NON-LINEAR DOMINANCE RELATIONSHIPS
BETWEEN S ALLELESK. F. THOMPSON and J. P. TAYLOR
Plant Breeding Institute, Trumpington, Cambridge

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1. INTRODUCTION

INFORMATION on dominance relationships between *S* alleles in a sporophytically controlled incompatibility system is limited. The primary objective in earlier studies of self-incompatibility in the Compositae and Cruciferae has been to establish the existence of sporophytic control in a species. Until very recently, the most extensive data on dominance relationships between *S* alleles for one species was given by Sampson (1958) for the crucifer *Lesquerella densipila* and in the F_1 hybrid *L. densipila* $\times$ *L. lescurii*. Relationships between alleles were established for about half of the possible combinations between nine *S* alleles and two levels of dominance were found in the pollen. Dominance was linear in that *S* alleles at the same dominance level were independent in all combinations, but in heterozygotes between alleles from different levels, the alleles from the upper were always dominant to an allele from the lower level. As Sampson (1958) states "there is no *a priori* reason to assume a linear dominance sequence except that almost all reliable data from other multiple allelic, sporophytic systems do fit a linear pattern".

However, Sampson mentions two definite exceptions to a linear pattern of dominance. One was reported by Bateman (1955) for S_5 in the pollen of *Brassica campestris*, in which both alleles were active in the heterozygotes $S_1 S_3$ and $S_1 S_5$ but S_3 was dominant to S_5 . A similar relationship occurred between S_1 , S_2 and S_5 in the stigma. The other example of non-linear dominance came from marrow-stem kale (*Brassica oleracea* var. *acephala*), in which Thompson (1957, Family 4) found that both *S* alleles were active in the stigma of $S_a S_f$ and $S_a S_e$ but S_f was dominant to S_e .

In order to provide a theoretical basis for understanding *S* allele interactions in self-incompatibility systems, controlled by a multiple series of *S* alleles at one locus in Angiosperms, Sampson (1960) has developed an hypothesis, with which he could explain linear and non-linear dominance in a sporophytically determined incompatibility system. While this present paper was in preparation, non-linear dominance in the stigma of *Raphanus raphanistrum* has been reported by Sampson (1964), although these alleles can be arranged in a linear order of dominance in the pollen. Results from some of the possible combinations between 28 different *S* alleles in marrow-stem kale, presented in this paper, demonstrate non-linear dominance relationships in both the pollen and stigma.

2. MATERIALS AND METHODS

Twenty-three of the 28 different *S* alleles, which were tested for dominance relationships, were identified from Cannell's variety of marrow-stem kale (*Brassica oleracea* var. *acephala*). However, only 15 of these alleles occurred frequently in this stock. Two alleles were obtained from Webb's purple stemmed variety of marrow-stem kale and three were identified only from thousand-head kale (*B. oleracea* var. *acephala*). The different *S* alleles were numbered in chronological order of recognition and their origin and their relative frequency in Cannell's stock of marrow-stem kale is given in table 1. There are real differences in the frequency of *S* alleles in Cannell's variety, but the division into "common" or "rare" in table 1 obviously over-simplifies the situation. This classification is based on the number of times an allele has been recognised in unrelated inbred lines or selections. Allowance has

TABLE 1
Source and relative frequencies of S alleles tested for dominance relationships

<i>S</i> allele No.	Source	Frequency in Cannell's marrow-stem kale	Cannell's thousand-head kale
1, 2, 3, 5, 8, 13, 14, 17, 20, 23	Cannell's marrow-stem kale	Common	Not found*
7, 9, 15, 16, 21	Cannell's marrow-stem kale	Common	Found
4, 6, 18, 22, 26	Cannell's marrow-stem kale	Rare	Found
10, 11, 12	Cannell's marrow-stem kale	Rare	Not found
24, 25, 27	Cannell's thousand-head kale	—	Found
28, 29	Webb's purple marrow-stem kale	—	Not found

* These *S* alleles may be present, because no attempt has been made to identify them in thousand-head kale. Relatively few thousand-head inbreds, homozygous for *S* alleles, were tested for homology with *S* alleles, obtained from marrow-stem kale.

been made for the apparently higher frequency of certain alleles, which are either closely linked to a distinct pigmentation marker gene (Thompson and Taylor, 1965), or are active in inbreds, used as testers for yielding ability.

Dominance relationships between two *S* alleles were determined by reciprocal crosses between the *S* allele heterozygote and the two component *S* allele homozygotes. Data came from two sources. *S* allele heterozygotes were produced by crossing known *S* allele homozygotes *e.g.* for heterozygotes involving alleles *S*₄, *S*₆, *S*₂₁, *S*₂₄ and *S*₂₆. Normally only one *S* allele heterozygote was tested and pollinations were not repeated; doubtful results were not included. However, many relationships were determined in the course of recognition of inbreds, homozygous for *S* alleles, from inbred lines selected for breeding purposes. In these lines, the relationships between alleles were often established many times.

Pollinations were made in an insect-proof glasshouse in early spring. At least three flowers were pollinated for each testcross, which was classified as incompatible

or compatible on seed set per fruit in comparison with seed set from a compatible cross with an unrelated plant and a self pollination made at the mature flower stage. If possible, crosses were also classified for darkening of stigmas two days after pollination. Thompson and Howard (1959) reported darkening of stigmas only after a compatible pollination. From a comparison of stigma darkening and seed setting, incomplete dominance between two alleles can be detected. This is, of course, only possible for self-incompatible plants, whose stigmas blacken clearly after a compatible pollination. If the stigmas of such a plant, with alleles S_1 S_2 , fail to darken on pollination with pollen from the S_2 homozygote, but give a full set of seed, it is assumed that S_1 is incompletely dominant to S_2 in the stigma.

3. RESULTS

(a) *In the pollen*

Dominance relationships for the combinations made between 28 S alleles in the pollen are given in table 2 and fig. 1. These alleles have been divided into seven groups. This classification is based on independence between S alleles within a group and on normally identical interactions of S alleles from one group with S alleles from other groups.

If these groups of alleles are considered in alphabetical order, both alleles are active in heterozygotes between the groups A and B and also between groups B and C. These three groups are necessary because S_{24} and S_{28} (group A) are dominant to S_1 (group C) and S_{24} is incompletely dominant to S_4 (group C). Dominance within these groups is non-linear, e.g. both S alleles are active in the heterozygotes S_1 S_6 and S_6 S_{24} but S_{24} is dominant to S_1 . Alleles S_{21} and S_{26} are put together in group D, although the interaction between these two alleles has not been determined. However, both these alleles are recessive in about half the combinations tested with alleles from groups A, B and C, although the interaction with any particular allele is not always the same. In fact, allele S_{21} is active with S_{24} , which is dominant to S_{26} , but S_{25} is dominant to S_{21} , and allele S_{26} is active with S_{25} . In the heterozygotes S_{24} S_{26} and S_{25} S_{21} , the recessive alleles in the pollen are active in the stigma (fig. 2), which confirms that these test plants are heterozygous for these S alleles. Dominance is non-linear whenever it occurs between alleles from groups A, B or C with alleles from group D.

The three remaining S alleles, S_2 , S_{15} and S_5 , are recessive in the pollen in all 35 combinations tested with alleles from groups A to D. Simple linear dominance occurs between the three recessive alleles which gives three more groups. Allele S_2 (group E) is dominant to S_{15} (group F) and to S_5 (group G), while S_{15} is dominant to S_5 .

(b) *In the stigma*

From the results of tests for dominance relationships in the stigma, the 28 S alleles have been divided into four groups. The basis for the division into groups A, B and C is the same as that given for interactions between alleles on the pollen. However group D should be sub-divided,

TABLE 2
Dominance relationships in the pollen between groups A and B and within group B

Group	<i>S</i> allele No.	B																											
		6	7	8	9	10	11	12	13	14	16	17	18	20	22	23	25	27	29										
A	24	*	*	*	.	*	*	*	.	*	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	28	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	*	*	*	.	*	*	*	.	*	*	.	*	*	.	.	*	.	.	.	.	.	.	.	.	.
	6	.	—	.	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	7	.	—	.	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	8	.	—	—	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	9	.	.	—	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	10	.	.	—	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	11	.	.	—	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	12	.	.	.	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	13	.	.	.	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	14	*	.	.	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	16	*	.	.	*	*	.	*	.	*	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	23	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

* Both *S* alleles active.
. Combination not tested.

Group		C	D	E	F	G
	S allele N ⁰	1 4	21 26	2	15	5
A	24	24 24	24	24	24	24
	28	28	28			
B	3			3		
	6		6	6	6	6
	7				7	7
	8			8	8	
	9				9	
	10		10 10	10		10
	11		11			
	12					
	13			13		
	16		16		16	
	17		17	17	17	17
	18		18 18			
	20		20	20	20	
	22		22		22	
	23				23	
	25		25	25		
	27					
	29					
C	1		1	1	1	1
	4			4	4	4
D	21			21	21	21
	26			26	26	
E	2				2	2
F	15					15

FIG. 1.—Dominance relationships between *S* alleles in pollen (excluding data in table 2).Key—Shaded square, both *S* alleles active.Number in square, *S* allele dominant.Number in shaded square, *S* allele incompletely dominant.

TABLE 3
Dominance relationships in the stigma within and between groups A, B and C

Group	S allele No.	A			B										C		
		11	17	18	20	3	6	7	10	12	14	16	22	24	27	28	29
A	11	—															
	17	.	—														
	18	.	.	—													
	20	.	.	.	—												
B	3	*	.	.	*	—											
	6	*	.	.	*	.	—										
	7	.	.	.	*	.	.	—									
	10	.	.	.	*	.	.	.	—								
	12	*	.	.	*	.	.	.	.	—							
	14	.	.	.	*	.	.	.	.	.	—						
	16	*	.	.	*	.	.	.	*	.	.	—					
	22	.	.	.	*	.	.	.	.	.	.	.	—				
	24	*	.	.	*	.	.	.	.	.	.	.	.	—			
	27	.	.	.	*	.	.	.	.	.	.	.	.	.	—		
	28	.	.	.	*	.	.	.	.	.	.	.	.	.	.	—	
	29	.	.	.	*	.	.	.	.	.	.	.	.	.	.	.	—
	17	*	.	.	*	.	.	.	.	.	.	.	.	.	.	.	.
C	2	.	*	.	*	*	6	.	*	.	.	.	.	*	.	.	.
	8	*	.	.	.	.	.	.	*	.	.	.	.	.	.	.	.
	23	.	.	.	.	.	.	.	*	.	.	.	*	.	.	.	.
	25	.	.	.	.	.	25	.	*	.	.	.	.	.	.	.	.
		.	.	.	.	.	.	.	*	.	.	.	.	.	.	.	.

* Activity of both S alleles.
 . Combination not tested.
 17 Allele 17 incompletely dominant.

because dominance occurs fairly frequently within the group (fig. 2). However, unexpected relationships within the group makes it difficult to sub-divide the group further. Thus, S_1 is incompletely dominant to S_{21} , S_{21} is dominant to S_5 , but S_1 and S_5 are independent.

Heterozygotes between the first three groups of S alleles, 20 S alleles

FIG. 2.—Dominance relationships between S alleles in stigma (excluding data in table 3).
 Key—Shaded square, both S alleles active.
 Number in square, S allele dominant.
 Number in shaded square, S allele incompletely dominant.

in all, show independence of both alleles, with the exception of incomplete dominance in three heterozygotes, but alleles from groups A, B and C can be distinguished by their dominance relationships with group D alleles. Thus with the exception of the combination $S_{13} S_{20}$, the four alleles S_{11} , S_{17} , S_{18} and S_{20} from group A are always dominant to alleles in group D. Group B alleles are dominant to group D alleles in about half of the heterozygotes tested, while both alleles are always active in heterozygotes between S_2 , S_8 , S_{23} and S_{25} from group C and alleles in group D. There is no clear pattern in the interaction between alleles from groups B and D. Incomplete dominance also occurs frequently in heterozygotes between group B alleles and S_{21} and S_{26} from group D. Four out of sixteen heterozygotes show incomplete dominance in crosses between group B alleles and alleles S_{21} and S_{26} in comparison with seven out of the remaining 122 combinations tested in the stigma.

The dominance of group A with group D alleles can be seen to be examples of non-linear dominance when compared with the independence of both alleles in heterozygotes between group C and D alleles and also between A and C alleles. If interactions between individual alleles are considered, S_{17} from group A and S_2 from group C are both active in the stigmas of heterozygotes in an inbred line, from which both S allele homozygotes were recognised. However S_{17} is dominant to S_5 , S_{13} , S_{15} and S_{26} , while all these alleles are active with S_2 in the stigma.

4. CHANGES IN THE GROUPING OF S ALLELES IF ALL COMBINATIONS TESTED

Slightly more than one third of the possible combinations between 28 S alleles have been tested in the pollen or in the stigma, *e.g.* 130 out of 378 possible combinations in the pollen. It is relevant therefore to consider whether any significant changes in the grouping of S alleles would be expected if all combinations were tested.

In the pollen, alleles in groups E, F and G are recessive to alleles in groups A to D in all 35 heterozygotes tested. Even when alleles in groups A to D have not been tested with alleles in groups E, F or G, they are active with at least two other alleles in groups A to D, which are dominant to alleles S_2 , S_5 or S_{15} . Thus, both S alleles are active in the heterozygotes $S_4 S_{27}$ and $S_{21} S_{27}$; both S_4 and S_{21} are dominant to S_2 , S_5 and S_{15} . Although S_{27} has only been tested with S_4 and S_{21} from groups A to D, it could not be placed in groups E, F or G.

However, a few alleles in group B, which have been tested with only two or three other alleles within the group and not at all with group D alleles, might be recessive to some of the other group B alleles and be put in group D, *e.g.* S_{12} , S_{13} , S_{14} , S_{23} and S_{27} . It is more likely that one or two alleles, not in group B would be transferred to group C, because the alleles in group A have only been tested with 10 of the 19 alleles in group B. There is less likelihood of the transfer of alleles from group

B to group A, because 14 of the 19 alleles in group B have not proved to be dominant to at least one of the alleles in group C.

Insufficient results in the stigma makes it impossible to decide whether S_{14} , S_{27} and S_{29} should be put in group B or C and they have been put in group B. The classification of S_{13} is also doubtful; it has been put in group D because it is recessive to S_6 and S_{17} , but it is active with S_{20} . The alleles S_8 , S_{23} and S_{25} have been grouped with S_2 in group C, because they are not dominant to alleles in group D, but they have not been tested against alleles in group A and may yet be recessive in some combinations.

Generally, no major changes are expected in the pattern of dominance relationships already established, even if all combinations were to be tested. Further examples of non-linear dominance would, however, be expected. The outcome of further tests for dominance relationships between this large group of S alleles may be to demonstrate that no two S alleles give identical interactions with all other S alleles. Already, although S alleles have been put into only four groups in the stigma, S_{17} in group A is incompletely dominant to S_{28} and dominant to S_{13} , whereas S_{20} , also from group A, is not dominant to S_{13} . In group C, S_2 is incompletely recessive to S_6 , but S_{25} is incompletely dominant to S_6 . While these unexpected results must be checked, there is a tendency for S alleles to show specificity in their dominance relationships, which would be expected, if, as Sampson (1960) has suggested in his hypothesis, each allele differs in the rate of production of incompatibility substance.

5. SPATIAL ARRANGEMENT OF S ALLELES IN KALE ACCORDING TO DOMINANCE RELATIONSHIPS

The groups of S alleles, as given in figs. 1 and 2, are based on dominance relationships in pollen and stigma respectively, and these groups have been arranged spatially in fig. 3. It is much easier to demonstrate diagrammatically a linear dominance sequence between groups of S alleles than examples of non-linear dominance between groups of S alleles, as exists in the stigma for kale. In particular, it is difficult to put group C, which is active with all other S alleles in the stigma, into a definite position on the diagram. However, if the explanation of non-linear dominance given by Sampson (1960) is accepted, group C can be put in an intermediate position between groups A and D (see explanation in section 6).

Although the dominance of group A with group D S alleles provides the only evidence for a linear order of dominance in the stigma, relationships in the pollen follow a basically linear order of dominance. In fact, non-linear dominance is always associated with one of four alleles in the pollen, *i.e.* S_{21} , S_{24} , S_{26} and S_{28} . If these four alleles had not been included in tests for dominance relationships between the 28 S alleles, relationships between the remaining 24 alleles would have

FIG. 3.—Groups of *S* alleles arranged spatially in accordance with their dominance relationships.

K—Entire lines with arrow, dominance of upper over lower group. Broken lines with arrow, *S* allele heterozygotes between groups show either activity of both alleles or alleles from upper group dominant to those from lower group. Dotted lines, both alleles active.

given a linear series with four levels of dominance. Furthermore, only one of these four S alleles, S_{21} , associated with non-linear dominance, is found commonly in Cannell's variety of marrow-stem kale. S_{26} occurs only occasionally, S_{24} came from thousand-head kale and S_{28} was obtained from Webb's purple marrow-stem kale (table 1). A study of dominance relationships between a smaller number of S alleles, taken only from Cannell's variety of marrow-stem kale, would probably not have detected non-linear dominance relationships in the pollen.

6. INTERPRETATION OF NON-LINEAR DOMINANCE IN KALE

The suggestion by East (1929), that the incompatibility substances from pollen and stigma interact like antigens and antibodies, has been confirmed by the serological tests of Mäkinen and Lewis (1962). These tests also demonstrate the protein nature of the incompatibility substances. Kroh (1964) obtained evidence from electron microscope studies in the Cruciferae that the barrier to self-fertilisation is the cuticle of the stigma and suggested that the incompatibility substance in the stigma irreversibly activates a cutinase enzyme system in the pollen from another cross-compatible plant, but inhibits this enzyme system in pollen with the same S alleles. However, these incompatibility substances are the end-product of allele interaction in the stigma and in the pollen mother cells and little is known about the chemistry of these allelic interactions. Sampson (1960) has developed a hypothesis to account for the S allele interactions in gametophytically and sporophytically controlled incompatibility systems in higher plants.

Sampson suggests that each S allele controls the production of a specific incompatibility substance, which must reach a threshold quantity before it causes activity. Both of these substances are produced in an S allele heterozygote, but the occurrence of dominance in heterozygotes implies limits on the effectiveness of S alleles. A limiting factor, L , for the production of incompatibility substances might be substrate or a limited number of sites for the incompatibility substance. Sampson suggests that S alleles might differ in their rate of production of incompatibility substance and that they would compete for a limited amount of substrate. Thus, if it is assumed that the threshold value for activity is the same for all alleles and if the limiting factor is not more than twice the threshold amount, the dominance sequence would be linear and would closely correspond with the production rates of individual alleles. If L were slightly higher, independence of S alleles with slightly different production rates would occur and with higher values of the limiting factor, non-linear dominance would be possible. When the limit is sufficiently high all S alleles will act independently.

Many of the examples of non-linear dominance in kale could be explained on the above hypothesis. This applies to the non-linear relationships between alleles S_1 , S_6 and S_{24} in the pollen (table 2 and fig. 1), where both alleles are active in the heterozygotes $S_1 S_6$ and S_6

S_{24} but S_{24} is dominant to S_1 . It must be assumed that the production rate of incompatibility substances for the S alleles is $S_{24} > S_6 > S_1$. The limiting factor is high enough to allow the threshold values to be exceeded by both alleles in the heterozygotes $S_{24} S_6$ and $S_6 S_1$, where differences in production rates are small, but the difference is large enough in $S_{24} S_1$ to prevent the threshold value of S_1 being reached. This instance of non-linear dominance appears to be very similar to the examples described by Sampson (1964) in the stigma of *Raphanus*. However, Sampson explained non-linear dominance in *Raphanus* by unequal competition, favouring S_{11} and S_{12} , for a special substrate that is required for the gene product of relatively few S alleles. In the stigma of *Raphanus* recessive alleles were found in only four of the 28 heterozygotes, i.e. S_{11} and S_{12} were both dominant to S_9 and S_{14} . This situation could be explained if the eight S alleles differed in their rates of production of incompatibility substance from a common substrate and that S_{11} and S_{12} had the highest rates and S_9 and S_{14} the lowest rates of production. Only in these particular combinations were the differences in production rates great enough to prevent the allele with the lower rate from reaching the threshold value for activity.

The low proportion of heterozygotes showing dominance in the stigma would indicate from Sampson's hypothesis that the limiting factor for substrate must be high in the stigma. Even so, S_2 (group C) is active but not dominant or recessive with all alleles with which it has been tested and frequently has non-linear dominance relationships with other S alleles. There are two possible explanations of this behaviour. Allele S_2 might require a different substrate to produce the incompatibility substance and so would not compete with the other S alleles, or it can be assumed that S_2 and other alleles in group C have an intermediate production rate between groups A and D. Differences in the production rates between alleles in groups A and C or between groups C and D are not large enough to prevent the allele with the lower production rate from reaching the threshold value for activity, but the greater differences in production rates between alleles in groups A and D result in the dominance of group A alleles. On this basis, group C is placed in an intermediate position between groups A and D in fig. 3(b).

Non-linear dominance relationships associated with S_{21} and S_{26} in pollen and stigma are difficult to explain. If fixed production rates for each allele are assumed, contradictory results are found. Thus, S_{24} is dominant to S_{26} in the pollen, but both alleles are active in the heterozygote $S_{21} S_{24}$. In the pollen S_{25} is dominant to S_{21} but in the combinations $S_{25} S_{26}$ both alleles are active (fig. 1). It would seem necessary to assume that S_{24} and S_{26} compete for one substrate and S_{25} and S_{21} compete for a second substrate or limiting factor. Although an attempt to repeat these results has not been made yet, the recessive S alleles in the pollen are active in the stigma (fig. 2), which confirms that these plants are S allele heterozygotes. Examples of similar contradictory

results are found in the stigma. The high incidence of incomplete dominance in heterozygotes between alleles from group B with S_{21} and S_{26} in the stigma suggest that these results are genuine. The high frequency of incomplete dominance indicates that alleles from group B differ sufficiently from S_{21} and S_{26} in production rates to ensure that S_{21} and S_{26} frequently just reach or fail to reach the threshold value for activity. Sampson (1960) explained incomplete dominance by assuming that "near-threshold quantities of incompatibility substances are produced and external conditions or modifying genes can swing the balance through degrees of activity to inactivity". Sampson concluded that evidence from incomplete dominance suggested a broad rather than the abrupt threshold value, which he had earlier suggested. If this were the case, an explanation can be given for the contradictory results with S_{21} and S_{26} without resort to different limiting factors for specific S alleles.

Finally, kale data in the pollen indicate that the percentage of heterozygotes with activity of both alleles depends on the degree of dominance of the S alleles tested. With the exception of a few instances of non-linear dominance, both alleles are normally active in heterozygotes between the 23 S alleles in groups A, B and C. However the five recessive S alleles are arranged in a strictly linear sequence of dominance with at least four different dominance levels. The same tendency occurs in *Raphanus raphanistrum*. Sampson (1964) found that five dominant S alleles in the pollen were all at the same level of dominance but the three recessive S alleles were each at a different level of dominance. If as Sampson proposes, the limiting factor is constant throughout a species, there must be a considerable difference in the production rates of incompatibility substance between alleles high and low in the dominance series. Such differences in production rates might explain the tendency for kale plants, homozygous for S alleles low in the dominance series, to be partially or completely self-compatible (Thompson 1965), although plants homozygous for the same alleles can be self-incompatible. The self-compatibility factors, which are inherited independently of the S allele system, do not affect the self-incompatibility of plants, heterozygous for S alleles high in the dominance series.

7. FREQUENCY OF DOMINANCE AND OCCURRENCE OF NON-LINEAR DOMINANCE

If Sampson's hypothesis is correct, a higher percentage of S allele heterozygotes, in which one allele is dominant, should occur in a population, from which S alleles can be arranged in a linear sequence of dominance than in one in which non-linear dominance relationships are found between S alleles. The percentages of heterozygotes, showing dominance, have been determined separately for pollen and stigma for four species from three genera in the Cruciferae (table 4). In this table the percentages of heterozygotes, showing dominance, are given

TABLE 4
Frequency of dominance in relation to type of dominance

Species	Pollen or Stigma	Authority	Percentage heterozygotes in which one allele is dominant	No. heterozygotes on which percentage based	Nature of dominance
<i>Raphanus raphanistrum</i>	Pollen	Sampson (1964)	64	28	Linear
<i>Lesquerella densipila</i>	Pollen	Sampson (1958)	58	19	Linear
<i>Brassica oleracea</i>	Pollen	This paper	42	128*	Some non-linear
<i>Brassica campestris</i>	Pollen	Bateman (1955)	30	10	Some non-linear
<i>Brassica campestris</i>	Stigma	Bateman (1955)	30	10	Some non-linear
<i>Brassica oleracea</i>	Stigma	This paper	26	127*	Mainly non-linear
<i>Raphanus raphanistrum</i>	Stigma	Sampson (1964)	14	28	Non-linear
<i>Lesquerella densipila</i>	Stigma	Sampson (1958)	0	15	None

* Heterozygotes in which incomplete dominance occurred were omitted.

in descending order, independently of genus or species and also without distinction between pollen and stigma. However, the percentages of heterozygotes showing dominance in the pollen, for all four species, are higher than any of the percentages from the stigmas.

With the exception of the kale and *Raphanus* data, these percentages are based on very small numbers of heterozygotes tested. It has already been mentioned that non-linear dominance in the pollen of kale might easily have been missed if a slightly smaller number of *S* alleles had been tested, so that the possibility cannot be excluded that *Lesquerella* might show non-linear dominance in the pollen, if a larger number of heterozygotes had been examined. However, for the results given in table 4, there is a very good correlation between the occurrence of non-linear dominance and a relatively low percentage of heterozygotes, in which one allele is dominant, as predicted in Sampson's hypothesis. Only linear dominance has been found in the pollen of *Raphanus* and *Lesquerella*, which, with 64 and 58 per cent. respectively, have the highest percentages of heterozygotes, in which one allele is dominant. Non-linear dominance does occur in kale pollen. Dominance has been found in 42 per cent. of the heterozygotes tested, but the percentage will probably be nearer 33 per cent., when all possible combinations have been tested. In *Brassica campestris*, the only other species in which non-linear dominance has been identified in the pollen, three of the ten heterozygotes showed dominance. Non-linear dominance was recognised in three of the species in the stigma and in none of these species did the percentage of heterozygotes, in which dominance occurred, exceed 30 per cent. In the fourth, *Lesquerella*, both alleles were active in all combinations in the stigma. From Sampson's hypothesis, it can be assumed that the value for the limiting factor is generally lower in the pollen than in the stigma for the Cruciferae examined, and that in the pollen the limiting factor is much lower in *Raphanus* and *Lesquerella* than in *Brassica*.

8. PRACTICAL SIGNIFICANCE OF DOMINANCE RELATIONSHIPS BETWEEN *S* ALLELES IN KALE

Studies of the self-incompatibility system in marrow-stem kale by Thompson (1957) and by Thompson and Howard (1959) made it possible to adapt the double-cross method for the production of distinct, vigorous and uniform hybrids to replace the more variable, mass-selected stocks of commercial kale (Thompson, 1959). A double-cross hybrid from marrow-stem kale will be marketed soon, but difficulties, largely inherent to the method, have occurred in the seed multiplication of this double-cross hybrid. Considerable labour is required to produce adequate quantities of selfed inbred seed by hand pollination of buds and the yields of single-cross seed from inbreds in the field are very low in comparison with seed yields from hybrids or from commercial stocks. Thompson (1964) has described a triple-cross hybrid method, which

would provide a much less laborious and more reliable method of seed multiplication than the double-cross method. From inbred seed to triple-cross hybrid takes three generations and the three successive stages consist of a single-cross, a three-way cross and a final cross between two three-way hybrids. Sporophytic control is essential for the production of 100 per cent. triple-cross seed, but the existence of dominance relationships between *S* alleles, which are characteristic of sporophytically controlled incompatibility systems, complicates use of the triple-cross method. For the production of 100 per cent. triple-cross seed, the *S* allele, homozygous in the inbred line, must be active in pollen and stigma with both *S* alleles from the single-cross hybrid, with which it is crossed to obtain three-way cross seed. If dominance occurs frequently and unpredictably in combinations between different *S* alleles, serious limitations are put on the arrangement of the six inbreds within a triple-cross hybrid. It was, therefore, necessary to examine dominance relationships between different *S* alleles in kale.

A joint consideration of dominance relationships in the pollen and in the stigma show that for combinations between the majority of *S* alleles examined, the occurrence of dominance is rare. In the pollen, with the exception of the four combinations between *S* alleles from groups A and C, dominance has not been found between the 23 *S* alleles in groups A, B and C (table 2). Dominance in the pollen is restricted to heterozygotes between *S* alleles from groups A, B and C with the five *S* alleles in groups D, E, F and G (fig. 1). In the stigma, a few combinations between the above-mentioned 23 *S* alleles show dominance (table 3 and fig. 2); in particular, allele *S*₉ is fairly frequently recessive and alleles *S*₁, *S*₄ and *S*₁₃ are occasionally recessive. However, even if the *S* allele in one inbred was recessive in the stigma to one of the *S* alleles in the single-cross, the maximum percentage of triple-cross seed in the final cross would only be reduced from 100 to 91 per cent. Such a reduction would not be of practical importance for a field forage crop. Thus, with the possible exception of *S*₉ inbreds, homozygotes for any of the other 22 *S* alleles could be used in any position in the triple-cross hybrid.

Inbreds, homozygous for the remaining alleles, *S*₂₁, *S*₂₈, *S*₂, *S*₅ and *S*₁₅, should only be used to produce single-cross seed and should not be crossed with the single-crosses to give three-way cross seed. These five *S* alleles are either frequently or always recessive in the pollen with *S* alleles from groups A, B and C, and with the exception of *S*₂, are often recessive in the stigma. The occurrence of non-linear dominance in the pollen and stigma of kales makes the prediction of dominance relationships between *S* alleles in an untested combination impossible; but non-linear dominance is largely associated with two alleles, *S*₂₁ and *S*₂₈, in both the pollen and stigma. The decision to use these two *S* alleles, together with the pollen recessive alleles, *S*₂, *S*₅ and *S*₁₅, only in the single-crosses, removes much of the unpredictability associated with non-linear dominance. Four of these five recessive *S* alleles are

common in marrow-stem kale, but they can be easily recognised if present in an inbred, homozygous for an unidentified S allele. One other recessive S allele, S_{30} , has been found, but the number of different recessive S alleles in kale populations are definitely few.

From these investigations into dominance relationships in kale, it can be concluded that the existence of dominance seems unlikely to restrict seriously the arrangement of inbreds within the triple-cross hybrid.

9. SUMMARY

1. Dominance relationships were determined for nearly a third of the possible combinations between 28 S alleles from marrow-stem and thousand-head kales.

2. Independent allele action is more common than dominance in S allele heterozygotes for both pollen and stigma, but dominance occurs more frequently in the pollen than the stigma.

3. Both alleles are normally active in heterozygotes between 23 S alleles, fairly high in dominance in the pollen. A few instances of non-linear dominance are found between these alleles and more frequently with two alleles slightly lower in the dominance series. Five recessive S alleles are arranged in a strictly linear sequence of dominance with at least four levels of dominance.

4. Non-linear dominance occurs more frequently in the stigma and examples of linear dominance are rare.

5. The relative frequency of dominance in kale and the occurrence of non-linear dominance in the pollen and stigma is in accordance with expectation based on Sampson's hypothesis of gene interaction at the S locus.

6. The arrangement of kale inbreds within a triple-cross hybrid will not be seriously limited by the pattern of dominance relationships, reported in this paper.

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