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Interactions of *S* Alleles in Sporophytically Controlled Self Incompatibility of *Brassica**

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Summary. The expressed activity in pollen and stigma was determined for both *S* alleles of sixteen *S*-allele heterozygous genotypes and for one of the two *S* alleles of two additional heterozygotes. Activities were measured using pollen tube penetration and seed set data from reciprocal crosses between each *S*-allele heterozygote and its two corresponding *S*-allele homozygotes.

In pollen the *S*-allele activities ranged from zero to 100% inhibition of pollen tube penetration and seed set, and in the stigma they ranged from 8 to 100% inhibition. Of the sixty-eight *S*-allele activities measured, thirty-three (48%) were 90 to 100% inhibition, nine (13%) were 80 to 89% inhibition and one to five were within each ten-unit range below 80% inhibition.

In an *S*-allele heterozygote, each subset of two *S* alleles had an activity for each allele in both pollen and stigma which was highly repeatable among duplicate pollinations within and among successive years. Each subset of two *S* alleles had a specific *S*-allele interaction in the pollen, and the same or another specific interaction in the stigma. In pairings with six other *S* alleles, allele S_2 had four calculated levels of activity in pollen that ranged from 88 to 94%, and five levels in the stigmas between 15 and 94%. When paired in a heterozygote, alleles S_3 and S_5 had activities ranging between 42 and 59%, representing mutual weakening of *S*-allele activity. Also, heterozygote $S_{15}S_3$ had pollen activities, respectively, of 25 and 6%, i.e. mutual weakening in the pollen.

These results indicate that in heterozygous combination with a series of other *S* alleles, each *S*-allele may have activity in pollen and also in stigma that potentially is between zero and 100% inhibition. They further indicate that the defined sexual-organ × *S*-allele-interaction Types I, II, III and IV are extremes; all intermediate variations including complete weakening of both alleles are possible. Recessiveness is weakening of the activity of but one of the two *S* alleles. The pollen tube penetrations into the style and seed set were highly correlated.

Key words: Incompatibility – Cabbage – *S* Alleles – Dominance – *Brassica*

Introduction

Sporophytically-controlled self incompatibility of plants differs from gametophytically-controlled in that:

1. All pollen grains from an *S*-allele heterozygous plant have the same incompatibility phenotype regardless of the *S*-allele received during meiosis. In contrast, with gametophytic control each grain has a phenotype that corresponds to the *S*-allele distributed to it during meiosis; therefore, there are two pollen phenotypes for a heterozygous plant.

2. As demonstrated by this study, in pollen, the activities of the two *S* alleles of a heterozygous plant are determined by *S*-allele interactions that range from dominance (complete or near-complete inactivity of one allele and complete or near-complete activity of the other) to codominance (full activity of both alleles), to partial dominance (and corresponding partial recessiveness), to mutual weakening (weakened or no activity of both alleles). With gametophytic control, interactions between *S* alleles do not occur in pollen of heterozygous plants; each grain has full activity of only that *S*-allele distributed to it during meiosis.

3. The female tissue of an *S*-allele heterozygous plant exhibits the same range of *S*-allele interactions as occurs in the pollen, but the *S*-allele interaction in the stigma of a heterozygous plant is often not the same as that in its pollen. In heterozygous plants with gametophytic control, simultaneous and full (codominant) activity of both alleles always occurs in the female tissues.

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The *S*-allele interactions reported prior to 1971 for the family *Cruciferae*, of which the genus *Brassica* is a member, were reviewed by Hoser-Krauze (1971). She cited reports of *S*-allele interactions for several species of crucifers by Bateman (1954, 1955), and for *Rhaphanus* species by Sampson (1964, 1967, 1957b) and Tatebe (1962). She also cited reports of interactions in several botanical varieties of *Brassica oleracea* by Odland (1962), Thompson (1957, 1965), Thompson and Taylor (1966), Haruta (1962) and Adamson (1965). And, she presented additional data for *S*-allele interactions in *Brassica oleracea*. More recent data on *S*-allele interactions in *Brassica* are reported by Ochendon (1975), Johnson and Blyton-Conway (1976), Lawson and Williams (1976a, 1976b), Mackay (1977), and Hodgkin (1977).

Additional physiological, anatomical and time-of-expression differences for self incompatibility under sporophytic as compared to gametophytic control are reviewed by de Nettancourt (1977), 1972) and Arasu (1968). The objective here is to more precisely define the *S*-allele interactions of *S*-allele heterozygous plants of *Brassica*.

Materials and Methods

Plant Material

Plants of homozygous *S*-allele genotype were inbreds of cabbage (*Brassica oleracea* var. 'capitata'). Heterozygous genotypes were derived from crosses between the homozygotes. Alleles S_2 and S_3 were used in previous studies at Cornell (Nasrallah and Wallace 1967a, 1967b, 1968; Nasrallah, Barber and Wallace 1970; Nasrallah, Wallace and Savo 1972; Wallace and Nasrallah 1968). Alleles S_8, S_9 and S_{11} have been identified only at Cornell. Alleles S_5 and S_{15} are in Cornell inbreds, but correspond to the S_5 and S_{15} of international nomenclature (Ochendon 1975a).

Pollination Procedures

All pollinations were on plants flowering in the greenhouse between February 15 and May 10 of indicated years. Night temperature was 15°C, and day temperature was 21°, until May when it was sometimes higher on sunny days. Racemes were selected with sufficient flowers for pollination of five adjacent flowers, including the most recently fully opened flower. Emasculation was not done prior to anthesis, but the dehisced anthers were removed to facilitate mechanical transfer of cross pollen to the stigmas. Anther removal always resulted in some self pollination. Planned cross or self pollination were done by brushing dehisced anthers against the stigmas. Reciprocal crosses were always made.

Scoring Pollen Tube Penetration

Sixteen to twenty-four hours after pollination, two of the five pollinated flowers were removed and the pistils were macerated and stained as described elsewhere (Wallace 1979). Using a fluorescent microscope each pistil was visually scored for pollen tube penetration into the upper style. Pollen tube penetration scores were as follows: 1 = 0-3 pollen tubes; 2 = 3-11; 3 = 12-50; 4 = 51-100 and 5 = more than 100 pollen tubes detected. (A score of 0 = zero tubes was also used in 1974 as discussed later.)

Determining S-Allele Activity in S-Allele Heterozygotes

In Table 1 each of the four columns beneath the heading for a heterozygous genotype contains data from one cross; the four crosses are derived from crossing the specified heterozygote reciprocally with each of its two homozygous parents. As an example, for genotype S_2S_5 (Table 1) the data are presented under two headings, male (♂) and female (♀), which are each further subdivided into a column for each of the two *S* alleles, S_2 and S_5, to give the four columns of data. All data under the column headed ♂ S_2 are from the cross S_2S_2 ♀ × S_2S_5 ♂. Since S_2S_5 was the ♂ and the ♀ carried only S_2, all the data in this column measure activity of allele S_2 in the male (♂), i.e. pollen, of the S_2S_5 heterozygote. All data under the column headed ♀ S_2 are from the reciprocal cross, i.e. from S_2S_5 ♀ × S_2S_2 ♂. Since S_2S_5 was the ♀ and the ♂ carried only S_2, these data measure activity of S_2 in the female (♀), i.e. stigma, of the S_2S_5 heterozygote. Similarly, data of the columns headed ♂ S_5 are from the reciprocal crosses between S_2S_5 and S_5S_5. Under ♂ S_5, S_2S_5 was ♂, and the activity of allele S_5 in the male (♂), i.e. pollen, of the heterozygote is measured. Under the column headed ♀ S_5, the S_2S_5 heterozygote was ♀, S_5S_5 was the ♂, and activity of S_5 in the stigma (♀) of the S_2S_5 heterozygote is measured.

Quantitating Reciprocal Differences

Calculation of reciprocal difference (RD) is more completely presented in Wallace (1979) where all pollen tube penetration scores and RD values are for a single pair of reciprocal pollinations. RD values used in this paper were also calculated for single pairs of reciprocal crosses. However, all RD values given herein (Table 1, Section C) are means of 2 to 41 repeats of such individual pollinations and corresponding calculations.

To elucidate interpretations derivable from RD values, calculation of single values is illustrated for a hypothetical heterozygote S_4S_6. This is only for illustration, neither allele occurs in a heterozygote for which actual data are presented. Each RD is derived from the pair of reciprocal crosses between S_4S_6 and one of the corresponding homozygotes, S_4S_4 or S_6S_6. The first pair of reciprocal crosses, A-1 and A-2, are respectively S_4S_6 × S_4S_4 and S_4S_4 × S_4S_6. The second pair, B-1 and B-2 are respectively S_4S_6 × S_6S_6 and S_6S_6 × S_4S_6. Assume the following pollen tube penetration scores for the two pistils scored for cross A-1 (1 and 1), cross A-2, (5, 5), cross B-1 (3, 4), and cross B-2 (4, 5). For the pair of reciprocal crosses A-1 and A-2, the respective sums of the two scores of pollen tube penetration are A-1 = 2 (1 + 1) and A-2 = 10 (5 + 5). Subtracting the smaller from the larger sum gives an RD of magnitude 8 (10 minus 2) for this A-1:A-2 pair of reciprocal crosses. Cross A-1 had the smaller sum (2) of pollen tube penetration scores, so a minus (−) sign is prefixed to make RD = −8. The RD is + 8 for cross A-2 because it had the largest sum (10) of scores. From the same steps for the B crosses, the RD values are −2 for cross B-1 and +2 for B-2.

Interpreting Reciprocal Difference and Pollen Tube Penetration Data Simultaneously

The quantified reciprocal difference measures the relative activity of an *S*-allele in the pollen (♂) and stigma (♀) of an *S*-allele

heterozygote. The ♂ or ♀ organ with the smaller sum of pollen tube penetration scores was given the (−) prefix and that with the larger sum the (+). The smaller sum represents fewer penetrated tubes and the larger sum more, which respectively indicate the higher and lower strengths of incompatibility. Therefore, the RD of a given cross, with its prefix and associated pollen tube penetration score, indicates exactly the numerical magnitude of the RD of the reciprocal cross, and thereby facilitates immediate approximation of the pollen tube penetration data of the reciprocal cross. The RD of the reciprocal cross will be numerically identical, but with a reversed (−) or (+) prefix. If RD of the observed cross is 0, −1 or −2, then the sum of the two pollen tube penetration scores of the reciprocal cross is identical (for reciprocalness = 0), or exceeds that of the observed cross by 1 (for reciprocalness = −1) or by 2 (for reciprocalness = −2), and strength of the incompatibility of the two reciprocal crosses is similar. If the RD is +8, the sum of scores of the reciprocal cross is 8 less than that of the observed cross. And, the observed cross has no incompatibility, i.e. activity for the tested allele in the observed (♂ or ♀) tissue of the heterozygote; while, on the contrary, the reciprocal cross has full incompatibility in the tissue of the opposite sexual organ (♂ or ♀) of the heterozygote.

Collecting Seed Set Data

About 60 days after pollination, pods from the three pollinated flowers left on the plant were harvested and the seeds were counted.

Quantifying S-Allele Activity

A seed set of 25 seeds per pod was semi-arbitrarily selected to represent full seed set because four heterozygotes that were crossed in 1975 to genotypes without a common *S*-allele gave average seed sets per pod between 17.8 and 29.0, with a grand mean of 25.5. Also, the average seed set from three pods for crosses between several homozygotes was about 20 seeds per pod and the maximum was 29. The relative activity (percent expressed compatibility of each *S*-allele in ♂ and also ♀ of each heterozygote) was calculated as follows:

$$\text{Percent } S\text{-allele activity} = 1 - \frac{S + P}{A + M} \times 100,$$

where S = average number of seeds per pod; P = average pollen tube penetration score; A = the selected full seed set, i.e. = 25; and M = the maximum possible pollen mean tube score, i.e. = 5.0.

Relative activities for the nine heterozygotes in Table 2, from data of Hoser-Krauze, were calculated entirely from an assumed full seed set of 25.0, since there were no pollen tube penetration data.

Pollen Tube Penetration Scores

Scores were obtained for the activity of both *S* alleles in both pollen (♂) and stigma (♀) of nine different *S*-allele heterozygotes (Table 1, Section A). Determination of these activities requires four crosses per heterozygote. Thus, the data are from a total of thirty-six different crosses. For each of sixteen crosses, representing all four required crosses for each of four *S*-allele heterozygotes, between thirty and eighty-eight pistils were scored per cross over a three year period. For eight, the four required crosses from two other *S*-allele heterozygotes, ten to thirty-two pistils were scored per cross, over two years. For the twelve required crosses from three additional *S*-allele heterozygotes, six to twenty pistils were scored during a single year.

Results

Pollen Tube Penetration Scores

The mean penetration scores varied from 1.0 (or below as explained later in this paragraph) to 5.0 (Table 1, Section A). For the six heterozygous genotypes tested for two or three years there was excellent reproducibility of data from year to year. The reproducibility held for the scores (measured activity) of each allele in ♂ and ♀ of each heterozygote, and for the relative scores, i.e. the activity, of one *S*-allele of the heterozygote as compared with the other. The mean penetration scores for 1974 which are lower than 1.0 resulted when – near the end of the 1974 pollinating season – a score of 0.0 was used for styles with no penetrated pollen tubes. In 1975 we again used the described 1-5 scale. Expansion to a 0-8 scale is recommended for future studies (Wallace 1979).

Seed Set per Pollination

Seed set (Table 1, Section B) was obtained from all crosses for comparison with the pollen tube penetration scores. Mean seed sets varied from 0.0 to 23.7 seeds per pollination, most being intermediate. For the six heterozygotes tested two or three years, reproducibility of seed sets from year to year was good, but was more variable than the pollen tube penetration scores. The reproducibility held for relative mean seed sets permitted by activity on an allele in ♂ and ♀ of each heterozygote, and for the relative sets permitted by the different *S* alleles of different heterozygotes. Relative *S*-allele activities indicated by seed set were generally comparable to those indicated by the pollen tube scores.

Reciprocal Differences

The mean reciprocal differences (RD) calculated from the pollen tube penetration data covered nearly the entire possible range of (0.0) to (8.0); the calculated extremes were 0.1 and 7.8 (Table 1, Section C). These RD values, especially with regard to positive and negative prefixes but also in numerical magnitude, were consistent from year to year with but slight variations. Reciprocal differences similarly derived by subtracting the smaller ♂ or ♀ grand mean seed set (Table 1, Section B) from the larger,

Table 1. Derivations from pollen-tube growth and seed-set data of the relative activities in pollen (♂ and stigma (♀) of each of the two alleles of nine

Genotypes of heterozygous plants		S_2 S_5				S_2 S_{15}				S_2 S_3				S_2 S_{11}			
		♂		♀		♂		♀		♂		♀		♂		♀	
		S_2	S_5	S_2	S_5	S_2	S_{15}	S_2	S_{15}	S_2	S_3	S_2	S_3	S_2	S_{11}	S_2	S_{11}
A. Mean pollen tube growth	1973	1.2>	4.1	1.0>	2.7	1.1 >	3.2	1.0 >	1.6	1.0 >	3.6	1.0 >	1.8	1.0 =	1.0	2.0 <	1.0
		16	10	16	10	20	12	20	12	10	14	10	12	20	4	20	4
	1974	1.0>	4.5	0.8>	2.4					1.1 >	4.8	1.5 =	1.5	1.0 =	1.0	1.3 <	0.6
		8	16	8	15					18	16	14	24	10	6	12	6
	1975	1.0>	3.2	1.0>	3.4					1.1 >	4.7	1.0 >	1.6				
		6	6	6	5					8	10	8	12				
	Grand Average	1.1>	4.1	0.9>	2.7	1.1 >	3.2	1.0 >	1.6	1.1 >	4.4	1.2 ⩾	1.6	1.1 =	1.0	1.7 <	0.8
		30	32	30	30	20	12	20	12	36	40	32	48	30	10	32	10
B. Mean seed set per pollination	1973	2.4>	8.5	1.2>	12.8	0.8 >	11.6	0.8 ⩽	0.2	0.8 >	16.5	3.3 >	6.5	2.6 ⩽	2.0	9.6 <	1.2
		30	24	30	24	30	15	30	24	15	21	15	21	30	6	30	6
	1974	1.6>	6.1	0.0>	13.3					0.6 >	10.3	6.8 <	2.0	0.9 ⩾	1.6	0.9 <	0.0
		12	29	12	27					27	24	18	27	15	9	18	9
	1975	0.3>	9.9	0.9>	15.0					2.3 >	13.2	0.1 >	1.0				
		12	9	12	9					15	15	12	18				
	Grand Average	1.8>	7.6	0.9>	13.4	0.8 >	11.6	0.8 ⩽	0.2	1.1 >	13.2	3.8 ⩽	3.2	2.0 =	1.8	6.3 <	0.5
		54	62	54	60	30	15	30	24	57	60	45	66	45	15	48	15
C. Reciprocal difference (from pollen tube data)	1973	+0.3	+3.2	−0.3	−3.2	+0.1	+3.6	−0.1	−3.6	0.0	+3.3	0.0	−3.3	−1.8	0.0	+1.8	0.0
		10	8	10	8	8	5	8	5	5	6	5	6	10	2	10	2
	1974	+0.3	+3.6	−0.3	−3.6					−1.1	+5.6	+1.1	−5.6	−0.5	+0.6	+0.5	−0.6
		4	7	4	7					7	7	7	7	6	3	6	3
	1975	0.0	+1.0	0.0	−1.0					0.0	+6.5	0.0	−6.5				
		3	3	3	3					4	6	4	6				
	Grand Average	+0.2	+3.0	−0.2	−3.0	+0.1	+3.6	−0.1	−3.6	−0.5	+5.2	+0.5	−5.2	−1.3	+0.4	+1.3	−0.4
		17	18	17	18	8	5	8	5	16	19	16	19	16	5	16	5
D. Reciprocal difference (from grand seed set)		+0.9	−5.8	−0.9	+5.8	0.0	+11.4	0.0	−11.4	−2.7	+10.0	+2.7	−10.0	−4.3	+1.3	+4.3	−1.3
		54	62	54	60	30	15	30	24	57	60	45	66	45	15	48	15
E. Relative activity of the allele		90%>	61%	94%>	46%	94% >	51%	94% =	94%	93% >	41%	83% =	84%	90% =	91%	73% >	96%
F. Relative weakening of the allele		10%	39%	6%	54%	6%	49%	6%	6%	7%	59%	17%	16%	10%	9%	27%	4%
G. Degree of dominance		partial		partial		partial		co-dom		partial		partial		co-dom		partial	
H. Sexual-organ x *S*-allele-interaction Type		I, or IV				II, or IV?				II, or IV?				III, IV?			

[a] See materials and methods and/or the respective sections in results for details of data collection and/or calculation procedures. The following statements will assist in interpreting the table. 1. A pollen tube penetration score of 1 = highly incompatible and a score of 5 = highly compatible. 2. The 'denominator' indicates the number of observations entering into the mean given in the 'numerator'. 3. A negative (−) prefix before a reciprocal difference indicates that the specified *S* allele is most active in the indicated (♂ or ♀) tissue of the

S-allele-heterozygous genotypes of cabbage[a]

S_2 S_8				S_2 S_9				S_{11} S_8				S_5 S_3				S_{15} S_3			
♂		♀		♂		♀		♂		♀		♂		♀		♂		♀	
S_2	S_8	S_2	S_8	S_2	S_9	S_2	S_9	S_{11}	S_8	S_{11}	S_8	S_5	S_3	S_5	S_3	S_{15}	S_3	S_{15}	S_3
1.0 <	1.8	4.6 <	1.1	1.1 ≤	1.0	4.8 <	1.0												
60	52	62	49	18	16	16	18												
1.0 >	1.8	4.3 <	1.0	1.0 ≤	0.7	5.0 <	1.0									4.8 <	2.5	5.0 <	1.1
22	18	20	18	10	10	10	4									8	12	8	11
1.0 >	1.7	5.0 <	1.1	1.0 ≥	1.6	5.0 <	1.0	1.0 >	2.6	1.0 =	1.0	4.1 <	2.5	2.9 ≥	3.2	3.0 <	2.7	1.3 <	1.0
6	10	6	10	12	18	12	18	6	7	8	8	10	12	8	12	6	6	6	6
1.0 >	1.8	4.6 <	1.1	1.0 =	1.2	4.9 <	1.0												
88	80	88	77	40	44	38	40												
1.6 >	2.8	15.9 <	0.8	3.3 <	0.7	18.9 <	0.4												
90	78	87	75	27	27	24	27												
0.2 >	1.3	12.6 <	0.1	0.3 ≤	0.1	19.9 <	0.0									17.7 <	9.4	22.6 <	2.1
33	27	40	27	12	12	15	6									11	18	12	18
1.1 >	3.1	19.5 <	0.1	2.8 >	7.6	23.7 <	0.1	0.6 >	8.2	0.2 =	0.3	9.3 >	14.1	14.4 <	9.2	6.4 <	0.6	0.0 <	0.6
9	15	6	15	18	27	18	27	9	15	12	12	15	18	12	21	9	9	9	9
1.2 >	2.5	15.1 <	0.5	2.5 >	3.4	20.7 <	0.2												
132	120	133	117	57	66	57	60												
−7.4	+1.6	+7.4	−1.6	−7.6	0.0	+7.6	0.0												
28	26	28	26	8	8	8	8												
−6.5	+1.7	+6.5	−1.7	−8.0	0.0	+8.0	0.0									−0.5	+2.8	+0.5	−2.8
10	7	10	7	5	2	5	2									4	6	4	6
−7.7	+1.2	+7.7	−1.2	−8.0	+0.9	+8.0	−0.9	0.0	+3.5	0.0	3.5	+3.5	+0.7	−3.3	−0.7	+5.0	+3.3	−5.0	−3.3
3	5	3	5	6	9	6	9	3	4	3	4	4	6	4	7	3	3	3	3
-7.2	+1.6	+7.2	−1.6	−7.8	+0.4	+7.8	−0.4												
41	38	41	38	19	19	19	19												
-13.9	+2.0	+13.9	−2.0	−18.2	+3.2	+18.2	−3.2												
132	120	133	117	57	66	57	60												
93% ≥	86%	34% <	95%	88% ≥	85%	15% <	96%	96% <	64%	96% =	96%	55% >	45%	42% <	59%	25% <	60%	8% <	89%
7%	14%	66%	5%	12%	15%	85%	4%	4%	36%	4%	4%	45%	55%	38%	41%	75%	40%	92%	11%
co-dom? or partial? reversal of dominance in ♂ & ♀		partial		co-dom		dom or partial?		partial		co-dom		co-dom in both? or partial in both? reversal of dominance in ♂ and ♀				dom or partial?		dom or partial?	
III, or IV? and reversal of dominance				III, or IV? and reversal of dominance						II or IV?		IV? mutual weakening						IV?	

respective heterozygous genotype, and that it is less active in the alternate (♂ or ♀) tissue. A numerically small recirprocal difference indicates little difference in activity for the indicated *S* allele in ♂ and ♀ while a large value indicates much difference in ♂ and ♀ activities. See the discussion section for descriptions of type and of degree of dominance. The indicated most-active (dominant) allele is to the open side of the symbol >, and the least active (recessive) is on the closed side. Each set of brackets encloses a set of somewhat contradicting data

gave near perfect interpretative agreement (Table 1, Section D) with those from pollen tube data (Table 1, Section C), except that for genotype S_2S_5 the signs indicated a reversal of the stronger ♂ vs. ♀ activity of allele S_5.

Range of S-Allele Activity

The thirty-six *S*-allele activities obtained for the Cornell-developed heterozygotes (Table 1, Section E) vary from 8% to 96%. Fifteen are between 90 and 96% and six between 80 and 89%. One *S*-allele activity is in the 70-79% range, three in the 60%, three in the 50, two in 40, one in 30, one in 20, one in 10 and one in the 0-9% range. Of the twenty-one *S*-allele activities below 90%, none are duplicates. There are duplicates for most activities above 89%, the maximum repeats being four and five for 94 and 96%, respectively. Distribution of ♂ and ♀ activities is about equal within each range, and the overall averages are 77 and 73%, respectively.

Table 2 presents relative *S*-allele activities for nine additional heterozygotes for which seed set data are given by Hoser-Krauze (1971). The calculated *S*-allele activities vary from 0-100%, with activities in all percentage ranges except 20-29 and 60-69%. Of the ten activities below 100%, none were duplicates. There were six ♂ activities of 100%. Of the ♀ *S*-allele activities, four were 100%, seven were 90-99%, three were 82 or 83%, one was 77% and the lowest was 46%. The overall mean ♀ activity was 90%, while the ♂ was 65%.

Activity of S Allele in Selfed Heterozygotes

Selfing was only done in 1975. Six, eight, twelve, and thirty self pollinations, respectively, for S_2S_5, S_2S_8, S_2S_9 and S_2S_3 each gave a mean pollen tube penetration score of 1.0. Mean seed sets/number of selfs were respectively, 2.1/13, 0.02/12, 0.7/18 and 0.4/45, indicating combined activities for both alleles in the respective heterozygotes of 90, 97, 94 and 95%.

Weakening of S-Allele Activity

The percentages of weakening of *S*-allele activities for both ♂ and ♀ are presented in Table 1, Section F, and in Table 2 for each of the two alleles of the eighteen heterozygous genotypes. The *S*-allele activities, i.e. % incompatibility, were subtracted from 100 to give the per-

Table 2. Relative S-allele activity, relative *S*-allele weakening and the sexual-organ X *S*-allele-interaction type of each of 9 heterozygous *S*-allele genotypes of cabbage (from seed set data in tables of Hoser-Krauze (1971))

Table		♂		♀		Degree of dominance		Sexual-organ X S-allele-interaction type
		S_x	S_y	S_x	S_y	♂	♀	
1	Relative activity	100%	16%	100%	96%	dominant or partial?	codominant	II, or IV?
	Relative weakening	0%	84%	0%	4%			
2	Relative activity	100%	50%	99%	83%	partial	codominant or partial?	II, or IV?
	Relative weakening	0%	50%	1%	17%			
3	Relative activity	100%	32%	99%	82%	partial	codominant or partial?	II, or I?
	Relative weakening	0%	68%	1%	18%			
4	Relative activity	79%	0%	90%	82%	dominant	codominant or partial?	II
	Relative weakening	21%	100%	10%	18%			
5	Relative activity	97%	39%	100%	77%	partial	partial or codominant?	I, or IV?
	Relative weakening	3%	61%	0%	23%			
6	Relative activity	–	36%	–	91%			
	Relative weakening		64%		9%			
7	Relative activity	–	54%	–	94%			
	Relative weakening		46%		6%			
8	Relative activity	100%	100%	100%	100%	codominant	codominant	IV
	Relative weakening	0%	0%	0%	0%			
9	Relative activity	98%	41%	98%	46%	partial	partial	I, or IV?
	Relative weakening	2%	59%	2%	54%			

cent compatibility which corresponds to weakening of the *S*-allele activity. Thus, activity and weakening are the inverse of each other.

Discussion

Summary of Procedures

Activities are presented for the two *S* alleles in nine heterozygous genotypes originally reported herein, and for nine from data of Hoser-Krauze (1971). The activities were derived from reciprocal crosses between each heterozygous *S*-allele genotype and its corresponding homozygous genotypes, except that for two heterozygotes data are presented for only the reciprocal crosses to one corresponding homozygote. Thus, the data are from sixty-eight of the possible seventy-two crosses, at two pairs of reciprocal crosses (four crosses) per heterozygote, and they represent thirty-four of the possible thirty-six *S*-allele activities in the pollen and also thirty-four of the possible thirty-six in the stigma.

Range of S-Allele Activity

For each of the thirty-six crosses (nine heterozygotes × four crosses) originally reported herein, there are two measures of *S*-allele activity, mean pollen tube penetration into the upper style and mean seed set per flower pollinated. Agreement is good for the two measures of *S*-allele activity, and the reproducibilities are excellent for: (A) multiple repeats of a given cross, (B) comparisons between the pollen and stigma activities in each heterozygote, (C) comparisons among the heterozygous *S*-allele genotypes, and (D) comparisons among years.

The *S*-allele activities were summarized by calculating the inhibition of full seed set, i.e. the percent of expressed incompatibility, for each of the sixty-eight crosses. These sixty-eight calculated *S*-allele activities ranged from zero to 100%, with thirty-three (14 ♂ and 19 ♀) being 90% or higher and nine (3 ♂ and 6 ♀) being 80-90%. One or more of the twenty-six other activities fell into each of the percentage ranges 0-9%, 11-20%, etc., through 70-90%; all but five (2 ♂ and 3 ♀) of these activities were above (15 ♂ and 6 ♀) 30%.

In heterozygote S_5S_3, the respective alleles had pollen (♂) and stigma (♀) activities of 55 and 42%, and 45 and 59%, and ♂ activities of the respective alleles of $S_{15}S_3$ were 25 and 60%. Allele S_2 was paired with a different allele in each of six heterozygotes, its ♀ activities being 94, 94, 83, 73, 34 and 15%. This range of variation in activity for one allele and the range from zero through all intermediate values to 100% for the sixty-two additional ♂ and ♀ activities indicate that each *S*-allele in a heterozygote may have ♂ and also ♀ activity at any intensity between zero and 100%.

S-Allele Interactions

Each *S*-allele has the potential to have zero to 100% activity in each sexual organ. But, the data indicate that the ♂ versus ♀ *S*-allele activities in a heterozygote cannot be more than semi-independent. The reproducibility over repeated crosses and years of the relative ♂ and ♀ activities of the two *S* alleles present in the individual heterozygotes, and the wide range of relative activities among the eighteen heterozygotes, indicate that the interaction is constant for each specific pair of *S* alleles when functioning in a given genetic background. The activities were only tested in one genetic background for each heterozygote since each heterozygous genotype was always derived from the same inbred parents. The data therefore provide no information about possible influence of genetic background on *S*-allele interactions as partially, but far from completely, investigated by Haruta (1962), Nasrallah and Wallace (1968), Webster (1973), Thompson and Taylor (1971), Richards and Thurling (1973), Nasrallah (1974), Lawson and Williams (1967a) and Hodgkin (1977). The minor variations in *S*-allele activity among repeated pollinations and years represent some sampling error; they also support conclusions that the two-allele subset-specific ♂ and ♀ activities may be modified, slightly at least, by environment (Nasrallah and Wallace 1968; Visser 1977; Lawson and Williams 1976b; Johnson 1971).

None of the sixteen heterozygotes tested for activity of both *S* alleles had full activity of one allele and no activity of the other. Therefore, full dominance was never observed. Heterozygote S_2S_9 had 15 and 96% activities for the two *S* alleles in ♀, i.e. near full dominance, and similar near full dominance (16 and 100%) occurred in ♂ of Hozer-Krauze's heterozygote No. 1. Activities of the two *S* alleles in No. 4 were 0% and 79%, which might be interpreted either as partial or full dominance, and $S_{15}S_3$ had similarly ambiguously interpretable activities of 8 and 89% for the respective alleles. Heterozygote No. 8 had 100% activity for both alleles (full codominance) in both ♂ and ♀. Heterozygotes No. 1, and S_2S_{15} and $S_{11}S_8$ had near full (94% or higher) activity of both alleles in o+ only, which would be interpreted as codominance or near codominance. Heterozygotes S_2S_{11}, S_2S_8 and S_2S_9 had ♀, and S_2S_3 and No. 4 had ♂ activities of 80 and 93% for both alleles, i.e. slightly weakened but near equal and therefore near codominant activity of both alleles. Heterozygote $S_{15}S_3$ had 25 and 60% activities for the respective alleles in ♂, obvious mutual weakening of *S*-allele ac-

tivities in the ♂ (Lawson and Williams 1976a). Heterozygote S_5S_3 had mutual weakening of activities of both *S* alleles in both ♂ and ♀; it also had a reversal of the most-active *S*-allele between ♂ and ♀, S_5 had 55% activity in ♂ and 42% in ♀ while S_3 had 59% in ♀ and 45 in ♂. Such reversal of *S*-allele activities are a weak reversal of dominance. Of the sixteen additional ♂ and twelve ♀ activities measured in the same heterozygote for both *S* alleles, eight ♀ had full or near full (90-100%) activity of one allele with 32 to 83% activity for the other, clearly indicating partial dominance, and eight ♂ had similar partial dominance with activities ranging from 90-100% for the most active *S*-allele and from 32 to 64% for the least active. These results support previous findings that partial dominance is much more frequent than full dominance (Thompson and Taylor 1966; de Nettancourt 1977).

Sexual-Organ × S-Allele-Interaction Types

Haruta (1962), Thompson and Taylor (1966), Wallace and Nasrallah (1968) and MacKay (1977) divided the *S*-allele heterozygous genotypes of sporophytic incompatibility in *Brassica* into four types as follows:

Type	♂	♀
I	Sa < Sb	Sa < Sb
II	Sa < Sb	Sa = Sb
III	Sa = Sb	Sa < Sb
IV	Sa = Sb	Sa = Sb

*S*a < *S*b indicates dominance of *S*b over *S*a and *S*a = *S*b indicates codominance, i.e. simultaneous action of *S*a and *S*b (Wallace and Nasrallah 1968). The sexual-organ × *S*-allele-interaction type (see Wallace 1979, for derivation of this terminology) that would most likely be assigned for each of the eighteen heterozygous genotypes of Tables 1 and 2 are indicated within the tables, as are the types that would next most likely be assigned. Most-likely and next-most-likely assignations occur because conclusions will usually be drawn with limited data, and because the assumptions of full dominance and of full intensity codominance as required for exact classification into the four types do not hold. From the data presented, because the activities of the two *S* alleles in ♂ and ♀ of heterozygotes have the potential to vary from 0-100%, it is evident that the range of possible sexual-organ × *S*-allele-interactions is continuous both within and among indicated Types I, II, III and IV.

Some Suggested Basic Research

The demonstrated full range of *S*-allele interactions in both the stigma and pollen of *Brassica* raises the following question. Why do all possible *S*-allele interactions occur in the female organ of heterozygous plants with sporophytic control of *S*-allele action in the pollen, while only codominance occurs in the female of plants with gametophytic control of *S*-allele activity in the pollen? That *S*-allele interactions of full or near full codominance, partial dominance, full or near full dominance and all gradations of mutual weakening all occur in the stigma, in addition to the pollen, suggests a more fundamental basis for sporophytic control than the commonly accepted assumption. This assumption is that sporophytic control is by *S*-allele-specified molecules that are synthesized in cells of the tapetum and are therefore of sporophytic origin – and that these *S*-allele-specific molecules are in the tryphine coating surrounding each pollen grain and/or are embedded in the numerous cavities of the sporopollenin that encases each pollen grain (Dickinson and Lewis 1973). This assumption permits the described logical explanation for control by the sporophyte of *S*-allele action in the pollen, but it cannot explain how all aspects of this sporophytic control of *S*-allele action in the pollen also occur in the stigma. Research should be undertaken to determine the molecular basis (Sampson 1960) for the codominance, dominance, partial dominance and mutual weakening of *S*-allele activities. The explanation will certainly be of fundamental biological importance.

Applied Benefits from this Research

As long as the investigator of self incompatibility recognizes existence of continuity within and between the sexual-organ × *S*-allele-interaction Types I, II, III and IV, assignation of type can greatly assist with identifying the two *S*-allele homozygous genotypes and the heterozygous genotype of first generation (I_1) inbred *Brassica* progenies. A companion paper (Wallace 1979) describes how determining these types using the pollen tube penetration assay and measuring the reciprocal difference, as done in this paper, can reduce by many fold the effort required to select and develop *S*-allele homozygous *Brassica* inbreds.

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