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Pollination in *Rosa multiflora*

Bestøvning hos Rosa multiflora

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Summary

The present work has shown, that seed production of *Rosa multiflora* requires at least 2 clones, due to self-incompatibility. Fruit and seed set, as well as germination of the seed, have been investigated by hand pollination of 22 clones, and among 49 cross-combinations 2 proved to be incompatible. With the aid of fluorescence microscopy of pollinated styles it has been concluded, that the inferior seed production following selfing and cross pollination between clone no. 9248 and 9249 is caused by the gametophytic type of incompatibility as the growth of the pollen tubes is inhibited half-way down the styles.

The trials showed a significant variation between clones in seedlings produced per pollinated flower. The most productive clone (no. 9247) was about 10 times as efficient as the least productive one (no. 5548). The eventual outcome is greatly influenced by an interaction between seed production and germination. Variation in seed production has been investigated in clone no. 5678 and 5679. The 1980-trials showed that it only made little difference to no. 5679, if a single pollination was postponed by 3 days, whereas fruit set in no. 5678 was reduced from 98.3% to 49.5%. No improvement of fruit and seed set occurred in the case of double pollination. Germination of seed harvested from all 8 clones in the trials showed considerable variation.

Key words: *Rosa multiflora,* pollination, incompatibility, fruit set, seed production, germination.

Resumé

Bestøvningsundersøgelser af *Rosa multiflora* har vist, at frøavl kræver mindst 2 kloner, da der ikke produceres afkom ved selvbestøvning.

Frugt- og frøsætning samt spiring er undersøgt i en række forsøg med håndbestøvning af 22 kloner, og blandt 49 krydskombinationer er der fundet 2 kombinationer, hvor såvel frugt- som frøsætning er meget lav.

Ved hjælp af fluorescens mikroskopi af bestøvede grifler er det påvist, at den manglende frøproduktion ved selvbestøvning og krydsbestøvning af de 2 kombinationer skyldes en hæmning af pollenrørenes vækst, inden de er nået frem til æganlæggene – en speciel form for sterilitet, der kaldes inkompatibilitet.

Antallet af kimplanter pr. krydsbestøvet blomst varierer meget. Således gav den mest udbytterige klon (nr. 9247) i gennemsnit ca. 10 gange større udbytte end den dårligste (nr. 5548). Udbyttet bestemmes af vekselvirkningen mellem frøproduktion (antal frø pr. bestøvet blomst) og spiringsevnen af frøet.

Klonforskelle med hensyn til frøproduktion er forsøgt klarlagt for klonerne 5678 og 5679.

Nøgleord: *Rosa multiflora,* bestøvning, inkompatibilitet, frugtsætning, frøproduktion, spiring.

Introduction

One of the greatest disadvantages of using *Rosa multiflora* Thunb. in the production of seedling rootstocks is lack of uniformity as this increases production losts considerably. The variation in the seedlings is a consequence of their genetic constitution, e.g. the degree of homozygosity and heterozygosity of the parental generation. Thereby, the variation will be determined by the natural mode of reproduction in *R. multiflora*.

The aim of the present work has been to analyse the reproductive system in *R. multiflora,* to obtain a fundamental knowledge for future research programmes on production of genetically improved seed.

R. multiflora belongs to the section *Synstylae* (14 chromosomes) of the genus *Rosa,* where the meiotic division proceeds in the normal way resulting in micro- and macrospores with 7 chromosomes (*Täckholm,* 1920, 1922). This is in contrast to the section *Caninae,* where a deviating course of meiosis, heterogamy, occurs. *Kroon* and *Zeilinga* (1974) have explained the presence of very uniform progenies from various selections of *Rosa canina* L. as a result due to both heterogamy and apomixis. With respect to prevalence of natural mode of crossing, various authors have described examples of self-incompatibility in the family *Rosaceae* (*Lewis,* 1956; *Linskens & Kroh,* 1967; *de Nettancourt,* 1977). The results of *Fagerlind* (1944) showed that *R. rugosa* was self-sterile, and *Sønderhousen* (1974) obtained a very limited fruit set (from 0 to 9.8%) in 4 self pollinated populations of *R. multiflora*. Nevertheless, *Wulff* (1952) and *Kordes* (1955) have described various cases of successful inbreeding (self pollination) of *R. multiflora*.

This paper presents results obtained on compatibility relationships for selected clones of *R. multiflora*.

Material and methods

The clones used for these studies were selected both in a clone collection located at the Institute of Landscaping Plants and within a seed production area kindly provided by a private nusery.

In 1979 self-incompatibility was investigated in 22 clones, and 10 of the 22 clones were selected for further investigations of intraspecific incompatibility. In 1980–81 the number of clones involved in cross pollinations was reduced to 8 (32 combinations).

Three methods of self pollination were examined:

1) Isolation of emasculated and hand pollinated buds.
2) Isolation of unemasculated buds without hand pollination.
3) Isolation of hand pollinated and unemasculated buds.

Emasculated and isolated buds were used for cross pollination in 1979. As the results from 1979 proved that the self-incompatibility was rather strict emasculation was omitted in 1980 and 1981.

Each combination was replicated on one or more mother plants by using 15–30 shoots with 2–6 flowers at the same stage. The total number of flowers per combination each year were 60–100.

Emasculation, or the mechanical removal of stamens, was delayed until 2 days before flower opening. One petal was removed to faciliate the excision of stamens, and the stamens were removed with a pair of needle forceps.

Flower buds prepared for hand pollination were isolated with pergamin bags to avoid contamination by unwanted pollen.

Pollen for hand pollinations were obtained by collecting anthers from isolated flowers 1 to 2 hours before the time of crossing. Little attention was given to the storage conditions because of the short range of time from collection of pollen to pollination of the female flower.

A small brush was used for pollen transfer, and the hand pollinations were carried out preferably in sunny weather between 9 a.m. and 5 p.m.

The fruits were harvested in October and the seed were cleaned and sown in boxes immediately after. The boxes were overwintered in a cold frame for natural stratification of the seed. In the spring the boxes were placed in a glasshouse where the seed germinated.

Compatibility relationships were determined by observations of fruit set, seed number and

Table 1. Clonal variation in flower characteristics (no. of styles per flower), fruit set (% fruit of pollinated flowers), seed set (no. of seeds per fruit and per pollinated flower), % germination and no. of seedlings produced per pollinated flower

Clone no.	Type of poll.	No. of styles/flow.	No. of comb.	% fruit	No. of seeds/ fruit	No. of seeds/ poll.flow.	% germina.	Seedl./ poll.flow.
5548	self[1])			12.5	1.0	0.1	0.0	–
	self[2])			0.0	–	–	–	–
	cross	4.5	2	73.5	5.5	4.0	14.7	0.6
	free				5.1		40.8	
5678	self[1])			0.0	–	–	–	–
	self[2])			0.0	–	–	–	–
	cross	6.7	4	92.5	5.6	5.2	40.1	2.1
	free				2.9		36.8	
5679	self[1])			40.0	1.0	0.4	0.0	–
	self[2])			0.0	–	–	–	–
	cross	7.7	4	86.1	7.7	6.7	36.3	2.4
	free				7.4		29.3	
9246	self[1])			44.4	1.0	0.4	0.0	–
	self[2])			1.0	1.8	<0.1	0.0	–
	self[3])			2.9	1.0	<0.1	0.0	–
	cross	7.0	7	91.7	7.9	7.3	57.2	4.2
	free				5.0		60.3	
9247	self[1])			0.0	–	–	–	–
	self[2])			0.3	1.0	<0.1	0.0	–
	self[3])			1.7	1.0	<0.1	0.0	–
	cross	10.8	7	80.4	11.8	9.4	69.3	6.5
	free				10.1		81.3	
9248	self[1])			0.0	–	–	–	–
	self[2])			0.0	–	–	–	–
	cross	9.1	2	86.4	7.9	6.7	58.9	3.9
	free				5.9		48.3	
9249	self[1])			0.0	–	–	–	–
	self[2])			0.0	–	–	–	–
	cross	10.7	2	87.8	9.1	7.9	74.5	5.9
	free				5.7		88.8	
9257	self[1])			0.0	–	–	–	–
	self[2])			0.0	–	–	–	–
	cross	9.8	4	71.4	8.7	6.0	54.1	3.2
	free				6.5		73.3	

[1]) Isolation of c. 10 emasculated and hand pollinated buds.
[2]) Isolation of 200–400 unemasculated buds without hand pollination.
[3]) Isolation of 50–100 hand pollinated and unemasculated buds.

Self pollinations were carried out in 1979 while the results from cross and free pollinations are mean values from 1980 and 1981.

germination of the seed. In all cases these results were correlated with pollen tube observations with the fluorescence method.

Flowers detached for further investigations by fluorescence microscopy were transferred to fixative 48 hours after pollination. The fixated flowers were stored in 70% ethanol at –18°C. The fixative, FAA, being a mixture of formalin, acetic acid and 80% alcohol (1:1:8 by volume). For each pollen pistil combination at least 2 pistillate clusters, each having 5–13 stigmatic styles, were macerated for 1 hour in 1N HCl at 60°C. Acid was removed by washing in distilled water and the styles were squashed directly in 0.1% aniline blue in 0.1 N K_3PO_4. In UV-light the callosic lining of the pollen tubes fluoresce yellow faciliating observation of the tubes in microscope. The styles were not subdivided horizontally because of the risk of damaging the pollen tubes. Instead the compatibility relationship between pollen and style was investigated by scoring pollen tubes at different levels of the style.

Results

Fruit set and seed production following cross pollination were excellent while self pollination resulted in a seed production near zero (Table 1). With respect to self pollinations none of the clones in the trial succeeded in producing progeny by selfing.

In four clones, no. 5548, 5679, 9246 and 9247, fruit set following selfing ranged from 0.3 to 44.4%. However the maximum seed set per pollinated flower was very limited (0.4) and the eventual outcome was zero due to failure in germination ability. Although the data of Table 1 shows that cross pollination by hand improved seed set per fruit when comparing with free pollination, conditions of natural pollination seemed to be very favourable with respect to clone no. 9247. Free pollination as well as hand pollination resulted in a seed production per fruit beyond 10.

This seed production is close to or more than the maximum production, expressed by the average number of styles per flower.

Table 2. The effect of pollen source on fruit and seed set in two experiments in 1979. Each combination includes c. 10 emasculated and hand pollinated flowers

Clone no.	Pollinator	% fruit	No. of seeds/ fruit	No. of seeds/ poll. flower
9248	9248[1])	0.0	–	–
	9248[2])	0.0	–	–
	9246	100.0	8.1	8.1
	9247	100.0	7.4	7.4
	9249	50.0	1.4	0.7
	9254	100.0	7.7	7.7
	9257	100.0	8.9	8.9
	Mean of comp. crosses	100.0	8.0	8.0
9249	9249[1])	0.0	–	–
	9249[2])	0.0	–	–
	9246	87.5	10.0	8.8
	9247	100.0	10.7	10.7
	9248	14.3	1.0	0.1
	9254	100.0	11.0	11.0
	9257	100.0	10.2	10.2
	mean of comp. crosses	96.9	10.5	10.2

[1]) Isolation of c. 10 emasculated and hand pollinated buds.
[2]) Isolation of 200–400 unemasculated buds without hand pollination.

The data from Table 2 indicates the presence of a barrier between clone no. 9248 and 9249, as both fruit and seed set in the combinations between the two clones were greatly reduced. On the other hand, it must be noted that in all compatible combinations but one, fruit set was 100% in the year 1979.

Table 3. Effect of time of cross pollination on fruit set in two experiments (1980)

	I		II		III	
Clone no.	No. of flowers	% fruit	No. of flowers	% fruit	No. of flowers	% fruit
5678	88	98.3	54	92.6	105	49.5
5679	19	89.5			136	80.9

I, II and III: One, two and three days after bagging.

The 1980-trials showed a strong negative effect on the fruit set in clone no. 5678 if the pollination was postponed by three days after bagging, whereas the response of clone no. 5679 was weaker (Table 3). The ideal time for pollination for both the two clones was one day after bagging. Pollination two days after bagging only gave a minor decrease in fruit set (clone no. 5678).

Table 4. Average fruit and seed set after single or double cross pollination in two experiments (1981)

	Single pollination				Double pollination			
Clone no.	no. of flowers	% fruit	no. of seeds per fruit	flower	no. of flowers	% fruit	no. of seeds per fruit	flower
5678	74	97.3	5.7	5.5	88	90.0	4.6	4.2
5679	57	81.2	8.5	6.9	50	96.0	6.9	6.6

Pollinating twice with the same pollen did not improve fruit and seed set (Table 4). The increase in fruit set in clone no. 5679 was followed by a decrease in no. of seeds per fruit. Consequently the seed set per pollinated flower remained at the same level as in single pollinations.

Fruit and seed set were correlated with observations of pollen tube growth (Fig. 1, 2 and 3). The observations showed that the failure in fruit and seed set following self pollinations was due to the presence of gametophytic incompatibility as the pollen tube growth was inhibited one third to half-way down the style (Fig. 2).

In all cases except two cross pollination resulted in a massive pollen germination on the stigma (Fig. 1) and subsequently growth of numerous tubes to the base of the style. The exceptions were the combinations between clone no. 9248 and 9249 (Fig. 3) in which growth of the pollen tubes was inhibited half-way down the styles as in the case of self pollinations (Fig. 2). This mutual inhibition of pollen tubes indicated the presence of intraspecific incompatibility between the two clones.

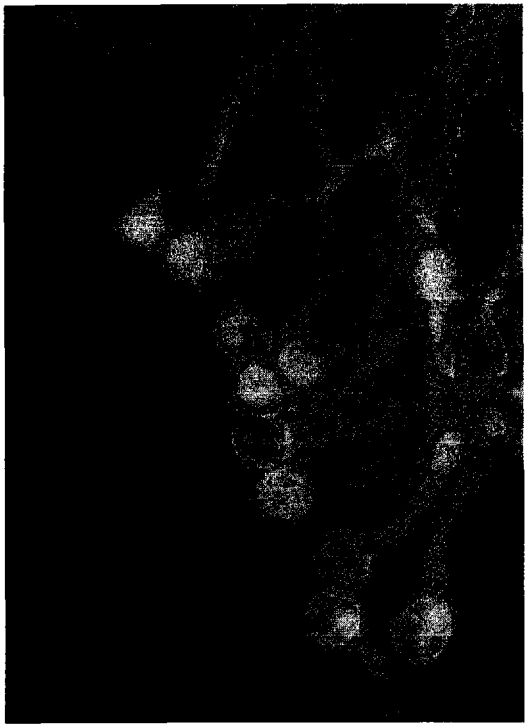

Fig. 1 Compatible pollen tubes from the stigmatic region of the style (clone no. 9247 ♀ × 9257 ♂). The tubes are stained in aniline blue and illuminated with UV-light.

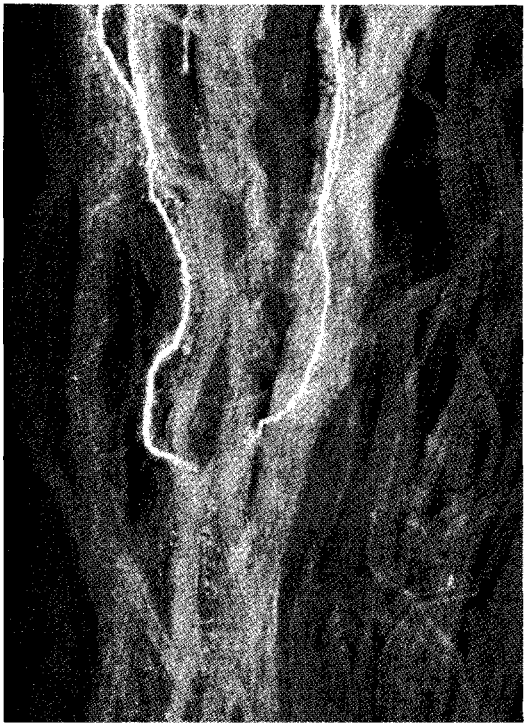

Fig. 2 The middle part of the style of clone no. 9246 after selfing. Incompatibility reaction inhibits further growth of the pollen tubes.

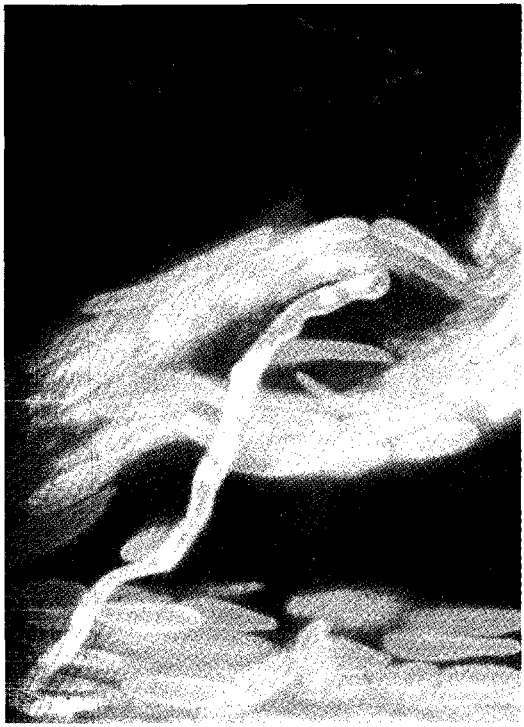

Fig. 3 Extremity of a pollen tube from an incompatible combination (clone no. 9248 ♀ × 9249 ♂). Callose plugs are seen in the tube apex.

Table 5. Compatibility relationship based on fruit and seed set and the fluorescence method. The pollinations were carried out in 1979, 1980 and 1981

♀ \ ♂	5547	5548	5577	5678	5679	9246	9247	9248	9249	9250	9251	9252	9253	9254	9255	9256	9257	9258	9259	9260	9261	9262
5547	o	+		+	+																	
5548	+	o		+	+																	
5577			o																			
5678	+	+		o	+	+	+															
5679	+	+		+	ϑ	+	+															
9246				+	+	ϑ	+	+	+					+			+					
9247				+	+	+	o	+	+					+			+					
9248						+	+	o	o					+			+					
9249						+	+	o	o					+			+					
9250										ϑ												
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9252												o										
9253													ϑ									
9254						+	+	+	+					o			+					
9255															o							
9256																ϑ						
9257						+	+	+	+					+			o					
9258																		o				
9259																			o			
9260																				o		
9261																					o	
9262																						o

+: compatibility
o: incompatibility
ϑ: pseudo-compatibility (no. of seeds/pollinated flower < 0.4)

Table 5 summarizes compatibility relationship between 22 clones. The scheme consists of results from both fluorescence microscopy of styles and estimation of fruit and seed set in field pollination trials in 1979, 1980 and 1981. The results of pollen tube growth as observed by fluorescence microscopy agree with those from the field trials except for those self pollinations showing pseudo-compatibility. The last phenomenon occuring so seldom that the pistillate clusters collected for fixation in FAA were not sufficient for detecting pseudo-compatibility by fluorescence microscopy.

Discussion

Although several apple cultivars are considered highly self-incompatible, environmental factors such as temperature and nutrition, are known to affect self-setting of apple flowers. *Williams* and *Mair* (1977) have found a considerable weakening of incompatibility in the cultivar 'Cox's Orange Pippin' at temperatures between 15° and 20°C. As our trials were carried out on plants grown outdoors, it was not possible to detect such temperature effects on seed set following selfing of *R. multiflora*.

However, self-incompatibility in *R. multiflora* appears to be a very constant phenomenon, as selfing of all the investigated clones (placed at different localities) induced a very limited seed set per pollinated flower (≤ 0.4).

The low seed number, that actually developed in selfed flowers could be attributed to a combined pseudo-compatibility and parthenocarpic re-

sponse, as reported from one apple cultivar, 'Cox's Orange Pippin' (*Goldwin & Swabe*, 1975). Besides this, contamination with foreign pollen sources could interfere. The total failure in germination nevertheless points to self-fertilization. Inbreeding is known to have a negative effect on the vigour of the embryo.

The variation between clones in germination ability must be taken with reservation. All combinations were investigated with fluorescence microscopy of pollinated styles and the ability of the pollen to germinate, penetrate through the style and reach the egg cell were examined. As allready mentioned, the inferior germination in three clones could be ascribed to later development or unfavourable weather conditions during the period of seed development. Finally, inbreeding can have a deleterious effect on seed development and germination. Information from rootstock producers and nursery advisers indicates, that the Danish rootstock material originates from a very limited plant population.

Williams (1970) and *Hansen* (1980) have found a very pronounced effect of temperature on the lifetime of the ovule of one apple cultivar, 'Cox's Orange Pippin'. This period from the time of receptiveness of the stigma to the death of the ovule is called the effective pollination period (EPP). The shortening in EPP at higher temperatures is antagonized by an increase in growth rate of pollen tubes.

Other environmental factors than temperature could affect EPP, as the clones in our trials were placed at different localities. However, with respect to clone no. 5678 and 5679, (planted alternately in one row) Table 3 shows a clear-cut case of clone variation.

In 1980 EPP of clone no. 5678 seems to last 1–2 days, whereas EPP of clone no. 5679 seems last 3 days or more, as it only made little difference to the outcome of clone no. 5679, if the pollination was postponed to the third day after bagging.

According to *Visser* and *Verhaegh* (1980) repeated pollination by hand increased the fruit and seed set in three apple cultivars. It is most probable that good results from pollinating twice at an interval of one day depend on the length of the EPP. Our data does not confirm this with respect to *R. multiflora*.

The two experiments in Table 4 did not show any positive result of double pollination – with respect to neither clone no. 5678 with the short EPP nor to clone no. 5679 with an EPP lasting 3 days or more.

Contrary to the results of *Visser* and *Verhaegh* (1980), our experiments with *R. multiflora* showed that the pollen applied first seemed so viable that the penetration through the stylar tissue to the egg cell was completed before the pollen applied secondly could intervene.

The excellent fruit set of emasculated and hand pollinated buds in 1979 (Table 2) is in contrast to the result of *Sønderhousen* (1974), where fruit set in similar experiments was about 38.8%. The most likely reason lies in the emasculation method, where the procedure of removing both petals and stamens with the aid of a scalpel seems far to drastic, leaving the styles to the risk of mechanical damage, draught and an altered metabolic activity.

In our seed production area at least 3 different insect species were involved in the natural pollination: Honey bees, bumble bees and syrphids (*Syrphus ribesii*).

The fluorescence method allows screening tests of numerous styles, both for the presence of pollen tubes in the entire length of the style or as shown in Fig. 3, a more detailed study of the tube apices. An increased number of callose plugs, as shown i Fig. 3, is one of the indications of a disturbed carbohydrate metabolism following an incompatible pollination (*Linskens*, 1964; *Linskens & Kroh*, 1967). Whereas pseudo-compatibility occurs among apple cultivars (*Williams & Maier*, 1977; *Spiegel-Roy & Alston*, 1982), self-incompatibility in *R. multiflora* seems to be very consistent. Although the micro-climate may vary considerably from one flower to another, inhibition of self-pollen tubes was very constant one third to halfway down the styles in flowers fixated 48 hours after the deposit of self-pollen on the stigma (Fig. 2). There was no reduction in the germination capability of self-pollen and the pollen tubes penetrated well through the stigma

zone. These results were in accordance with earlier findings in *Malus* (*Stougaard,* 1982).

Table 5 shows, that *R. multiflora* must be characterized as highly self-incompatible. Dense deposits of self-pollen did not affect the self-incompatibility reaction seriously. Only six clones showed a weakening in the reaction, but the resulting seed production per pollinated flower was below 0.4.

Detailed studies on the correlation between stigma type and incompatibility system has lead *Heslop-Harrison* and *Shivanna* (1977) to conclude, that sporophytic self-incompatibility systems are associated with dry, papillate stigmas while gametophytic systems are associated with wet stigmas. Within the family *Rosaceae,* this correlation holds for the genera *Malus, Pyrus* and *Prunus,* where reports on gametophytic control corresponds to the wet stigmas. The correlation is broken in the genus, *Rosa,* where the stigma belongs to the dry and papillate type and consequently, the incompatibility system should be of the sporophytic type. The recent work strongly suggests gametophytic control in *R. multiflora* functioning together with a dry stigma.

Conclusion

The present work has shown, that the natural mode of reproduction in *Rosa multiflora* is cross pollination. A significant variation between clones has been found in the number of seedlings produced per pollinated flower. The most productive clone was about 10 times as efficient as the least productive. Variation in number and lifetime of ovules (EPP) accounts for part of the differences, but besides this, the final outcome has been shown to be strongly influenced by the variation concerning germination ability. Inability of germination has been explained by several factors, e.g. variation in susceptibility to unfavourable weather conditions during the period of seed development and/or the deleterious effects of inbreeding.

Cross pollination requires activity of insects within the period where the stigmas are receptive and the ovules fertile. Hence, clones with short EPP strongly depend on this activity in a very short period. Besides the allready mentioned variations in productivity, clones for seed production must be carefully selected concerning pollination barriers. Among 49 cross-combinations, 2 proved to be incompatible. Fluorescence microscopy of pollinated styles seems to indicate that this cross-incompatibility, as well as the failure of self-pollen to effect fertilization can be explained on the basis of a gametophytic control system, inhibition of the pollen tube growth occuring one third to half-way down the style. This is in accordance with earlier findings of the same control system in the genera *Malus* and *Pyrus,* both belonging to the family *Rosaceae.*

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