*Brassica oleracea* var 'gemmifera'). Euphytica **24**, 805-813.

Gilbert, N. (1967): Additive combining abilities fitted to plant breeding data. Biometrics **23**, 45-49

Haruta, T. (1966): Studies on the Genetics of self and cross incompatibility in cruciferous vegetables. Takii Plant Breed. Exper. Sta., Kyoto, Japan: Northrup King & Co.

Hodgkin, T. (1975): Genetic control of self-compatibility levels in Brussels sprouts. Proc. Eucarpia Meeting-Cruciferae 1974, Scot. Hort. Res. Inst., 27-35

Hodgkin, T. (1976): Studies on the inheritance of pseudo-compatibility in *Brassica oleracea*. Ph.D. Thesis, Dundee University

Hodgkin, T. (1978): The inheritance of partial self-compatibility in *Brassica oleracea* L.: results from a half diallel homozygous for a highly recessive S-allele. Theor. Appl. Genet. **53**, 81-87

Hodgkin, T. (in press, 1980): The inheritance of partial self-compatibility in *Brassica oleracea* L.: results from a half diallel homozygous for a moderately recessive S-allele. Euphytica **29**

Marrewijk, N.P.A. van; Visser, D.L. (1975): The influence of alternating temperatures and relative humidity on the activity of S-alleles in *Brassica oleracea* L. var 'gemmifera' (D.C.). Proc. Eucarpia Meeting-Cruciferae 1974, Scot. Hort. Res. Inst., 20-26

Nasrallah, M.E.; Wallace, D.H. (1968): The influence of modifier genes on the intensity and stability of self-compatibility. Euphytica **17**, 495-503

Ockendon, D.J. (1975): Dominance relationships between S-alleles in the stigmas of Brussels sprouts (*Brassica oleracea* var 'gemmifera'). Euphytica **24**, 165-173

Thompson, K.F. (1957): Self-incompatibility in marrowstem Kale, *Brassica oleracea* var 'acephala' 1. Demonstration of a sporophytic system. J. Genet. **55**, 45-60

Thompson, K.F.; Taylor, J.P. (1966a): The breakdown of self-incompatibility in cultivars of *Brassica oleracea*. Heredity **21**, 637-648

Thompson, K.F.; Taylor, J.P. (1966b): Non-linear dominance relationships between S-alleles. Heredity **21**, 345-362

Thompson, K.F. (1972): Competitive interaction between two S-alleles in a sporophytically-controlled incompatibility system. Heredity **28**, 1-7

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