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Intraspecific Unilateral Incompatibility in *Vicia faba* L.

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Summary. Unilateral incompatibility was discovered when crossing was attempted between different self-compatible types and subspecies of *V. faba*. Crossing in the direction female less self-fertile × male more self-fertile failed, whereas the reciprocal-crossing succeeded. Unilateral incompatibility developed with the evolution of less fertile and large seeded field bean types. How a cross fertilized (and self-incompatible) system may develop from a self fertilized one is discussed.

The unilateral incompatibility in *V. faba* and other plant species is compared. The two-power competition hypothesis can explain all kinds of unilateral incompatibility reported so far in the literature. Breeding field beans for improved self-fertility is discussed.

Key words: *Vicia faba* - Unilateral Incompatibility - Self-fertility - Self-Compatibility - Self-Incompatibility

Introduction

The phenomenon in which the crossing between two parents succeeds only in one direction has been widely referred to as unilateral incompatibility. However, other terms have also been used: unilateral hybridization, unilateral inhibition, unidirectional crossability, one-way isolation, unilaterial incongruity and SI × SC inhibition. The last term was used because of the discovery that such behaviour occurs predominantly when crossing is attempted between self-incompatible (SI) plants as female and self compatible (SC) as male. Later, unilateral incompatibility (UI) was discovered, with less frequent occurrence, in the direction SC × SC, SC × SI and SI × SI.

Some authors lumped together all kinds of unilateral relation (UR) as unilateral incompatibility. It would be better to reserve the term unilateral incompatibility for those cases of UR in which:

1) Both parents possess the same chromosome number;

2) Crosses succeed in one direction and hybrids are obtained;

3) Failure of the cross is not due to particular maternal- or paternal-effects or interactions;

4) Consistent occurrence of such phenomenon in the same parental combinations is the rule.

Unilateral incompatibility occurs in different plant species (see review of Abdalla 1970, 1974a; Abdalla and Hermsen 1972): in *Antirrhinum*, *Lolium* species (Spoor 1976), *Lycopersicon* (see also de Nettancourt et al. 1973, 1974), *Nicotiana*, *Pelargonium*, *Petunia*, *Solanum* (see also Hermsen et al. 1974; Hermsen and Ramanna 1976), and in *Vicia faba* (Abdalla 1974b). Unilateral incompatibility was reported to occur when crossing was attempted between species of the same genus, of different genera and of different families. In the case of *V. faba* and in some cases in *Lycopersicon*, UI was detected between plants of the same species.

V. faba is a self-compatible species. It is generally accepted that this species is divided into 2 subspecies: ssp. *paucijuga* and ssp. *eu-faba*. The latter subspecies comprises 3 botanical types differing in seed size and shape: 'major', 'equina' and 'minor'. Unilateral incompatibility was discovered when crossing - done mainly to broaden the genetic base - was attempted between different field bean populations. The question then arose as to whether UI in *V. faba* could be explained on a similar basis to that reported for other plant species. And is there any relation between the occurrence of UI and the evolution of this crop? Answers to the above questions are attempted here.

Materials and Methods

Materials. The field bean materials used in these studies differ in origin. In this article mention will be made of the results obtained from 4 populations: C_2, a 'major' population originating from Equador but grown for many generations under Egyptian conditions; C_3, a 'major' stock from the Netherlands; C_6, a *paucijuga* type from Pakistan that had been handled in Egypt for at least 8 generations; and an Egyptian local stock (C_9) that lies on the border between 'equina' and 'minor'. Scientifically it would not make any difference if it was alloted to either type. C_9 will be referred to as 'equina' type.

Methods. Artificial self-pollination was attempted on different plants from each stock. For crossing, buds were emasculated at a later stage and were protected from contamination. Pollination took place a few days later. Crossing was made on 26-50 emasculated flowers from each female parent. To test pollen tube growth in styles, pollinated pistils were fixed after 72 hrs in a mixture of acetic acid-formalin-80% alcohol in a 1:1:8 proportion. They were refrigerated till checked according to the method used by Ramanna and Mutsaerts (1971).

Results

Self-compatibility. All the plants selfed from ssp. *paucijuga* and the types 'major', 'equina', (and 'minor', not included in this article) set pods containing seeds. Therefore the presence of self-incompatibility of the type known as the *Nicotiana* gametophytic system is ruled out.

Fig. 1. Inhibition of pollen tubes of 'equina' C_9 into styles of 'major' C_3

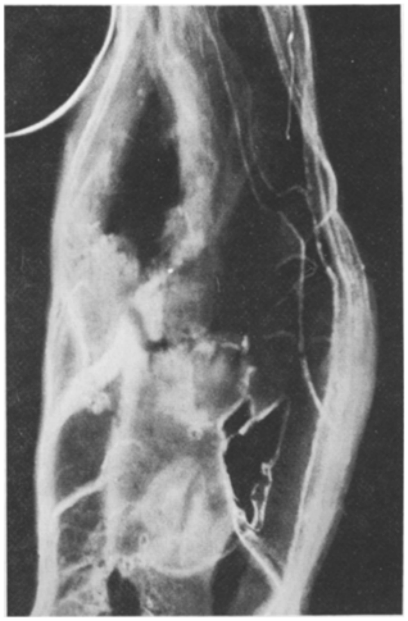

Fig. 2. Normal growth of pollen tubes of 'equina' C_9 into styles of 'major' C_2

Crossing. The crossing was not designed to take in all possible combinations. For breeding purposes, our primary interest was to cross divergent populations. The reciprocal crossings were also attempted. The results were as follows:

1. 'Major' C_3 × 'Equina' and *Paucijuga:* no pod set. The reciprocal cross succeeded. The F_1 as well as F_2 were raised from some of such crosses (Abdalla 1977).
2. 'Major' C_2 × *Paucijuga:* No pod set. Reciprocal cross succeeded.
3. 'Major' C_2 × 'Equina': 5% pod set; reciprocal 35%.
4. 'Equina' × *Paucijuga:* both reciprocal crosses succeeded. All the seed set from the above mentioned crosses proved to be of hybrid origin.

Pollen tube growth. In the crosses which failed to set seed, inhibition of pollen tube growth was observed in the styles (Fig. 1). In successful crossings, pollen tubes were detected traversing the styles (Fig. 2) and reaching very close to the ovules.

Fertility. The data on natural pod and seed set presented in Table 1 have been collected from 48 plants from C_2, 33 plants from each of C_3 and C_6 and 99 plants from C_9. The values are generally higher than those found under less suitable environ-

Table 1. Natural pod and seed set in the different *V. faba* stocks (between parentheses are relative percent of C_3)

Character	*Paucijuga*	'Equina'	'Major' C_2	'Major' C_3
No. pods/ plant	100(625)	63(394)	38(237)	16(100)
No. seeds/ plant	298(709)	190(452)	72(171)	42(100)

mental conditions, but the relative comparisons are what interest us here. It is clear from Table 1 that the different populations varied widely in fertility. 'Major' C_2 is twice as fertile as 'major' C_3. The 'equina' population is 4 times as fertile and *paucijuga* is 6 to 7 times as fertile compared with C_3.

Discussion

It is believed that the unilateral intraspecific incompatibility in *V. faba* is associated with evolution of this crop. The evolution of field bean will be reported elsewhere. It is accepted that the small-seeded populations are the oldest forms - in this study *paucijuga* is the smallest seeded stock - whereas the largest seeded 'major' type is the more recently developed one. 'Major C_3, which inhibited pollen tube growth of 'equina' and *paucijuga*, proved to be the least fertile stock (1/2 to 1/7 the fertility of others). 'Major' populations are known to possess bigger seeds (100 seed weight may be more than 200 gr), whereas 'equina' possesses intermediate seed size, followed by 'minor' type. The smallest seeds are those of *paucijuga* (100 seed weight is less than 20 gr). Combining this and other information led us to hypothesize on the origin of UI in this crop.

Origin of unilateral incompatibility in *V. faba*

Paucijuga population is the most autofertile *faba* bean studied by us up to now. 'Minor' and 'equina types may possess good self-fertile populations. From types such as *paucijuga*, *'pliniana'* (discovered in Algeria) and 'minor', less self-fertile ones may have evolved. 'Equina' is more self-fertile than 'major'. What could happen then, when such populations meet? The most fertile types (small-seeded ones) will reproduce more and yield more offspring. They will also cross with 'major' populations, one result being the 'erosion' of 'major' characteristics and identity (Abdalla 1977). On the other hand, 'major' populations will produce only limited numbers of offspring because they are less fertile (Table 1). They may also suffer other drawbacks (lower germination, slower development, especially at early stages of growth, etc.). In addition crossing with the highly fertile populations will lead to inbreeding depression of the 'major' type because of its sensitivity to inbreeding (Abdalla 1975). Under such conditions, 'major' populations may develop barriers against the introduction of genes that affect its fertility and endanger its identity and persistence. One such barrier will be specific genes (unilateral incompatibility genes = <u>UI</u>) that reject fertilization from the more self-fertile populations. Consequently 'major' would be able to cross as male with more self-fertile populations while the reciprocal crosses fail. The cross

♀ more fertile × ♂ less fertile succeeds,
♀ less fertile × ♂ more fertile fails.

That is the behaviour known as unilateral incompatibility. The 'major' - or other - populations that did not possess such a barrier could either have never developed this barrier, or have lost the barrier in the absence of selection pressure preserving it, or they may represent recessive segregants of the <u>UI</u> genes (<u>uiui</u>-genotypes).

The 'major' C_2 may be one such population with respect to 'equina' C_9, but it still maintains its rejecting unilateral incompatibility with *paucijuga*.

UI in *V. faba* and other species

In discussing the hypotheses accounting for UI (Abdalla 1970, 1974a; Abdalla and Hermsen 1972) the conclusion reached was that the "two-power competition" hypothesis could explain the occurrence of UI in different plant species whether the failure of the cross was in the direction SI × SC, SC × SC, SC × SI or SI × SI.

The two-power competition hypothesis was worked out (Abdalla 1970) to explain the UI that frequently occurs when crossing is tried between SI species as females and SC relatives as males. It was assumed that the hybridization between SI and SC powers, resulting in adverse effects of introducing self-compatibility into the heterozygous SI populations, led to the evolution of the $\underline{UI}$ genes on the side of SI plants. The $\underline{UI}$ genes prevent fertilization by specific $\overset{S}{\underline{c}}$ (self-compatibility) alleles of the SC species, not only leading to UI, but also rendering the reciprocal F_1 plants (SC × SI) self-incompatible and consequently preventing the "self-compatibility disease" from threatening the SI populations. The evolution of a $\underline{UI}$-gene $\overset{S}{\underline{c}}$-gene system as a result of the challenge of hybridization between SI and SC powers (comparable to the gene-for-gene system of host-parasite relations) was published in detail in 1972 by Abdalla and Hermsen.

Unilateral incompatibility in *V. faba* is the first reported occurrence of this phenomenon among different self-compatible populations of the same species lacking SI relatives. It can be explained on the similar basis of the evolution of unilateral incompatibility, as outlined in the two-power competition hypothesis. The $\underline{UI}$ genes present on the side of low self-fertile populations will protect them from the drawbacks of the "self-fertility disease". The "self-fertility disease" expected to occur in progenies of lower self-fertile when crossed with higher self-fertile populations is comparable to the "self-compatibility disease" that occurs after crossing self-incompatible with self-compatible species.

Evolution of self-incompatibility from self-compatibility

It may be argued that *V. faba* evolved from an autogamous ancestor, or from an allogamous one - never found - that was forced to inbreed and has undergone a change leading to atuogamic nature. Whatever the ancestor was, the cultivated *V. faba* is assumed to have developed from highly self-fertile populations that possess genes specific for high fertility (SHF). A change could have happend leading to self-fertile populations (SF), similar to some small-seeded and some medium-seeded stocks. Another change could have happened leading to low fertility populations (SLF), comparable to some 'major' stocks. A third change could have occurred, leading to cross-fertilized populations (SC) but maintaining self-compatibility. A fourth change might occur - never proved till now - resulting in self-incompatible populations (SI). A self-compatible plant may develop into a self-incompatible one through a change of $\underline{S}$ specificity from $\overset{S}{\underline{c}}$ (self-compatibility allele) to $\overset{S}{\underline{i}}$ (self-incompatibility allele) or through the development of $\underline{UI}$ rejecting genes against its $\overset{S}{\underline{c}}$ alleles ($\underline{\overset{S}{c}_1}\ \underline{\overset{S}{c}_1}\ \underline{UI_1}\ \underline{UI_1}$ is a self-incompatible plant).

It is possible that some *V. faba* populations are already at the stage of the third change (percentages of cross fertilization reaching more than 60% have been reported in fild beans by some authors).

The hypothesized steps express the possibility of the evolution of a cross-fertilized system from a self-fertilized one (see also Abdalla and Hermsen 1972). It is also possible that self-incompatible species have evolved from self-compatible ones following some or all of the following steps leading to the different changes:

$$\text{SHF} \rightarrow \text{SF} \rightarrow \text{SLF} \rightarrow \text{SC} \rightarrow \text{SI}\ (\underline{S_{c_1}}\ \underline{S_{c_1}}\ \underline{UI_1}\ \underline{UI_1}\ \text{ or }\ \underline{S_i}\ \underline{S_i}).$$

The UI in *V. faba* or any other species will develop on the side of populations that are threatened and endangered in their evolutionary pathways or in their persistence. In *V. faba* the $\underline{UI}$-genes will develop favouring low fertility populations against highly fertile ones. In SI species, $\underline{UI}$ genes will develop favouring self-incompatible populations against self-compatible relatives.

The scheme above rules out the possibility of the dual function of self-incompatibility alleles (Lewis and Crowe 1958 and others). It also implies that SI species should possess $\underline{UI}$ genes against SC relatives, especially 'old' ones; and that $\underline{UI}$ genes may be present favouring different SC populations against other SC ones, in particular on the side of low self-fertility against high self-fertility and cross-fertilized against self-fertilized.

Unilateral intraspecific incompatibility in *Lycopersicon*

Cases of unilateral intraspecific incompatibility were reported in *Lycopersicon* by Martin (1961, 1963, 1964). These involved SI and SC populations. The results reported by Martin (1964) on the lines Baños and Surco of the botanical types 'glabratum' and 'hirsutum' of *L. hirsutum* are interesting. The two lines are SC but differed in their fertility. Baños being more fertile (40 · 3 seeds per fruit), and Surco less fertile (18 · 9 seeds per fruit). Surco rejected fertilization by pollen from Baños; the reciprocal-cross succeeded. The failure of the cross was in the direction of female less fertile × male more fertile, agreeing with the present model. The SI line (Cajamarca) rejected fertilization from both SC lines which also agrees with the model presented above.

The fact that UI occurs between plants of the same species (*Vicia* and *Lycopersicon*) is interesting. This justifies the argument that this phenomenon evolved due to the challenge of hybridization between different plants, and controlled by specific $\underline{UI}$ genes. It also shows that UI occurs before speciation takes place. UI (and self- and cross-incompatibility) functions equally well among plants of the same species and between plants of different species. This contradicts the reports that UI functions only between populations (Hogenboom 1973 and others).

The incongruity model

Hogenboom (1973) presented what he called the incongruity model to account for unilateral relations. The model is essentially Martin's (1963) hypothesis of the polygenically controlled balance of substances affecting pollen tube growth and stylar inhibition (see also Pandey 1969). In addition to arguments presented earlier against such ideas (Abdalla 1970, 1974a; Abdalla and Hermsen 1972; de Nettancourt et al. 1974) it is observed that the incongruity model: (1) failed to differentiate between widespread occurrence of certain behaviour (SI × SC inhibition) and findings of rare events; (2) ignored the importance of inbreeding depression occurring in SI populations following the introduction of $\underline{S}_c$ alleles, although such depression was clearly demonstrated also in *Lycopersicon* inbreds (Hogenboom 1972a); (3) rejected the role of evolution and natural selection in building up a $\underline{UI}$-gene-$\underline{S}_c$-gene system (Abdalla and Hermsen 1972).

Compared with the two-power competition hypothesis, the incongruity model cannot furnish an acceptable explanation for the differing results reported in the literature, such as: behaviour of hybrids between SC and SI parents and their segregating progenies in connection with self-compatibility and self-incompatibility; the association of self-incompatibility and unilateral incompatibility in hybrids between SC and SI parents; the occurrence of SC progenies among SI × SI hybrids and SI progenies in SC × SC hybrids. Also the results of Grun and Aubertin (1966), Hogenboom (1972d), Hermsen et al. (1974) and Spoor (1976), and the behaviour of 'major' C_2 in our results, are antagonistic to the incongruity model. These results dealt with the successful reciprocal crossing between plants that accept and those that reject $\underline{S}_c$-carrying pollen. All the results reported can be simply explained on the basis of the two-power competition hypothesis.

Dr. Hogenboom's (1972b, c) results can be explained on the basis of the two-power competition hypothesis as follows: the SC inbreds obtained through mutation, inbreeding and selection may possess different $\underline{S}_c$ structures; some differ from those unable to fertilize $\underline{UI}$ genotypes present in *Lycopersicon peruvianum*, and will cross reciprocally with sister SI plants; mutation and inbreeding may have resulted in different $\underline{UI}$ genotypes, inbreeding leading to $\underline{uiui}$ ones against *L. esculentum* pollen (mutation of $\underline{UI}$ genes is not ruled out), and consequently some may also cross reciprocally with *L. esculentum*. The segregation of $\underline{UI}$-genes in Hogenboom's material may explain all his results. The explanation of Hogenboom (1973) of the model of Lewis and Crowe (1958) of the gradual mutation from SI species through Sc and Sć to SC ones is based on disputable suppositions: "lowering capacities of many barrier genes" and "maintaining penetration capacity" and "adjusting penetration capacity" are too many assumptions without proof. The mutants assumed in the model of Lewis and Crowe (1958) are easily explained as a one-gene mutation step in $\underline{S}_c$ or $\underline{UI}$-genes. On the basis of the two-power competition hypothesis the mutants may be given such genotypes as the following to account for their assumed behaviour [see also Abdalla and Hermsen (1972) and Abdalla (1974a) for more details]:

Lewis and Crowe (1958) species		Expected genotype according to the two-power competition hypothesis
SI	=	$\underline{S_iS_i\ UI_1..ui_2ui_2ui_3ui_3}$
Sc	=	$\underline{S_{c3}S_{c3}UI_1UI_1ui_2ui_2ui_3ui_3}$
Sć	=	$\underline{S_{c2}S_{c2}ui_1ui_1ui_2ui_2ui_3ui_3}$
SC	=	$\underline{S_{c1}S_{c1}ui_1ui_1ui_2ui_2ui_3ui_3}$

So far as it has been tested, the two-power competition hypothesis can satisfactorily and simply furnish a basis to explain the results of unilateral interspecific and intraspecific incompatibility published up to now. From the practical point of view $\underline{uiui}$ genotypes are being used in research in different plant species. The studies of mutation, incompatibility and intra- and interspecific crossings are expected to reveal interesting discoveries in the potentialities of $\overset{S}{\underline{i}}$, $\overset{S}{\underline{c}}$ and $\underline{UI}$ genes and their interactions. Compared with $\overset{S}{\underline{i}}$ alleles, $\overset{S}{\underline{c}}$ alleles have been given less attention.

Fertility and field bean breeding

With respect to the fertility characteristic, differing specificities are known in *V. faba*, different ones of which may be present in similar or different botanical types. The nature of the $\overset{S}{\underline{c}}$ alleles remains to be thoroughly investigated. An interesting discovery by Abdalla and Hussein (1977) is the mutation of an 'equina' to a 'major' type.

'Major', 'equina' and 'minor' types possess stocks with different fertilities, *paucijuga* is highly 'autofertile' but a very low yielder. Improving fertility through individual-plant selection may be achieved in certain stocks but not in others (Abdalla 1976). Small-seeded populations are generally more self-fertile. 'Major' stocks are mostly low in fertility. In order to improve the fertility of such populations, one may try to change the $\overset{S}{\underline{c}}$-specificity towards better fertility but at the same time greatly inaffecting the 'major' characteristic. C_2 is a 'major' type with better fertility compared with C_3.

Hybrids are good yielders and express high fertility, but they still are difficult to produce commercially. Some inbreds with high self-fertility and which are least affected by environmental conditions may be equally good as hybrids.

Hybridization between 'major' and other varietal types is possible. Reciprocal crossing and facilitating the recovery of useful segregants necessitates using $\underline{uiui}$ gentoypes (see Abdalla and Hermsen 1972). However, the practicability of recovering the original typical 'major' with fertility similar to *paucijuga* or 'minor' types may be questioned. It is being experimentally tested. Handling 'equina' populations may be promising in different aspects. It would be interesting to throw more light on the relationship and the products of recombination of the different $\overset{S}{\underline{c}}$ alleles in *V. faba* (see Abdalla 1977).

The discovery of the presence of unilateral incompatibility in *V. faba* calls for re-assessment of the degree of natural cross-fertilization reported in this crop. If some of the plants used in the earlier studies happened to be carrying $\underline{UI}$ rejecting genes, such plants would fail to cross as females; therefore, it is possible that earlier results may need to be rechecked.

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Note Added in Proof

The discussion in this and in previous papers assumed the rejecting UI genes to be dominant. Preliminary results in *V. faba* showed that this may not be a rule.