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AN S-ALLELE SURVEY OF CABBAGE (*BRASSICA OLERACEA* VAR. *CAPITATA*)

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INDEX WORDS

Brassica oleracea var. *capitata,* cabbage, recessive S-alleles, S-allele collection, F_1 hybrids.

SUMMARY

A total of 31 S-alleles was found in a survey of 197 cabbage plants representing 11 cultivars of diverse type. Most of these S-alleles also occurred in either kale or Brussels sprouts, but five of them have not been found previously and apparently occur only in cabbage. A more detailed study of five cultivars of spring cabbage showed only 12 S-alleles in all, with 6–10 S-alleles in four older cultivars and only 3 S-alleles in the newer more highly selected cultivar. S2 was by far the commonest S-allele, as it is in *B. oleracea* as a whole. The highly recessive alleles S5 and S15 were not particularly common in cabbage and this may partly explain why the sib problem in F_1 hybrids is apparently less in cabbage than in Brussels sprouts. Three cases were found in which an S-allele was completely recessive in both the stigma and the pollen. The problems for the breeder created by this rather unusual situation are discussed.

INTRODUCTION

Most of the commercially important cabbage cultivars in the USA are F_1 hybrids (RYDER, 1979), and there is a similar trend in Western Europe (INNES, 1975). These F_1 hybrids are based on self-incompatibility, yet little has been published about the S-alleles which occur in cabbage. HARUTA (1962) found ten S-alleles in breeding material derived from six cultivars of cabbage, and WALLACE (1979) was apparently working with seven S-alleles in inbred lines of cabbage. Some private breeding companies have information about the S-alleles in their cabbage breeding material, and may have their own S-allele collections, but this information is not generally available. With the creation of the standard Brassica S-allele collection, it became feasible to make a survey of the S-alleles which occur in cabbage. This collection was started in Cambridge (THOMPSON, 1968) and has been housed at the National Vegetable Research Station since 1971 (OCKENDON, 1975b). A further aim was to add to the collection any new S-alleles.

Knowledge of the S-alleles present in his material is useful to the breeder of F_1 hybrids because he must ensure that his inbreds are homozygous for their S-alleles, and this is greatly facilitated by knowledge of the S-alleles originally present in the inbred families. Information is available about the S-alleles present in kale (THOMPSON & TAYLOR, 1966a), Brussels sprouts (OCKENDON, 1974) and Cape broccoli (OCKENDON, 1980), and it is useful to know if the S-alleles in cabbage differ markedly from those of the other cole crops.

Because of the wide range of cabbage types, a complete survey of the S-alleles in cabbage would be very time-consuming. For the present study, cultivars which were not highly selected were chosen to represent a wide range of types, and relatively few plants of each cultivar were tested. However, for spring cabbage several cultivars were tested to detect the variation between cultivars of a single morphological type, and to compare the highly selected cv. Avon Crest with some of the older more variable cultivars.

MATERIAL AND METHODS

S-allele tests were made on 11 cultivars of cabbage. Five of these were spring maturing cabbages with conical heads, and the others (Table 2) can be described according to JENSMA (1956) as white cabbage (cvs Brunswick and Christmas Drumhead), savoy (cvs Winter and January King Compact) and red cabbage (cv. Red Niggerhead); cv. Purple Flatpoll is a large coarse cattle cabbage, not mentioned by JENSMA (1956). Four of the five spring cabbage cultivars (Table 1) were traditional open-pollinated forms, whereas the fifth, cv. Avon Crest is a more highly selected form released in 1970, and derived from crosses between cvs Liverpool Market and Severn Stoke (JOHNSON & FAULKNER, 1967). The aim was to test 20 plants of each cultivar, but this was not always possible. A total of 197 plants was tested, including 30 plants of cv. Avon Crest.

The plants were tested against the standard *Brassica* S-allele collection. As far as possible, both S-alleles in each plant were identified. As S-alleles are more often masked by dominance in the pollen than in the stigma, the S-allele tester plants were normally used as the male parents. When testing for an S-allele known to be more recessive in the stigma than in the pollen, the S-allele tester plants were used as females. Because of the unusual dominance relationships of S2 and S5 it was possible to identify plants homozygous for either of these two S-alleles using the method already described by OCKENDON (1977a). For some plants in which only one S-allele could be identified initially, selfed-progenies were raised and the second S-allele isolated in the progeny.

Two freshly opened flowers were used in each test and test pollinations were assessed as compatible or incompatible by examining pollen tube growth 24 hours after pollination. Pollinated styles were stained with decolorised aniline blue and the pollen tubes observed with a fluorescence microscope (KHO & BAER, 1968).

RESULTS

A total of 12 different S-alleles was found in the four older cultivars of spring cabbage tested (Table 1) with each cultivar having 6–10 S-alleles. The four S-alleles which were common to all four cultivars also occurred at the highest frequency within a cultivar. Three of these four S-alleles were recessive either in the pollen or in the stigma.

With cv. Avon Crest, more difficulty was encountered with the S-allele identifications than in the other cultivars, because in many of the plants tested only one of the two S-alleles present could be identified with certainty. Despite testing 30 plants only 3 different S-alleles were found, and in only 12 plants could both S-alleles be identified initially. The problem was largely resolved when the selfed progeny of a

Table 1. S-allele frequencies in four cultivars of spring cabbage. The figures indicate the percentage of plants carrying the allele. PR = recessive in the pollen, SR = recessive in the stigma.

S-allele	Sutton's April	Durham	Offenham	Severn Stoke
S2 PR	13	36	4	18
S5 PR	27	24	7	14
S6		5	11	4
S12	7		7	11
S13				4
S14 SR			11	
S15 PR	7		7	7
S23		12		7
S24	7	9	7	7
S25 SR	13	7	14	14
S45 PR	10		7	
S50			4	
unknown	17	7	21	14
Total S-alleles	7	6	10	9
Number plants tested	15	21	14	14

plant in which only S6 could be detected, was found to contain plants which were S5.5. In this progeny S6.6 plants could not be distinguished from S5.6 plants because S6 was completely dominant to S5 both in the pollen and the stigma. In other plants of cv. Avon Crest, S6 was found to be dominant to S13 in the stigma but not in the pollen. As plants homozygous for recessive S-alleles are expected to occur naturally, but those homozygous for dominant S-alleles are not (OCKENDON, 1974), plants in which S6 alone could be detected were considered to be S5.6, whereas plants in which S5 alone or S13 alone were found, were considerd to be homozygous. On this basis the S-allele frequencies were estimated to be S5 = 35%, S6 = 25%, S13 = 40%.

Two further examples of plants in which one of the S-alleles was completely recessive in both the pollen and the stigma were found in cv. Durham. By testing selfed progenies it was established that one plant was S23.5 and the other S24.2. Although S2 is usually recessive in the pollen, it is very rarely completely recessive is the stigma as well (THOMPSON & TAYLOR, 1966a; OCKENDON, 1975a).

The six cultivars representing a wide range of cabbage types had a total of 25 S-alleles (Table 2). The largest number of S-alleles (11) was found in cv. Purple Flatpoll, and the smallest number of S-alleles (4) was found in cv. Red Niggerhead. S2 occurred at a high frequency in five of the six cultivars, but surprisingly was absent from cv. Purple Flatpoll. The commonest S-alleles were S2, 3, 4, 7, 16, 45 and each of these occurred in at least half of the cultivars tested. S26 was found in only one of the cultivars, but at a high frequency, and may well be more widespread than the present data indicate. The pollen recessive S-alleles S5 and S15 were relatively uncommon in the six cultivars tested in Table 2, although both occurred in spring cabbage (Table 1), with S5 at a particularly high frequency. The six cultivars tested (Table 2) were clearly less similar in their S-alleles than the four cultivars of spring cabbage (Table

Table 2. S-alleles in various cabbages. Figures represent the percentage of plants carrying a particular S-allele.

	Purple Flatpoll	Brunswick	Red Niggerhead	January King Compact	Christmas Drumhead	Savoy Winter King
S2 PR		34	56	25	44	24
S3	3			7		3
S4	6				3	13
S5 PR	6					
S6	8					
S7		13		4		18
S8		6				
S12	3					
S14 SR				11		
S15 PR	6	13				
S16	3	13		7	3	
S17					14	
S18	19					
S22				4	3	
S23					8	
S26 SR				32		
S28 SR			17		3	
S29			14			
S33	8					
S36		6				
S45 SR	11		14		11	
S55					3	21
S56	17					
S58						18
S63		3				
unknown	11	13	0	11	3	3
Total S-alleles	11	7	4	7	9	6
Plants tested	18	16	18	14	18	19

1), and spring cabbage contained four S-alleles (S13, 24, 25, 50) not found in the other cabbage types tested.

Most of the 31 S-alleles found in cabbage also occur in kale, Brussels sprouts or Cape broccoli (Table 3). but five of them have not been found previously and are confined to cabbage. One of these (S53) has only been found in a line derived from the savoy cv. Ostara, which was received from the Institute for Horticultural Plant Breeding in Wageningen. Another, (S54), has only been found in an inbred line derived from cv. Copenhagen Market, which was received from Mr R. M. Adamson. The total number of S-alleles in cabbage (Table 3) is similar to that in kale, but appreciably greater than in Brussels sprouts and Cape broccoli. This is probably related to the degree of morphological variation, which is much greater between cultivars of cabbages and kales than between cultivars of Brussels sprouts or Cape broccoli.

Table 3. Occurrence in kale, Brussels sprouts and Cape broccoli of S-alleles found in cabbage.

	Cabbage	Kale[1]	Brussels[2] sprouts	Cape broccoli[3]
S2	+	+	+	+
S3	+	+		
S4	+	+		
S5	+	+	+	
S6	+	+		
S7	+	+	+	
S8	+	+		+
S12	+	+		+
S13	+	+	+	
S14	+	+	+	+
S15	+	+	+	+
S16	+	+		+
S17	+	+		
S18	+	+		+
S22	+	+	+	
S23	+	+	+	+
S24	+	+		+
S25	+	+		+
S26	+	+		+
S28	+	+		
S29	+	+	+	+
S33	+	+		
S36	+	+	+	+
S45	+		+	+
S50	+			
S53	+			
S54	+			
S55	+			
S56	+			
S58	+			+
S63	+		+	
Total	31	23 (33)	12 (19)	15 (20)

The total number of S-alleles in kale, Brussels sprouts and Cape broccoli are indicated in brackets.
[1] THOMPSONS & TAYLOR (1966a); [2] OCKENDON (1974); [3] OCKENDON (1980).

DISCUSSION

The recessive S-alleles in *Brassica oleracea* are typically recessive either in the pollen or in the stigma (THOMPSON & TAYLOR, 1966a), but seldom totally recessive in both. Totally recessive S-alleles (S_R) present a problem because they can only be detected in a selfed progeny of a plant which is S_DS_R (S_D = dominant S-allele), and not in the original plant. Furthermore there is no way of distinguishing S_DS_R from S_DS_D plants except by testing their selfed progenies. This is a particular problem for a breeder wishing to obtain an inbred line homozygous for a dominant S-allele which occurs together with a totally recessive S-allele.

THOMPSON & TAYLOR (1966b) suggested that intense selection for uniformity could lead to the loss of S-alleles and the accumulation of high frequencies of recessive S-alleles. Cv. Avon Crest is a good example of this, although the extent of allele loss is not quite as great as in the cabbage cv. Avon Coronet which has only 2 S-alleles (OCKENDON & CURRAH, 1979).

Because of the greater morphological diversity and the smaller number of plants tested, the S-allele data for cabbage given here is less complete than that for Brussels sprouts (OCKENDON, 1974) although the majority of S-alleles in cabbage have probably been detected. The more detailed data for spring cabbage revealed 12 S-alleles, and it is likely that the other major types of cabbage have a similar number of S-alleles, with many of these alleles common to at least two types.

Although most of the S-alleles in cabbage also occur in other cole crops, reflecting their common ancestry, the distribution of S-alleles in cabbage differs from that of other cole crops. As these crops are fully interfertile, they must be kept separate if they are to retain their distinctive features. This splitting up of the cole crop gene pool has led to differences in the S-allele distribution, which are maintained despite evidence that S-alleles can be transferred from one cole crop to another (OCKENDON, 1977b).

The most recessive S-alleles in *B. oleracea* are S5 and S15, and these are often associated with poor self-incompatibility both in kale (THOMPSON & TAYLOR, 1971) and Brussels sprouts (SMITH, BLYTON-CONWAY & MEE, in press). These weak S-alleles are considerably less common in cabbage than in Brussels sprouts. Furthermore there is a wider range of dominant S-alleles available in cabbage than in Brussels sprouts. This helps to explain the report by HODGKIN (1981) that sib rates were considerably lower in F_1 hybrid cabbages than in F_1 hybrid Brussels sprouts.

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