Theor. Appl. Genet. 53, 81-87 (1978)

The Inheritance of Partial Self-Compatibility in *Brassica Oleracea* L.: Results from a Half Diallel Homozygous for a Highly Recessive S-Allele

T. Hodgkin
Scottish Horticultural Research Institute, Invergowrie, Dundee (Scotland)

Summary. In a study of partial self-compatbility in *Brassica oleracea*, flower number, seeded siliqua and seed production were recorded on self- and cross-pollinated inflorescences of the progenies of a half diallel between five unrelated inbred plants homozygous for the same recessive *S*-allele.

On cross-pollinated inflorescences significant amounts of additively controlled genetic variation were found for seed set per flowering site and its two components, seeded siliquae per flower and seeds per seeded siliquae. Considerable heterosis and gene interaction were also present and a simple additive dominance model did not fully explain the observed variation.

On self-pollinated inflorescences, additive gene action was absent for the seed production variates although differences between progenies were highly significant and heterosis was present. Complex gene interactions were considered to be responsible. The characteristics of the method of assessment used and the relationship between self- and outcross seed production are discussed. It appears unlikely that the component lines could be selected for reduced self seed set, but selection for higher outcross seed set may be possible.

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

Introduction

The efficiency of the sporophytic self-incompatibility system in *Brassica oleracea*, which is controlled by a single locus with approximately 50 *S*-alleles (Thompson 1957; Thompson and Taylor 1966a), is extremely variable, and some degree of partial self-compatibility is common in most varieties of the species. When fully functional, the self-incompatibility system prevents either the germination of pollen or the penetration of pollen tubes through the stigmatic surface (van Hal 1968) if pollen and pistil possess the same active *S*-allele. When partial self-compatibility occurs, pollen tubes penetrate the stigma surface and grow normally through the style to the ovary in spite of the common *S*-allele possessed by pollen and pistil.

Self-incompatibility in *B. oleracea* has been utilised in the production of F_1 cultivars, particularly of Brussels sprouts and cabbage. However, when partial self-compatibility is present in the parent lines of F_1 cultivars, sibs occur in the hybrid crop and reduce both its agronomic and commercial value.

Various factors have been shown to affect the stability of the self-incompatibility mechanism. The occurrence of modifier genes affecting the *S*-locus was suggested by Haruta (1966) and Nasrallah and Wallace (1968) although Ockendon (1973) found little evidence for their occurrence in Brussels sprout. Thompson and Taylor (1966a) showed that it was possible to classify *S*-alleles according to their dominance relationships and found evidence (1966b) that recessive S-alleles were most common in crops with the highest partial self-compatibility. Environmental variation can also affect self-incompatibility, and both high relative humidity (Carter and McNeilly 1975) and high temperature (van Marrewijk and Visser 1975) have been shown to increase self-compatibility levels. Increasing plant and flower age can also result in a rise in the level of partial self-compatibility (Hodgkin 1976).

In most reported experiments self-compatibility levels have been measured either by pollen tube counts in the pistil (van Hal 1968), by seed set (Thompson and Taylor 1966b) or by a combination of both and, in nearly all of them, considerable variation in the effect of a particular factor was reported. Even with identical material under uniform conditions both measures are extremely variable (Hodgkin 1976) and there is evidence that they may not be correlated (Gates and Ockendon 1975). In addition, fertility cannot be assessed when pollen tube counts alone

0040-5752/78/0053/0081/$ 1.40

are employed as a measure of self-compatibility, although factors that affect fertility will almost certainly influence the observed level of partial self-compatibility. Thus, while these methods have provided evidence of the sensitivity of the self-incompatibility system in *B. oleracea*, much of the information obtained is not of direct relevance to the problem of developing inbred lines with enhanced self-incompatibility for F_1 cultivar production.

The demonstration of usable heritable variation for partial self-compatibility would have important consequences for brassica breeding. This would be especially true for breeding lines which contained those recessive *S*-alleles which are most frequent in the crops (e.g. Thompson and Taylor 1966b; Ockendon 1974) and for measurements of partial self-compatibility which gave results relevant to the conditions used in hybrid seed production. This paper describes the results of the first of a series of experiments which have been carried out at the Scottish Horticultural Research Institute to measure the genetic components of variation in partial self-compatibility and fertility as expressed in a natural environment.

Materials and Methods

Seed of the 15 progenies of a half diallel with selfs from five inbred *Brassica oleracea* plants was obtained by bud pollination in a glasshouse. The parents used were two purple sprouting broccoli inbreds (parents 1 and 2), two Brussels sprout inbreds (parents 3 and 4) and one marrow stem kale inbred (parent 5). One of the Brussels sprout inbreds was homozygous for a recessive glossy foliage gene. All parents were homozygous for the incompatibility allele S_{15} a highly recessive *S*-allele (Thompson and Taylor 1966a).

In March 1973, 50 seeds of each progeny were sown individually into Jiffy 7 Pots in an unheated greenhouse. On germination, 21 seedlings of each progeny were randomised individually into three blocks each containing seven plants per progeny. A row of plants of the Brussels sprout F_1 cv 'Gleneagles' was placed between each row within each block and as a guard surrounding the blocks. At the end of May the plants were transplanted to the field in their same relative positions at a spacing of 0.46 × 0.76 m. The following spring (1974) four plants of each progeny in each block were randomly chosen for use in the experiment.

Characteristically, the plants produced one primary and about ten secondary inflorescences, each of which flowered for three to four weeks and produced the bulk of the plants' seed. On each plant two secondary inflorescences were selected for visual similarity and concurrent flower bud development. Just before flowering began one was bagged with a paper-backed cellophane bag (380 × 280 mm) to exclude foreign pollen and supported with a cane. The other was left unbagged to permit free cross pollination with the Gleneagles' plants. During August, after the seed had ripened but before any dehiscence of the siliquae, all the inflorescences were collected and counts were made of the number of flowers, the number of siliquae with seeds and the number of seeds present on each inflorescence. Technically the number of flowers was the number of floral petiole scars and may have included aborted buds or abnormal flowers. In this way, measurements of the amount of seed produced by natural self- and cross-pollination were made so that a measure of partial self-compatibility was obtained which could be compared with one of fertility.

In one block certain bagged inflorescences were severely damaged by wind and rain and a considerable number of plants were found to show late rotting and death. The results from this block were therefore excluded from the analysis.

The procedures outlined by Mather and Jinks (1971) for diallel analysis were used to analyse variation in flower number, mean number of seeds per flower, the proportion of seeded siliquae and the mean number of seeds per seeded siliqua on bagged and unbagged inflorescences respectively. For the seed set variates a log transformation of the data was found appropriate for analysis while flower number was analysed without transformation. The results from the analysis of flower number are not presented here since they do not bear directly on the seed set results, but the progeny and array means are given in Tables 1 and 3.

In Tables of results the means of the untransformed data are given to aid interpretation but all analyses and Wr Vr data are based on the transformed data. Block interaction terms were found to show no evidence of heterogeneity using Bartlett's test and all tests of significance were carried out against the block interaction total (B*t*).

Results

Seed Production on Unbagged Inflorescences

The log transformation of the numbers of seeds per flower was found to be an appropriate expression of seed production for analysis. The most important sources of variation for this variate were found to be a and b_1 ($P < 0.001$ for both, Table 2) although b_2 and b_3 were also significant ($P < 0.05$). Additive gene action and heterosis were thus complemented by the presence of different numbers of dominant genes in the different arrays and by specific gene interaction effects.

An average of 4 seeds per flower was obtained on the unbagged inflorescences and, although two progenies gave more than 7 seeds (5.1, 5.3, Table 1), four gave less than two. All the self progenies were poor seed producers. Array means were markedly different in that arrays 3 and 5 clearly contained progenies with higher seed set than arrays 1, 2 and 4 (Table 3).

The analysis of Wr + Vr and the regression of Wr on Vr were significant ($P < 0.05$ and $P < 0.01$, respectively) and there was no evidence of heterogeneity. As calculated from progeny means, over blocks the slope of the regression line was 0.50 ± 0.121 (Fig. 1), a clear deviation from the expectation of unity for an additive, dominance model. The position of the intercept was evidence that the average level of dominance was high ($H_1 \leqslant D$), and it appeared that parents 1 and 2 possessed mainly recessive genes and parents 3, 4 and 5 mainly dominant ones. The correlation between Wr + Vr and array means was significant ($P < 0.05$), so that increased seed set was usually under the control of dominant genes.

Seed production per flower on unbagged inflorescences

can be partitioned into two separate components, the number of seeded siliquae per flower and the number of seeds per siliqua. As Table 1 shows, the proportion of flowers at which successful pollination occurred and at which siliquae with seed were produced ranged from 0.41 to 0.87 and the number of seeds in such siliquae from 2.02 for progeny 2.1 to 9.93 for progeny 5.3. Overall, just over two thirds of flowers gave seeded siliquae and these contained almost 5.5 seeds.

The main features of the separate analyses were similar

Table 1. Progeny means for flower number and seed set data on unbagged and bagged inflorescences (untransformed data)

	Unbagged inflorescences				Bagged inflorescences			
Identifier	Flower number	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae	Flower number	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae
1.1	27	1.51	.52	2.92	40	0.22	.12	1.78
2.1	31	0.92	.44	2.11	39	0.24	.16	1.69
2.2	35	1.56	.57	2.72	35	0.23	.15	1.62
3.1	42	5.73	.87	6.61	42	0.16	.07	2.27
3.2	41	6.62	.83	7.98	37	0.65	.23	2.85
3.3	27	1.96	.57	3.42	26	0.72	.34	2.14
4.1	44	2.59	.68	3.82	40	0.39	.21	1.89
4.2	50	3.19	.72	4.46	45	0.96	.35	2.75
4.3	52	5.46	.78	7.02	41	0.96	.36	2.70
4.4	33	2.15	.62	3.44	43	0.03	.02	1.38
5.1	58	7.37	.87	8.45	53	1.21	.34	3.55
5.2	56	5.72	.68	8.45	53	0.86	.25	3.38
5.3	50	8.33	.84	9.93	62	0.31	.14	2.14
5.4	64	5.46	.81	6.71	52	0.70	.28	2.53
5.5	56	2.07	.62	3.32	67	0.17	.13	1.31
Overall Mean	44	4.27	0.71	5.66	44	0.54	0.21	2.39

Table 2. Analysis of the log transformation of seeds per flower on unbagged and bagged inflorescences and its two components, the proportion of flowers producing seeded siliquae and the number of seeds per seeded siliquae

		Seeds per flower		Seeded siliquae per flower		Seeds per seeded siliquae	
Item	d.f.	Unbagged M.S.	Bagged M.S.	Unbagged M.S.	Bagged M.S.	Unbagged M.S.	Bagged M.S.
Line *a*	4	6.089***[1]	0.697	0.611***	0.504	2.370***	0.174
b_1	1	33.185***	15.531***	2.440***	24.499***	14.038***	3.850*
b_2	4	2.551*	5.311**	0.091	6.530	1.421**	0.391
b_3	5	2.074*	1.651	0.214*	1.160	0.760	0.569
b	10	5.376***	4.503***	0.387**	5.642**	2.352***	0.826
Blocks	1	0.127	0.963	0.028	2.934	0.033	0.074
B*a*	4	0.591	0.509	0.035	0.205	0.341	0.491
Bb_1	1	0.010	1.118	0.055	0.156	0.051	0.234
Bb_2	4	0.683	0.122	0.089	2.852	0.217	0.638*
Bb_3	5	0.456	0.875	0.068	1.346	0.117	0.136
B*b*	10	0.502	0.511	0.075	1.830	0.150	0.557*
B*t*	14	0.528	0.510	0.064	1.365	0.203	0.538*
Within family variance		0.307 (83)[2]	0.764 (80)	0.041 (83)	1.305 (80)	0.139 (83)	0.216 (80)

[1] *, **, *** indicate significance at the 0.05, 0.01 and 0.001 levels respectively; main effects tested against Bt, block interaction effects against the residual

[2] a variable number of inflorescences were lost for bagged and unbagged variates. The number in parenthesis following the mean square gives the appropriate degrees of freedom

Table 3. Array means for flower number and seed set data on unbagged and bagged inflorescences (untransformed values)

Array	Unbagged inflorescences				Bagged inflorescences			
	Flower number	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae	Flower number	Seeds per flower	Seeded siliquae per flower	Seeds per seeded siliquae
1	40.2	3.61	0.67	4.77	43.0	0.44	0.17	2.42
2	42.6	3.55	0.64	5.10	41.6	0.59	0.23	2.41
3	42.5	5.62	0.78	6.99	41.5	0.56	0.23	2.54
4	48.8	3.78	0.72	5.10	44.1	0.61	0.24	2.25
5	56.9	5.81	0.77	7.39	55.5	0.65	0.23	2.58

except that the b_2 item was significant for seed production per seeded siliqua but not for seeded siliqua per flowering site (Table 2). There was a close phenotypic relationship between the proportion of flowers producing seeded siliquae and the numbers of seeds per seeded siliqua ($r = 0.71$, $P < 0.001$, Table 4). This was even higher for progeny means ($r = 0.93$, $P < 0.001$).

For neither variate was the analysis of Wr + Vr significant over blocks although the regression of Wr on Vr was significant for both with no between block heterogeneity. The slopes of the regression lines (Fig. 1) were markedly different from 1. It appeared that a much higher level of gene interaction was present, for the number of seeds per seeded siliqua, although the ordering of the arrays along the regression line was the same for both variates.

For these progenies, seed production on the unbagged inflorescences was adequately explained in terms of seed set per flower and little was gained from analysing seeded siliqua and seed production separately. There was, however, some evidence of differences between the parents for the two variates. There were also differences in gene expression, shown as unequal distribution of dominant genes (b_2), and more gene interaction (Vr Wr slope) for seeds per seeded siliqua.

Seed Production on Bagged Inflorescences

On bagged inflorescences seeds can only be produced when self-incompatibility is incomplete. Out of 113 plants from which data on bagged seed set was obtained, only 19 gave no seed at all and no progeny was completely self-incompatible (Table 1). In contrast, a few plants were found for which up to 50% of the flowers produced seeded siliquae with 3-4 seeds in them.

Analysis of variance showed that for the number of seeds per flower (log transformed) a was not significant but b_1, b_2 and b_3 were ($P < 0.001$, 0.01, 0.05, respectively, Table 2). Thus, it appears that only dominance variation is important and that heterosis, asymetry of gene distribution among the parents and gene interaction in individual progenies all play a part in determining bagged seed set levels.

Only 0.5 seeds per flower were produced on average, 12% of the number obtained on unbagged inflorescences. Progeny means (Table 1) show that while all progenies set

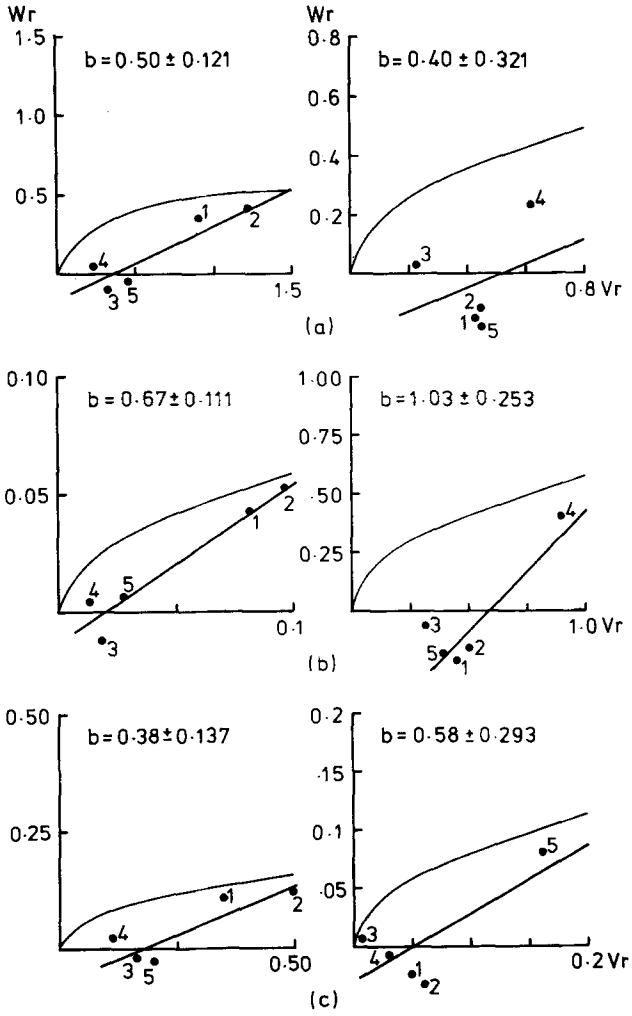

Fig. 1. Wr Vr graphs for unbagged (left) and bagged (right) seed set measures as transformed for analysis: (a) seeds per flower, (b) seeded siliquae per flower, (c) seeds per seeded siliqua

Table 4. Correlation coefficients for seed set data in *Brassica oleracea* calculated from the data after transformation. Top right triangle contains phenotypic correlations (d.f. = 90) and bottom left, genotypic ones (d.f. = 13)

Unbagged seeds per flower	1	–	0.33**	0.88***	0.21*	0.96**	0.42***
Bagged seeds per flower	2	0.50	–	0.34***	0.91***	0.28**	0.86***
Unbagged seeded siliquae per flower	3	0.97***	0.45	–	0.25*	0.71***	0.39***
Bagged seeded siliquae per flower	4	0.37	0.94***	0.32	–	0.16	0.61***
Unbagged seeds per seeded siliquae	5	0.99***	0.50	0.93***	0.39	–	0.39***
Bagged seeds per seeded siliquae	6	0.76***	0.78***	0.72**	0.64*	0.77***	–
		1	2	3	4	5	6

some seed, lines 3.1, 2.1 and 5.3 gave low bagged seed set levels and 4.1 gave a lower seed set than other progenies derived from parent 4. Array means (Table 3) show that parents 4 and 5 contributed a high seed set and parent 1 a low one, but the differences were slight.

The analysis of Wr Vr relationships was inconclusive since neither the Wr + Vr nor the regression analysis were significant, although the array points are plotted in Fig. 1 for completeness.

When the partition of seed number per flower into its two components was done as for unbagged seed set, the phenotypic and genotypic correlation coefficients obtained between seeded siliquae per flower and seeds per seeded siliqua were similar to each other (0.61 and 0.64, $P < 0.001$ and 0.05, respectively, Table 4). However, both of the correlation coefficients are lower than the equivalent unbagged variates and for the genotypic one the drop is dramatic.

In the analysis of variance (Table 2) the block line interaction terms were high but in contrast to the analysis for unbagged inflorescences, more of the variation for seeded siliqua production than for seed production was due to a and b sources. For seeded siliqua production b_1 and b_2 were significant ($P < 0.01$ and 0.05, respectively) whilst for seeds per seeded siliqua only b_1 was significant ($P < 0.05$).

The array means (Table 3) indicated that parental behaviour differed for the two variates, despite the generally close correlation between them. Particularly noticeable in this respect were the means obtained for arrays 3 and 4. Array 3 had low bagged seeded siliqua production and array 4 low bagged seed per seeded siliqua production. The Wr Vr graphs for bagged seeded siliqua and seeds per seeded siliqua are given in Fig. 1 although in neither case was the analysis successful in revealing the sources of variation in these characters.

Comparison of Bagged with Unbagged Seed Set

Seed set on unbagged inflorescences is a record of the fertility level of the plants tested and depends on a large number of factors including pollen, ovule and zygote viability. On bagged inflorescences, the presence of seed demonstrates the presence of partial self-compatibility, but the amount of seed produced will depend, at least in part, on the fertility levels.

The phenotypic and genotypic correlation coefficients between equivalent bagged and unbagged variates (Table 4) suggest that there is considerable variation in siliquae per flower and seeds per flower on bagged inflorescences independent of fertility differences. For seeds per seeded siliqua the correlations are closer, especially the genotypic one ($r = 0.77$, $P < 0.001$). Differences in the relative importance of the components of seeds per flower on bagged and unbagged inflorescences were also suggested by the genotypic correlations. On unbagged inflorescences seeded siliquae per flower and seeds per seeded siliquae were closely correlated with each other ($r = 0.93$, $P < 0.001$) and with seeds per flower ($r = 0.97$ and 0.99 respectively). However, on bagged inflorescences the genotypic correlation between the two components was low ($r = 0.64$, $P < 0.05$), and seeds per seeded siliqua were less closely correlated with seeds per flower ($r = 0.78$) than seeded siliquae per flower ($r = 0.94$).

Analyses of the relative number of self seeds to outcross seeds per flower and other comparative variates were carried out, but none proved more informative than direct comparison of the means. These showed that progenies from array 3 gave the lowest proportion of self to outcross seeds per flower, largely as a result of high outcross seed set. Arrays 2 and 4 gave the highest proportion of self seed due to low outcross seed set. Individual progenies with low relative self seed set were 4.4, 3.1, 3.2 and 5.3.

Discussion

Partial self-compatibility was measured as the number of self seeds produced after self-pollination of all the flowers on an inflorescence during 3-4 weeks. During this period temperature, relative humidity, plant and flower age varied considerably, and the particular combinations of these factors occurring will have affected the seed set of each flower and hence, the total seed set. Fertility was measured as outcross seed set in a comparable way, so

that its effect on partial self-compatibility could be investigated, and so that direct comparisons could be made of the proportion of self to outcross seed produced under conditions similar to those used to produce F_1 seed. Thus, although the results of the experiment refer to only one site in a single year, and hence afford no information on the specific interaction of genotypes and the environment, it is considered that a more realistic measure of the overall performance of the progenies has been obtained than would have been possible using conventional test pollination procedures.

No direct comparisons of the two methods of measurement were carried out and it is difficult to determine what the significance of such comparisons would be, but some general points can be made. It was expected that the numbers of seed set on unbagged inflorescences would be lower than those from controlled test pollinations. Poor weather (low temperature or wet conditions) would reduce the acitivity of pollinating agents, a factor which would effect all progenies equally. In addition, Faulkner (1974) has shown that similarity in flower colour and plant height are important in determining the extent to which bees cross pollinate rather than self or sib-pollinate. No attempt was made to measure the similarities between the tested progenies and the pollinator plants, but the progenies least similar in appearance to the pollinator were the two broccoli and the glossy Brussels sprout selfed progenies and, when their outcross seed was compared with that obtained by hand pollination of the parents, no reduction attributable to bee discrimination could be identified.

On bagged inflorescences, three factors may affect the results obtained. First, since no active pollinating agent is involved, pollination depends on natural deposition. Second, less pollen is present on the stigmas than when they are actively pollinated. Third, the environment of the bag is different from ambient; night temperatures are lower, day temperatures and relative humidity are higher. Hodgkin (1976) examined the effect of these factors and concluded that there was usually an adequate supply of pollen on the stigmas, and that the conditions in the bag would tend to increase the level of partial self-compatibility (Visser 1977; Carter and McNeilly 1975).

Finally, counts of pollen tubes penetrating the stigmas in test self pollinations were made on the parents of the progenies (Table 5). These show no relation to seed set numbers obtained from the selfed progenies on the array means, in agreement with results obtained by Gates and Ockendon (1975) and Hodgkin (1975).

Genetically determined variation in partial self-compatibility was present, but inheritance was complex and only unequal gene distribution between the parents and heterosis were significant. Although, with so few parents caution should be excercised in drawing detailed conclusions, it is clear that an additive dominance model is not appropriate. Deviations from the simple model may result from a number of factors (Hayman 1954) but the most likely ones in this experiment would seem to be interactions between non-allelic genes and non-random gene distribution between the parents. The assumptions of parent homozygosity and diploid gene action appear reasonable and, although the *S*-locus is a multi-allelic locus, there seems no reason to suppose that this is true of genes which modify its action.

Table 5. Mean pollen tube numbers penetrating stigmas on self-pollinated parent plants of the half diallel

	Parent				
	1	2	3	4	5
Pollen tubes	4.8	1.2	8.0	0.4	0

Hodgkin (1975) reported that there was additive gene action for self seed set in inbred Brussels sprout material and that, as in this experiment, the production of seeded siliquae was the most important component. He also found a close relation between partial self-compatibility and fertility for the progenies tested. In this experiment the independent inheritance of partial self-compatibility and fertility levels has been demonstrated. The existence of progenies which give extremely low levels of self seed set compared with their outcross seed set levels has also been demonstrated for material homozygous for a highly recessive *S*-allele. However, the results suggest that the existence of different levels of self-compatibility does not necessarily mean that selection for lower levels will be possible.

Both correlation coefficients and genetic analysis have shown that the most important component of self seed set is the proportion of flowers which give seeded siliquae. These results could suggest that one of the major factors determining the level of self seed set was the proportion of flowers in which self-incompatibility failed to some extent, rather than the extent to which such failure occurred in each flower producing self seed. Once the self-incompatibility reaction ceases to operate with complete efficiency, the number of self seeds produced may depend much more on fertility factors than on partial self-compatibility ones, as shown by the correlation between bagged and unbagged seeds per seeded siliqua. Such a situation would obviously account for the lack of agreement between pollen tube counts and seed set measures noted above.

Whatever the combination of fertility and partial self-compatibility that results in a given self seed set, the breeder will wish to compare self and outcross seed set numbers to identify those progenies or plants with the

lowest relative self seed production. The results suggest that the methods used in this experiment can give good discrimination between progenies with respect to their self and outcross seed set, and that progenies with low levels of partial self-compatibility can be identified. In the material used, however, there was little evidence of usable genetic variation for partial self-compatibility and most improvement would come from selecting for high outcross seed set, for which significant additive variation was present, with an assessment of the proportion of self pollinated flowers producing seeded siliquae.

Acknowledgement

Thanks are due to Eveline Wiseman for her excellent technical assistance and to P.B. Topham and J.B. Cowan for statistical advice and to Dr A.B. Wills for helpful criticism.

Literature

Carter, A.L.; McNeilly, T.: 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 (1975)

Faulkner, G.J.: Factors affecting field-scale production of seed of F_1 Brussels sprouts. Ann. Appl. Biol. **77**, 181-190 (1974)

Gates, P.J.; Ockendon, D.J.: Seed set and pollen tube growth as a measure of self incompatibility in *Brassica oleracea*. Incompatibility Newsletter **6**, 56-60 (1975)

Hal, J.G. van: Identification of S-alleles in Brussels sprouts. Brassica Meeting of Eucarpia: 1968, Nat. Veget. Res. Sta., 32-33 (1968)

Haruta, T.: Studies on the genetics of self and cross incompatibility in Cruciferous vegetables. Takii Plant Breed. Exper. Sta., Kyoto, Japan: Northrup King and Co. 1966

Hayman, B.I.: The theory and analysis of diallel crosses. Genetics **39**, 789-809 (1954)

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

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

Marrewijk, N.P.A. van; Visser, D.L.: 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 (1975)

Mather, K.; Jinks, J.L.: Biometrical Genetics. London: Chapman and Hall 1971

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

Ockendon, D.J.: Selection for high self-incompatibility in inbred lines of Brussels sprouts. Euphytica **22**, 503-509 (1973)

Ockendon, D.J.: Distribution of self-incompatibility alleles and breeding structure of open pollinated cultivars of Brussels sprouts. Heredity **33**, 159-171 (1974)

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

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

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

Visser, D.L.: The effect of alternating temperatures on the self-incompatibility of some clones of Brussels sprouts. Euphytica **26**, 273-278 (1977)

Received March 29, 1978
Communicated by A Gustafsson

T. Hodgkin
Scottish Horticultural Research Institute
Invergowrie, Dundee DD2 5DA (Scotland)