Euphytica 12 (1963): 323–340

INVESTIGATIONS INTO THE BREEDING SYSTEM OF CAULIFLOWER *BRASSICA OLERACEA* VAR. *BOTRYTIS* (L.)

I. Studies of self-incompatibility

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With 7 figures

Received 27 May 1963

Abstract

Incompatibility reactions of 21 varieties of summer, autumn and winter type cauliflowers were assessed by

(a) comparing the seed sets per siliqua from separate inflorescences of the same plant which were self-pollinated and mixed-pollinated with self and Brussels sprout pollen,

(b) correlating the percentage hybrids from the mixed-pollinations with those from natural cross-pollination,

(c) differentiating between the self- and mixed-pollinations by the proportions of seed set in each quarter of the siliquas, and

(d) calculating the percentage of hybrid seed in each quarter of the siliquas following mixed-pollination.

All three cauliflower types set similar amounts of seed upon artificial self-pollination, but the autumn and winter cauliflowers exhibited a "facultative self-incompatibility" by their ability to set more seed following mixed-pollination with self and Brussels sprout pollen. The percentage of hybrids in the progenies from the mixed-pollinations were – summer cauliflowers 18.2, autumn cauliflowers 57.1, and winter cauliflowers 71.9. These results were similar to those found after natural cross-pollination.

Calculations of the percentage of hybrid seeds in each quarter of the siliqua showed that the ratio of hybrid : self seeds was the same in all quarters of the siliqua, indicating that restrictions of pollen tube growth in these cauliflower types is confined to the stigmatic surface.

It is suggested that the annual type summer cauliflowers were derived from biennial types by constant selection of a small number of plants for uniformity and quality which has led to self-compatibility as a correlated response. It is also suggested that under similar intense selection self-compatibility may possibly be attained in the autumn and winter types.

Introduction

The cauliflowers grown in Britain fall into three main types, summer, autumn and winter which differ in time of sowing, period of market maturity, and subsequent flowering and seed-setting. Varieties of the autumn and winter types are noticeably more variable both between and within varieties than those of the summer cauliflower type.

LAMM, HINTZE, and AVALL (1957) described the difficulties in identifying varieties and suggested that cauliflowers were mainly cross-fertilised, although JENSMA (1957) found a low percentage of cross-fertilisation (with the exception of an individual plant) in a single variety of summer cauliflower, and concluded that cauliflowers were self-compatible and mainly self-fertilised. BATEMAN (1955) showed that while many *Brassica* species exhibit sporophytic self-incompatibility, the degree of self-incompatibility varies with different species. Few investigations into the breeding system of cauliflowers have been reported, but SAMPSON (1957) showed that sprouting broccoli (a species which is cross-compatible with cauliflower and morphologically resembles it more closely than other Brassicas), possesses a sporophytic incompatibility system.

An attempt has been made to clarify the breeding system by making a study of

(a) the variations in self-compatibility shown by differences in seed set between self- and mixed-pollinated (with Brussels sprout and self-pollen) inflorescences of individual plants,

(b) the amount of cross-pollination occurring under natural conditions.

(c) the expression of self-incompatibility as shown by the number and position of seeds within the siliqua following self-pollination, and

(d) the effect of the incompatibility reaction by assessing the numbers and positions of hybrid seeds within the siliqua.

MATERIALS AND METHODS

In order to make controlled pollinations upon the three cauliflower types, twenty plants of eight varieties of each type were raised direct from seed sown in pots in mid-April out-of-doors, and were transferred to an insect-proof glasshouse when curds or heads were produced. By this method, the winter cauliflower types received the cold stimulus necessary for curd initiation (VERKERK, 1954), and flowering periods of the three types overlapped one another. Because of deaths, the number of varieties was eventually reduced to the twenty one shown in Table 1.

As each plant came into flower, its inflorescence was divided into three parts, each consisting of 50 to 100 flowers, which were covered by cellophane bags to prevent contamination by foreign pollen. Part one of the inflorescence was then self-pollinated, by brush, three times per week, while part two was shaken vigorously at these times to encourage pollen dispersal within the bag. The seed-set from both forms of self-pollination supplied a measure of the degree of auto-compatibility (DRAYNER, 1959) for plants and varieties, as well as providing an indication of the facility with which selfed seed could be produced under bags in the field. Part three of each inflorescence was pollinated with a brush bearing compatible pollen of Brussels sprouts, and by thus overcoming any effect of self-incompatibility, an indication was given of the potential seed-set for a particular plant. This pollination is referred to in the text as mixed-pollination since the brush picked up both foreign pollen and self-pollen during the transfer of pollen from Brussels sprouts to unemas-

TABLE 1. SUMMER, AUTUMN AND WINTER CAULIFLOWER VARIETIES USED IN POLLINATION EXPERIMENTS

Ref. No.	Variety	Supplier	Type and normal cultivation
S1	Cambridge No. 5	N.V.R.S.	Summer cauliflower
S2	Cambridge No. 6	N.V.R.S.	(Sown October or January and maturing
S3	Cambridge No. 7	N.V.R.S.	late May to late June)
S4	No. 8	N.V.R.S.	
S5	All the Year Round	Finney	
S6	No. 35	Van den Berg	
S7	Six Weeks	Van den Berg	
A1	Autumn Giant	E. W. King	Autumn cauliflower
A2	Everest	Elsoms	(Sown in March and maturing late
A3	Early September	Woodwards	August to late October)
A4	Majestic	Harrison (L.)	
A5	Primus	Dippe	
A6	Lenormand	de Corato	
W1	Cluseed Princess	Clucas	Winter cauliflower
W2	Early Feltham	Cooper-Taber	(Sown in May and maturing March to
W3	April Queen	Cooper-Taber	May)
W4	Avalanche	Webb (Stourbridge)	
W5	Camb. Dwarf April	N.V.R.S.	
W6	Giant Easter	D.T. Brown	
W7	St. George	Cooper-Taber	
W8	Camb. Hardy Late	N.V.R.S.	

culated cauliflowers. From an earlier experiment the most satisfactory method of assessing seed-set in cauliflower was found to be that of counting the number of seeds per pod or siliqua. Ovaries of all varieties used in the experiment contained similar numbers of ovules.

MARKER GENES

As there are no cauliflower marker genes which can be reliably identified in the seedling stage, pollen of Brussels sprout (*B. oleracea* L. var. *gemmifera* ZENKER), which is cross-compatible with cauliflower (CRANE, 1943), provided marker genes for pollinations on the third part of the inflorescence. The Brussels sprout plant characters, reflexed habit, elongated epicotyl, rounded lamina, entire edge, and presence of axillary buds behave as dominants in F_1 (figures 1–3).

Identification of hybrids was possible at the two leaf stage but, since the hybrids became progressively more like the male parent with increasing age, seedlings were left in the seedbed until five or more leaves were produced.

In order to determine whether either type of pollen possessed an advantage over the other in germination or subsequent growth, eight cauliflower plants were emasculated and pollinated with a mixture of pollen from Brussels sprout and an unrelated cauliflower variety which possessed a marker gene identifiable in the mature plant. A total progeny of 143 Brussels sprout hybrids and 187 cauliflower hybrids

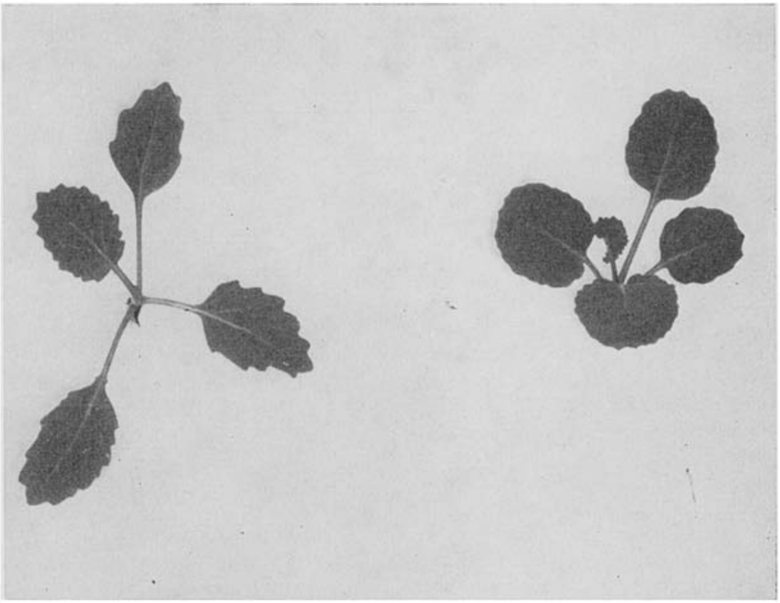

FIG. 1. Seedling of cauliflower (left) and cauliflower/sprout hybrid (right).

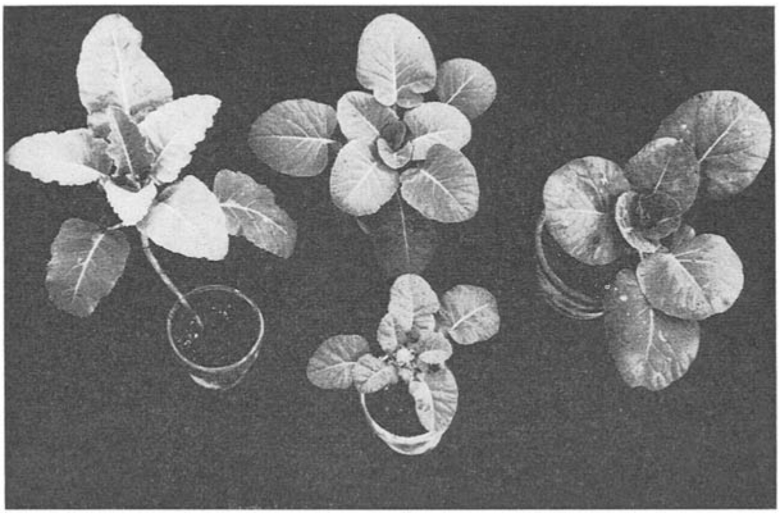

FIG. 2. Cauliflower (left), Brussels sprout (right). Two cauliflower/Brussels sprout hybrids centre (lower one with "curd").

were produced and although this ratio differed significantly from a 1 : 1 ratio (x^2 = 5.86), the difference was mainly due to the performance of one plant which gave 14 Brussels sprout and 56 cauliflower hybrids in its progeny. Excluding this progeny, the ratio became 129 : 131 (x^2 = .01 P = .90) – three plants giving an excess of

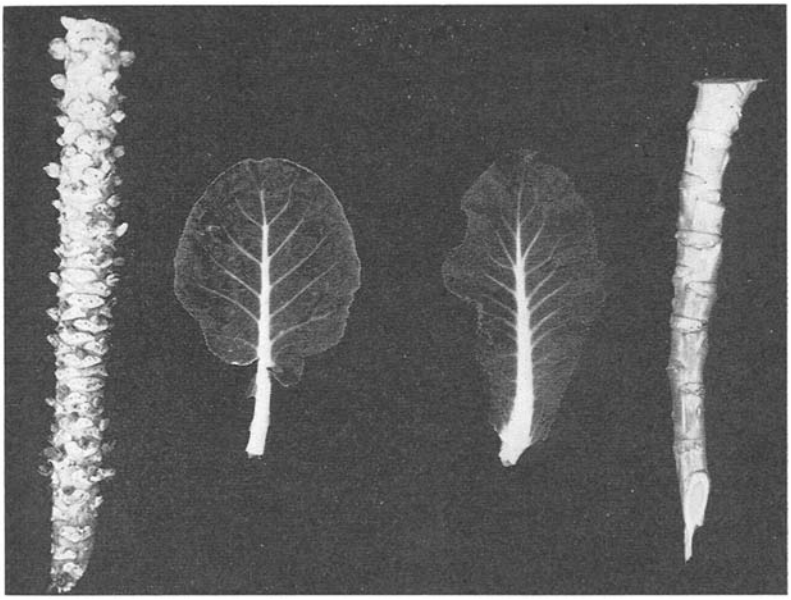

FIG. 3. Leaf and stem (no axillary buds) of cauliflower (right). Leaf and stem of cauliflower/ Brussels sprout hybrid (left).

Brussels sprout hybrids, and five plants an excess of cauliflower hybrids in their progenies, – and as neither type of pollen showed a consistent advantage over the other it was concluded that the use of Brussels sprout pollen would give a reliable indication of cross-compatibility.

(a) POLLINATION RESULTS

Auto-compatibility

BATEMAN (1935) indicated that natural self-pollination in *Cruciferae* is automatic, although pollen may not reach the stigma if the anthers show any tendency to become reflexed. Table 2 shows the seed-set for both forms of self-pollination, with and without brushing, and indicates that apart from two varieties (S1 and W7), brush pollination resulted in greater seed-set. All varieties set some seed without application of pollen by brush and although the differences between means for pollination with and without brushing were significant for the three cauliflower types, there was evidence of a greater tendency towards auto-compatibility in the summer and autumn types than in the winter types.

It may be concluded from table 2, that selfing of selected cauliflower plants (especially summer cauliflower) under bags in the field without mechanical aid will give a reduced yield of seed, but this may well be compensated by economy in labour, particularly as the plants can be seeded *in situ*. Some varieties, however, e.g. W1 and W2, may be found to need the additional stimulus of brush pollination.

TABLE 2. SEED-SET PER SILIQUA FROM SELF-POLLINATION BY BRUSH AND BY AGITATION

Seed set per pod from	Summer Types Variety: S1	S2	S3	S4	S5	S6	S7		Mean
Self by brush	4.2	7.5	4.8	6.6	5.9	5.9	7.1		6.0 ± .33
Self by agitation	5.8	6.7	4.7	2.9	5.2	3.2	6.7		5.0 ± .38
Differences, Brush minus agitation	−1.6	0.8	0.1	3.7	0.7	2.7	0.4		1.0 ± .42
Seed set per pod from	Autumn types A1	A2	A3	A4	A5	A6			
Self by brush	9.6	5.4	9.0	6.0	4.9	8.3			7.2 ± .71
Self by agitation	6.8	3.7	5.3	5.8	3.8	8.1			5.6 ± .79
Differences, Brush minus agitation	2.8	1.7	3.7	0.2	1.1	0.2			1.6 ± .79
Seed set per pod from	Winter types W1	W2	W3	W4	W5	W6	W7	W8	
Self by brush	6.8	7.8	4.3	5.7	9.3	6.4	5.1	7.0	6.6 ± .48
Self by agitation	2.2	2.6	3.4	3.6	6.0	4.5	6.7	4.6	4.2 ± .41
Differences, Brush minus agitation	4.6	5.2	0.9	2.1	3.3	1.9	−1.6	2.4	2.4 ± .51

TABLE 3. SEED SET PER SILIQUA FROM MIXED- AND SELF-POLLINATION BY BRUSH

Seed set per pod from	Summer types Variety S1	S2	S3	S4	S5	S6	S7		Mean
Mixed-pollination	6.3	4.6	3.4	4.9	4.8	4.9	5.1		4.9 ± .32
Self-pollination	4.5	7.5	4.8	6.6	5.9	6.6	6.5		6.1 ± .41
Difference. Mixed minus self	1.8	−2.9	−1.4	−1.7	−1.1	−1.7	−1.4		−1.2 ± .52
Seed set per pod from	Autumn types A1	A2	A3	A4	A5	A6			
Mixed-pollination	7.2	5.8	8.8	6.9	6.3	9.9			7.5 ± .63
Self-pollination	8.2	5.4	7.7	5.8	5.6	8.3			6.8 ± .56
Difference. Mixed minus self	−1.0	0.4	1.1	1.1	0.7	1.6			0.7 ± .85
Seed set per pod from	Winter types W1	W2	W3	W4	W5	W6	W7	W8	
Mixed-pollination	7.8	8.5	8.9	6.8	7.1	9.9	10.3	10.7	8.8 ± .52
Self-pollination	6.4	6.7	4.8	5.3	9.0	6.4	4.8	6.2	6.2 ± .48
Difference. Mixed minus self	1.4	1.8	4.1	1.5	−1.9	3.5	5.5	4.5	2.6 ± .71

Expressions of self-incompatibility

The differences in seed-set between self- and mixed-pollination by brush are shown in Table 3.

The summer cauliflowers (with the exception of variety S1) were significantly more self-fertile than cross-fertile. Out of 63 plants, 49 gave more seed with self-pollination than with mixed-pollination. The autumn cauliflowers showed a slight trend towards increased cross-fertility, but this was not significant. The winter cauliflowers (with the exception of variety W5) were significantly more cross-fertile than self-fertile. The three cauliflower types set similar numbers of seeds per siliqua with self-pollination, however, and it appeared that the winter cauliflowers and, to a lesser extent, the autumn cauliflowers, exhibit what may be described as a "facultative self-incompatibility" – selfing was not prohibited although there was a greater likelihood of fertilisation when foreign pollen was available.

Only about 30 per cent of the ovules of most varieties formed seed, but this may have been caused by the limitation of nutrients since the whole inflorescence was pollinated in this experiment, and every siliqua and seed was counted. In another experiment, when only five flowers were cross-pollinated on each of 21 plants, thirteen seeds were set per siliqua, but when complete "branches" of the same plants were pollinated the seed-set was reduced to ten per siliqua.

Assessment of self-incompatibility by pollination of emasculated flowers

As an extension of the first experiment, plants from the three cauliflower types were selected at random, and an inflorescence of each was emasculated in the late bud stage. Mixtures of Brussels sprout and self pollen, made by shaking anthers of each plant alternately over a glass slide where the pollen was mixed further, were applied when the flowers were fully open, and the progenies were classified as shown in Table 4.

These results indicated that self-pollen tended to be at a disadvantage in competition with foreign-pollen, although summer cauliflower plants S4/2 and S4/19 appeared to exhibit a "preferential" or "selective" self-fertilisation effect, and summer cauliflowers were, on average, more self-compatible than the other two types.

The self-incompatibility reaction was more pronounced in the autumn and winter cauliflowers, although only three plants did not set any selfed seed.

Evidence of incompatibility effects from observations on progeny of the mixed-pollinations

Because the mixed-pollinations of the first experiment were made three times per week, some flowers came into contact with foreign pollen immediately after opening, while others received no pollen, other than that deposited by their own anthers, for a longer period. Thus for the majority of flowers, the opportunity for self-fertilisation appeared to be greater than that for cross-fertilisation. By determining the ratio of hybrids: selfs in the progeny of the mixed-pollinated inflorescence it was possible to assess the strength of any self-incompatibility reaction. Seed samples from the

TABLE 4. NUMBERS OF SELFS AND HYBRIDS IN PROGENIES OF SINGLE PLANTS FOLLOWING APPLICATION OF POLLEN MIXTURE TO EMASCULATED FLOWERS OF SUMMER, AUTUMN AND WINTER CAULIFLOWERS

Variety and plant no.	Nos. hybrids	Nos. selfs	% hybrids
S1/7	31	19	62.0
S1/34	11	3	76.6
S2/1	7	7	50.0
S2/20	70	29	70.7
S3/21	17	11	60.7
S4/2	2	15	11.8
S4/15	55	32	63.2
S4/19	16	37	30.2
Total S types	209	153	57.7
A2/17	29	4	87.9
A2/18	16	3	84.2
A4/30	28	0	100.0
A5/E	69	10	87.3
Total A types	142	17	89.3
W1/1	4	2	66.7
W1/3	34	5	83.2
W4/7	45	9	83.3
W4/21	14	0	100.0
W5/12	45	0	100.0
W7/13	27	1	96.4
W8/1	39	12	76.5
W8/6	12	2	85.7
Total W types	220	31	87.6

mixed-pollinations of individual plants were sown in boxes adjacent to their appropriate parental controls, and the results are shown in table 5.

The progeny of the summer cauliflowers consisted mainly of selfs, with one variety in particular having 93 per cent. This variety, S4, was shown previously to contain plants which were higly self-compatible.

The autumn cauliflowers appeared to be more self-incompatible but the winter cauliflowers, with a mean of 72 per cent hybrids, showed the greatest self-incompatibility. No variety was so self-incompatible that the progeny consisted only of hybrids, the highest percentage of hybrids being 88.4 in variety W8, but the self-incompatibility reaction of the majority of winter cauliflowers was strong enough to delay self-fertilisation, thus allowing fertilisation by foreign pollen in spite of the self-pollen frequently having possessed a two-day advantage in time of application.

Variety W5 (Cambridge Dwarf April) produced only 16.6 per cent of hybrids in its progeny in contrast with the high percentage of hybrids produced by the other winter cauliflowers, and was the only one of the winter type varieties to set more seed by self than by mixed-pollination (Table 3). This variety has been quite intensively inbred over the last thirty years, and this may have caused a modification of the self-incompatibility reaction.

TABLE 5. NUMBER OF HYBRIDS AND SELFS PRODUCED FROM MIXED-POLLINATIONS OF SUMMER, AUTUMN AND WINTER CAULIFLOWERS VARIETIES

Variety	No. hybrids	No. selfs	% hybrids
S1	56	316	15.1
S2	114	487	19.0
S3	147	629	20.0
S4	77	1044	6.9
S5	112	494	18.5
S6	117	532	18.0
S7	338	832	28.9
Total S types	961	4334	18.2
A1	181	52	77.7
A2	33	65	33.7
A3	643	419	60.5
A4	251	182	58.0
A5	134	60	69.1
A6	556	572	49.4
Total A types	1798	1350	57.1
W1	533	149	78.2
W2	544	121	81.8
W3	375	77	83.0
W4	316	63	83.4
W5	79	396	16.6
W6	295	211	58.3
W7	543	140	79.5
W8	411	54	88.4
Total W types	3096	1211	71.9

(b) ASSESSMENT OF SELF-INCOMPATIBILITY BY AN EXPERIMENT ON NATURAL CROSS-POLLINATION

In order to study the pollination behaviour of cauliflower types under field conditions, cauliflower plants chosen at random from the original material, either as cuttings, or plants which were showing secondary flowering growth, were transplanted into the field. Brussels sprout plants were grown as male parents and interplanted with cauliflowers in a plot so designed that every fourth plant in each direction was a cauliflower. Brussels sprout plants were transplanted into position but cauliflowers were left in their pots which were buried below the soil surface to ensure that they could be moved to the glasshouse without a check for pod ripening when flowering was complete. By using clonal material it was possible to make direct comparisons of the incompatibility reactions under controlled and uncontrolled conditions of pollination.

BATEMAN (1956) concluded that the limitations of natural crossing experiments were (i) the isolating effect of differences in flowering time, (ii) the possibility of localised effects because of differences in insect activity, and (iii) preferences by the pollinating insects for flowers of similar colours. Differences in flowering time were overcome in this experiment because representatives of all cauliflower types were flowering over the same period. Regarding (iii), some of the winter cauliflowers possessed white flowers instead of the more common yellow flowers but observations suggested that there was no colour discrimination by the insects. This was

TABLE 6. COMPARISON OF NUMBERS OF SELFS AND HYBRIDS IN PROGENIES OF SINGLE PLANTS SUBJECTED TO BOTH NATURAL POLLINATION AND MIXED-POLLINATION

Type, Var. & Plant No.	Type of pollination	Progeny		χ^2 relationship of (a) to (b)	Probability
		Hybrids	Selfs		
S2/1	(a) Nat. poll.	17	46		
	(b) mixed poll.	60	113	1.25	0.10
S2/16	(a)	13	167		
	(b)	14	80	*3.27	0.05
§ S6/17	(a)	3	35	1.72	0.10
	(b)	7	32		
	(a)	18	70	0.11	0.50
S7/15	(a)	42	324	0.99	0.10
	(b)	16	90		
§ A2/5	(a)	10	20	*4.2	(a) & (b) Differ sig.
	(b)	20	12		
	(a)	308	9	*55.8	(a) & (b) Differ sig.
A6/3	(a)	3	48	4.09	(a) & (b) Differ sig.
	(b)	28	118		
A6/10	(a)	227	45	0.01	0.90
	(b)	73	14		
W2/6	(a)	116	6	2.24	0.10
	(b)	78	9		
§ W4/3	(a)	203	96	*10.27	(a) & (b) Differ sig.
	(b)	44	4		
	(a)	36	66	*39.44	(a) & (b) Differ sig.
§ W4/11	(a)	14	7	*5.22	(a) & (b) Differ sig.
	(b)	25	1		
	(a)	37	2	0.06	0.50
	(a)	12	2	1.43	0.10
W4/15	(a)	28	3	1.60	0.10
	(b)	74	18		
W4/16	(a)	64	1	0.45	0.50
	(b)	29	0		
W6/3	(a)	43	13	*6.23	(a) & (b) Differ sig.
	(b)	71	5		
W6/14	(a)	68	11	*16.48	(a) & (b) Differ sig.
	(b)	25	22		
W7/1	(a)	69	21	0.03	0.50
	(b)	84	27		
W8/5	(a)	98	167	*50.73	(a) & (b) Differ sig.
	(b)	58	10		

* Corrected for continuity.

§ Clones duplicated and randomised in position in field expt.

borne out by the similarity in the proportion of hybrids in the progeny of both white and yellow flowered plants.

After assessing the number of hybrids and selfs in the progeny of the cauliflower plants, the results were compared with those obtained on the same material after mixed-pollination under glass.

The chi squared tests in table 6 showed that nine out of sixteen plants gave progenies with similar ratios of hybrids : selfs under both glasshouse and field conditions, while two plants of a clone grown in the field (W4/11) gave similar ratios in their progenies, and one gave a different ratio from that produced under glass. Of the remaining six plants, four gave lower proportions of hybrids in their progenies when grown in the field than when grown in the glasshouse, one gave a higher proportion of hybrids, and the two clonal plants of the other gave contrasting proportions of hybrids and selfs.

All summer cauliflower plants performed similarly to one another in both field and glasshouse, giving a majority of selfs in their progenies. One out of three autumn cauliflower plants and three out of nine winter cauliflower plants gave similar results to one another in field and glasshouse, but nearly all plants of autumn and winter cauliflowers gave an excess of hybrids in their progenies.

Results from both glasshouse and field pollinations indicated that the summer cauliflowers were self-compatible while the autumn and winter cauliflowers were more self-incompatible, although the strength of the self-incompatibility reaction varied between plants.

It is possible that the plants in the field experiment were cross-pollinated less frequently than those in the glasshouse, particularly as the cold, wet weather during the flowering period in 1959 tended to restrict insect activity.

Table 6 shows that randomly positioned duplicates of clones S6/17 and W4/11 behaved similarly to one another in the field, whereas duplicate plants of the other two clones (A2/5 and W4/3) gave progenies differing significantly from one another in their ratio of hybrids to selfs. These differences may be attributable to localised insect activity. If the plants were highly self-incompatible it is likely that their progenies would each have similar ratios of hybrids to selfs, with a majority of hybrids. With a facultative self-incompatibility system, however, one plant (visited occasionally by insects) could produce a majority of hybrids, while its sister plant (seldom visited by insects) could produce a majority of selfs.

(c) The further expression of self-incompatibility: by the position of seeds in siliquas

Although it has been suggested by Bateman (1955) that Brassicas possess a sporophytic system of incompatibility, one characteristic of which is the failure of incompatible pollen tubes to grow through the stigma, the results from the previous pollination experiments indicated that the reaction was so modified in the cauliflowers that pollen-tubes grew through the stigma and achieved fertilisation.

In order to test the possibility that self-pollen-tubes might, nevertheless, be restricted in their growth, twenty siliquas, ten of which were self-pollinated and ten mixed-pollinated, were taken at random from each of twenty plants. Counts were made of the number of seeds in each quarter of each siliqua, and the results are shown in figures 4a and 4b as percentage of the total number of seeds in the siliqua. Plants were grouped by cauliflower types in figure 4a and by their relative fertility indices, regardless of cauliflower type, in figure 4b.

The relative fertility index, as used in figure 4b, is a modification of KAKIZAKI's (1930) method of classification, and is a measure of self-incompatibility obtained by dividing the seed-set per siliqua from mixed-pollination by that from self-pollination on each plant. Thus, a self-compatible plant should have a relative fertility index of 1.0 or near, while self-incompatibility would cause the index to exceed 1.0. Three summer, two autumn and one winter cauliflower plant had relative fertility indices of less than 1.0, four autumn and five winter cauliflower plants were between 1.0 and 2.0, and three autumn and two winter cauliflower plants had relative fertility indices above 2.0.

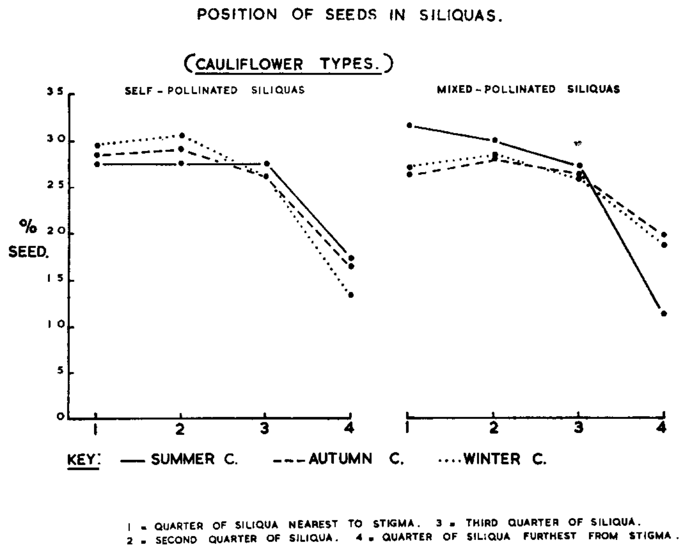

FIG. 4a. Seed positions in siliqua (grouped by maturity types).

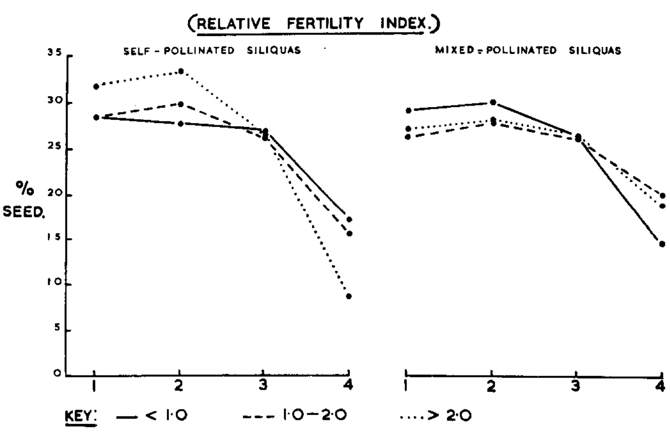

FIG. 4b. Seed positions in siliqua (grouped by relative fertility indices).

Figure 4a shows that there was a reduced seed-set at the distal end of the siliquas following either method of pollination. This indicated that in general the self-pollen tubes were no more restricted in their growth than the Brussels sprout pollen-tubes. More seed, however, was set in the distal quarter of the mixed-pollinated than the selfed siliquas, with the exception of summer cauliflowers which suggested that fewer self-pollen grains germinated or that their tubes were unable to penetrate as far as those of Brussels sprout pollen. The winter cauliflowers were the most self-incompatible as they had the lowest percentage of seed in the distal quarter following self-pollination. Figure 4b provides a further demonstration of the effect of self-incompatibility as plants with an r.f.i. above 2.0 set only 8.7 per cent seeds in the distal quarter after self-pollination.

As the main differences between seed sets of self-compatible and incompatible plants were confined to the distal region of the siliquas, by deducting the percentage seed set in this region from the mean of the other three regions, a measure of the degree of incompatibility could be obtained. An analysis of the results for self-pollination (Table 7) when plants were grouped according to their relative fertility indices, showed that the difference between the more self-incompatible (rel. fert. index > 2.0) and the less self-incompatible plants was significant. When plants were grouped according to their maturity type, however, the differences were not significant because of the variation in differences within each type.

TABLE 7. DIFFERENCE BETWEEN PERCENTAGE SEED SET IN DISTAL QUARTER AND MEAN OF REMAINING THREE-QUARTERS OF SILIQUAS FOLLOWING SELF-POLLINATION

Grouped by maturity types	Probability	Grouped by rel. fert. indices		Probability
Summer cauliflower 11.0 ± 3.2	Not sig. (19 DF)	r.f.i. < 1.0	11.4 ± 2.1	Sig. at P = .01 (19 DF)
Autumn cauliflower 14.5 ± 2.2		1.0–2.0	13.4 ± 1.7	
Winter cauliflower 16.9 ± 2.3		> 2.0	21.8 ± 2.3	

There was a considerable difference between the reactions of groups above and below rel. fert. index 2.0, but there appeared to be little inhibition of pollen-tube growth in plants relative fertility indices of 1.0 to 2.0. As plants with an r.f.i. of 1.0–2.0 tended to set more seed in the distal region of the siliqua by mixed than by self-pollination, however, they may possess the rudiments of a self-incompatibility mechanism, albeit a relatively ineffective one.

Analysis of the results from mixed-pollination showed that the summer cauliflowers set a significantly smaller proportion of seeds in the distal quarter of the siliquas than either of the other cauliflower types, thus suggesting a high degree of self-compatibility or cross-incompatibility, and corroborating the results shown in Table 3 where foreign pollen appeared to be at a disadvantage. Figures 5 and 6 show the result of self- and mixed-pollination upon a winter cauliflower plant with

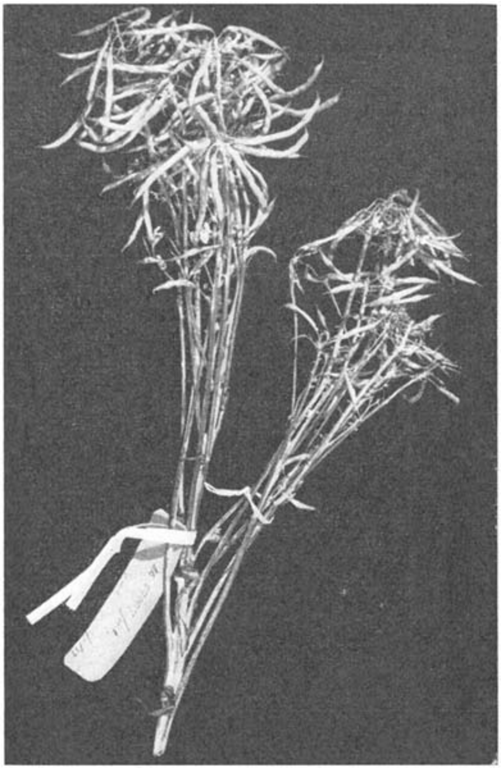

FIG. 5. Mixed-pollinated branch (left), self-pollinated branch (right) of plant having rel. fert. index of 2.52.

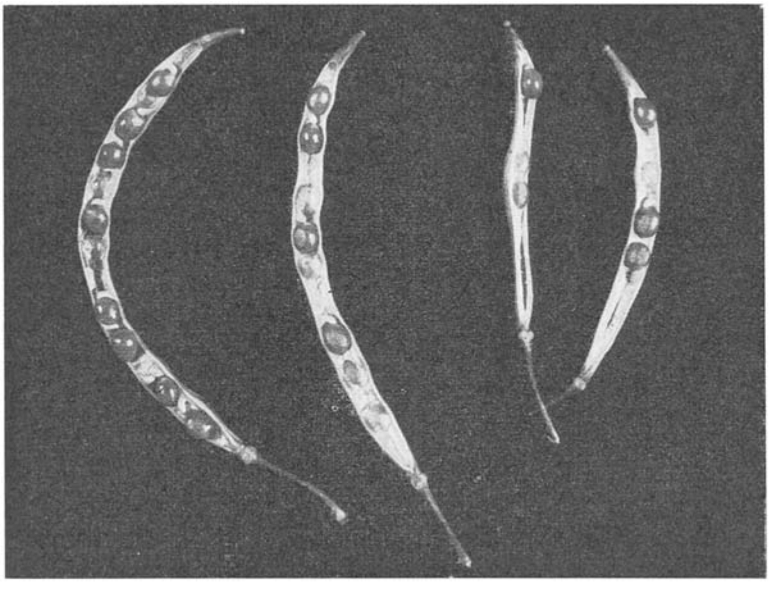

FIG. 6. Sample of siliquas from fig. 5, showing reduced seed set in selfed siliquas and lack of seed in distal region (from stigma).

a relative fertility index of 2.52–a comparatively high degree of self-incompatibilty for cauliflowers.

(d) Comparative efficiency of self and foreign pollen

Following the previous investigations, a count was made of the numbers of hybrids and selfs derived from each quarter of the mixed-pollinated siliquas, with results as shown in figure 7.

Although the results have again been grouped in two ways they follow the same pattern. There was a sharp distinction in the percentage of hybrids between cauliflower types and a constancy of the hybrid to self ratio throughout the siliquas. It

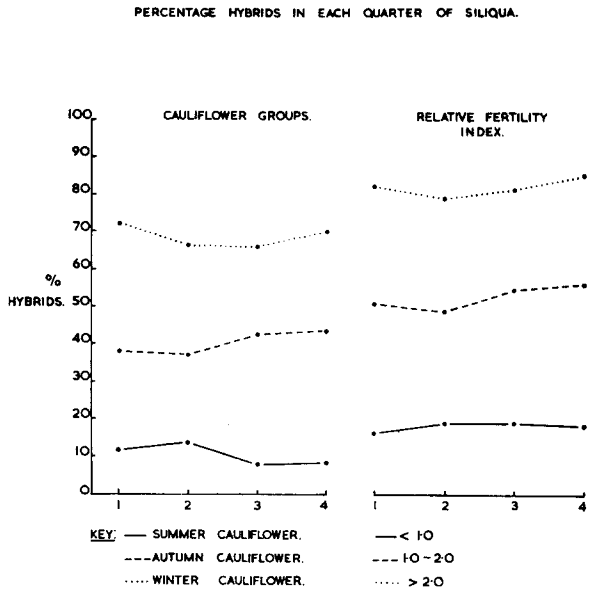

Fig. 7. Percentage hybrids in each quarter of mixed-pollinated (but unemasculated) siliquas.

appeared that for any particular level of self-incompatibility, there was an optimum level of cross or self-fertilisation and self-pollen-tubes did not seem to be retarded any more than foreign pollen tubes, once they had penetrated the stigma.

Discussion

Sporophytic incompatibility in the *Brassicae* is widespread (Bateman, 1955), but although the floral structures in cauliflower are adapted to outcrossing, as are those of most other members of the genus, the present results tend to indicate that cauliflowers exhibit more self-compatibility than the majority of related species. Mather (1943) attributed the greater self-compatibility of some species or types, when compared with the marked incompatibility of their related species, to their hybrid origin (e.g. *Nicotiana sanderae*), and suggested that reshuffling, by hybridisation, of polygenic combinations which were balanced with their associated incompatibility system, led to a lower efficiency in the hybrid. LEWIS (1951) showed that mutations of the S allele to the fertile Sf allele occurred quite frequently. In plants or species which possess balanced polygenic combinations, the mutation of active S alleles to Sf would cause disruption of the incompatibility mechanism and, if these Sf alleles and their polygenic backgrounds were not mutually adapted it seems likely that the general result, in a large population, would be a continuous range in the intensity of inhibition.

If, in a system of this type, it was possible for certain plants and progeny to be continually self-pollinated, it is conceivable that the polygenic combinations associated with the fertility allele would become so stable that self-pollen would exhibit few disadvantages in competition with foreign pollen and this appears to be particularly applicable to the summer cauliflower.

Self-pollen of summer cauliflowers may possibly possess some advantage over foreign pollen which is demonstrated by selective self-fertilisation.

Investigations on one of the summer cauliflower plants which produced more selfed than hybrid progeny following application of a pollen-mixture showed that the proportion of hybrids decreased from 20 per cent at the proximal end to 5 per cent in the distal quarter. Further, when pollen-tube growth was examined *in vitro,* the pollen-tubes of this and another summer cauliflower plant were longer when grown in a solution of sucrose and self-style extract than in either sucrose solution alone or in style extract from another, cross-compatible plant. KEARNEY and HARRISON (1924) applied a mixture of self- and foreign-pollen to cotton, and obtained 75 per cent self-fertilised seed, although germination of each type of pollen was normal when applied to separate stigmas, and similar examples have been described in maize, by JONES (1922) and in cotton, by BALLS (1919). It seems likely, therefore, that selective self-fertilisation does occur in summer cauliflowers although its method of action and mode of inheritance require further elucidation.

Years of artificial selection in cauliflowers have probably modified the original breeding system to the present one in which the summer cauliflowers are largely self-compatible and homozygous, while both the autumn and winter cauliflowers have reached a stage which is intermediate between this and complete self-incompatibility. The morphological similarity of the three maturity types is so marked that it seems unlikely that they have always been differentiated by their breeding behaviour. STEBBINS (1957) suggested that self-fertilised types or species have probably been derived from cross-fertilising ancestors, and he mentions that a high proportion of the self-fertilising species are annuals. KIRCHNER (1905) and WILLIAMS (1951) showed that annual species of *Leguminosae* tend to be self-compatible, while biennials or perennials are mainly self-incompatible. The cauliflowers tend to be analogous because the summer type behaves as an annual and the winter type behaves as a biennial, while the autumn type cauliflower tends to have an extended "annual" season.

CROSBY (1954) showed that the flexibility of natural populations of *Primula vulgaris,* was such that the breeding system gradually altered from outbreeding to inbreeding although there had been no artificial selection. MATHER and DE WINTON (1941) quoted the great increase of self-compatible *Primula sinesis* plants and remarked that "commercial seed raisers prefer plants which may be selfed, as this enables them to keep pure stocks with relative ease". It seems axiomatic that crops in which uniformity is desired, and where diversity is easily recognisable, are more likely to be subjected to intense selection and possible enforced inbreeding. Continuous strict selection over numerous generations, as practised in summer cauliflower, could lead to the establishment of self-compatibility as a correlated response. Selection for uniformity over the years would thus induce the type of breeding system which is necessary to ensure the maintenance of the character under selection.

Although varietal self-compatibility appears to be confined mainly to the summer cauliflowers, it is also exhibited by one winter cauliflower variety, Cambridge Dwarf April. The following history of the variety indicates that it has undergone a condensed process of that which has happened with summer cauliflowers. Cambridge Dwarf April was derived by rigid selection following a cross between two plants of the variety St. George (W7). From the initial cross, up to the present time, selections and subsequent pollinations have been made upon very small numbers of plants. The variety is notably uniform and yields well, showing no symptoms of loss of vigour after successive generations of inbreeding. Its parent variety, on the other hand, appears to be one of the most self-incompatible of the winter cauliflowers.

It seems possible, therefore, that diligent testing within a "self-incompatible" variety may reveal self-compatible individuals whose progeny will compete quite successfully commercially with their heterozygous sibs. There would probably be a greater likelihood of success in producing an inbreeding line, however, if selection was not too intensive at the outset, but was concentrated upon a limited number of plants tending towards self-compatibility, thus providing a gene pool for future selection.

Different methods of seed production may have contributed to the diversification of the cauliflower breeding system. Summer cauliflowers are normally seeded in Britain or in the Low countries, following rigid selection for uniformity, while the autumn and winter cauliflowers are seeded in the Mediterranean region where selection is less intensive, and where less attention is paid to varietal uniformity.

Two other *Brassicas,* cabbage and sprouting broccoli, are comparable with cauliflower in having types with different maturity periods, but they are mainly seeded in the British Isles. Nevertheless, it has recently been shown (FROST unpub.) that sprouting broccoli form two distinct classes based on incompatibility reactions, (although the inhibitory reaction is stronger than that of the cauliflowers) and the cabbage may well provide a third example of differing responses to intensities of selection pressure.

ACKNOWLEDGEMENTS

I wish to express my appreciation of the advice given during this project by DR. J. C. HAIGH and the help of MR. R. A. T. GEORGE.

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