

THE BREAKDOWN OF SELF-INCOMPATIBILITY IN CULTIVARS OF *BRASSICA OLERACEA*

K. F. THOMPSON and J. P. TAYLOR
Plant Breeding Institute, Cambridge

Received 1.iii.66

1. INTRODUCTION

THE wild ancestors of the cultivars of *Brassica oleracea* L., a diploid species ($2n = 18$), are believed to have been self-incompatible. Some cultivars, however, have either preferential self-compatibility (summer cauliflowers) or partial to complete self-compatibility. In marrow-stem kale, which is morphologically relatively unspecialised and which has been less intensively inbred than cultivars in other botanical varieties of the species, self-compatibility is rare and is usually found only in inbreds homozygous for a *S* allele, low in the dominance series (Thompson, 1961 and 1965). This association in marrow-stem kale between self-compatibility and recessive *S* alleles suggests that the more self-compatible cultivars of other botanical varieties may have a high frequency of *S* alleles, low in the dominance series and Thompson and Taylor (1965) did find that five *S* alleles, low in the dominance series in marrow-stem kale, occurred frequently in some other botanical varieties. These earlier results have been extended by examining both a wider range of cultivars and more plants of each.

2. MATERIAL AND METHODS

The botanical varieties of *B. oleracea* and the sources of the stocks, from which plants were tested, are given below.

- var. *acephala* —green marrow-stem kale (Cannell and Sons Ltd.)
- var. *acephala* —green dwarf curled kale (Bees Ltd.)
- var. *capitata* —January King cabbage (transplants—Cambridge market)
- var. *capitata* —Niggerhead cabbage (Charles Townsend Ltd.)
- var. *gongyloides*—Purple kohlrabi “Matouska Modra Rana” (Institut für Kulturpflanzenforschung, Gatersleben, near Aschersleben, the seed having been produced by Forschung Institut Gemüsebau, Olomouc, Czechoslovakia)
- var. *botrytis* —Summer cauliflower, All the Year Round (Bees Ltd.)
- var. *botrytis* —Summer cauliflower, Early Snowball (F. W. Woolworth and Co. Ltd.)
- var. *botrytis* —Winter cauliflower, St George (Rule Bros.)
- var. *italica* —Purple sprouting broccoli (Bees Ltd.)

About ten flowers on each plant were selfed at the open flower stage to test for self-compatibility. All plants were tested for cross-incompatibility with pollen from four inbreds, homozygous respectively for the recessive alleles S_2 , S_5 , S_{15} , and S_{28} . At least four flowers were pollinated in each test-cross. The tests reveal the presence of these alleles because allele S_2 is active in the stigma in combination with any other *S* allele and because alleles S_5 , S_{15} , and S_{28} are active in the stigma with about half of

TABLE 1
Frequency of recessive S alleles active in the stigmas of plants from different botanical varieties of B. oleracea

Botanical variety of <i>B. oleracea</i>	Type and source	No. plants examined	No. plants with activity in stigma of S alleles				Percentage of S alleles low in dominance
			2	5	15	26	
<i>acephala</i>	Bees' green dwarf curled kale	20	2 (0)	1	0	2	12.5
<i>acephala</i>	Cannell's green marrow-stem kale	17	3 (0)	4 (1)*	1 (1)	0	26.5
<i>capitata</i>	Niggerhead cabbage	18	8 (4)	3 (1)	0	0	42.0
<i>capitata</i>	January King cabbage	17	14 (3)	0	0	1	52.0
<i>italica</i>	Bees' purple sprouting broccoli	21	7 (1)	1 (0)	9 (2)	0	47.6
<i>botrytis</i>	Winter cauliflower	17	6 (1)	1	8 (1)	0	47.0
<i>gongylodes</i>	Purple kohlrabi Matouska modra rana	17	13 (11)	7 (3)	0	0	88.0
Totals		127	53	17	18	3	

* () No. of plants in which allele also active in pollen.

the other S alleles with which they have been tested (Thompson and Taylor, 1966). If possible, incompatible and compatible pollinations were distinguished on the browning or darkening of stigmas, which occurs two days after a compatible pollination—see Thompson and Taylor (1966). The mean seed set per fruit was also recorded about six weeks after pollination and these results were checked with information on cross-incompatibility, obtained from colour changes in the stigma after pollination. If the stigmas of a plant did not darken clearly after a compatible cross, pollinations were classified as compatible or incompatible solely on the number of seed set per fruit. Clear darkening of stigmas after a compatible cross occurred in the majority of plants examined from marrow-stem kale, kohlrabi, January King cabbage and winter cauliflower, but this test could be used for very few plants of curled kale, red cabbage or purple sprouting broccoli. If stigmas darken after a compatible cross, the activity of self-incompatible S alleles can be detected in self-compatible plants. The stigmas of a self-compatible plant normally fail to darken after selfing at the open flower stage or after an incompatible cross, although, in both instances, a full set of seed is produced. Fortunately, completely self-compatible plants were not found in varieties of curled kale, red cabbage or purple sprouting broccoli, in which darkening of the stigma is rare. However, none of the four recessive S alleles could be identified in the summer cauliflower varieties “All the Year Round” and “Early Snowball”, because all plants in both varieties were completely self-compatible and the stigmas of selfed flowers darkened as much as those crossed with the four tester inbreds.

If a plant has one of the recessive alleles, S_2 , S_5 , or S_{15} , it is easy to determine whether the other S allele in the plant is also recessive. These three S alleles were always recessive in the pollen in combination with twenty-three different S alleles from marrow-stem kale (Thompson and Taylor, 1966). Activity of alleles S_2 , S_5 , or S_{15} in the pollen indicates that the other S allele in the plant is also very low in the dominance series. Nearly all plants, active for one of these recessive alleles in the stigma, were tested for activity of that allele in the pollen, and from this information the minimum percentages of recessive S alleles in the populations (table 1) were estimated.

3. RESULTS

The number of times the alleles S_2 , S_5 , S_{15} and S_{28} were active in the stigma in plants from stocks of different botanical varieties of *B. oleracea* is given in table 1. The number of plants, in which the alleles S_2 , S_5 and S_{15} were active in the pollen, as well as in the stigma, is shown in brackets. The percentage of S alleles, low in dominance, for each stock examined, is also presented in table 1.

The allele S_2 was found in every stock examined and in all botanical varieties. It was infrequent in Cannell's marrow-stem kale and in dwarf curled kale; but it was common in purple sprouting broccoli, winter cauliflower and Niggerhead or red pickling cabbage and a very high proportion of plants from January King cabbage and purple kohlrabi had this allele active in the stigma. This allele was usually recessive in the pollen, but it was active in the pollen from four of the eight plants, which had this allele, in Niggerhead cabbage. In Matouska kohlrabi S_2 was active in the pollen from at least 11 of the 13 plants, which had this allele. Alleles S_5 and S_{15} occurred much less frequently than S_2 . Allele S_5 was identified in all stocks except January King cabbage, but it occurred frequently only in the purple kohlrabi. Allele S_{15} was surprisingly not recognised in Bees' stock of dwarf curled kale, although it had been earlier identified twice in dwarf curled kale

selections (Thompson and Taylor, 1965). This allele was not found in purple kohlrabi, although it has been obtained from a variety of green kohlrabi, but it was common in both purple sprouting broccoli and in the winter cauliflower. Allele S_{15} was only rarely active in the pollen and, on two of the four occasions, allele S_5 was present (S_{15} is dominant to S_5 in the pollen). The allele S_{26} was not identified from Cannell's marrow-stem kale, in which it is known to occur rarely, but, as in the earlier series, it was found twice in dwarf curled kale and it was also active once in January King cabbage.

The percentage of recessive S alleles in a stock can be determined from the number of times recessive S alleles are active in the stigmas and also from the activity of these alleles in the pollen of plants, which have one of these recessive alleles active in the stigma. The activity of these S alleles in the pollen was tested for all plants with the exception of a marrow-stem kale plant, active for S_2 in the stigma, a curled kale plant, which had S_5 and two winter cauliflower plants active for alleles S_5 and S_{15} respectively. The percentage of S alleles, low in dominance, cannot be estimated directly by adding together the figures given in table 1 for the number of recessive S alleles in the stigma and the activity of these alleles in the pollen, because, particularly in Matouska kohlrabi, several plants were active in the stigma for two different recessive alleles. Some kohlrabi plants were heterozygous for alleles S_2 and S_5 (table 3); allele S_2 is dominant to S_5 in the pollen so that, if activity of these alleles in pollen and stigma were added together, the percentage of recessive S alleles in the population would be overestimated. In fact, the figures given for the percentage of recessive S alleles are probably too low, because other unknown recessive alleles might be active in plants, not active for any of the four tester S alleles, and also because the alleles S_5 and S_{15} , in particular, might be recessive and therefore undetected in the stigma.

Neglecting these possible errors, considerable differences for the percentage of recessive S alleles occurred between the different stocks. The lowest percentage of 12.5 was found in dwarf curled kale and the value of 26.5 per cent. for Cannell's marrow-stem kale was also low. Between 40 and 50 per cent. of the S alleles were recessive in Nigger-head cabbage, January King cabbage, purple sprouting broccoli and in the winter cauliflowers but the highest value occurred in Matouska kohlrabi, in which 88 per cent. of the S alleles were very low in dominance.

Plants were classified as self-compatible if the seed set on selfing at open flower was at least 80 per cent. of that set on bud pollination or 60 per cent. of that set from a compatible out-pollination. If the seed set on selfing varied between 40 and 80 per cent. of that set on bud pollination or between 25 and 60 per cent. of that set from a compatible outcross, the plant was described as partially self-compatible. It is assumed that most plants are heterozygous for recessive lethal genes and will set less seed on selfing than from a cross with an unrelated plant.

Few partially self-compatible or completely self-compatible plants were found in marrow-stem kale, dwarf curled kale, purple sprouting broccoli or in Niggerhead cabbage (table 2). One of the two self-compatible marrow-stem kale plants had the constitution $S_5 S_{15}$ and in the other plant allele S_5 was active in the stigma (table 3). One dwarf curled kale plant, which had allele S_5 active in the stigma, was partially self-compatible, but the remaining plants were almost completely self-incompatible. One partially self-compatible plant from Niggerhead cabbage was heterozygous for S_2 and S_5 and in the other S_5 was active in pollen and stigma. Three of the 17 January King cabbages were self-compatible, one of these was heterozygous for S_2 and S_{26} . Partial self-compatibility was common in the kohlrabi, variety Matouska; four of the winter cauliflowers were self-compatible and another three were partially self-compatible.

4. FREQUENCY OF S ALLELES IN RELATION TO DOMINANCE RELATIONSHIPS

The results given in this paper and also the earlier results of Thompson and Taylor (1965) show that the recessive alleles S_2 , S_5 and S_{15} are widely distributed throughout the botanical varieties of *Brassica oleracea*. The fourth recessive allele S_{26} has, however, only been found rarely in marrow-stem kale, occasionally in curled kale and once only in January King cabbage. Allele S_2 occurs very commonly and is active in all botanical varieties and all stocks tested. Excluding marrow-stem kale, it is active in 48 per cent. of all plants tested (table 1). Alleles S_5 and S_{15} are active in 12 per cent. and 15 per cent. respectively. Whereas allele S_5 is found in all botanical varieties, allele S_{15} , although identified earlier in curled kale and green kohlrabi, was found in these tests only in purple sprouting broccoli and winter cauliflower; unlike allele S_5 , it was as common in these stocks as S_2 . The dominance relationships between these four S alleles and also with other S alleles offers a partial explanation for the differences in distribution and frequency.

Of 28 different S alleles, obtained from marrow-stem and thousand-head kale and tested for dominance relationships by Thompson and Taylor (1966), only five were recessive in the pollen. Two of these alleles, S_{21} and S_{26} , were recessive to about half the remaining S alleles in the pollen, and three, S_2 , S_5 , and S_{15} , were recessive to all the other S alleles with which they were tested. A simple linear dominance relationship, $S_{26} > S_2 > S_{15} > S_5$, exists in the pollen between the four alleles, used for tests in this paper. In the stigma, S_5 , S_{15} and S_{26} are recessive in about half the combinations tested, but S_2 is active in combination with all but two of the alleles tested. Allele S_2 is incompletely recessive with the two exceptional alleles. Even so, S_2 can always be recognised in the stigma. Thus, the outstanding characteristic of the three alleles, S_2 , S_5 , and S_{15} , is that they are pollen-recessive alleles and the fact that allele S_{26} is only sometimes recessive in the

pollen may account for the differences in frequency between this allele and S_5 .

The activity of S alleles, recessive in the pollen with the majority of other alleles, will normally be masked to permit compatible crosses between plants, heterozygous for the same recessive S allele. Consequently, recessive S alleles can be expected to occur more frequently than dominant S alleles in a population. Sampson (personal communication, Jan. 26th 1965) found that the frequencies of pollen-recessive S alleles were three times higher than those for dominant alleles in a wild population of *Raphanus raphanistrum*.

Although both S_2 and S_5 are widely distributed throughout *B. oleracea*, allele S_2 occurs at least three times as frequently as S_5 . Allele S_2 is always active in the stigma in combination with any other S allele and can be easily detected, whereas allele S_5 is recessive in the stigma with half the other S alleles. Masking of the presence of S_5 cannot, however, account for the difference in frequencies between these two alleles. Allele S_5 is active in the stigma in combination with either S_2 or S_{15} and these two alleles are active in about 60 per cent. of plants examined, excluding marrow-stem kale; hence only one fifth of the total number of S_5 alleles would be expected to be undetected in the populations. On the other hand, allele S_5 might be anticipated to be more frequent than S_2 in these populations, because S_2 is dominant to S_5 in the pollen and is always active in the stigma. However, allele S_2 occurs twice as frequently as S_5 in the purple kohlrabi, which has a very high percentage of recessive S alleles in the population and in which allele S_2 is normally active in pollen and stigma. It is possible that S_2 has other inherent selective advantages.

Allele S_{15} is found in fewer stocks than S_5 , but when it occurs, the frequency of this allele in a population is comparable to that of allele S_2 . Although plants, homozygous for alleles S_2 or S_{15} can be very self-incompatible, competition occurs between these alleles and the S allele heterozygote is self-compatible (Thompson, 1965). In earlier work, one plant of purple sprouting broccoli was found to be self-compatible and to be heterozygous for these two alleles. This may explain the high frequencies of allele S_{15} in populations also active for S_2 . As suggested in section 6, the frequencies of S alleles, associated with self-compatibility, would be expected to increase in rigorously selected cultivars, based on relatively few selections.

5. PERCENTAGE OF RECESSIVE S ALLELES IN STOCKS AND THE OCCURRENCE OF SELF-COMPATIBILITY

Stocks of different botanical varieties vary considerably in the frequency of recessive S alleles (table 1). In marrow-stem kale, self-compatibility has often been found in selections or inbreds, in which only S alleles, low in the dominance series, are present. The self-compatibility factors are genetically independent of the self-incompatibility system and self-compatibility is usually expressed only in the

TABLE 2
Number of partially and completely self-compatible plants in cultivars from different botanical varieties of B. oleracea with the frequency of recessive S alleles in these stocks

Botanical variety of <i>B. oleracea</i>	Type	No. plants examined	Number of plants		Percentage of <i>S</i> alleles low in dominance
			Self-compatible	Partially self-compatible	
<i>acephala</i>	Green dwarf curled kale	20	0	1	12.5
<i>acephala</i>	Green marrow-stem kale	17	2	2	26.5
<i>capitata</i>	Niggerhead cabbage	18	0	2	42.0
<i>capitata</i>	January King cabbage	17	3	1	52.0
<i>italica</i>	Purple sprouting broccoli	21	0	0	47.6
<i>botrytis</i>	Winter cauliflower	17	4	3	47.0
<i>gongylodes</i>	Purple kohlrabi	17	2	8	88.0

absence of S alleles, high in the dominance series (Thompson, 1961, 1965). However, self-compatibility has occasionally occurred in plants, active for a dominant S allele. It is, therefore, of interest to compare the percentage of recessive S alleles in different stocks with the occurrence of partial and complete self-compatibility.

Self-compatibility is less common in stocks than recessive S alleles, and, for this reason, is more liable to sampling error. Thus the numbers of self-compatible plants for marrow-stem kale in table 2 are higher than would be expected from the proportion of selections, taken from this stock for breeding purposes, which are self-compatible. Other

TABLE 3

S allele constitution of partially and completely self-compatible plants from different botanical varieties of *B. oleracea*

Botanical variety of <i>B. oleracea</i>	Type	S allele constitution of plants	
		Self-compatible	Partially self-compatible
<i>acephala</i>	Green dwarf curled kale	...	$S_D^* S_5$
<i>acephala</i>	Green marrow-stem kale	$S_D S_5; S_5 S_{16}$	$S_D S_5; S_D S_D$
<i>capitata</i>	Niggerhead cabbage	...	$S_2 S_5; S_5 S_R^\dagger$
<i>capitata</i>	January King cabbage	$S_2 S_{20}; S_2 S_{23}; S_D S_2$	$S_2 S_{23}$
<i>botrytis</i>	Winter cauliflower	$S_2 S_{15}; S_D S_2; S_D S_5$	$S_D S_{15}; S_D S_{15}; S_D$
<i>gongyloides</i>	Purple kohlrabi	$S_D S_{16}$	S_D
		$S_5 S_R; S_D S_D$	Five plants $S_2 S_R$
			Three plants $S_2 S_5$

* S_D —unidentified S allele; in heterozygotes dominant to recessive S alleles in pollen.

† S_R —unidentified S allele; with which recessive S allele is active in pollen.

botanical varieties of *B. oleracea* have a much higher proportion of recessive S alleles than marrow-stem or dwarf curled kale from var. *acephala*. Dwarf curled kale and purple kohlrabi had respectively the lowest and highest percentages of recessive alleles of the stocks tested. Only one of the curled kale plants was partially self-compatible, but more than half of the kohlrabi plants were either partially or completely self-compatible. Four stocks had from 40 to 50 per cent. of recessive S alleles, but January King cabbage and winter cauliflower had more self-compatible plants than purple sprouting broccoli and red cabbage. A dominant allele was present in the majority of plants from these four stocks, because, with the exception of allele S_2 in red cabbage, the tester S alleles were rarely active in the pollen.

The S allele constitution of partially and completely self-compatible plants are given in table 3. As mentioned at the end of section 3, several of the self-compatible plants in marrow-stem kale, January King and red cabbage had only recessive S alleles. Eight partially self-compatible and the completely self-compatible plant from the purple kohlrabi had only recessive S alleles; one completely self-compatible plant was not

active for any of the four recessive tester S alleles and was recorded in table 3 as $S_D S_D$. However, this plant might have been active for a different recessive S allele. One self-compatible plant from winter cauliflower was heterozygous for alleles S_2 and S_{15} , but the other three self-compatible plants each had an S allele, dominant either to S_2 , S_5 , or S_{15} in the pollen. At least two different dominant alleles occurred in these three plants. Four plants from January King cabbage were heterozygous for alleles S_2 and S_{23} , in which S_{23} was dominant to S_2 in the pollen. One of these four plants was completely self-compatible and two were very self-incompatible. Allele S_{23} may also be fairly low in the dominance series, because alleles S_2 and S_{23} were both active in the pollen from a wild cabbage plant. All purple sprouting broccoli plants were very self-incompatible, except for one self-compatible plant from the earlier series, which was heterozygous for alleles S_2 and S_{15} . It is possible that self-compatible genes are rare in purple sprouting broccoli.

Although self-compatible plants in different botanical varieties of *B. oleracea* often carry only recessive S alleles, some self-compatible plants have alleles, higher than the pollen-recessive alleles in the dominance series, but the position of these dominant alleles, e.g. S_{23} , in the dominance series may still be relatively low. Thus, although the frequency of recessive S alleles is not always matched by the degree of self-compatibility in individual stocks, there appears to be a tendency for self-compatibility to be more common in varieties with a high proportion of recessive S alleles.

6. EFFECTS OF INTENSIVE SELECTION ON THE FREQUENCY OF RECESSIVE S ALLELES AND SELF-COMPATIBILITY IN *B. OLERACEA*

The different frequencies of recessive alleles and the association between self-compatibility and a high frequency of recessive alleles can be explained by the effect of intensive selection in certain botanical varieties of *B. oleracea*. When plants of *B. oleracea* were first taken into cultivation, they were probably highly self-incompatible. Thus Sampson (1964) has found that one striking difference between two crop species (broccoli and radish) and two wild species (*Lesquerella densipila* and *Raphanus raphanistrum*) was "the commonness of self-compatible individuals in the crops and their absence from the weeds."

The agricultural kales, and perhaps curled kales, are morphologically relatively unspecialised and have been less intensively bred than the other botanical varieties. Mass-selected stocks of marrow-stem kale may be based on several hundred selections. In marrow-stem kale self-compatibility is rare and at least 24 different S alleles have been identified in one stock, although only 15 of these occurred frequently (Thompson and Taylor, 1966). Similarly, plants of dwarf curled kale were very self-incompatible and no dominant allele occurred more than three times in the 20 plants tested.

In wild populations, masking of the activity of recessive S alleles

permits a much higher frequency of recessive than dominant S alleles. In the weed species, *Raphanus raphanistrum*, Sampson (personal communication, Jan. 28th 1965) found that three pollen-recessive alleles had a mean frequency three times that of four dominant S alleles. Under cultivation, in which small numbers of selected plants are seeded together, there would be a greater selection pressure than in the wild. The total number of S alleles in the population would fall as the proportion of recessive S alleles increased. If self-compatible genes, independent of the S allele system, were present, seed multiplication would favour the retention of partially or completely self-compatible plants with S alleles, low in the dominance series, especially if insect pollinators were rare.

Stocks of January King cabbage, purple sprouting broccoli, winter cauliflower, red cabbage and probably Brussels sprouts are at this stage in the breakdown of the self-incompatibility system. In many of these stocks the number of different dominant S alleles has been reduced. Only five different dominant S alleles were found in the 17 plants of January King cabbage examined; allele S_{23} was active in four plants and another dominant allele was active in five plants. In winter cauliflower one dominant S allele was active in seven of the 17 plants and in red cabbage one dominant allele was identified in seven of the 18 plants.

A further stage towards a self-fertilised crop is shown in the purple kohlrabi variety "Matouska," in which dominant S alleles are almost absent and 88 per cent. of the S alleles are recessive and represented mainly by alleles S_2 and S_5 . Partial and complete self-compatibility is common, but self- or cross-incompatible pollinations can still be distinguished from cross-compatible pollinations, by the failure of stigmas to darken after pollination. Finally, the summer cauliflowers represent the most self-compatible type in *B. oleracea*, in which it is not possible to distinguish incompatible from compatible crosses on darkening of stigmas, because the stigmas of selfed flowers darken considerably. For this reason, S alleles in two varieties of summer cauliflower could not be identified. Watts (1965) found that there is little if any inbreeding depression in summer cauliflowers in contrast to the more self-incompatible autumn and winter cauliflowers, in which even self-compatible plants showed marked inbreeding depression on selfing. He said that "records of summer cauliflower production can be traced to the middle of the 19th century, prior to which only the coarser autumn and winter types seem to have been grown. It is highly possible that the increasing interest in horticulture at that time led to the selection of an "annual" earlier maturing type, which, under continuous close selection and mating evolved a system of homozygous balance."

The evolution of self-compatibility in the summer cauliflower may be paralleled by the breeding of the winter cauliflower cultivar, Cambridge Dwarf April, which was obtained by rigid selection over the last

thirty years following a cross between two plants of the winter cauliflower cultivar St George (Watts, 1963). The results of tests for activity of recessive S alleles in plants from the cultivar, St George, are given in this paper (table 1), and Watts considered this cultivar to be one of the most self-incompatible of the winter cauliflowers. Watts found that Cambridge Dwarf April was the only cultivar from the winter cauliflowers to set more seed by self than by mixed pollen. He also states that this cultivar is "noticeably uniform and yields well, showing no loss of vigour after successive generations of inbreeding."

7. INTERPRETATION OF DISTRIBUTION AND FREQUENCY OF ALLELE S_2 IN *B. OLERACEA*

Allele S_2 has been found in all stocks of any botanical variety of *B. oleracea*, in which at least 17 plants were tested. The total number of plants, in which this allele has been identified, is surprisingly high, and the frequency of this allele in January King cabbage, Niggerhead cabbage and purple kohlrabi is probably even higher than is suggested by data in table 1. In these stocks, plants, in which S_2 is active in the pollen and S_5 or S_{15} are not identified, are probably homozygous for allele S_2 . Reasons for the widespread distribution and high frequency of this allele in *B. oleracea* must be considered.

Plants from all the different botanical varieties of *B. oleracea* cross readily with each other to give fertile hybrids. However, as suggested by Thompson and Taylor (1965) it is unlikely that allele S_2 has been spread in the last century by cross-pollination between the distinct, basic, breeders' stocks of Brussels sprouts, cabbages, kohlrabi, purple sprouting broccoli or cauliflower. Although mutations are normally recessive and the number of different recessive S alleles in *B. oleracea* appears to be limited, independent mutation to S_2 in different botanical varieties is not probable, because S alleles are remarkably stable. Lewis (1951) reported no new self-incompatible mutations at the S locus after screening 22 million gametes of *Oenothera* and Dodds (1961) found the same S alleles in diploid cultivated species of potato and in polyhaploids of autotetraploid Andigena potatoes which must have been isolated for a long time. It is much more likely that allele S_2 , and perhaps S_5 and S_{15} , occurred in the ancestral *B. oleracea*, from which the modern botanical varieties have evolved.

The widespread occurrence of the three pollen-recessive alleles S_2 , S_5 and S_{15} in different botanical varieties of *B. oleracea* can be satisfactorily explained by the effect of intensive selection on the frequency of recessive S alleles in populations. It does not account for the very high frequency and ubiquitous distribution of allele S_2 , relative to alleles S_5 and S_{15} . Some horticultural cultivars are based on very few selections and it would be expected that by chance one or other of the pollen-recessive S alleles would be eliminated sometimes from a stock. This would appear to happen to alleles S_5 and S_{15} . From table 1, allele S_{15} was not detected in January King cabbage, red cabbage or in

the purple kohlrabi variety, while S_5 was not found in January King cabbage. The self-compatibility of the heterozygote, S_2, S_{15} confers an advantage on alleles S_2 and S_{15} , compared with allele S_5 , but it is allele S_{15} , which most frequently was not found in stocks. Otherwise the dominance relationships of allele S_2 do not give it any advantage compared with the other two alleles and it must be assumed that allele S_2 must have some other inherent advantages.

8. SUMMARY

1. Three pollen-recessive S alleles, S_2 , S_5 and S_{15} , which were identified in marrow-stem kale, are frequently active in the stigmas of a wide range of botanical varieties within the species *Brassica oleracea*.

2. Populations from different varieties differed in the frequency of recessive S alleles (table 1). High frequencies of recessive S alleles in a population are often associated with a higher proportion of partially and completely self-compatible plants.

3. Intensive selection for morphological and physiological characters by plant breeders is probably responsible for both these properties.

4. Allele S_2 was found more commonly than the other pollen-recessive alleles and has been recognised from all the botanical varieties examined. This allele was active in 48 per cent. of plants tested, apart from marrow-stem kale. It may have been present in the ancestral *B. oleracea*, from which the modern botanical varieties have evolved.

9. REFERENCES

- DODDS, K. S. 1961. *Ann. Rep. John Innes Institute*, 52, 22.
- LEWIS, D. 1951. Structure of the incompatibility gene. III. Types of spontaneous and induced mutations. *Heredity*, 5, 399-414.
- SAMPSON, D. R. 1964. A one-locus self-incompatibility system in *Raphanus raphanistrum*. *Can. J. Genet. Cytol.*, 6, 435-445.
- THOMPSON, K. F. 1961. *Ann. Rep. Plant Breeding Institute, Cambridge*, (1959-1960), 41.
- THOMPSON, K. F. 1965. *Ann. Rep. Plant Breeding Institute, Cambridge*, (1963-1964), 71.
- THOMPSON, K. F., AND TAYLOR, J. P. 1965. Identical S alleles in different botanical varieties of *Brassica oleracea*. *Nature*, 208, 306-307.
- THOMPSON, K. F., AND TAYLOR, J. P. 1966. Non-linear dominance relationships between S alleles in kale. *Heredity*, 21, 345-362.
- WATTS, L. E. 1963. Investigations into the breeding system of cauliflower, *Brassica oleracea* var. *botrytis* (L.). I. Studies of self-incompatibility. *Euphytica*, 12, 323-340.
- WATTS, L. E. 1965. Investigations into the breeding system of cauliflower. II. Adaptation of the system to inbreeding. *Euphytica*, 14, 67-77.