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Reaction of pollen after transfer from one stigma to another (Contribution to the character of the incompatibility mechanism in *Cruciferae*)

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Summary. The investigation dealt with the question, whether after self-pollination active pollen cutinase is irreversibly inactivated, or if after cross-pollination, inactive pollen cutinase is irreversibly activated. To answer this question, a short time after pollination pollen grains of the self-incompatible *Cruciferae* species *Arabis arenosa* and *Brassica nigra* were transferred onto a second stigma with other incompatibility genes and their behavior observed. The pollen grains were used under the following pollination conditions: I. crossing → crossing (control), II. selfing → crossing, III. selfing → selfing (control), IV. crossing → selfing. While the two controls indicated that the reaction of pollen is not changed by the mode of transfer, penetration of the pollen tubes into the second stigma (selfing) could be observed in combination IV.

This result suggests an irreversible activation of pollen cutinase by the first stigma (crossing). Because under favourable conditions only short contact of the pollen grain with the stigma is necessary for the activation of cutinase, we suppose that the reaction which induces activity of cutinase takes place between specific structures situated in the wall of pollen grain and papilla.

The question whether activation and blockage of activation of the cutinase system is dependent on S-alleles is discussed in connection with the concept of SAMPSON (1962) on „species-area"- and the „S-allele-area"-combination between pollen and stigma.

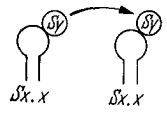
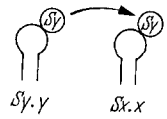
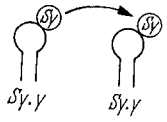
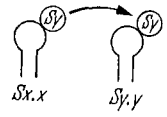
Many plant species have developed a physiological barrier against self-fertilization, which is the mechanism of self-incompatibility. For the geneticist and breeder, who often need homozygote material or descendants of self-incompatible plants for their investigations, the self-incompatibility can be a disturbing obstacle. But it can also be advantageous, for example, in the production of F_1-hybrids (REIMANN-PHILIPP, 1965). Because the *Cruciferae* represent a large part of our vegetables, they can be considered as a valuable object for incompatibility investigations.

In self-incompatible *Cruciferae* the number of pollen grains which germinate is less in the case of self-pollination and the few pollen-tubes which are formed cannot penetrate the stigma (CHRIST, 1959). One can overcome the inhibition of germination by bringing the self-pollinated plant into a humid atmosphere; but the then formed pollen tubes are still unable to grow into the stigma (CHRIST, 1959). However, if one brings pollen grains directly into the stigma, thus by-passing the cuticle, normal fertilization results (SEARS, 1937; TATEBE, 1939; KROH, 1956). Therefore the inhibition is limited to the surface of the stigma. The stigma is covered with papillae-like epidermis cells, whose walls consist of a cuticle and a pectin-cellulose layer (CHRIST, 1959). After cross-pollination the pollen tubes penetrate the cuticle of the papillae and grow in the cellulose-pectin layer to the base of the papillae by dissolving the pectin parts and onward intercellulary through the stigma- and style tissue to the seed ovules (KROH, 1964). The dissolving of the cuticle at the point of contact between the tip of the pollen tube and the papilla wall is done enzymatically (LINSKENS and HEINEN, 1962). After self-pollination the dissolving of the cuticle doesn't take place.

It depends on the incompatibility- or S-genes of the crossing partners if the pollen tubes grow into the stigma after a pollination. If identical S-genes meet in stigma and pollen (self-pollination), the pollen tubes don't penetrate the stigma. However, if stigma and pollen differ in their S-alleles (cross-pollination), the mentioned penetration of the tubes into the stigma can be observed. The incompatibility reaction is thus very specific.

There are 2 hypotheses for the explanation of the incompatibility mechanism (CHRIST, 1959). By the inactivation-hypothesis, the cutinase system present in the pollen becomes inactivated after a self-pollination under the influence of identical S-alleles in pollen and style. According to the activation-hypothesis the cutinase system of the pollen is present in an inactive form and becomes activated after a cross-pollination. To determine which is the correct explanation, experiments were performed based on the following reflection: If the pollen undergoes an irreversible influence of positive or negative kind after cross- or self-pollination, this should appear if one

Table 1.

Results of different pollen-stigma combinations						correspondence with	
No. of combination	Sequence of pollination*	Species	Number of pollen grains transferred onto the 2nd stigma	% germinated	% germinated pollen grains which penetrate	Inactivation-Hypothesis	Activation-Hypothesis
I (control-1)	crossing -crossing 	*A. arenosa*	765	53.2	36.7	+	+
		B. nigra	227	70.4	17.5	+	+
II	selfing-crossing 	*A. arenosa*	259	51.7	49.3	+*	+
		B. nigra	257	68.9	13.0	+*	+
III (control-2)	selfing-selfing 	*A. arenosa*	122	36.0	0	+	+
		B. nigra	123	77.2	0	+	+
IV	crossing-selfing 	*A. arenosa*	1558	39.5	20.4	−	+
		B. nigra	284	75.7	10.7	−	+
	* Sx and Sy represent different S-alleles					* Inactivation reversible	

brings the pollen on another stigma which differs from the first by possessing other incompatibility alleles.

Materials and Methods

Self-incompatible but cross-compatible clones from *Arabis arenosa* and *Brassica nigra* were used. The experiments were done over five periods of vegetation.

1. Pollen transfer. For the experiments of pollen transfer the stigmas with a piece of style were cut off and the cut surface fastened on a slide with gelatine. To prevent drying, the stigmas were surrounded by a wet strip of filter paper. The pollen grains to be tested were brought on the papillae under the preparation microscope with a glass needle and the prepared slide was kept in a humid petri dish. An average of three stigmas were brought on each slide. The number of pollen grains per stigma was 3 to 7 depending on the number of papillae which offered a favourable position for the following micromanipulation. Since some of the pollen grains grow into the papillae within 10 minutes after cross-pollination, the transfer of the pollen grains after self-pollination, as well as after cross-pollination, started 4 minutes after the grains were brought on. The removal of the pollen grains from the first stigma and their transfer onto papillae of the second stigma was performed with a glass needle while using the micromanipulator (Fonbrune) with an enlargment of 100 ×. Whether the transferred pollen grains had germinated and grown in was controlled with an enlargement of 450×. If from the microscopic picture it was doubtful whether the pollen tubes were in the wall or on the surface of the papilla, an attempt was made to lift the pollen grain with the adhering tube from the papilla. In the first case, this is only possible by tearing the pollen grain from the piece of the pollen tube which is present in the wall, while in the second case one generally succeeds in removing the pollen grain with the tube uninjured from the surface of the papilla.

Pollen and stigma were combined as follows (Tab. 1):

I. A stigma is cross-pollinated and 4 min later, the pollen is transferred onto a second stigma, containing the same S-alleles as the first; thus the pollen remains under conditions of cross-pollination (control-1: crossing → crossing).

II. The pollen is placed on the first stigma under conditions of self-, and after transfer onto the second stigma under conditions of cross-pollination (selfing → crossing).

III. The pollen is under conditions of self-pollination on both stigmas (control-2: selfing → selfing).

IV. One places the pollen on the first stigma under conditions of cross-, and onto the second stigma under conditions of self-pollination (crossing → selfing).

2. Conditions of swelling. As a measure of swelling of the pollen grains their maximum length and breadth were estimated. These were determined by measuring 100 pollen grains which were taken a) from an anther, b) after having been 30 min on the stigma under conditions of self-pollination, c) after having been 30 min on the stigma under conditions of cross-pollination.

Table 2. *Comparison of percentages in Tab. 1 using the χ^2-method.*

combination-results compared	Species	germination	germinated pollen grains which penetrated
		P^+	P^+
I with II	*Arabis arenosa*	0.68	0.01
	Brassica nigra	0.78	0.32
III with IV	*Arabis arenosa*	0.50	0.002
	Brassica nigra	0.84	0.002
I with IV	*Arabis arenosa*	—	$<$0.001
	Brassica nigra	—	0.08

$^+$ two sided testing (α = 0.05 level of significance).

Results

Transfer of pollen

The results of the pollen transfer experiments are summed up in tab. 1. The two controls indicate that the pollen is not changed in its reaction by transferring it from one stigma to another. In control-1 the tubes penetrate the papillae of the second stigma; in control-2 they don't. Assuming that the pollen on the first stigma don't undergo an irreversible influence, combinations I and II should display the same reaction on the second stigma (cross-pollination). Combinations III and IV (self-pollination on second stigma) must also react alike but not in the same manner as I and II. From the results in tab. 1 and 2 it is seen that this assumption turned out to be true for the pollen germination. On the other hand, if we compare the number of pollen tubes entering the second stigma, we find statistically significant differences in dependence on the sequence of pollination. Under conditions of cross-pollination, more pollen tubes of *A. arenosa* penetrate the stigma if they have been under conditions of self-pollination on the first stigma. Furthermore, both in *A. arenosa* and *B. nigra* a penetration of pollen tubes into the stigma after self-pollination can be observed if the pollen grains were first used for a cross-pollination. These findings clearly indicate that the pollen grains have undergone an irreversible, positive influence by the first stigma in respect to penetration of their tubes into the second stigma.

The penetration of pollen tubes into the stigma after self-pollination in combination IV cannot be explained by the inactivation-hypothesis. In that case, the cutinase system of the pollen should have been inactivated on the second stigma and the pollen tubes should not have been allowed to penetrate this stigma. Also the results of combination II can only be explained by the inactivation-hypothesis if one supposes that the cutinase activation on the first stigma is reversible. Assuming irreversibility, no pollen tube should have been allowed to penetrate the second stigma. With the activation-hypothesis and the additional acceptance of the irreversibility of activation, however, all experimental results can be explained. The differences in the percentages, regarding the penetration of pollen tubes into the stigma found with *A. arenosa* between combination I and II can be interpreted in this manner. In combination I the process of fastening of the pollen grain to the papilla wall is interrupted by the event of transferring, while this disturbance does not exist with combination II. This phenomenon could not be observed with *B. nigra*. Accepting an irreversible activation of the pollen cutinase, one should really expect that in combination IV as many pollen tubes penetrate the stigma as in combination I. With *B. nigra* a weak hint is given for this (tab. 1, 2). With *A. arenosa*, however, in combination IV clearly less pollen tubes have penetrated the second stigma than in combination I (tab. 1, 2). This result can be explained in the following way: in combination I the pollen grains, which still have not been activated on the first stigma get a further possibility for activation on the second one. However, in combination IV only the pollen tubes, which have been activated on the first stigma, can penetrate the second stigma. Pollen grains, which have not yet undergone an activation on the first stigma at the moment of transferring to the second one, don't get a chance for it on the last one.

Duration of contact and activation

As mentioned, we started 4 min after pollination of the first stigma to transfer the pollen grains from the first to the second stigma. The time lapse between the transfer of the first and the last pollen grain was as long as 30 min. The pollen grains transferred to the second stigma therefore differ by their duration of contact with the first stigma. Statistically, no dependence between penetration of pollen tubes into the second stigma and the duration of contact of the corresponding pollen grains with the first stigma can be proved. Therefore, how long the pollen grains have lain on the first stigma should be unessential for the penetration of the pollen tubes into the second stigma. This result is a consequence of the method of evaluation. In the statistical calculations we started from the principle that the pollen grains were transferred aselect, that means each pollen grain brought onto the second stigma had the same chance to become activated by the first stigma. Because the pollen grains were not transferred at the same time, we have in fact applied a negative selection. Namely, if one observes the behavior of pollen grains after a cross-pollination, it is striking that with proceeding time more and more pollen grains germinate and penetrate the papillae. 25 min after pollination only few transferable pollen grains are met on the stigma. These belong either to the group which is not able to penetrate the stigma at all or to the portion which needs a longer contact for the activation. Different factors can be responsible for the different behavior of the pollen after a cross-pollination. On one hand, surely not all pollen grains take a favourable position for the activation on the stigma, e.g. only some of the grains will directly lay with a germination pore against the papilla wall, possibly a position advantageous for activation. On the other hand, as homozygote material was not used, the different genetic composition of the pollen grains will effect the physiological behavior.

The behavior of pollen grains after pollination

Two phenomena must be explained which occur after self-pollination:

Table 3. *Length and breadth in μ of C. pratensis-clone C-6 pollen grains; a) from anther, b) 30 min after selfing (C-6 × s), c) 30 min after crossing (C-8 × C-6)*

source	length	P^+	breadth	P^+
a) anther	37,8	<0,001	21,1	<0,01
b) selfing	34,0	<0,001	32,2	<0,001
c) crossing	33,69	0,48	22,7	0,41

* χ^2-method ($\alpha = 0.05$ level of significance).

1. the inhibition of germination of pollen grains,

2. the inability of pollen tubes to penetrate the wall of the papilla.

Because the inhibition of germination can be overcome by addition of moisture from without, one must suppose that after a self-pollination, the pollen is not supplied with enough moisture for the germination. If the germination tube becomes visible, we consider a pollen grain as germinated. The germination is preceded by the swelling of the pollen grains, which is also dependent on water consumption. Tab. 3 shows that there is no difference between self- and cross-pollination with respect to the amount of swelling of the pollen grains. The pollen grains therefore acquire the moisture necessary for the swelling from the atmosphere surrounding the stigma. After the swelling of the pollen grains, which is a preliminary condition for enzymes to become active, the influence of the genetic condition of pollen and stigma begins to manifest. After a cross-pollination, the pollen cutinase becomes activated. This is followed by the onset of the dissolving of the papillae cuticle at the point of contact between pollen grain and papilla wall. During this process the permeability of the cuticle to moisture from the papilla cells increases and the swollen pollen grain begins to germinate. In the case of self-pollination, however, the activation of the cutinase does not take place as a result of the effect of identical S-alleles in pollen and stigma. The condition of permeability of the cuticle is not influenced. The inhibition of germination of the pollen grains after self-pollination is therefore conditioned by a shortage of moisture on the stigma surface. The moisture present there is sufficient for the swelling but not for the germination of the pollen grain.

As stated, after a self-pollination, the activation of the pollen cutinase is blocked under the influence of identical S-alleles in pollen and stigma. Therefore, the pollen tubes induced by artificial increase of the air humidity cannot succeed in dissolving the cuticle of the papilla wall and growing into the cellulose-pectin layer. In which way the cutinase activation is blocked is not yet known.

Conclusions

Under certain conditions, e.g. self-pollination, the cuticle represents a barrier to the penetration of the pollen tubes into the stigma which is not only of a mechanical nature. It serves as a barrier which lowers the permeability to water and water soluble compounds. One can conclude from the experimental results that in order for the pollen grain to overcome the barrier of the stigma after cross-pollination, its cutinase system becomes irreversibly activated. At present we can't give any concrete explanations of the mechanism of activation. We don't know where the cutinase is located in the pollen grain. The fact that under favourable conditions only a short contact of the pollen grain with the stigma is necessary for the activation of the pollen cutinase suggests that the reaction inducing the activity of the cutinase occurs between specific structures present in the wall of pollen grain and papilla. Whether the reaction product effects an activation at the cutinase molecule itself or only serves as a trigger for bringing the enzyme system into force are questions whose answers are reserved for further investigations.

We have seen that the activation of the cutinase takes place if pollen and stigma differ in their S-alleles. Must we conclude from this that the activation is dependent on the S-alleles, or is it possible that principally each stigma of a self-incompatible *Cruciferae* species is able to activate the cutinase of pollen of the same species? Although *Cruciferae* are representative of the homomorphic-sporophytic incompatibility system and dominance is often found in pollen and style so that the whole pollen as well as the styles of a plant can be determined by one of the two S-alleles, there is often present individual action of the incompatibility alleles in the style. With a specific activation of the pollen cutinase under the influence of different S-alleles in pollen and stigma, a self-pollination as e.g. $S_1 S_2 \times S_1 S_2$ with dominance of $S_1 > S_2$ in the pollen and independent action of the alleles in the style should also come out as compatible. The pollen determined by S_1 should have become activated by the S_2-gene of the style. This is not the case. The findings point more to the interpretation of SAMPSON (1962) that pollen and stigma of one species on a molecular level are in principle able to experience a complementary binding, which in our case would have an activation of the cutinase system as consequence. Opposite to this "species-area"-combination exists the "S-allele-area"-combination, which is formed exclusively in presence of identical S-alleles in pollen and stigma and should cause the blocking of the cutinase activation. The "S-allele-area" combination would thus represent the specific reaction responsible for the incompatibility.

Moreover, the existence of self-compatible *Cruciferae*, as well as the bud-compatibility of self-incompatible species, is further evidence against a S-alleles-dependent cutinase activation. With a bud-pollination identical S-alleles meet in pollen and style. An activation of the cutinase would therefore not be possible under the given genetic conditions. Consequently, the penetration of the pollen tubes into the stigma after bud-pollination is brought back either to the non-functioning of the "S-allele-area" combination between pollen and stigma surface or to the lack of the barrier in the budstage at all. The investigations by SAMPSON (1962) with *Brassica oleracea* and by us with *Brassica nigra* have indicated that young stigmas have developed a cuticle also. If its structure is the same as that of fully differentiated stigmas is still being investigated. Possibly it presents only a low resistance against the pollen germination and the penetration of the pollen tubes into the stigma.

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Zusammenfassung

Anlaß für die Untersuchung war die Frage, ob eine aktive Pollencutinase nach Selbstbestäubung irreversibel inaktiviert, oder ob eine inaktive Pollencutinase nach Kreuzbestäubung irreversibel aktiviert wird. Zur Beantwortung dieser Frage wurden Pollenkörner der selbstinkompatiblen Cruciferenarten *Arabis arenosa* und *Brassica nigra* kurze Zeit nach Bestäubung auf eine zweite Narbe mit anderen Inkompatibilitätsgenen übertragen und ihr Verhalten beobachtet. Die Pollenkörner wurden unter folgende Bestäubungsbedingungen gebracht: I. Kreuzung → Kreuzung (Kontrolle), II. Selbstung → Kreuzung, III. Selbstung → Selbstung (Kontrolle), IV. Kreuzung → Selbstung. Während die beiden Kontrollen zeigten, daß der Pollen durch den Vorgang des Übertragens in seiner Reaktion nicht verändert wird, war bei der Kombination IV ein Eindringen der Pollenschläuche in die zweite Narbe (Selbstbestäubung) zu beobachten.

Dieses Ergebnis spricht für eine irreversible Aktivierung der Pollencutinase durch die erste Narbe (Kreuzbestäubung). Da für die Aktivierung der Cutinase unter günstigen Umständen nur ein kurzer Kontakt des Pollenkorns mit der Narbe notwendig ist, nehmen wir an, daß sich die Reaktion, welche die Cutinasetätigkeit auslöst, zwischen spezifischen, in der Wand von Pollen und Papille gelegenen Strukturen abspielt. Die Frage der S-Allel-Abhängigkeit von Aktivierung und Blockierung der Aktivierung des Cutinasesystems wird im Zusammenhang mit der Vorstellung von SAMPSON über das Zustandekommen einer "Species-Areal"-Kombination und einer "S-Allel-Areal"-Kombination zwischen Pollen und Narbe diskutiert.

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Eine polyploide Serie von „Ruderalkartoffeln" (*Solanum* sect. *Tuberarium*) aus der argentinischen Kordillere

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A polyploid series of "Ruderal potatoes" (*Solanum* sect. *Tuberarium*) from the Argentinian Andes

Summary. A number of non-cultivated, tuber bearing *Solanum* species, collected by the author between 1955 and 1963 in the Argentinian Andes, are grouped together under the designation "Ruderal potatoes". They are karyologically and morphologically distinct from *Solanum sparsipilum*, a species known in Peru and Central Bolivia as a "weed" potato. Diploid, triploid and tetraploid Ruderal potatoes from the provinces Catamarca, Salta and Jujuy are reported here for the first time. The future will have to decide if they deserve species status. They may have played a role in the evolution of the tetraploid cultivated potato *S. tuberosum* (= *„andigenum"*). Their importance for practical breeding was recognised by the author some years ago, when he pointed out that some of these "Ruderal Potatoes" have a high grade of field resistance against virus leafroll and nematodes. Preliminary tests with *Meloidogyne hapla*, *M. javanica*, *M. thamesii* and *M. incognita* which were undertaken by the author in South-Africa showed that "Ruderal Potatoes" (Exp. No. 1059) from the Juella Region can withstand rootrot disease.

Mit der Gruppenbezeichnung „Ruderalkartoffeln" trennen wir eine in Argentinien festgestellte polyploide Serie nichtkultivierter *Solanum* (*Tuberarium*-)-Formen von den typischen Wildkartoffeln einerseits und den primitiven Indianerkartoffeln andererseits ab. Das Vorkommen von Ruderalkartoffeln ist in Argentinien auf die nordwestlichen Provinzen Catamarca, Salta und Jujuy beschränkt, wo man sie gelegentlich zwischen Mais-, Bohnen-, Oka- und Kartoffel-Pflanzungen der Eingeborenen, aber auch in der Nähe verlassener Siedlungen antreffen kann.

In der Literatur finden sich bisher keine Angaben über die Existenz von Ruderalkartoffeln in der Republik Argentinien. Hingegen ist über das Vorhandensein von „weed-potatoes" in Ecuador, Peru und Bolivien mehrfach berichtet worden. Russische und britische Autoren schufen hierfür eine Reihe von nov. spec. und Synonyma.

Offensichtlich verlangt es ein jahrelanges Vertrautsein mit den örtlichen Gegebenheiten und intensives Studium der autochthonen Kartoffelvarietäten sowie

[1] Die Sammlungen und Beobachtungen in den argentinischen N.W.-Provinzen wurden seinerzeit durch Mittel der „Deutschen Forschungsgemeinschaft" und des „Consejo Nacional de Investigaciones Cientificas y Tecnicas, Buenos Aires" unterstützt, wofür auch an dieser Stelle gedankt wird. Für die Anfertigung von Zeichnungen und Fotografien danke ich unseren Mitarbeitern SIXTO GARCIA und MARIO FARIÑAS, Botan. Inst. Caracas.