SELF-COMPATIBILITY IN KALE

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1. Introduction

Self-compatibility is uncommon in plants selected from commercial stocks of marrow-stem kale, *Brassica oleracea* var. *acephala*, but when selfed, about a quarter of these selections produce some self-compatible inbreds (Thompson, 1961). In this paper details on the inheritance of self-compatibility and on the relationship between the expression of self-compatibility and the position of the *S* alleles for self-incompatibility in the dominance series are given; the results have been reviewed briefly by Thompson (1967).

2. Materials and methods

Most of the marrow-stem kale selections were taken from commercial stocks produced by Cannell and Sons, but one inbred, B120/24, was selected from a commercial stock produced by Dunns Farm Seeds. The curled kale plant, Cr1, was found as an extra hairy seedling in plants raised from seed bought at Woolworths.

All pollinations were made in glasshouses in which minimum temperatures of about 10° C. were maintained but in which maximum temperatures were not controlled closely. The glasshouses were insect-proofed and pollinations were not bagged. Pollinations were started a few days after the plants began to flower and all material in an inbred line or a cross was pollinated over a short period of time. Different families were pollinated, however, at any time from early March to late May in different years.

Plants were tested for self-compatibility by selfing at least six, and usually ten, flowers at the mature flower stage and within 2 days of a flower opening. As a test for seed fertility, plants were either selfed in the bud or crossed at the mature flower stage with an unrelated inbred which was usually homozygous for an *S* allele. In making seed for crosses, ten, or occasionally only six, flowers were pollinated at the mature flower stage immediately after emasculation.

The darkening of stigmas 2 days after pollination was used as a rapid means of determining whether a cross was compatible in tests with the curled kale line (Thompson and Howard, 1959; Thompson and Taylor, 1966*a*, *b*). Because no darkening of stigmas occurred after incompatible crosses or after selfing a self-compatible plant, it was possible to determine *S* allele activity in self-compatible plants even though a full set of seed would be produced. For all material, counts of seed set were made about 6 weeks after pollination.

3. Results

(*a*) *Inbred line from plant 31*

The self-incompatible marrow-stem kale selection, plant 31, produced on selfing a number of self-compatible inbreds (table 1—plants 31/6 of 1952

and plants 31/24/47 and 48 of 1956). No compatible crosses were found in the intra-pollinations made between the 15 self-incompatible, first-generation inbreds (Thompson, 1957, table 8). Plant 31 was, however, heterozygous for *S* alleles because four different incompatibility groups were identified in the progeny from a cross between plant 31 and plant 300 (Thompson, 1957, family 1 of table 2). The recessive allele from plant 31 was not active in any of the four combinations.

Ten of the 15 self-incompatible inbreds from plant 31 were crossed with an inbred, plant 300/7, homozygous for a recessive *S* allele and the progeny from the crosses were tested for activity of the dominant *S* allele present in plant 31. Only one inbred, plant 31/35, was found to be homozygous for the dominant *S* allele, the remaining nine being *S* allele heterozygotes

TABLE 1

Self-compatibility in family 1 (plant 31 selfed).

Year	Inbred No.	Average no. seeds/fruit from selfing: at mature flower	selfing: in the bud	pollination: by inbred 31/44
1952	1	0·1	9·1	—
	2	1·9	5·7	—
	3	0·1	17·0	—
	7	1·6	13·0	—
	10	0·0	10·1	—
	6	24·0	16·1	—
	5*	0·5	2·0	—
	8*	0·5	0·2	—
	Plant 31 (parent)	0·3	15·4	—
1956	46	0·9	13·0	1·5
	24	10·7	12·8	18·0
	47	17·3	—	12·6
	48	30·4	—	30·6

* Inbreds with poor seed fertility.

(Thompson and Howard, 1959, tables 3 and 4). As inbred 31/35 was cross-incompatible as female parent with the remaining 14 inbreds (Thompson, 1957, table 8), none of them was homozygous for the recessive allele.

The self-compatible inbred, plant 31/48 (see table 1), produced on selfing seven self-compatible and three fairly self-incompatible inbreds, all of which were cross-compatible with plant 31 (table 2 (*a*)). Progeny from the cross plant 31/48 with inbred 300/7 were all self-incompatible and all cross-compatible with plant 31 (table 2 (*b*)), showing that 31/48 must be homozygous for the recessive allele of plant 31. One of the self-incompatible inbreds, 31/48/6, was back-crossed to inbred 31/48; three of the progeny were self-compatible and four were fairly self-incompatible (table 2 (*c*)). The self-incompatible seedlings were cross-compatible with plant 31 (*i.e.* the seedlings did not possess the dominant *S* allele) but were cross-incompatible with the self-incompatible first generation inbred, 31/59.

All the above results can be explained by postulating that plant 31 is heterozygous for a single, dominant self-compatibility factor, *SC*, which is

TABLE 2

Self-compatibility in plant 31 derivatives

(*a*) Self-compatibility of selfs from self-compatible inbred 31/48

Inbred No.	Average no. seeds/fruit from selfing at mature flower	Average no. seeds/fruit from selfing in the bud	Average no. seeds/fruit from pollination by plant 31
1	8·4	6·7	—
2	10·0	10·3	—
3	7·9	2·3	—
5	19·8	14·2	—
7	19·1	15·6	—
9	2·9	3·4	—
10	8·9	15·4	—
4	5·8	15·3	—
6	3·2	10·1	16·3
8	2·4	13·4	17·3

(*b*) Test of progeny from cross between inbreds 31/48 and 300/7 for activity of dominant allele, S_1, from plant 31

Progeny No.	Average no. seeds/fruit from selfing at mature flower	Average no. seeds/fruit from crossing with following inbreds as male 31/35 $S_1\ S_1$	300/7 $S_{15}\ S_{15}$	B89/1 $S_7\ S_7$
1	1·0	27·7	0·2	27·8
2	0·1	21·5	0·3	31·3
4	0·7	24·2	0·2	23·7
5	0·2	9·2	0·7	11·4
7	1·4	25·0	2·9	26·0
3	4·3	18·8	3·6	15·8
6	3·6	14·7	4·0	16·7

(*c*) Self-compatibility of progeny from cross between self-compatible inbred 31/48 and self-incompatible inbred 31/48/6

Progeny No.	Average no. seeds/fruit from selfing at mature flower	Average no. seeds/fruit from selfing in the bud	Average no. seeds/fruit from pollination by plants 31 $S_1\ S_{15}$	31/59 $S_{15}\ S_{15}$	169 $S_5\ S_{18}$
1	0·4	19·0	17·2	0·5	21·0
3	6·8	13·4	17·0	7·5	12·7
6	2·4	14·5	17·5	1·3	23·0
7	2·8	19·5	17·0	3·8	21·0
2	17·3	14·0	18·3	12·7	18·7
4	12·7	12·7	13·7	—	13·0
5	17·3	15·0	16·7	—	19·7

independent of the *S* allele system and expressed only in the absence of the dominant *S* allele present in plant 31 (fig. 1). The two alleles in plant 31 were identified later as S_1 (fairly high in the dominance series) and S_{15} (recessive, *i.e.* low in the dominance series).

(b) *Inbred line from curled kale, plant Cr*1

The self-incompatible selection of curled kale, Cr1, the stigmas of which darkened clearly after compatible pollinations, produced on selfing a progeny containing self-compatible inbreds. Plant Cr1 possessed the recessive allele S_{15} which was active in its stigmas and another allele which was dominant to allele S_{15} in its pollen; the latter allele was not identical with any previously studied and was designated as S_{35}. A plant homozygous for S_{35} was obtained in the F_2 generation of a cross between plant Cr1 and a marrow-stem kale inbred.

The first generation inbreds from plant Cr1 were crossed as female parents with plants homozygous for alleles S_{15}, S_{35} or S_7. Results of testing these inbreds for self-compatibility and for S allele constitution are given in table 3. Of the 12 self-compatible inbreds tested, the stigmas of 11 darkened after

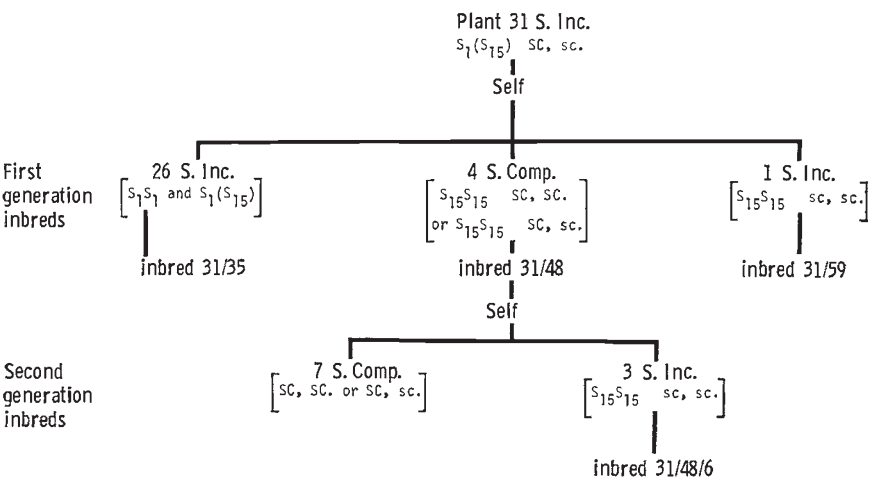

FIG. 1.—Inbred line from plant 31; proposed S allele and self-compatibility constitution of inbreds.

S.Inc. = Self-incompatible plant. S.Comp. = Self-compatible plant. (S_{15}) = Allele S_{15} recessive.

crossing with inbred B89/1 but did not darken when crossed with the inbred homozygous for S_{15}; this means that they were all S_{15} homozygotes (the constitution of the other inbred, Cr 1/29, could not be determined because its stigmas did not darken when pollinated with B89/1, a S_7 homozygote).

The other 37 inbreds from plant Cr1 were self-incompatible (Cr 1/41, however, produced a rather large number of seeds from selfing and plants 20 and 31 were partially self-compatible). Three of these self-incompatible inbreds were homozygous for S_{15}, 18 were S_{15} S_{35} heterozygotes and 10 were homozygous for S_{35} (the constitution of six others was either S_{35} S_{35} or S_{15} S_{35}). One of the self-incompatible inbreds, Cr 1/30, homozygous for S_{15}, was very weak and died early. Although the seed set could not be counted accurately, the plant was self-incompatible and cross-incompatible with S_{15} and a much larger number of seeds were set in the cross with S_{35}. The stigmas of inbreds heterozygous for S alleles did not darken on crossing with the inbred K108/10 homozygous for S_{15}, so that S_{15} was active in the stigma. Plants 11 and 14 set very few seeds in crosses by K108/10 but many set a large number of seeds;

TABLE 3

Segregation for self-compatibility and S *alleles in inbreds from selfing curly kale plant, Cr*1

Inbred No.	Average no. seeds/fruit from selfing: at mature flower	selfing: in the bud	crossing as female with plants homozygous for: S_{15}	S_{35}	S_7	*S* allele constitution
Cr1/10	16·4	21·2	20·0	16·0	18·8	
18	10·8	16·6	13·5	17·8	15·3	
32	9·9	13·0	5·3	20·0	20·7	
34	13·1	16·8	6·0	18·0	19·2	
37	12·5	8·7	8·8	7·5	12·8	
38	15·8	11·7	14·2	16·5	16·5	15, 15
45	17·8	14·3	12·8	16·6	20·8	
51	22·8	—	21·0	29·7	30·0	
53	18·2	20·3	21·0	18·2	20·7	
54	10·3	17·5	17·7	19·3	15·1	
60	18·8	16·7	18·0	21·3	18·8	
29*	21·2	—	16·7	24·2	21·2	15, 15
15	1·7	—	1·7	15·0	17·7	
27	3·1	13·0	2·6	12·8	11·8	15, 15
30	2·0	—	Few	20·0‡	20·0‡	
11	0·2	16·4	3·4	0·5	25·0	
12	0·0	—	8·3	1·3	7·2	
14	0·5	7·7	2·8	0·0	7·0	
16	0·6	7·5	2·5	0·1	23·7	
19	2·3	19·7	10·8	0·0	14·5	
21	2·7	—	8·0	0·5	12·6	
23	0·1	—	17·8	0·4	22·8	
28	1·5	10·0	8·6	0·0	14·2	
31	8·2	—	22·5	1·8	21·7	
33	0·0	10·4	8·0	0·1	14·8	
35	1·0	12·7	11·2	0·2	13·3	15, 35
41	16·7	—	28·4	2·1	33·6	
41†	8·9	17·9	15·2	0·6	28·3	
42	2·0	—	10·0	12·2	12·6	
42†	—	—	6·6	14·7	10·0	
44	0·3	—	21·7	0·3	9·2	
47	3·6	—	17·5	4·7	14·7	
48	0·0	14·3	22·3	2·2	27·0	
50	0·1	2·2	5·0	0·3	6·6	
56	0·2	19·8	12·3	0·6	31·6	
17	0·1	8·5	11·6	0·0	11·2	
24	0·2	13·8	15·3	0·0	15·5	
26	0·0	—	23·2	12·5	19·5	
36	1·7	12·7	15·0	0·0	14·7	
43	0·1	5·0	10·6	0·1	9·0	
46	0·1	17·1	23·5	0·7	24·4	35, 35
49	0·0	13·0	18·7	0·0	14·7	
55	0·1	—	15·4	0·4	15·7	
57	0·3	14·1	12·9	0·0	16·2	
59	0·3	12·3	18·5	0·1	17·6	
13*	1·0	—	20·0	0·5	20·0	
20*	8·7	—	20·5	5·8	20·6	
22*	0·0	5·3	8·0	0·2	9·6	35, 35
40*	3·6	—	20·0	3·8	22·0	or
52*	0·6	—	6·6	0·8	12·2	15, 35
58*	1·2	15·2	21·3	1·0	20·7	

* Stigmas not darkening clearly after compatible pollination.

† Repeat pollinations.

‡ Approximate number—plant died early.

in the latter plants S_{35} was incompletely dominant to S_{15}. The ten inbreds, homozygous for S_{35}, were extremely self-incompatible although Cr 1/26 set some seed when pollinated with Z209/65, homozygous for S_{35}.

The occurrence of three inbreds which were homozygous for S_{15} and self-incompatible showed that the factor for self-compatibility in this line was independent of the *S* allele system and not an S_F type allele. On the other hand all self-compatible inbreds (with the exception of one plant, the allele constitution of which was not determined) were homozygous for S_{15}. This suggests an explanation similar to that given for the inbred line from plant 31; plant Cr1 is heterozygous for a single, dominant self-compatibility gene, *SC*, which is independent of the *S* allele system and the expression of which can only take place in the absence of the dominant allele S_{35}. The segregation expected on selfing plant Cr1 is 12 self-incompatible plants, heterozygous or homozygous for S_{35}; three self-compatible plants homozygous for S_{15}; one self-incompatible plant homozygous for S_{15}. The segregation found (omitting Cr 1/29) was 34 : 11 : 3 which is in good agreement with a 12 : 3 : 1 ratio (X_2 d.f.) = 0·55; P = 0·70-0·80).

(c) *Inbred lines from plants A168 and 169*

Plant A168 (Thompson and Howard, 1959, family 7 and table 5) gave on selfing one fairly self-compatible inbred, A168/2, which set 10 to 20 seeds per fruit when pollinated with five of the self-incompatible inbreds from plant A168. Of 14 self-incompatible inbreds only one, A168/20, was homozygous for the recessive allele S_5. The self-compatible inbred, A168/2, was crossed with inbred B91/7. homozygous for the recessive allele S_{15}; four of the progeny were self-incompatible and three were partially self-compatible (table 4 (*a*)). All seven seedlings were incompatible when pollinated by the self-incompatible inbred, A168/5/1, homozygous for S_5, and all six plants tested were compatible with inbred A168/19, homozygous for the dominant allele S_4. The self-compatible inbred A168/2 was therefore homozygous for the recessive allele S_5.

One completely self-compatible inbred, 169/4, was found in 13 inbreds, obtained by selfing the self-incompatible selection, plant 169. Seven first-generation inbreds, including 169/4, were crossed as males to the self-incompatible inbred 300/7, homozygous for the recessive allele S_{15}, and the progenies were pollinated by plant 169 to test for activity of the dominant allele. The six seedlings from the cross between inbreds 300/7 and 169/4 were all compatible with plant 169 (table 4 (*b*)) so that the self-compatible inbred 169/4 was homozygous for the recessive allele, later identified as S_5. The other six self-incompatible family 169 inbreds were all heterozygous for the dominant *S* allele.

(d) *Progenies from crosses between inbreds, heterozygous for the self-compatibility gene, and inbred 300/7*

Tests for homology between recessive *S* alleles showed that both of the self-incompatible inbreds, 31/48/6 and 300/7, were homozygous for the recessive allele S_{15}. From the explanation of the inheritance of self-compatibility in the inbred line from plant 31, the progeny of a cross between the self-compatible inbred, 31/48, heterozygous for the self-compatibility gene, and inbred 300/7 would be expected to give a one-to-one ratio of self-compatible and self-incompatible plants. However, of the seven seedlings from this

TABLE 4

Tests for activity of dominant S *alleles in self-compatible inbreds*

(*a*) Test of progeny from self-compatible inbred A168/2 × inbred B91/7 for activity of dominant allele S_4, from plant A168

	Average no. seeds/fruit from					
	selfing		crosses with following inbreds as male			
Progeny No.	at mature flower	in the bud	A168/5/1 $S_5\ S_5$	A168/19 $S_4\ S_4$	B91/7 $S_{15}\ S_{15}$	B91/2 $S_8\ S_8$
2	0·0	29·0*	0·2	26·5*	0·5	29·0*
3	0·2	23·0	0·0	24·5	0·0	30·0
5	1·2	28·5	6·2	32·0	8·0	30·5
7	3·2	29·5	0·2	28·5	0·6	28·5
1	12·8	24·5	1·6	—	10·0	27·5
4	15·6	28·5	1·2	26·5	3·4	29·5
6	17·0	24·5	1·4	28·5	7·0	28·5

* Mean of seed counted from only two fruits.

(*b*) Test of progeny from self-compatible inbred 169/4 × inbred 300/7 as female for activity of dominant allele, S_{18}, from plant 169

	Average no. seeds/fruit from			
		crosses with following plants as male		
Progeny No.	selfing at mature flower	300/7 $S_{15}\ S_{15}$	169 $S_{15}\ S_{18}$	B89/1 $S_7\ S_7$
1	0·2	0·0	26·6	21·7
3	2·0	0·5	23·5	27·6
4	6·1	1·2	25·5	22·5
5	9·9	1·0	29·8	23·3
6	3·6	1·7	22·7	26·2
7	4·0	2·1	25·2	19·7

TABLE 5

Partial self-compatibility in plants, heterozygous for a dominant S *allele and plants, homozygous for a recessive* S *allele, in families obtained by crossing plants with inbreds, homozygous for a recessive* S *allele*

Family	*S* allele constitution	No. of plants with a percentage self-compatibility						Total no. plants
		0-10	10-20	20-30	30-40	40-50	over 50	
Plant 31 inbreds	$S_1\ S_{15}$	17	7	2	0	2	0	28
× inbreds 300/7 or 300/14	$S_{15}\ S_{15}$	12	7	7	7	3	5	41
Plant 169 inbreds	$S_{15}\ S_{18}$	16	0	0	0	0	0	16
× inbred 300/7	$S_5\ S_{15}$	5	4	2	5	6	6	28
Single cross B120/24 × Z2/23	$S_{11}\ S_{15}$	14	4	0	0	0	0	18
× inbred Z2/23	$S_{15}\ S_{15}$	5	8	2	0	0	3	18

cross tested, five were self-incompatible and two, plants 3 and 6, were slightly less self-incompatible and also set a few seeds in back-crosses with inbred 300/7 (table 2 (*b*)); none was self-compatible.

Self-compatible seedlings would also be expected in progenies from the cross between plant 31 inbreds and inbred 300/14 (Thompson and Howard, 1959, table 4). With the addition of data from progenies of crosses between five plant 31 inbreds, crossed with inbred 300/7, results are given in table 5. Percentage self-compatibility was determined by comparing seed set per

fruit on selfing at mature flower stage with seed set from the compatible out-pollination. Seedlings heterozygous for the dominant allele S_1 from plant 31 were self-incompatible with only four out of 28 seedlings partially self-compatible. Of 41 plants homozygous for S_{15}, only two were self-compatible, a high proportion were partially self-compatible but separation into distinct self-incompatible and partially self-compatible groups was not possible. Approximately a quarter of the progeny homozygous for S_{15} would be expected to be self-compatible, because only half the plant 31 inbreds would be expected to be heterozygous for the self-compatibility gene and from crosses between those inbreds with inbreds 300/14, only half the progeny homozygous for S_{15} would carry the self-compatibility gene.

Progeny from a cross between the self-compatible inbred 169/4 and inbred 300/7 gave only partially self-compatible and self-incompatible plants (table 4 (*b*)). Results for progenies from plant 169 and its inbreds, crossed with inbred 300/7, are given in table 5. Plants heterozygous for the dominant allele S_{18} from plant 169 were extremely self-incompatible; about half of the seedlings heterozygous for the recessive alleles S_5 and S_{15} were partially self-compatible and only two out of 28 were self-compatible. About a quarter of the progeny heterozygous for S_5 S_{15} would be expected to be self-compatible if plant 169 is heterozygous for a dominant self-compatibility gene.

These results, obtained in different years, suggest that the expression of the self-compatibility gene in plants, active only for *S* alleles low in the dominance series, can be modified by independent genes to give partial self-compatibility.

(e) *Back-cross generation from single-cross (B120/24 × Z2/23) × Z2/23*

The kale inbred, B20/24, is homozygous for allele S_{11}, high in the dominance series in the stigma (Thompson and Taylor, 1966*a*, table 3 and fig. 2). In the production of single-cross seed for the double-cross hybrid, Maris Kestrel, this inbred is crossed with inbreds from plant Z2/23, homozygous for the recessive allele S_{15}. Inbreds from Z2/23 are sometimes partially self-compatible and a few are fairly self-compatible.

In an attempt to improve seed fertility in the Z2/23 inbreds, the seed-fertile F_1 hybrid, B120/24 × Z2/23, was back-crossed to inbred Z2/23 and the progeny tested for *S* alleles and self-compatibility. The results are given in table 5. For this family percentage self-compatibility was determined from the proportion of seed set by selfing at mature flower as compared with selfing in the bud stage. Eight of the 18 seedlings homozygous for S_{15} were more partially self-compatible than any of the 18 plants heterozygous for S_{11}. One of the progeny homozygous for S_{15} was self-compatible. The mean set of seed for 18 plants heterozygous for alleles S_{11} S_{15} was $16{\cdot}9 \pm 3{\cdot}6$ for selfing by bud pollination and $0{\cdot}8 \pm 0{\cdot}9$ for selfing at mature flower. The corresponding figures for 18 plants homozygous for S_{15} were $18{\cdot}2 \pm 3{\cdot}4$ and $4{\cdot}0 \pm 4{\cdot}6$.

Both the mean seed set on selfing and the standard deviation of the mean was much lower for plants heterozygous for the dominant allele S_{11} than for those homozygous for S_{15}.

4. Inheritance of self-compatibility in *Brassica oleracea*

In two inbred lines, one from marrow-stem and the other from curled kale, self-compatibility was determined by a single dominant factor, in-

herited independently of the *S* allele system but expressed only in the absence of *S* alleles high in the dominance series. The same type of self-compatibility probably occurred in the two marrow-stem kale lines from plants 169 and A168, in which the single self-compatible inbred from each line was homozygous for the recessive *S* allele. Sampson (1957) found that three self-incompatible inbreds obtained from selfing a self-compatible plant of Calabrese green-sprouting brocoli (*B. oleracea* var. *italica*) were heterozygous for alleles S_1 and S_4 (Sampson's nomenclature) like their self-compatible parents. If both *S* alleles were low in the dominance series, the results agree with the hypothesis of an independent dominant gene for self-compatibility, although Sampson noted that the self-compatible gene permitted some activity in pollen and stigma of the *S* allele completely recessive in the self-incompatible *S* allele heterozygote. Wallace and Nasrallah (1968) reported that in cabbage, *B. oleracea* var. *capitata*, a self-compatible mutant from a self-incompatible inbred line homozygous for an *S* allele was determined by a dominant gene unrelated to the *S* allele system.

Mutual weakening of the activity of two recessive *S* alleles to give a self-compatible kale plant heterozygous for *S* alleles was reported by Thompson (1967). Plants homozygous for either of the alleles S_2 or S_{15} were self-incompatible. Allele S_2 was dominant to S_{15} in the pollen of the heterozygous plant and both alleles were active in the stigma. In a few partially self-compatible plants heterozygous for *S* alleles, allele S_2 was incompletely dominant to S_{15} in the stigma. This change in both self-compatibility and dominance relationships was probably determined by a recessive gene. With the possible exception of the heterozygote, S_{20} S_2, no other example of mutual weakening or competitive interaction was recognised in kale, but van Hal (personal communication) found several instances of mutual weakening between different *S* alleles in Brussels sprouts, *B. oleracea* var. *gemmifera*.

Further examples of self-compatibility have been reported, some of which are determined by different genetic factors. Self-compatible kale inbreds, homozygous and active in the stigma for the dominant allele S_{16}, were selected for good seed fertility from a seed multiplication plot (Thompson, 1967). Another self-compatibility gene, independent of the *S* allele system and more effective than those described in this paper, is probably present in this material. Recessive self-compatibility genes occurred in a Brussels sprout inbred line homozygous for allele S_2, and in a marrow-stem kale line homozygous for allele S_5 (Thompson, 1967). The level of self-incompatibility in *B. oleracea* is controlled also by modifer as well as major genes and in cabbage modifer genes affected the intensity and stability of self-incompatibility (Nasrallah and Wallace, 1968).

Finally, although several genetically distinct types of self-compatibility have been found in *B. oleracea*, the type described in this paper occurs frequently in kale and is probably widely distributed through the species.

5. Interpretation of self-compatibility in kale

The breakdown of self-incompatibility in kales is incomplete; self-compatible inbreds, which give a full set of seed on selfing at mature flower, may be 70 per cent. cross-fertilised in the field with adequate insect pollinators (Thompson, unpublished). In contrast, only 30 to 40 per cent. of

hybrid seed was produced in the field from summer cauliflowers (Watts, 1963) and in oil-seed rape, *Brassica napus* (Olsson, 1960). Thompson (unpublished) found that the stigmas of both summer cauliflowers and oil-seed rape darkened on selfing at mature flower as much as from a compatible cross-pollination. But activity of incompatibility substances occurred in the stigmas of self-compatible kale plants, because their stigmas failed to darken after selfing at mature flower. Sampson (1957) found *S* allele activity in self-compatible plants of green sprouting broccoli by the stigma squash method. Nasrallah and Wallace (1967) demonstrated that cabbage inbreds, each homozygous for a different *S* allele, were antigenically distinguishable by immunodiffusion tests using antisera produced in rabbits from stigmas of each type. A self-compatible mutant from one self-incompatible line was active for the same antigen as in the parental line, but smaller quantities were present.

Our knowledge is insufficient to explain self-compatibility in terms of molecular genetics, but a hypothesis has been developed by Sampson (1960) to account for *S* allele interaction in both gametophytically and sporophytically controlled incompatibility systems in higher plants. He proposed that dominance might be explained if the production rate of incompatibility substances differed for different *S* alleles. In an *S* allele heterozygote, these alleles would compete for a common limiting factor, possibly substrate, so that the recessive allele would not produce sufficient antigen to reach a certain threshold value for activity. Thompson and Taylor (1966*a*) were able to explain the results for dominance relationships between 28 *S* alleles from kale on Sampson's hypothesis and it can also be applied to understand some of the self-compatibility results.

The presence of less antigen in stigmas from the self-compatible than the parental self-incompatible cabbage (Nasrallah and Wallace, 1967) supports the existence of a threshold value for expression of self-incompatibility. Serological tests by Wallace and Nasrallah (1968) indicated a greater concentration of a specific antigen in stigmas of a plant homozygous for a certain *S* allele, than in stigmas of plants heterozygous for this allele. Both alleles were active in the heterozygote. If the recessive alleles, S_5 and S_{15}, were relatively slow and ineffective in the production of antigen in the *S* allele homozygote, the quantity of antigen might be reduced below the threshold value by the inactivation of some of the antigen by products of the self-compatible gene, making the plant self-compatible. Inactivation of a similar quantity of antigen would not give self-compatibility in a plant, homozygous for an *S* allele high in the dominance series, because a much higher concentration of antigen would be initially present. Similarly, competition between two weak, self-incompatible *S* alleles for substrate would reduce the amount of each specific antigen below the threshold value to make the *S* allele heterozygote self-compatible, although both *S* allele homozygotes were self-incompatible. However, if mutual weakening involved an *S* allele high in the dominance series, as may occur, this explanation would be inadequate.

6. Practical significance of self-compatibility studies

The production of almost 100 per cent. F_1 hybrid seed is being attempted in Brussels sprouts (Johnson, 1966) and in other horticultural Brassicas

(Nieuwhof, 1963; Wallace and Nasrallah, 1968). Apart from vigour, considerable uniformity is required from crops of horticultural Brassicas, so that only a very small percentage of selfs can be tolerated in F_1 hybrids and it is important to use parental lines, which produce very self-incompatible inbreds. Extremely self-incompatible parental inbreds are desirable but not so essential in field kales, because consistent individual performance is less necessary in closely spaced crops. Also, with the larger quantities of seed required to grow the greater acreage of the commercial kale crop, double or triple-cross hybrids must be produced (Thompson, 1964). In a field of two mixed single-cross hybrids for production of double-cross seed, the occasional, weaker inbreds will be overgrown and will contribute, at the most, a few three-way cross seeds to the yield of double-cross seed.

Studies on the inheritance of self-compatibility in kales indicate that inbreds homozygous for *S* alleles high in the dominance series will give more strongly self-incompatible inbreds than plants homozygous for *S* alleles low in the dominance series. The three self-incompatible inbreds homozygous for the recessive allele S_{15} set a mean of 2·3 seed per fruit on selfing at mature flower, in comparison with a mean of 0·3 seeds per fruit for the 10 sibs homozygous for the dominant allele S_{35} (table 3). Three self-incompatible inbreds from selfing the self-compatible inbred 31/48 averaged 3·8 seeds per fruit (table 2 (*a*)). In material segregating for an independent self-compatible gene (table 5) or self-compatible genes with smaller effects (table 5), a much higher proportion of the plants, heterozygous for the dominant alleles S_{18} and S_{11} respectively, were very self-incompatible in comparison with plants active only for the recessive alleles S_5 and S_{15}.

Of a group of 28 alleles from kale investigated by Thompson and Taylor (1966*a*), alleles S_5 and S_{15} were the lowest in the dominance series in the pollen and often recessive in the stigma. Alleles S_{11} and S_{18} were two of the highest alleles in the stigma; alleles S_1 and S_4 were intermediate and the dominance relationships of S_{35} were not tested except that it was dominant to the recessive alleles S_2 and S_{15} in the pollen.

High frequencies of recessive *S* alleles in populations of various cultivars of *B. oleracea* were often associated with a higher frequency of partially and completely self-compatible plants (Thompson and Taylor, 1966*b*). However, in purple-sprouting broccoli all plants were self-incompatible although 47 per cent. of *S* alleles in the population were recessive and a plant heterozygous for S_2 and S_{15} was still fairly self-incompatible. Van Hal and Verhoeven (1968) found three Brussels sprout inbred lines, all homozygous for the recessive allele S_2, which showed very different levels of self-incompatibility. There is no reason why inbreds which are homozygous for a recessive *S* allele should not be used to produce F_1 hybrids, if they give very self-incompatible inbreds on selfing. But, if three-way or more complex hybrids are to be marketed, inbred lines, homozygous respectively for alleles S_2 and S_{15}, should be checked for mutual weakening in the *S* allele heterozygote before being used for hybrid production.

In conclusion, although a self-incompatible inbred homozygous for a recessive *S* allele and known to give self-incompatible progeny can be safely used as a parent for an F_1 hybrid, inbreds homozygous for a dominant *S* allele are more likely to produce very self-incompatible inbreds. If the mutual weakening of the recessive alleles S_2 and S_{15} in a plant heterozygous for these alleles is considered, it is better to use *S* alleles higher in the domin-

ance series for three-way, double-cross and triple-cross hybrids. In partially self-compatible breeding material with a high proportion of recessive *S* alleles, introduction by back-crossing of *S* alleles, high in the dominance series, may be necessary.

7. Summary

1. Self-compatibility was determined in two inbred lines of kale by a single dominant gene independent of the *S* allele system, but the self-compatibility was expressed only in the absence of *S* alleles high in the dominance series. Two other inbred lines of kale probably segregated for the same type of self-compatibility.

2. In progeny from outcrosses with a self-incompatible inbred line homozygous for the same recessive *S* allele, partial rather than complete self-compatibility occurred in plants homozygous for recessive *S* alleles and active for the dominant self-compatibility gene. The modification from complete to partial self-compatibility was determined probably by modifer genes rather than environmental factors.

3. The dominance relationship between alleles S_{35} and S_{15} in the stigma differed between first-generation curly kale inbreds from both alleles active to incomplete dominance of S_{35}.

4. The interpretation of self-compatibility is discussed in relation to Sampson's hypothesis on gene interaction at the *S* locus and with consideration for recent serological information about *S* allele relationships.

5. In order to obtain very self-incompatible inbreds for F_1 hybrid production from partially self-compatible breeding material, it may be necessary to introduce *S* alleles high in the dominance series.

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