FACTORS AFFECTING SEED SET IN BRUSSELS SPROUTS, RADISH AND CYCLAMEN

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MET EEN SAMENVATTING

FACTOREN, DIE DE ZAADZETTING IN SPRUITKOOL, RADIJS EN CYCLAMEN BEÏNVLOEDEN

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TER VERKRIJGING VAN DE GRAAD
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A. I. M. EL MURABAA

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VOORWOORD

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INTRODUCTION: RELEVANT LITERATURE AND SCOPE OF EXPERIMENTS

1. The problem

One of the major difficulties in plant breeding is to obtain sufficient seed after certain pollinations. In Brussels sprouts and radish the cause is incompatibility; a given plant may yield a large quantity of seed when pollinated by certain plants, but not by others or by itself. In *Cyclamen persicum* insufficient seed set is apparently due to other causes.

2. Review of relevant literature

In *Brassica* and certain other plants it has been shown that incompatibility may be overcome by pollination of the flowers before or after anthesis.

Pearson (25, 1929)[1] was the first to show that in the common cabbage, flower buds pollinated two days before opening gave good seed while those pollinated one day later failed to set seed. This was confirmed by Kakizaki (14, 1930), who selfed flowers from 5 days before until 3 days after anthesis. Optimal seed set was obtained when buds were pollinated two days before anthesis. Flowers self-pollinated three days after anthesis showed a small increase in the seed set compared with flowers that had just opened.

The advantages of bud pollination in self- or cross-incompatible plants were also demonstrated with Chinese cabbage (*Brassica pekinensis*) and radish (Kakizaki and Kasai 15, 1933); Indian toria and Indian sarson (*Brassica campestris* var. *dichotoma* and *Brassica campestris* var. *sarson*) (Mohammad 23, 1935); broccoli and radish (Sears 28, 1937); radish (Tatebe 32, 1940); *Brassica chinensis* var. *rosularis* (Lee 17, 1948) and *Raphanus raphanistrum* (Kroh 16, 1956). The usefulness of bud pollination for the breeding of cole crops has also been demonstrated by other authors (Myers and Fisher 24, 1944; Haigh 12, 1954; Zeevaart 39, 1955).

[1]) First number refers to "Literature" on page 32, second number is the year of publication.

Generally when flowers are self-pollinated a decline in compatibility occurs shortly before opening whereas flowers that are cross-pollinated, are compatible. This was clearly demonstrated by ATTIA (1, 1950) who pollinated flower buds of green cabbage with pollen from the same plant, followed by pollen from red cabbage plants. At 10–15 °C flower buds pollinated three or less days before opening yielded seed that gave more than 50% of hybrid plants. At a higher temperature (15–20 °C) more than 50% hybrids were obtained when flower buds were pollinated one day before opening.

PEARSON (25, 1929; 26, 1932) presumed that the incompatible pollen tubes would grow more slowly than the compatible ones and bud pollination would give the former tubes more time to reach the ovules. ATTIA (1, 1950) on the other hand attributed the seed set primarily to a low concentration or absence of an inhibiting substance in the styles before the flower buds reached a certain physiological maturity.

In 1941 EYSTER (10) reported that self-incompatibility in certain *Petunias* could be overcome by spraying the flowers immediately before or after self-pollination with an aqueous solution containing 10 p.p.m. α-naphthylacetamide (NAd). This substance also favoured the seed set in highly self-incompatible strains of African marigold, cabbage and red clover. NAd and other growth substances were used with success by EMSWELLER and STUART (9, 1948) to obtain seed from certain incompatible selfings and crosses of Easter lilies. CRANE and MARKS (7, 1952) and BROCK (4, 1954) obtained pear-apple hybrids by brushing the pear ovaries with an aqueous solution containing 40 p.p.m. β-naphthoxyacetic acid at the time of pollination and again 24 hours later. DARROW (8, 1956) obtained seeds from some heteroploid blueberry crosses by the use of NAd as 1 per cent lanolin paste.

In other cases, which showed no incompatibility or sterility, growth substances improved the fruit set or both the fruit and the seed set. BURREL and WHITAKER (5, 1939) in breeding muskmelons increased the fruit set by applying 1 per cent 3-indoleacetic acid in lanolin to one lobe of the stigma after the flowers had been pollinated. WHITAKER and PRYOR (37, 1946) tried six growth substances to improve the fruit set in artificially pollinated flowers of *Cucumis melo*. Only the use of para-chlorophenoxyacetic acid at the time of pollination improved the fruit set. WESTER and MARTH (36, 1949) were able to increase both the number of successful crosses and seeds per cross in lima bean by applying a mixture of indolebutiric acid and para-chlorophenoxyacetic acid in lanolin to scratches made at the flower base.

3. SCOPE OF EXPERIMENTS

The practical difficulties encountered in selfing or crossing Brussels sprouts, radish and *Cyclamen persicum* led to the following experiments.

From the literature it is evident that much work has already been done to overcome incompatibility in *Brassica* and *Raphanus*. This work has been repeated and extended in Brussels sprouts (*Brassica oleracea* var. *gemmifera*) and radish (*Raphanus sativus*). Buds and flowers have been selfed or cross-pollinated in all stages and at different temperatures. The effect of growth substance applications on flowers pollinated at different stages has also been studied.

Little work has been done so far on seed set in cyclamen crosses. It soon became evident that the problem here is different from that in Brussels sprouts and radish, as incompatibility does not play a role of any importance. The general aspects of floral biology have been studied, while extensive investigations have been made on the causes of fruit stalk decay and the possibilities to overcome this by growth substance applications.

The investigations will be described and discussed separately for the three experimental plants. A general discussion is not given, since the problems in Brussels sprouts and radish on the one hand and in cyclamen on the other hand are quite distinct from each other.

II

BRUSSELS SPROUTS

1. Pollination experiments

1.1. *Experimental methods.* The work was carried out with plants of the cultivars 'Kolom' (K) and 'Spiraal' (S) growing in the open field at Wageningen in 1955 and 1956. At the beginning of the experiments, plants with good inflorescences were selected and covered with paper bags after all open flowers had been removed. Then for the next ten days the buds were emasculated shortly before opening and tagged on the day of anthesis. At the end of this period all emasculated flowers (ranging in age from 0 to 10 days after opening) and buds (forming an age series from 15 to 1 day before opening) were pollinated simultaneously. Emasculation and tagging of buds to mark days of anthesis continued until the remaining buds had opened. Two weeks later the paper bags were removed. The number of flowers which opened daily on one plant ranged from 0 to 11.

Pollen for self-pollination was gathered from flowers (age 0) on the same inflorescence which were not emasculated before opening. Pollen for crossing was taken from a plant belonging to the other cultivar.

The average temperature was determined from graphs drawn by a thermograph. Temperature below 5 °C was neglected as it did not cause bud development. The temperature area on the thermograph paper was measured and transferred into degrees centigrade according to the equation:

$$\left(\frac{\text{area per day in cm}^2}{3.95} \times \frac{5.00}{0.75}\right) + 5.0$$

This was done because a height of 0.75 cm on the paper represented 5 °C and the thermograph turned 3.95 cm a day. In the cases of bud pollination, the temperature was determined for the average number of days before opening which was suitable for sufficient seed set. When old flowers were used the temperature for the average number of days after opening was established. A day was considered to begin at noon. Average seed numbers of more than 10 seeds were considered as sufficient seed setting except when flowers were self-pollinated after opening (5 or more seeds). These figures have been chosen from general experience as being practically justified.

1.2. *Results*

1.2.1. Bud pollination. The results obtained from self-incompatible plants are given in table 1. They show the following:

(a) The average seed number increases with the age of the bud at pollination until it reaches a maximum 6 to 2 days before anthesis.
(b) After this, it decreases rapidly so that the seed set of buds pollinated 3 to 0 days before anthesis is very low.
(c) As the temperature increases, the period before anthesis during which the bud may be selfed successfully becomes shorter and lies closer to anthesis.
(d) The number of seeds yielded by one bud pollinated at the time of maximal response to selfing appears to be about the same at different temperatures.

Figure 1 illustrates the main results.

In table 2, the data from compatible cross-pollinations are given. These show:

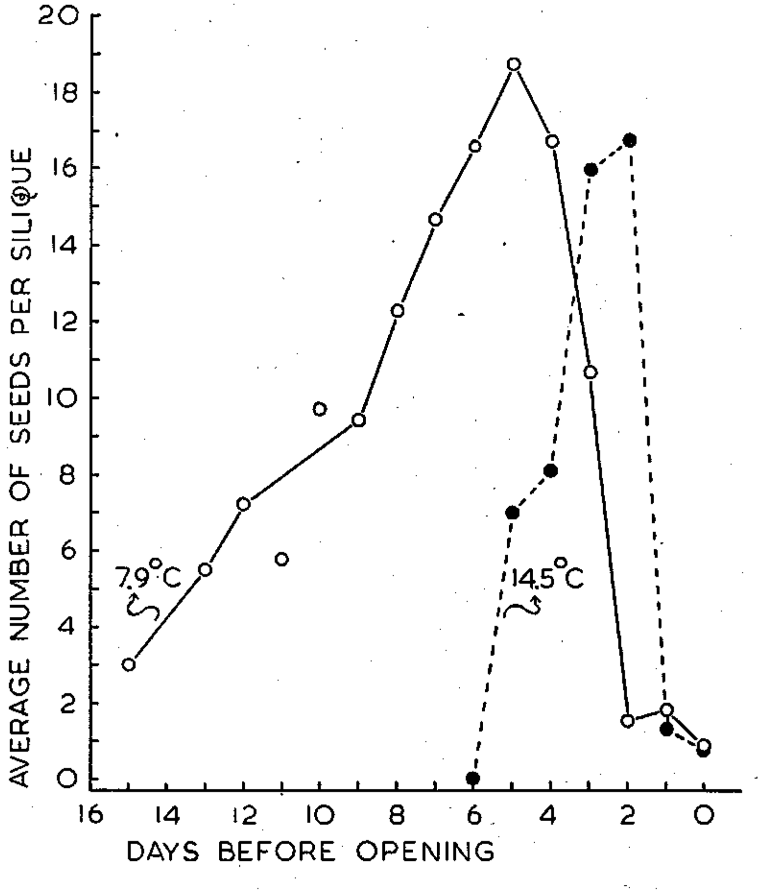

FIG. 1. Brussels sprouts: Self-pollination of buds at varying numbers of days before opening and at different temperature conditions.

TABLE 1. Average seed numbers obtained from incompatible plants, when flowers were self-pollinated at or before opening.

Plant number	Date of selfing (1955)	Average temperature	Number of days before opening															
			15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
K 3	17 May	7.4 °C				1.0	3.0	6.6	7.6	*20.5*	*18.0*	*18.0*	*22.2*	*15.0*	*19.0*			0
K 2	15 May	7.9	3.0		3.0	8.0		*10.5*	*17.0*		*18.0*	*18.0*	*16.0*	*15.5*	5.5	1.5	2.0	3.0
K 3	19 May	8.0						0	1.5	1.0	4.0	*12.0*	*13.3*	*19.0*	0			0
K 2	16 May	8.2			8.0	12.6	8.6	*22.0*	*21.0*	*15.5*	*19.5*	*20.0*	*24.0*				1.6	1.5
K 1	14 May	8.4							0		*14.3*	*15.0*		*18.0*	*18.3*			0
K 1	13 May	9.7						0			*13.0*			*21.0*		*11.0*	7.0	0
S 5	22 May	10.2							0		0.3	9.0	*22.0*	*21.0*	*17.0*		0	0
K 7	25 May	10.4							0	0	2.0	3.5	9.8	*20.0*	*17.5*	*16.5*	1.7	1.0
K 7	27 May	11.2										0	2.3	6.0	*11.3*	*12.0*	0	1.5
S 8	28 May	11.6							0		3.0	2.6	6.0	*14.3*	*17.0*	*11.0*	0.4	1.0
S 9	30 May	14.1											7.0	*11.3*	*16.0*	*18.0*	2.0	1.3
S 9	31 May	14.9									0	0		5.0		*15.6*	0.6	0.3

TABLE 2. Average seed numbers obtained from compatible combinations, when flowers were cross-pollinated at or before opening.

Number of female parent	Date of crossing (1955)	Average temperature	Number of days before opening													
			13	12	11	10	9	8	7	6	5	4	3	2	1	0
K 2	16 May	8.2 °C	1.0	2.0	8.0	7.0		*18.0*	*24.0*	*24.0*	*26.0*	*21.6*	*19.0*	*26.0*	*25.0*	24.0
K 4	21 May	8.2					1.0	5.5	*12.5*	*14.0*	*22.0*	*16.3*	*13.0*			17.0
K 1	14 May	8.5				6.0	*10.3*		*14.0*		*15.0*	*15.5*	*13.0*	*12.0*	*18.0*	19.0
K 1	20 May	9.1			5.0	*12.4*	*15.6*	*16.0*	*16.0*		*18.8*	*17.0*			*19.5*	22.0
K 7	25 May	10.4						0	6.0	10.0	*15.2*	*13.0*	*13.0*	*26.0*	*22.5*	22.5
S 5	22 May	10.4							5.0	*11.0*	*17.0*	*21.0*	*19.0*			18.0
K 6	24 May	11.1					0	2.5	6.0	7.6	9.5	*18.5*	*15.0*	*22.5*	*22.0*	19.0
K 6	23 May	11.2				0	1.0	2.4	5.2	8.3			*14.0*	*21.0*	*19.0*	19.0
S 9	30 May	13.9										4.5	*16.7*	*19.0*	*18.0*	21.2
S 9	31 May	15.0									4.3	*12.6*	*14.5*	*21.0*	*20.0*	21.5

(a) Buds may be pollinated successfully 10 to 1 days before anthesis; younger buds yield little or no seed.
(b) The number of seeds does not decrease as buds approach anthesis.
(c) At higher temperatures the number of days before anthesis during which buds may be successfully pollinated decreases.

Figure 2 illustrates the main results.

From tables 1 and 2 it will be seen that plants K1, K2, K7, S5 and S9 were both selfed and cross-pollinated on the same dates and consequently give

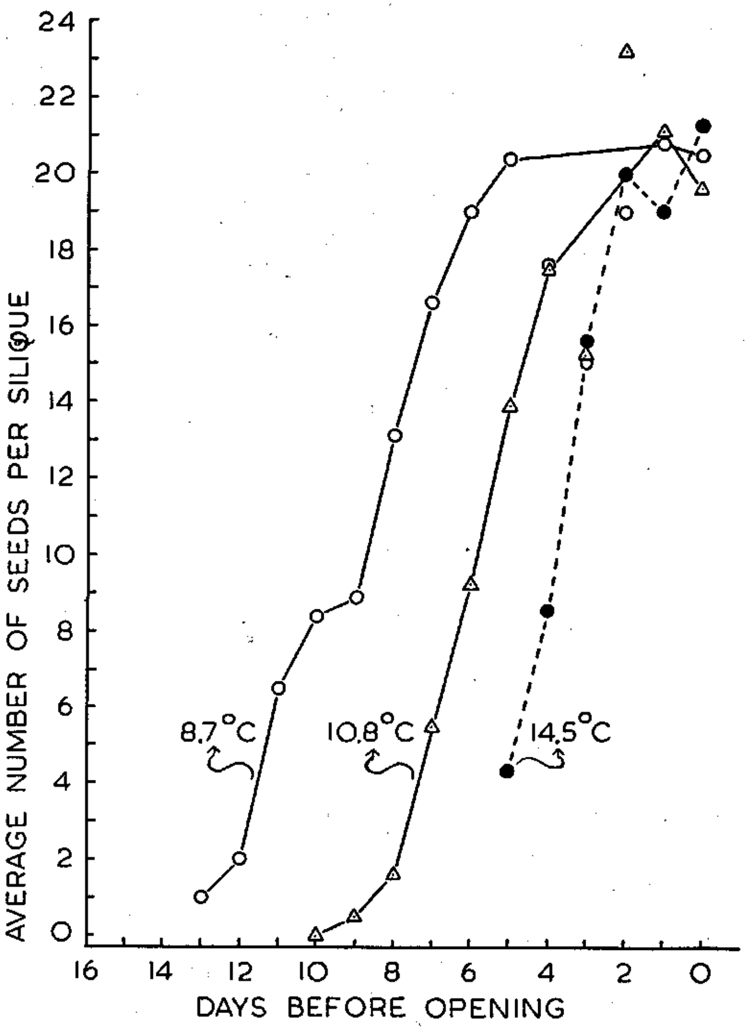

FIG. 2. Brussels sprouts: Cross-pollination of buds at varying numbers of days before opening and at different temperature conditions.

suitable data for a comparison of both methods. From this comparison it is evident that:

(a) During a period before anthesis flower buds of Brussels sprouts may be selfed or cross-pollinated with equal success;

(b) The length of this period decreases at higher temperatures;

(c) Three to zero days before opening, the effect of self-pollination drops suddenly to become slight or nil, whereas the buds remain just as sensitive to cross-pollination as before.

Figure 3 gives a comparison for one plant.

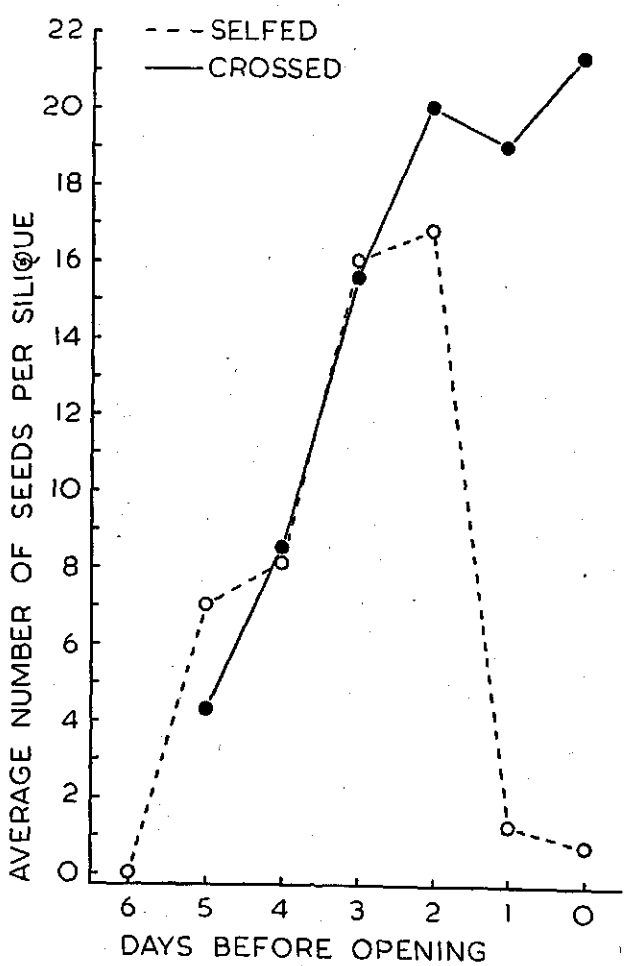

FIG. 3. Brussels sprouts: Comparison between selfing and crossing of flower buds. Data of plant S 9 at an average temperature of about 14.5 °C. Approximately the same seed set was obtained when flower buds were pollinated 3 to 6 days before anthesis.

1.2.2. Late pollination. The results obtained from some plants, when flowers were self-pollinated on different days after anthesis are presented in table 3. The data obtained from other plants are not given as they showed smaller seed numbers although the behaviour of the seed set is nearly the same.

TABLE 3. Average seed numbers obtained from incompatible plants, when flowers were self-pollinated at or after opening.

Plant number	Date of selfing	Average temperature	Number of days after opening									
			0	1	2	3	4	5	6	7	8	9
K 2	15 May 1955	10.1°C	3.0	*5.5*		*7.0*	*9.0*	*5.0*				
K 1	14 May 1955	10.4	0	*5.7*		*9.0*	*7.0*	1.5	3.4			
K 24	15 May 1956	11.7	1.0	*7.3*	*10.5*	*11.8*	*5.8*	1.8	0.2			
K 14	14 May 1956	12.6	4.2	*9.4*	*10.0*	*6.7*	4.6	1.7	2.3	0.3	0	0

The data indicate:

(a) The seed set reaches a minimum when flowers are pollinated at opening; when they are selfed at a later stage there is a marked increase in yield although it never reaches a high value.

(b) When flowers become very old, the seed set following self-pollination again decreases.

(*c*) At higher temperatures the period during which selfing has some success is shorter.

Figure 4 illustrates the main results.

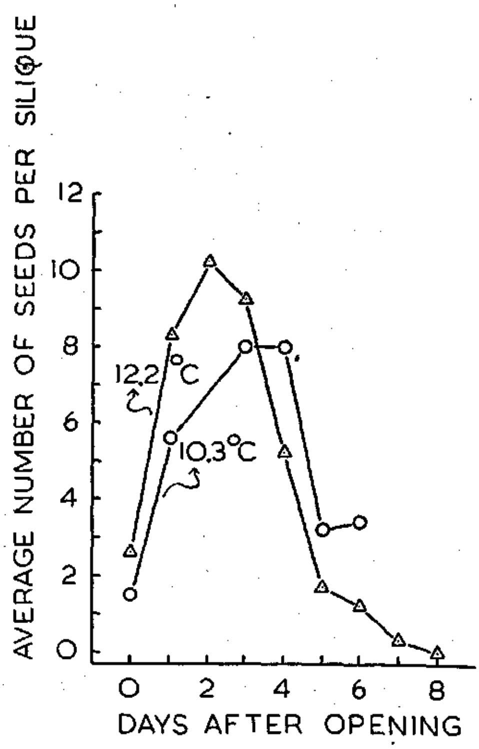

FIG. 4.
Brussels sprouts: Self-pollination of old flowers at varying numbers of days after opening and at different temperature conditions.

TABLE 4. Average seed numbers obtained from compatible combinations, when flowers were cross-pollinated at or after opening.

Number of female parent	Date of crossing	Average temperature	Number of days after opening											
			0	1	2	3	4	5	6	7	8	9	10	11
S 5	22 May 1955	6.9 °C	18.0	*21.0*	*20.0*			*16.0*	*12.0*		*13.0*	5.0	0	0
K 2	16 May 1955	9.3	24.0	*20.0*			*18.6*	*11.0*						
K 1	14 May 1955	10.4	19.0	*15.0*	*18.0*	*27.0*	*10.5*	5.0	3.5					
K 24	15 May 1956	11.8	18.3	*14.3*	*13.5*	10.0	7.0	5.1	0.5					
K 25	13 May 1956	12.0	19.4	*16.4*	*14.6*	7.7	3.6	3.1	1.5	0.1	0.5	0		

Again, the results obtained from cross-pollination are markedly different. These are given in table 4 and in figure 5 and may be summarized as follows:

(a) During a period of about 3 days after anthesis the response of the flower to cross-pollination appears to be maintained at the same level; after that it gradually drops to zero.

(b) At higher temperatures the number of days during which pollination is successful decreases.

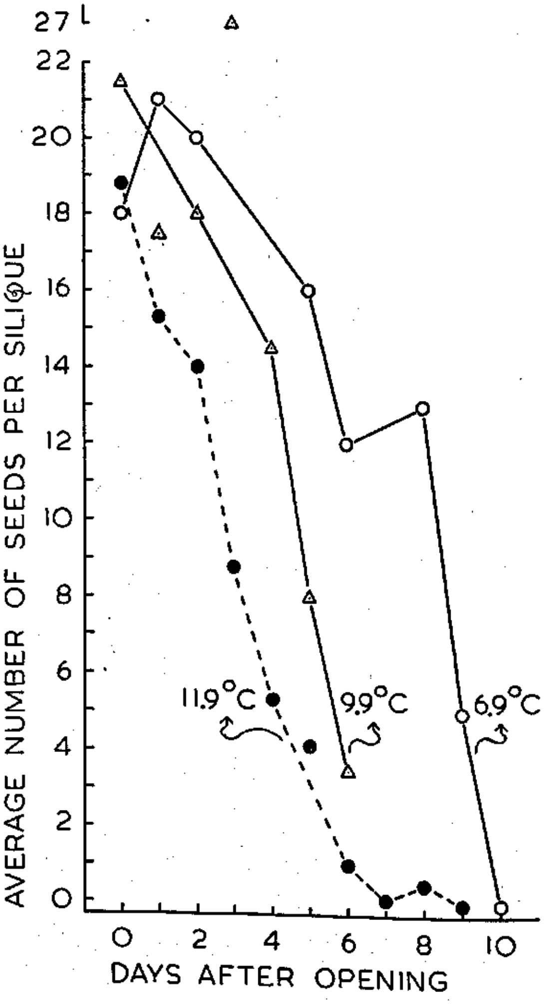

FIG. 5.
Brussels sprouts: Cross-pollination of old flowers at different numbers of days after opening and at different temperature conditions.

In figure 6 a comparison is made between the effects of crossing and selfing in one plant at different days after anthesis.

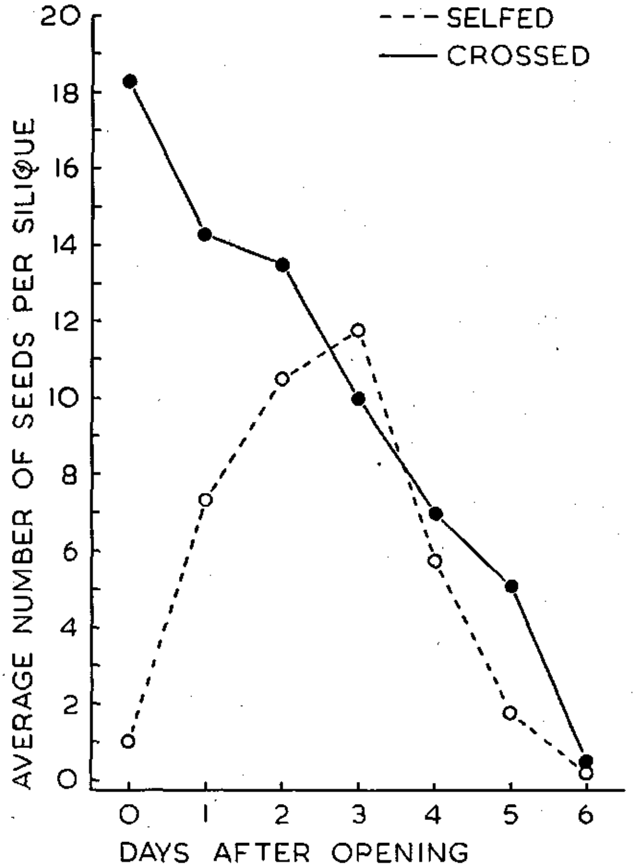

FIG. 6. Brussels sprouts: Comparison between selfing and crossing of old flowers. Data of plant K 24 at an average temperature of 11.8 °C. No significant difference in the seed set after selfing or cross-pollination when flowers were pollinated 3 to 6 days after anthesis.

Photograph 1 (at the end) illustrates the results obtained from flower buds, flowers at anthesis and old flowers when selfed or cross-pollinated.

1.2.3. Behaviour of incompatible pollen. In one highly self-incompatible plant flowers were self-pollinated at anthesis. Forty eight hours after self-pollination the stigma was cut by hand into longitudinal slices. These were stained with cotton blue and examined microscopically.

The mean diameter of the pollen grains was about 25μ. Only 45% had germinated: 35% had pollen tubes less than 20μ long, 7% had tubes from 20 to 40μ and 3% tubes from 40 to 60μ. These short pollen tubes were mostly found between the stigmatic papillae; nowhere did they penetrate the stigmatic tissues.

2. Experiments with α-naphthylacetamide

2.1. *Methods.* The inflorescences were treated in the same way as described in the preceding experiments, except that after pollination the flowers were sprayed with an aqueous solution containing 10 p.p.m. α-naphthylacetamide (NAd) dissolved in a few drops of aethanal.

On each plant three inflorescences of approximately the same vigour were selected. On one inflorescence the NAd solution was applied by means of a small hand sprayer immediately after self-pollination and once again 24 hours later. A second inflorescence was treated in a similar way with a control solution, containing only water and a few drops of aethanal, while the third was not sprayed at all.

In two plants the NAd or control solution was rubbed on the stigmas by means of a piece of cotton wool prior to self-pollination, which was done at anthesis.

To study the effect of NAd on cross-pollination, two inflorescences were selected on each plant. One of these was sprayed with the NAd solution immediately after pollination and once again 24 hours later; the other was not sprayed.

The average seed numbers per silique obtained from different treatments are compared by the Student's method devised by Love & Brunson (21, 1924). Flowers on the same plant, pollinated simultaneously and at the same number of days before or after opening are used as parallels.

2.2. *Results.* The average seed yield of selfed flowers, sprayed or not sprayed after pollination, is given in table 5.

TABLE 5. Effect of NAd applications on the seed set obtained from incompatible Brussels sprouts plants, when flowers were self-pollinated at different stages.

Flower stages	Treatment	Mean number of seeds	Comparison between parallels in the different treatments			
			Treatments compared	Mean difference	n	
Flower buds at suitable stages	Untreated	15.7 ± 0.7	Untreated-control	6.59 ± 1.50	24	S[1])
	Control	9.1 ± 1.3	Untreated-NAd	4.69 ± 1.14	24	S
	NAd	11.0 ± 1.4	Control-NAd	1.89 ± 1.80	24	–
Flower buds at other stages	Untreated	3.8 ± 0.6	Untreated-control	1.10 ± 0.75	27	–
	Control	2.7 ± 0.6	Untreated-NAd	0.34 ± 0.65	27	–
	NAd	3.5 ± 0.7	Control-NAd	-0.77 ± 0.72	27	–
Flowers at opening	Untreated	0.6 ± 0.2	Untreated-control	0.41 ± 0.27	16	–
	Control	0.2 ± 0.1	Untreated-NAd	-0.11 ± 0.32	16	–
	NAd	0.7 ± 0.4	Control-NAd	-0.52 ± 0.48	16	–
Flowers after opening	Untreated	3.3 ± 0.6	Untreated-control	0.23 ± 0.74	19	–
	Control	3.1 ± 0.6	Untreated-NAd	0.55 ± 0.74	19	–
	NAd	2.8 ± 0.6	Control-NAd	0.32 ± 0.61	19	–

[1]) S = 1% significance – = less than 5%

These data show that the number of seeds obtained after self-pollination at suitable bud stages is decreased by applications of NAd, while there is also a significant unfavourable effect of the control solution. Flowers pollinated at earlier or later bud stages, at opening or a few days after that, set very little seed in all cases.

The same holds true for plants, the stigmas of which were rubbed with the solutions before self-pollination at opening. The seed set per silique was very low (0.42 ± 0.21), and neither affected by NAd (0.47 ± 0.16) nor by the control solution (0.66 ± 0.24).

The data obtained from cross-pollinated flowers are summarized in table 6.

TABLE 6. Effect of NAd applications on the seed set obtained from compatible combinations of Brussels sprouts, when flowers were cross-pollinated at different stages.

Flower stages	Treatment	Mean number of seeds	Comparison between parallels in the different treatments			
			Treatments compared	Mean difference	n	
Flowers at suitable stages (flowers at or near opening)	Untreated NAd	17.5 ± 0.5 14.6 ± 0.9	Untreated-NAd	2.89 ± 0.76	61	S[1])
Flower buds (earlier stages)	Untreated NAd	4.7 ± 0.8 3.9 ± 0.8	Untreated-NAd	0.75 ± 0.71	16	–
Flowers after opening (later stages)	Untreated NAd	3.1 ± 1.2 1.6 ± 0.6	Untreated-NAd	1.43 ± 0.89	7	–

[1]) S = 1% significance – = less than 5%

The general trend is obviously the same as in the experiments on self-pollination. There is a slightly unfavourable effect of NAd applications, and this is significant only in cases of a sizable seed yield.

3. Discussion and conclusions

The fact that bud pollination increases the seed set is in agreement with previous findings of several authors cited in the introduction. Pearson (25, 1929) and Kakizaki (14, 1930) obtained the largest amount of seeds from buds selfed 2 days before opening, while Sears (28, 1937) obtained good results 4 to 7 days before opening. This may have been due to a different temperature, yet it should be mentioned that they worked with different varieties of *Brassica oleracea.*

In our experience medium sized flower buds which are about 7 to 9 mm long yield the highest amount of seed after selfing. At 15–17 °C these buds open after 3 or 4 days, at 10–13 °C after 5 to 7 days and at 2–6 °C after 13 to 21 or even more days. When the buds have passed this stage they become strongly self-incompatible. This was shown to be the case in cabbage by Attia (1, 1950), who found that a high percentage of hybrid seed was obtained when buds were pollinated 3 to 1 days before opening according to the prevailing temperature.

The small decrease in self-incompatibility a few days after opening of the flower is in agreement with the results of KAKIZAKI (14, 1930) with cabbage and MOHAMMAD (23, 1935) with Indian toria and Indian sarson.

The observation that self-incompatibility at anthesis is due to inhibition of pollen germination and tube growth is in agreement with the conclusions of STOUT (31, 1931), SEARS (28, 1937) and TATEBE (34, 1951) who worked with other *Brassicas*. BATEMAN (2, 1954; 3, 1955) reported that in all crucifers which he had examined, pollen tubes were inhibited before the stigma had been penetrated. This inhibition has been assumed to be due to a substance formed by the stigma (TATEBE 33, 1947; 35, 1955 and KROH 16, 1956). This substance is probably responsible for the reaction between style and pollen assumed by SEARS (28, 1937) and BATEMAN (2, 1954; 3, 1955). It follows from fig. 3 and 6 (pages 8 and 11) that this hypothetical substance begins to affect the pollen a few days before anthesis and reaches its maximum at the opening of the flowers. Later on there is a decrease in the inhibition. In very old flowers there is no difference in the seed set following self- or cross-pollination, so the incompatibility substance has probably disappeared again.

PEARSON (25, 1929) concluded that bud pollination enabled the tubes of the incompatible pollen to reach the ovules before degeneration of the egg cells. This explanation is unsatisfactory because, as the data show (table 3), the number of seeds obtained from flowers selfed a few days after opening is significantly larger than that obtained from flowers selfed at opening, although the latter have shorter styles than the former. Moreover, egg cells do not degenerate quickly as shown by the excellent results of flowers cross-pollinated some days after opening.

KAKIZAKI (14, 1930) attributed incompatibility in cabbage to slow growth of the pollen tubes caused by an inhibiting substance produced abundantly when the pistil was in its prime, but in lesser quantities when it was losing vigour. The present experiments with Brussels sprouts indicate that early in the life of the bud and late in the life of the flower the inhibitory substance is not produced at all.

ATTIA (1, 1950) found that flower buds of cabbage when pollinated at an early stage gave more seeds when selfed than when crossed. He assumed that at this moment the inhibitory substance was at a low concentration, at which it might promote pollen tube growth rather than inhibit it. The present data with Brussels sprouts give no reason for this explanation. Meanwhile we agree with ATTIA that the style length at the time of self-pollination is not the prime factor governing the seed set.

Alpha-naphthylacetamide did not overcome incompatibility in Brussels sprouts. The same growth substance and the same method were previously used by EYSTER (10, 1941) and claimed to be very helpful with petunias, marigolds, cabbage and red clover plants. EYSTER assumed that NAd applications increased the growth of incompatible pollen tubes by neutralizing the incompatibility substance.

LEWIS (18, 1946) found that NAd applied to the styles in 20 p.p.m. aqueous solution had no effect on incompatible or compatible pollen tubes of *Prunus* species and *Oenothera organensis*. The style abscission was delayed by 2–3 days but the incompatible pollen tubes stopped growing as in the normal cases. When high concentrations were used all the pollen tubes burst, and in *Oenothera* empty seeds and parthenocarpic fruits were obtained. According to LEWIS (20, 1949) the seeds obtained by EYSTER might have been empty.

MCGUIRE and RICK (22, 1954) used the same growth substance to obtain seeds from incompatible crosses of *Lycopersicum peruvianum* without success. The only effect of the growth substance was to prevent flower drop.

The large seed numbers obtained by NAd (EMSWELLER and STUART 9, 1948), from incompatible crosses of the Easter lily may be due to the delay of style abscission allowing the slow growing pollen tubes to reach the ovules (LEWIS 20, 1949).

Although beta-naphthoxyacetic acid stimulated pollen tube growth to some extent in pear-apple hybridization (BROCK 4, 1954), the success achieved was due mainly to parthenocarpy. This is concluded because pear-apple hybrids were only obtained from varieties capable of parthenocarpy and reciprocal crosses (apple-pear) were not successful. It was also observed by LEWIS (19, 1948) that growth substances could induce fruit development preventing the loss of the few seeds which developed in *Oenothera* and by DARROW (8, 1956) in blueberry heteroploid crosses.

In Brussels sprouts incompatible pollen tubes do not penetrate the stigma (see page 11). The cause of incompatibility is not the slow growth of the pollen tubes and the early abscission of flowers. Owing to parthenocarpy pollinated flowers of Brussels sprouts remain on the plant with the styles until maturity, although the siliques may contain no seeds. For these reasons negative results could be expected.

III

RADISH

1. POLLINATION EXPERIMENTS

1.1. *Experimental methods.* The plants used belonged to the cultivars 'Kleine Ronde Witpunt' (RW) and 'IJskegel' (IJ). As they began to flower, the plants which were grown in pots, were removed to a greenhouse where the temperature was kept at 20 °C at night and between 22 and 25 °C (occasionally higher, up to 28 °C) during the day. Flower buds and open flowers of different ages were selfed or cross-pollinated in the way described for Brussels sprouts.

1.2. *Results.* The data obtained from self-pollinated plants which are summarized in table 7 show nearly the same trend as those of Brussels sprouts (cf. tables 1 and 3). In radish also the average number of seeds set after self-pollination increases as buds are selfed at a later stage of development and here also there is a sudden decrease in yield when the buds reach anthesis. A difference from Brussels sprouts is that the increase in the seed number when flowers are pollinated after opening is stronger; the optimal seed set of flowers selfed after opening reached the same value as the seed set of buds selfed before opening.

At the slightly higher temperature the rise and fall of the seed yield is somewaht more abrupt, although the maximum and minimum values are about the

TABLE 7. Average seed numbers obtained from incompatible radish plants when flowers were self-pollinated at, before, or after opening.

Plant number	Date of selfing (1955)	Temperature	Number of days before opening						Number of days after opening				
			5	4	3	2	1	0	1	2	3	4	5
RW 1	27 June	20–25°C			3.2	5.0	4.2	0.5	2.7	6.3	5.3	3.0	
RW 1	28 June	20–25°C		2.0	2.0	6.0	4.6	0	3.0	6.3			
RW 3	30 June	20–25°C		1.0	3.0	2.8	4.0	0.5	1.0	1.2	3.0	0	0
IJ 4	5 July	20–25°C	1.0	1.0	4.0	2.6	3.0	0.5	2.0	3.5	3.0	1.5	1.0
IJ 5	6 July	20–25°C				4.0	7.0	0.6	2.5	6.5	2.0	2.6	0.8
RW 1	15 July	20–28°C				4.5	5.0	0.6	6.2	6.8	2.2	0.5	0
RW 3	15 July	20–28°C		1.0	2.0	2.0	4.0	1.0	4.5	2.6	2.0	0	

same. In both temperature ranges the only moment at which seed set following selfing is unsatisfactory is at the day of anthesis. When the temperature was 20–25 °C, flower buds yielded the maximal seed set 3 to 1 days before opening, but when the temperature rose to 28 °C the maximal seed set was obtained only on the day before opening. At the lower temperature the seed set after opening did not reach its peak until 2 or 3 days after anthesis but at the slightly higher temperature it was already reached the first or the second day after the opening of the flower.

The data from cross-pollinated plants (table 8) also confirm the observa-

TABLE 8. Average seed numbers obtained from radish plants when flowers were cross-pollinated at, before, or after opening.

Number of female parent	Date of crossing (1955)	Temperature	Number of days before opening					Number of days after opening				
			4	3	2	1	0	1	2	3	4	5
RW 1	27 June	20–25°C		4.0	5.0	7.1	7.8	8.2		2.5	3.0	
RW 2	28 June	20–25°C			7.0	7.0	6.0	7.0	7.0	0		0
RW 3	30 June	20–25°C	1.5	3.2	3.5	7.0	7.5	7.5	3.5	4.5	0	0
IJ 4	5 July	20–25°C			3.5	7.0	7.5	7.0	5.0	2.6	1.3	1.0
IJ 5	6 July	20–25°C					7.0	8.0	7.3	1.0	0	2.0

tions made on Brussels sprouts (cf. tables 2 and 4). In radish too there is a gradual increase in the seed set as the buds are pollinated at a later stage. The optimum is reached one day before opening at 20–25 °C; this high level is maintained at opening and for one day after that. Then the seed yield decreases.

For a further comparison of the results of self- and cross-pollination we will use the data from plants RW1, RW3, IJ4, and IJ5, which were selfed as well as crossed. The most striking difference is the average seed number obtained when plants have been pollinated at anthesis. This is 7.0 to 7.8 when flowers have been cross-pollinated and only 0.5 to 0.6 when they have been selfed. When flowers are pollinated in the bud stage the difference is less pronounced but at all stages selfing was significantly less successful than crossing. The same holds true for the seed yield of flowers pollinated 1 or 2 days after the opening of the

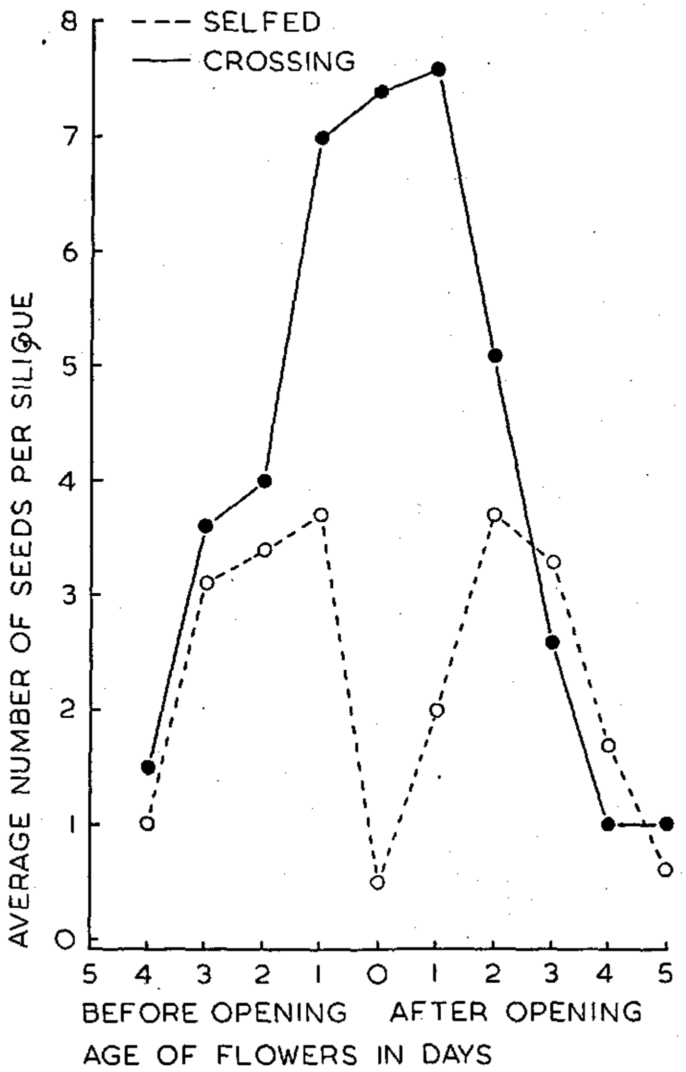

FIG. 7. Radish: Comparison between selfing and crossing at 20–25 °C. At all bud stages selfing was less successful than cross-pollination. No significant difference in the seed set when flowers were selfed or cross-pollinated 3 to 5 days after anthesis.

flower. In later stages the seed yield is very low and differences are not significant. In figure 7 the results of crossing and selfing, both before, at and after opening of the flowers, are represented. Photograph 2 also illustrates the results.

The behaviour of the pollen tubes in a highly self-incompatible plant was studied using the same method described for Brussels sprouts. Forty eight hours after self-pollination at flower opening only 30 % of the pollen had germinated.

The pollen grains were about 20μ in diameter. Twenty five per cent had pollen tubes less than 20μ long; 3% had tubes from 20 to 40μ and 2% had tubes from 40 to 60μ long. Penetration of the stigma was not observed.

2. Experiments with growth substances

2.1. *Methods.* Alpha-naphthylacetamide (NAd) and para-chlorophenoxy-acetic acid (CPA) were used in 10 p.p.m. aqueous solutions. The flowers were treated in the way described for Brussels sprouts.

2.2. *Results.* The average seed set of selfed flowers obtained in the different treatments is given in table 9.

TABLE 9. Effect of NAd or CPA applications on the seed set obtained from incompatible radish plants, when flowers were self-pollinated at different stages.

Flower stages	Treatment	Mean number of seeds	Comparison between parallels in the different treatments			
			Treatments compared	Mean difference	n	
Flower buds and flowers after opening at suitable stages	Untreated	4.4 ± 0.3	Untreated-control	1.54 ± 0.46	15	S[1]
	Control	2.9 ± 0.6	Untreated-NAd	3.17 ± 0.47	15	S
	NAd	1.3 ± 0.4	Untreated-CPA	2.59 ± 0.56	15	S
	CPA	1.8 ± 0.5	Control-NAd	1.63 ± 0.69	15	S
			Control-CPA	1.05 ± 0.75	15	–
Flowers at opening	Untreated	0.6 ± 0.1	Untreated-control	-0.05 ± 0.27	4	–
	Control	0.7 ± 0.2	Untreated-NAd	0.40 ± 0.19	7	–
	NAd	0.2 ± 0.1	Untreated-CPA	0.40 ± 0.16	7	S
	CPA	0.2 ± 0.1	Control-NAd	0.50 ± 0.18	4	–
			Control-CPA	0.50 ± 0.25	4	–
Flowers at other stages	Untreated	1.8 ± 0.2	Untreated-control	0.35 ± 0.19	14	–
	Control	1.5 ± 0.2	Untreated-NAd	1.05 ± 0.26	14	S
	NAd	0.8 ± 0.3	Untreated-CPA	0.88 ± 0.23	15	S
	CPA	0.9 ± 0.2	Control-NAd	0.70 ± 0.26	14	S
			Control-CPA	0.52 ± 0.25	14	–

[1]) S = 5% significance or better – = less than 5%

In radish also, the number of seeds obtained after self-pollination at the suitable stages is decreased by the growth substance applications. A difference from Brussels sprouts is that NAd has an unfavourable effect compared with the control solution. Flowers self-pollinated at unsuitable stages do not show the significance between treatments which is obtained when the seed set is higher.

The data obtained from cross-pollinated flowers are summarized in table 10. The seed set is also decreased by the growth substance applications, especially when the flowers are pollinated at the suitable stages that yield relatively large quantities of seed.

TABLE 10. Effect of NAd or CPA applications on the seed set obtained from compatible combinations of radish plants, when flowers were cross-pollinated at different stages.

Flower Stages	Treat-ment	Mean number of seeds	Comparison between parallels in the different treatments			
			Treatments compared	Mean difference	n	
Flowers at suitable stages (Flowers at or near opening)	Untreated	7.0 ± 0.1	Untreated-NAd	1.32 ± 0.37	17	S[1])
	NAd	5.6 ± 0.4	Untreated-CPA	3.11 ± 0.50	18	S
	CPA	3.9 ± 0.5				
Flowers at other stages	Untreated	2.2 ± 0.5	Untreated-NAd	0.78 ± 0.48	11	–
	NAd	1.8 ± 0.6	Untreated-CPA	1.00 ± 0.36	13	S
	CPA	1.2 ± 0.4				

[1]) S = 2% significance or better – = less than 5%

3. Discussion and conclusions

As the results on Brussels sprouts have been fully discussed, the comments on the data from the experiments on radish may be short.

The results show that radish may be successfully self-pollinated both in the bud stage and after anthesis, although the seed yield will never attain the same values reached after cross-pollination. The most suitable stage for bud pollination is when the buds are 6 to 8 mm long, that is 1 to 3 days before anthesis at a temperature of about 20 °C. Flowers should be pollinated 2 or 3 days after anthesis at a temperature of about 20 °C and 1 day after anthesis at a higher temperature.

The fact that self-pollination of radish is much more successful when done in the bud stage than at opening was already shown by Kakizaki & Kasai (15, 1933). Tatebe (32, 1940) was the first to show that good results may also be obtained with old flowers.

One may assume that at anthesis a substance is produced that inhibits germination and tube growth of incompatible pollen. In radish the period during which this substance completely inhibits self-pollination lasts only for the day of anthesis, at least at 20–28 °C. In Brussels sprouts, this substance was effective for a longer time; this may be due to a genetic difference between the two, and also to the fact that the prevailing temperature during the experiments with Brussels sprouts was much lower.

In radish the fact that the seed set obtained after selfing is always less than after cross-pollination indicates that the inhibition is never completely absent, unless perhaps at very early bud stages or very late in the life of the flower. This means that in radish self-incompatibility cannot be overcome completely.

The behaviour of incompatible pollen in radish was studied by Tatebe (32, 1940). Our data are in accordance with his results.

The growth substance applications did not overcome incompatibility in radish. The results obtained agree with those of Brussels sprouts. However, in radish NAd applications had an unfavourable effect compared with the control solution. Growth substances may have different effects on different kinds of plants and under variable conditions.

In radish incompatible pollen tubes do not penetrate the stigma (see page 17). The flowers remain on the plant with the styles at least for some weeks after pollination although the siliques may contain no seeds. Further details have been previously discussed with Brussels sprouts.

IV

CYCLAMEN

1. Introduction

The low fruit set obtained from cyclamen crosses led to the present experimental work.

There is no incompatibility in cyclamen, as although small numbers of fruits are obtained in many cases the fruits always contain seeds.

2. General observations

2.1. *Growth of fertilized ovules and ovaries.* Plants of the cultivar 'Perle von Zehlendorf' were used. At different intervals after pollination, 3 to 6 ovaries and 10 to 20 ovules from each ovary were studied. The data collected were the area of one side of the ovule and the area of the ovary base in mm^2. The average values are given in table 11. These show that *ovules and ovaries start to grow about three weeks after pollination.*

TABLE 11. Growth of ovules and ovaries of 'Perle von Zehlendorf' after pollination.

Number of weeks after pollination	Average area per ovule	Average area per ovary base
0	0.08 mm^2	16.2 mm^2
1	0.08	16.9
2	0.07	16.3
3	0.13	18.9
4	0.32	22.0
6	4.07	122.0

2.2. *Decay of the flower stalks.* Cyclamen flowers have fleshy stalks. In most cases a large number of the stalks on a plant loose their turgidity and rot away during the first month after pollination. When the number of decayed stalks is lower, the decay occurs more gradually over a longer period. However, in all cases the stalks which later decay stop elongating before the fruit develops. The pattern of this decay is shown by the figures given in table 12.

2.3. *Correlation between number of seeds and seed weight.* The cultivars 'Wit' and 'Perle von Zehlendorf' were used for observations on seed weight and number of seeds per fruit. These data are summarized in table 13. It is

TABLE 12. Numbers of decayed flower-stalks at different intervals after pollination.

Cultivar	Experimental series (cf. table 19, the untreated groups)	% decayed stalks at 4 weeks after pollination			Total decayed stalks %
		1–4	5–8	more	
Perle von Zehlendorf	2	86.3	2.2	0	88.6
„	3	77.5	2.5	0	80.0
„	1	58.9	6.5	0	65.5
„	4	50.9	5.8	1.9	58.8
Wit	5	47.4	13.5	1.6	62.7
„	7	19.0	9.5	3.1	31.7
„	9	20.0	8.0	2.0	30.0
„	6	7.8	5.2	10.5	23.6
„	8	7.5	15.0	0	22.5

TABLE 13. Correlation between the average number of seeds per fruit and the average seed weight.

Average number of seeds per fruit	Average seed weight in mg		Number of fruits	
	Wit	Perle von Zehlendorf	Wit	Perle von Zehlendorf
1– 25	6.88	10.03	26	12
26– 50	7.89	12.56	27	20
51– 75	7.06	11.59	45	13
76–100	6.68	11.33	45	9
101–125	6.50	9.78	13	1
126–160	6.44	–	3	–
1– 12	6.81	7.77	18	5
13– 25	7.05	11.87	8	7

evident that *as far as the seed weight is concerned there is an optimal seed number per fruit.* This number lies between 26 and 50. If less seeds develop, their average weight is lower, and the same holds true when there are more seeds per fruit.

3. POLLINATION EXPERIMENTS

3.1. *Effect of emasculation.* The effect of emasculation on seed set was studied on plants of the cultivars 'Donkerrood' and 'Lichtrood'. On each plant one flower was emasculated and one was left intact. Both were pollinated at opening time and again three days afterwards.

According to the results presented in table 14 *the effect of emasculation is unfavourable,* as the fruit set or both the fruit set and the number of seeds per fruit are higher in the controls.

TABLE 14. Effect of emasculation on fruit and seed set of cyclamen.

Cultivar	Per cent of fruits set		Average number of seeds per fruit	
	Emasculated	Not emasculated	Emasculated	Not emasculated
Donkerrood	30	50	6.0	7.2
Lichtrood	40	100	21.0	47.3

The effect of emasculation on decay of flower stalks was studied in 'Perle von Zehlendorf'. The stalks were marked in ink at 1 cm intervals. On each plant, two flowers were emasculated, two more were kept intact; in both cases one flower was pollinated while the other one was not.

After ten days it was observed that all stalks of intact flowers, whether pollinated or not, had elongated. Elongation of the emasculated flower stalks was only 64% of those that had been pollinated and 73% of the others. The stalks which had not elongated decayed 1 to 2 weeks afterwards. This shows that *emasculation tends to shorten the life of the flower stalk.*

3.2. *Method of pollination.* Flowers of various cultivars were emasculated at the bud stage. One group was pollinated immediately; the other was pollinated twice, viz. at anthesis (4 to 7 days after emasculation) and again three days later. In all cases pollen from other plants belonging to the same cultivar was used.

TABLE 15. Effect of bud pollination on the fruit and seed set.

Cultivar	Per cent of fruits set		Average number of seeds per fruit	
	Pollinated at the bud stage	Pollinated at opening and three days later	Pollinated at the bud stage	Pollinated at opening and three days later
Reinrosa fimbriata	0	56.2	–	33.3
Rood	20.0	100.0	6.0	19.0
Rosa v. Mariental rococo . .	9.1	53.8	55.0	41.0
Vuurbaak	16.6	54.5	38.0	42.0
Jubileum	12.5	30.0	20.5	28.6
Reinrosa	20.0	27.2	23.5	27.3
Rosa v. Mariental	33.3	25.0	24.8	25.0

The results given in table 15 show that the second method of pollination gave the best result.

4. Experiments with growth substances

4.1. *Material and methods.* The following growth substances were used:

α-naphthylacetamide (NAd)
para-chlorophenoxyacetic acid (CPA)
β-naphthoxyacetic acid (NOA).

They were applied both in lanolin and in aqueous solutions. Lanolin paste was used mainly to apply NAd. The growth substance was dissolved in aethanal 96% and mixed with hydrated lanolin (1 part wool fat + 1 part distilled water).

Hydrated lanolin plus a few drops of aethanal was used as a control. Pastes containing 5 or 10 mg NAd per gram were applied to the wound caused by removing the corolla and the anthers.

To prepare the aqueous solutions, the growth substance was dissolved in a few drops of aethanal 96% which were then mixed with distilled water. The concentrations used were 10×10^{-6} and 50×10^{-6}. In some cases sodium lauryl sulphate in a concentration of 10^{-7} was used as a wetting agent. The control solution was prepared in the same way but without a growth substance. The solutions were applied with a small hand sprayer at the base of the ovary to the wound caused by removing the corolla and the anthers and on the upper part of flower stalks.

Pollination was done at the time of opening of the flower (4 to 7 days after emasculation) and again three days afterwards. Pollen was used from plants belonging to the same cultivar.

4.2. *Effect of application at pollination.* In preliminary experiments during 1954 and '55 NAd, CPA and NOA were applied in lanolin pastes (containing 5 or 10 mg growth substance per g) at pollination. As only NAd showed promising results, the work was continued with this substance.

In 1955 and '56 NAd was applied in lanolin paste at the time of pollination to the flowers of 27 plants of 'Perle von Zehlendorf' and 32 plants of 'Wit'. The results are summarized in table 16.

TABLE 16. Effect of NAd in lanolin paste on the fruit and the seed set when applied at the time of pollination. Parthenocarpic fruits are shown between brackets.

Cultivar and observed character	Treatments			
	Untreated	Lanolin	5 mg NAd/g	10 mg NAd/g
Perle von Zehlendorf				
Per cent of fruits set	11.1	22.2	14.8	37.0+(7.4)
Average number of seeds per non-parthenocarpic fruit . .	44.6	53.6	44.0	39.0
Average number of seeds per pollinated flower	4.9	11.9	6.5	14.4
Average seed weight in mg . .	11.8	12.7	12.2	11.0
Wit				
Per cent of fruits set	53.1	53.1+(3.1)	40.7+(3.1)	50.0+(6.2)
Average number of seeds per non-parthenocarpic fruit . .	65.5	74.3	53.0	65.3
Average number of seeds per pollinated flower	34.8	39.5	21.5	32.6
Average seed weight in mg . .	5.9	6.2	6.0	7.0

These figures show that there is a difference in response between the two cultivars. In 'Perle von Zehlendorf', there is a marked increase in the fruit set and consequently a similar effect on the average number of seeds yielded by one flower. Lanolin alone appears to have a stimulating effect on the fruit set. In 'Wit' only the number of parthenocarpic fruits is increased by lanolin and NAd applications.

Similar experiments were carried out with growth substances in aqueous solutions, containing 50 mg growth substance per liter, a wetting agent and a few drops of aethanal. The control solution contained water, a wetting agent and a few drops of aethanal. Each treatment consisted of 6 plants with a total of 25 to 30 flowers. The plants used were chosen from an arbitrary group with the same phenotype and the same vigour. The results are given in table 17.

TABLE 17. Effect of growth substances in aqueous solutions on fruit and seed set when applied at the time of pollination.

Treatments	Per cent of fruits set	Average number of seeds per fruit	Average number of seeds per flower	Average seed weight in mg
Untreated	20.0	50.4	10.1	11.5
Control solution	9.5	62.5	5.6	11.5
CPA	23.0	44.9	10.5	14.2
NAd	17.0	59.2	10.2	16.4
NOA	20.0	48.8	9.8	12.7

The growth substances have no effect when they are applied at pollination while the control solution appears to have a harmful effect.

4.3. *Effect of application at both emasculation and pollination or only at emasculation.* In the last experiment CPA was also applied at the time of emasculation and again a few hours before pollination. This treatment gave a fruit set of 34.6%, which is considerably higher than the normal treatment (20.0%). This seemed a promising result. Consequently a large scale experiment was carried out in 1956 with all three growth substances applied at both emasculation and pollination or only at emasculation.

There were nine series, differing in the cultivar used, date of pollination and a few other respects. They are reviewed in table 18.

TABLE 18. Review of treatments in 9 series of experiments with NAd, CPA and NOA.

Experimental series	Cultivar	Number of plants per treatment	Approximate number of flowers per plant	Date of pollination	Concentration of growth substance per litre	Wetting agent	Number of applications
1	Perle v. Zehlendorf	12	4	Nov. 25, '55	50 mg	+	2
2	,,	12	4	Dec. 21, '55	50 mg	+	2
3	,,	8	5	Dec. 6, '55	50 mg	—	2
4	,,	8	5	Jan. 23, '56	50 mg	—	2
5	Wit	12	4	Dec. 21, '55	50 mg	+	2
6	,,	8	5	Jan. 18, '56	50 mg	—	2
7	,,	12	4	Jan. 30, '56	50 mg	+	1
8	,,	8	5	Feb. 6, '56	50 mg	—	1
9	,,	8	5	Feb. 4, '56	10 mg	+	1

TABLE 19. Effect of NAd, CPA and NOA on fruit and seed set (the treatments are reviewed in table 18).

Character	Experimental series	Untreated (actual values = 100%)	% of the untreated group			
			Control solution	NAd	CPA	NOA
Per cent of fruits set	1	34.4	123	190[1]	145	88
,,	2	11.3	81	382[1]	203	58
,,	3	20.0	78	333[1]	75	117
,,	4	41.1	55	188[1]	67	89
,,	5	37.2	73	145[1]	61	131
,,	6	76.3	76	102	70	54
,,	7	68.2	71	125[1]	85	103
,,	8	77.5	104	114[1]	99	77
,,	9	70.0	–	123[1]	114	109
Average number of seeds per fruit	1	52.6	106	82[2]	91	100[2]
,,	2	77.2	56	52[2]	59	49[2]
,,	3	58.6	85	65[2]	89	80[2]
,,	4	31.2	87	70[2]	85	71[2]
,,	5	74.0	89	89	67[2]	50[2]
,,	6	66.9	92	102	72[2]	86[2]
,,	7	53.0	101	106	89[2]	80[2]
,,	8	64.6	110	109	81[2]	85[2]
,,	9	55.6	–	108	110	89
Average seed weight in mg	1	11.4	96	106	106	93
,,	2	10.2	125	125	104	128
,,	3	12.5	94	103	89	94
,,	4	11.6	100	114	96	100
,,	5	6.2	100	110	95	87[3]
,,	6	7.0	89	100	114	80[3]
,,	7	7.2	114	110	110	94[3]
,,	8	7.1	100	94	111	87[3]
,,	9	7.1	–	100	97	107
Average number of seeds per pollinated flower	1	18.1	131	156[1]	132	88
,,	2	8.7	46	198[1]	121	28
,,	3	11.7	67	217[1]	67	95
,,	4	12.8	48	133[1]	57	63
,,	5	27.5	65	130[1]	41	66
,,	6	51.0	69	105	50	47
,,	7	36.1	71	133[1]	75	83
,,	8	50.1	115	124[1]	80	66
,,	9	38.9	–	134[1]	126	97

[1] Significantly higher (at 5% level or better) than the untreated group.
[2] Significantly lower (at 5% level or better) than the control treatment.
[3] Significantly lower (at 2% level or better) than the untreated or the control treatment.

In series 7 to 9 the growth substances were applied at the time of emasculation only. In series 1 to 8, there were five treatments per series: not sprayed, sprayed with the control solution, and sprayed with one of the three growth substances. In series 9, the treatment in which the plants were sprayed with the control solution was omitted.

The Student's method devised by LOVE and BRUNSON (21, 1924) was used to compare the data.

The results of the experiments are summarized in table 19. They show the following:

a) The fruit set was better in 'Wit' than in 'Perle von Zehlendorf'.

b) Application of the control solution reduced the fruit set in most cases.

c) NAd applied twice in 50 p.p.m. concentration increased the fruit set in the cases where the normal fruit set was low; in series 2 and 3 (fruit set 11.3 and 20.0 % respectively) it increased by more than 200 %, while in series 1 and 4 (fruit set of the untreated groups 34.4 and 41.1 %) about 90 % increase was obtained. In 'Wit' when the fruit set was 37.2 % this application increased the fruit set by 45 % (series 5) but when the fruit set was high (76.3 %, series 6) no increase was obtained. NAd applied in 50 or 10 p.p.m. once at emasculation gave 14 to 25 % increase although the fruit set was high (series 7 to 9).

d) In 'Perle von Zehlendorf' the average number of seeds per fruit was reduced by NAd more than by the control solution. However, there was a large increase in the total seed yield.

e) Applications of NAd did not decrease the seed weight.

f) CPA applied in 50 p.p.m. concentration increased the fruit set in 'Perle von Zehlendorf' when a wetting agent was used (series 1 and 2); this increase was smaller than that obtained by NAd. In 'Wit' it had an unfavourable effect on the fruit set and the average number of seeds per fruit. When applied in 10 p.p.m. the increase in the fruit set was smaller than that obtained by NAd (series 9).

g) The figures showing the effect of NOA on the fruit set are not clear. In both cultivars the average number of seeds per fruit was decreased. The seed weight was also reduced in 'Wit'.

4.4. *Effect on decay of flower stalks.* Aqueous solutions of NAd, CPA and NOA (50 mg per litre + few drops of aethanal + wetting agent) were sprayed

TABLE 20. Effect of growth substances in aqueous solutions on decay and elongation of flower stalks.

Number of weeks after emasculation	Per cent of decayed stalks			
	Untreated	NAd	CPA	NOA
4	70	20	44	0
8	80	48	76	100
12	100	88	100	
16		100		
Per cent of elongation during the first ten days	14	37	20	35

on the wound caused by emasculation and on the upper part of the flower stalk at the time of emasculation and again 5 days later. The flowers were not pollinated. Each treatment consisted of 5 plants of 'Perle von Zehlendorf' with 20 to 25 flowers. The results are given in table 20.

These data show that all three growth substances tend to stimulate the elongation of the flower stalk and to prolong its life, NAd being the most active in both respects. CPA is less active than NAd. NOA has injurious effect on the ovaries and therefore the flower stalks decay some weeks earlier.

In another experiment, NAd (50 p.p.m.) was applied in aqueous solution: (1) on the upper part of the flower stalk, (2) at the same place and also on the wound caused by emasculation. The second treatment was better than the first; four weeks after application 70% of the control stalks had wilted, 30% of the first group and 0% of the second had decayed.

The effect of NAd in lanolin was also studied. The growth substance was applied at emasculation on the wound caused by removing the corolla and the anthers. Ten plants of 'Perle von Zehlendorf' were used and the flowers were not pollinated. The results are given in table 21.

TABLE 21. Effect of NAd in lanolin on decay of flower stalks.

Number of weeks after treatment	Per cent of decayed stalks			
	Untreated	Lanolin	5 mg NAd/g	10 mg NAd/g
4	70	70	10	10
8	100	100	30	40
12			60	60
16			60	60
19			80	70
Per cent of parthenocarpic fruits	0	0	20	30

NAd in lanolin was also applied to the cut surface of flower stalks from which the flowers had been removed. The results are given in table 22 and photo 3.

TABLE 22. Effect of NAd on decay of flower stalks after the flowers had been cut.

Number of weeks after treatment	Per cent of decayed stalks		
	Untreated	Lanolin	5 mg NAd/g
4	100	100	30
8			40
12			50
15			60

In a further experiment NAd in lanolin paste was applied on the flower stalk about 2 to 3 cm from the ovary. This application did not prevent the decay of the upper part on which the growth substance paste was not smeared (photo 4).

5. Discussion and conclusions

In the present experiments there is no evidence of *spontaneous* parthenocarpy in *Cyclamen persicum*, consequently pollination is a limiting factor for the fruit set. Bud pollination is not effective because it does not increase the number of fruits and seeds compared with pollination at the time of opening.

Undoubtedly, unsatisfactory seed set in cyclamen is due to many factors. The role of the environment is evident from the differences in both the fruit and the seed set when the plants are pollinated on different dates (cf. table 19). Tables 15 and 19 show that there are also differences between cultivars.

Our data leave little doubt that generally emasculation has an unfavourable effect on fruit set owing to an early decay of the flower stalks, although there are differences between varieties. It is known that young stamens are very rich in auxin (Wittwer 38, 1943; Hatcher 13, 1945). The control of flower stalk elongation has been demonstrated by Söding (29, 1936; 30, 1938) to be due to the amount of auxin diffused from the flower. The result of emasculation is not only a decrease in the fruit set but also a reduction in the number of seeds per fruit in some cultivars.

The growth of cyclamen ovules has been studied by Gorter (11, 1955) and was found to start ± 4 weeks after pollination. This is in accordance with our results. The decay of large numbers of stalks before the fruits develop causes the loss of many fruits and consequently decreases the fruit set.

The three growth substances used stimulate elongation of the fruit stalks and thereby decrease the chances of decay; CPA is less effective. NOA has severe injurious effect on the growth of the small fruits and also on the seed set. Therefore no helpful results can be achieved by the use of either CPA or NOA.

NAd stimulates the growth of the stalks and prolongs their life more than CPA and NOA, and evidently has no harmful effect on the growth of the fruits except when applied too frequently or in too high concentrations. Therefore, when the fruit set is high, no increase is obtained by the use of this growth substance in lanolin (5 or 10 mg/g) or by applying twice an aqueous solution containing 50 p.p.m. In this case one application (50 or 10 p.p.m.) at the time of emasculation is beneficial.

Clore (6, 1948) found in lima bean, that the higher the concentration of α-naphthaleneacetic acid used, the higher the reduction in the yield and the average number of beans per pod.

It should be mentioned that different cultivars may react differently to the same concentration of a growth substance.

Applications of growth substances have been found to prevent the drop of flowers and small fruits in melon crosses by Burrel and Whitaker (5, 1939) and by Whitaker and Pryor (37, 1946) and in lima bean crosses by Wester and Marth (36, 1949). Growth substances sprayed onto plants increased the pod set and the yield of shelled lima beans under conditions which favoured flower and pod drop (Rahn 27, 1955). The case of cyclamen seems to be analogous to those investigated by the authors mentioned.

V

SUMMARY

I. In Brussels sprouts and radish incompatibility was studied. In *Cyclamen persicum* decay of the flower stalk is the important factor which affects seed set.

II. *Brussels sprouts*

1. In selfing, the seed set increases with the age of the bud until it reaches a maximum few days before anthesis to decrease rapidly afterwards. At higher temperature the period during which the bud may be selfed successfully is shorter and lies closer to anthesis. Medium sized flower buds which are about 7 to 9 mm long are considered to yield the highest seed set.
2. In crossing, the seed set does not decrease as the buds approach anthesis. At higher temperature the number of days prior to anthesis during which buds may be successfully pollinated decreases.
3. There is a period before anthesis during which flower buds may be selfed or cross-pollinated with equal success. The length of this period decreases at higher temperature.
4. After anthesis there is a slight increase in seed set after self-pollination. At later stages the seed set decreases again. At higher temperature the period during which selfing has some success is shorter.
5. In crossing, the seed set appears to be maintained for about two days after anthesis at the same level as at opening when the temperature is low, after that it gradually drops to zero. At higher temperature the number of days during which pollination is successful decreases.
6. Flowers at later stages may be selfed or cross-pollinated with equal results.
7. There is no correlation between style length at the time of self-pollination and the seed set.
8. When flowers of incompatible plants are self-pollinated at anthesis a large per cent of the pollen does not germinate and the pollen tubes do not penetrate the stigma.
9. The inhibition of the pollen by the style occurs a few days before anthesis and reaches its maximum at the opening of the flower. Later on it decreases and then disappears.
10. Alpha-naphthylacetamide applications do not overcome incompatibility.

III. *Radish*

The data on the time of pollination show nearly the same trend as those of Brussels sprouts; however there are a few exceptions.

1. Old flowers yield approximately the same seed set as flower buds. Buds which are 6 to 8 mm long are suitable for selfing.
2. The seed set obtained from buds after selfing is always less than after cross-pollination.
3. Alpha-naphthylacetamide or para-chlorophenoxyacetic acid applications do not overcome incompatibility.

IV. *Cyclamen*

1. There is no incompatibility. Although small numbers of fruits are obtained in many cases, the fruits always contain seeds.
2. Ovules and ovaries start to grow about three weeks after pollination.
3. In many cases a large number of flower stalks loose turgidity and decay early, causing the loss of the fruits.
4. Emasculation tends to shorten the life of the flower stalks and decreases the fruit set or both the fruit set and the number of seeds per fruit.
5. Bud pollination does not increase the number of fruits or seeds compared with pollination at the time of opening.
6. In 'Perle von Zehlendorf' and 'Wit' the optimal seed weight is reached when the fruits contain 26–50 seeds. The seed weight decreases if less or more seeds develop.
7. Alpha-naphthylacetamide applied in 50 or 10 p.p.m. to the upper part of the flower stalks and the wound caused by removing the corolla and the anthers, at the time of emasculation or both at emasculation and at pollination, increases the fruit set and consequently the total seed yield. Applications of para-chlorophenoxyacetic acid or β-naphthoxyacetic acid are not beneficial.
8. Alpha naphtylacetamide stimulates the elongation of flower stalks, decreases the chances of their decay, and has no injurious effect on the small fruits except when used in high concentrations.

ACKNOWLEDGMENTS

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SAMENVATTING

FACTOREN, DIE DE ZAADZETTING IN SPRUITKOOL, RADIJS EN CYCLAMEN BEÏNVLOEDEN

I. In spruitkool en radijs werd incompatibiliteit bestudeerd. In *Cyclamen persicum* is het voortijdig verwelken van de bloemsteel de belangrijkste factor, die de zaadzetting beïnvloedt.

II. *Spruitkool*

1. De zaadzetting neemt met de leeftijd van de knop op het moment van zelfbestuiving toe tot een maximum, dat enige dagen voor het opengaan van de knoppen wordt bereikt, daarna neemt de zaadzetting snel af. Wanneer de temperatuur hoger is, wordt de periode, waarin de knop met succes kan worden zelfbestoven, korter en ligt zij dichter bij het tijdstip waarop de

bloemknoppen opengaan. Bloemknoppen, die ongeveer 7–9 mm lang zijn, blijken het grootste aantal zaden op te brengen.

2. Bij kruisbestuiving neemt de zaadzetting niet af als de knoppen het tijdstip van het opengaan naderen. Bij hogere temperatuur neemt het aantal dagen, waarin de knoppen met succes bestoven kunnen worden, af.
3. Er is een periode vóór het opengaan van de bloemen, waarin zelfbestuiving en kruisbestuiving hetzelfde resultaat leveren. Bij hogere temperatuur is deze periode korter.
4. De zaadzetting neemt iets toe als de bloemen na het opengaan worden zelfbestoven en neemt in latere stadia weer af. Bij hogere temperatuur wordt de periode, waarin de bloemen met enig succes kunnen worden zelfbestoven, korter.
5. De goede zaadzetting na kruisbestuiving blijft bij lage temperatuur ongeveer twee dagen na het opengaan der bloemen op de zelfde hoogte, hierna daalt zij geleidelijk tot nul. Het aantal dagen, waarin bestuiving met succes kan worden toegepast, is bij hogere temperatuur kleiner.
6. Bij oude bloemen is de zaadzetting na zelf- en kruisbestuiving gelijk.
7. Bij zelfbestuiving is er geen correlatie tussen de lengte van de stijl en de zaadzetting.
8. Wanneer de bloemen van incompatibile planten bij het opengaan worden zelfbestoven, kiemt een groot percentage van het stuifmeel niet en dringen de pollenbuizen de stempel niet binnen.
9. De remming van stuifmeel door de stijl treedt enige dagen voor het opengaan van de knoppen op, en bereikt een maximum bij het opengaan. Daarna vermindert en verdwijnt zij.
10. Toepassing van alpha-naftylacetamide kan incompatibiliteit voorkómen nòch opheffen.

III. *Radijs*

De gegevens van radijs vertonen op enkele uitzonderingen na hetzelfde beeld als die van spruitkool.

1. Bij zelfbestuiving vertonen oude bloemen bijna de zelfde zaadzetting als bloemknoppen. Knoppen die 6–8 mm lang zijn, zijn geschikt voor zelfbestuiving.
2. De zaadzetting van de knoppen na zelfbestuiving is altijd minder dan na kruisbestuiving.
3. Toepassing van alpha-naftylacetamide of para-chloorfenoxyazijnzuur kan incompatibiliteit voorkómen nòch opheffen.

IV. *Cyclamen*

1. Bij cyclamen bestaat geen incompatibiliteit. De vruchten bevatten altijd zaden.
2. De ovulae beginnen ongeveer drie weken na de bestuiving te groeien.
3. Vele bloemstengels verliezen voortijdig hun turgescentie en gaan rotten, waardoor vele vruchten verloren gaan.
4. Ten gevolge van de castratie wordt het percentage stengels dat wegrot groter, en dientengevolge het aantal vruchten kleiner. Bij sommige rassen vermindert als gevolg van de castratie ook het aantal zaden per vrucht.

5. Knopbestuiving heeft geen voordelen boven bloembestuiving.
6. Bij 'Perle von Zehlendorf' en 'Wit' wordt het optimale zaadgewicht bereikt wanneer de vrucht 26–50 zaden bevat. Wanneer het aantal zaden per vrucht kleiner dan 26 of groter dan 50 is, vermindert het zaadgewicht.
7. Alpha-naftylacetamide verhoogt de vruchtzetting en daarmede de totale zaadopbrengst, indien het direct na castratie, of zowel na castratie als op het tijdstip van bestuiving, in 50 of 10 d.p.m. op bloemstengels en castratiewonden wordt toegediend. Para-chloorfenoxyazijnzuur en beta-nafthoxyazijnzuur werken niet of schadelijk.
8. Alpha-naftylacetamide bevordert de strekking van de bloemstengels, vermindert de kans op rotting en heeft geen schadelijke invloed op de jonge vruchten, behalve wanneer het in hoge concentraties toegepast wordt.

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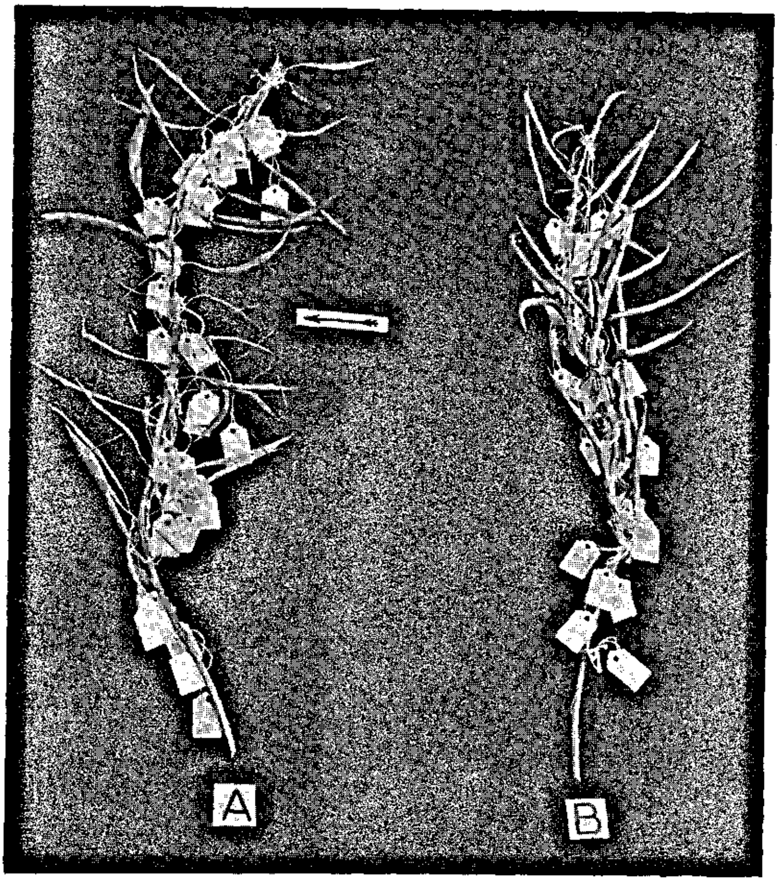

PHOTO 1. *A*. Self-pollination of an incompatible Brussels sprouts plant. Flowers self-pollinated either at the bud stage (top) or after anthesis (base) give siliques with seeds, while flowers pollinated at anthesis (marked by the arrow) give small siliques without seed. *B*. Cross-compatible pollination of the same plant. Flowers pollinated at the three stages give good siliques.

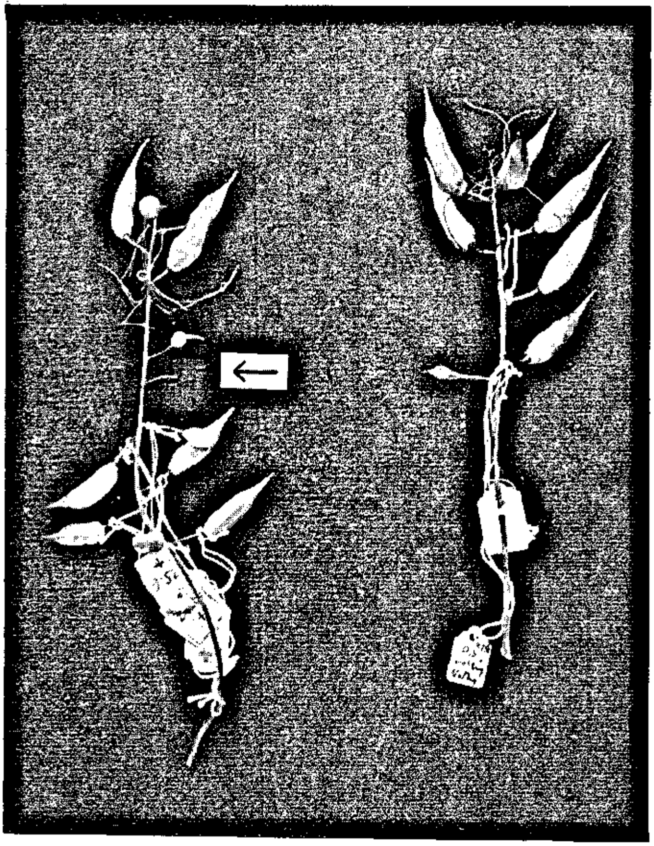

PHOTO 2. *Left.* Self-pollination of an incompatible radish plant. Both flowers self-pollinated at the bud stage and after anthesis give siliques with good seed set. Flowers self-pollinated at anthesis give no or small siliques (marked by the arrow).
Right. Cross-compatible pollination of the same plant. Flowers cross-pollinated at the three stages give good siliques.

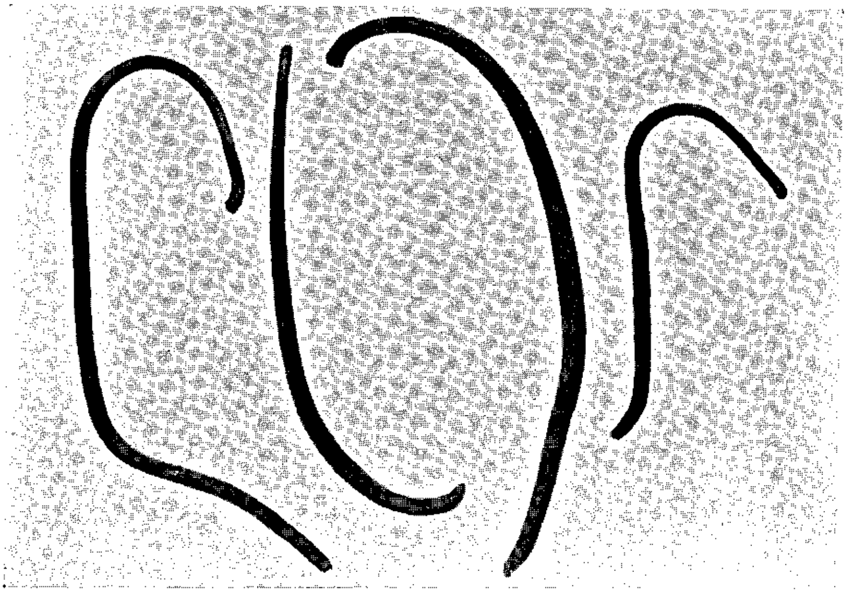

PHOTO 3. The effect of alpha-naphthylacetamide in lanolin on cyclamen flower stalks after removing the flower. Flower stalks keep growing and do not decay. The photo is taken 15 weeks after treatment.

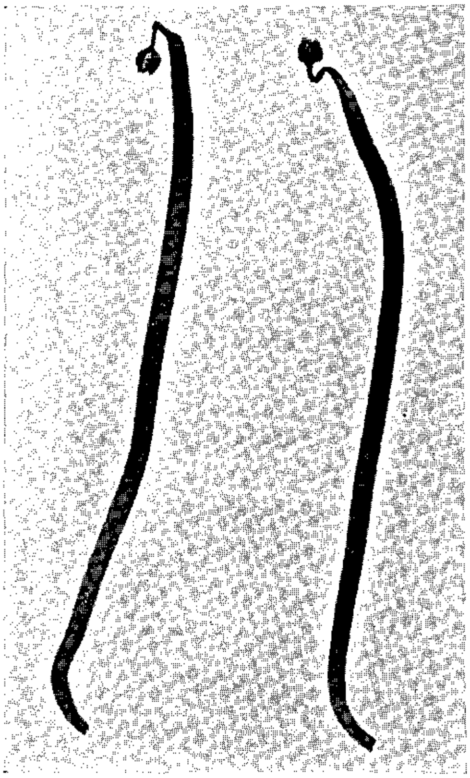

PHOTO 4. Alpha-naphthylacetamide applied in lanolin paste (10 mg/1 g) to flower stalks of cyclamen 2–3 cm from the ovary. The upper part of the stalk decays.

THEOREMS

I

PEARSON's theory that bud pollination enables the slow growing pollen tubes to reach the egg cells before they degenerate cannot be accepted.

This thesis.

II

It is advisable for the commercial grower to plant peach nursery trees in the small size classes.

SAVAGE and COWART, Proc. Amer. Soc. hort. Sci. **65** (1955): 149–154.

III

The introduction of Dutch light frames "bakken" in Egypt would benefit horticulture.

IV

There is no evidence for EYSTER's conclusion that alpha-naphthylacetamide applications could overcome incompatibility by accelerating the slow growth of the pollen tubes.

EYSTER, Science **94** (1941): 144–145.

V

In all probability the "parthenogenetic" seeds obtained by VON TSCHERMAK [Biologia Generalis **19** (1949): 3–50] are the result of amphimixis.

WELLENSIEK *et al*, Euphytica **1** (1952): 123–129.

VI

Although it is generally accepted that low temperature may decrease incompatibility in some kinds of plants, high temperature may have the same effect in others.

VII

The so-called Japanese seedless watermelon, "the dream of the breeder and consumer", reported by W. EMERSON [Seed World **67** (9) 1950: 12], has no market future.

VIII

In artichoke growing cultural methods can be helpful to control the root rot disease caused by *Sclerotium rolfsii* SACC.

IX

Without industrialization it is not possible to develop agriculture properly and to improve effectively the standard of living in Egypt.