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Cross-incompatibility Between Two Sympatric Polyploid *Solanum* Species

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Summary. Preliminary results from a large number of reciprocal crosses between the closely related sympatric species *S. gourlayi* Hawkes ($2n = 4x = 48$) and *S. oplocense* Hawkes ($2n = 6x = 72$) indicated that they are difficult to hybridize. Pollen-pistil incompatibility barriers were detected via fluorescent microscopy. The cross incompatibility reaction occurred at three sites in 6x × 4x crosses; on the stigma, in the first one-third of the style, and in the first two-thirds of the style. In the reciprocal 4x × 6x crosses the incompatibility reaction invariably occurred in the ovary. Backcrosses of interspecific pentaploid hybrids (that were occasionally formed) to both parental populations were fully compatible, partially compatible, and fully incompatible with three sites of cross-incompatibility reaction similar to those observed in 6x × 4x crosses, respectively. Both polyploid species were found to be self-compatible, whereas their F1 hybrids were found to be self-incompatible. An hypothesis based on interactions of dominant cross-incompatibility (CI) genes in pistils and dominant specific complementary genes in pollen grains is postulated to explain these observations. The cross-incompatibility system that appears to be operating in nature between 4x *S. gourlayi* and 6x *S. oplocense* provides a way for gene exchange between sympatric populations without threatening the identity of either species.

Key words: Cross-incompatibility – *Solanum* – Reproductive barriers – Introgression – Evolution

Introduction

The organization of breeding populations into reproductively isolated species is a necessary accompaniment of the sexual process in a heterogeneous environment (Grant 1971). Each species is adapted to a particular ecological niche and, therefore, unrestrained hybridization would result in an appalling number of hybrids which would not be adapted to any one mode of life (Dobzhansky 1937; Cain 1954). Many and diverse barriers to hybridization, thus, had to develop between sympatric populations in order for them to maintain their identity. These barriers have been divided into three main classes; spatial, environmental and reproductive, the latter being internal and external (Grant 1971).

Tuber-bearing *Solanum* species are outcrossers with very similar floral structures, closely related cytogenetically, and interfertile within wide limits (Howard and Swaminathan 1952). Related species are considered to be isolated in nature by ecological and other external factors (Hawkes and Hjerting 1969).

Natural populations of the polyploid tuber-bearing species *Solanum gourlayi* Hawkes (grl[1], $2n = 4x = 48$) and *Solanum oplocense* Hawkes (opl[2], $2n = 6x = 72$) are sympatric in some areas of NW Argentina (Okada 1974). These species are very closely related (Hawkes and Hjerting 1969), self-compatible (our observations), and both have an Endosperm Balance Number (EBN) of four. The EBNs are qualitative genetic factors whose balance in the endosperm in a 2:1 female to male ratio is a necessary prerequisite for normal development of this tissue and therefore of the seed (Johnston et al. 1980). Hybridization should, therefore, occur readily in nature, unless barriers to prevent or restrict interspecific crossing would have developed between the two polyploid species.

Preliminary results from a large number of reciprocal crosses between these species, carried out both in a greenhouse and in the field in different seasons, indicated that they are difficult to hybridize. Hybrids with the expected pentaploid number of chromosomes are occasionally obtained. These pentaploid hybrids, which in contrast to their parents are self-incompatible, can be backcrossed to the original populations of 4x grl and 6x opl to give rise to tetraploid and pentaploid progeny, respectively.

[1,2] Abbreviations according to Simmonds (1963)

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It is apparent from these results that a cross-incompatibility system is operating between populations of 4x grl and 6x opl. The study of this system and the discussion of its possible genetic basis and evolutionary significance are the main concerns of this report.

Materials and Methods

An extensive crossing program between a large number of plant introductions of 4x grl and 6x opl was carried out in a greenhouse and in the field in the fall of 1978 and in the spring and summer of 1979, to obtain some information on the effect of environment and genotype on the crossability of these species. Only 48 pentaploid hybrids were obtained, regardless of the direction of the cross. Plants of 4x grl, 6x opl and a sample of these pentaploid (opl-grl) hybrids were grown in a greenhouse in the fall of 1979. Tetraploids, pentaploids and hexaploids were selfed; pentaploids were also intercrossed and backcrossed as females to both parental populations. Pollen grain germination and pollen tube growth following selfing and backcrossing were observed, as will be described later.

The results of these interspecific crosses, backcrosses, and selfings suggested that a cross-incompatibility system was operating between populations of 4x grl and 6x opl. To investigate the cytological and genetic basis of this system, four introductions of each of these two polyploid species were grown in the field in the summer of 1980. Each introduction was represented by 14 plants. Reciprocal interspecific crosses and backcrosses were made using the cut-stem technique (Peloquin and Hougas 1959). Inflorescences were cut from plants in the field and taken to an airconditioned greenhouse. Open flowers were removed and buds one day prior to opening were emasculated. Fresh pollen from tetraploids and hexaploids and pollen from pentaploid hybrids, that had been stored at low temperatures, was abundantly applied to the stigmata later the day of emasculation or the next morning. Either pistils or styles were removed 48 hrs. after pollination and fixed in FAA (1:8:1 formalin: 80% ethanol:glacial acetic acid). When only styles were removed, a drop of a 6 ppm solution of 2-4D (Dionne 1958) was applied to the attached ovaries in order to promote fruit development, providing a situation in which even a single fertilized ovule could develop and ripen into a seed.

Following fixation, pistils were rinsed with tap water, treated with a nearly saturated aqueous solution of sodium hydroxide (8 N), rinsed, and stained with a solution of 0.1% water soluble aniline-blue dye in 0.1 N K_3PO_4, as described by Martin (1958). Pistils were then mounted in one drop of stain on glass slides, covered with cover slips, and squashed very gently. A conventional microscope with ultraviolet light was used for observations at 100 magnification.

Some of these crosses and backcrosses were repeated on plants in the field, to verify expectations based on microscopic observations.

Results

The combined microscopic observations and crossing results are presented in table 1.

Table 1. Pollen tube growth and seed set following selfing, crossing and backcrossing plants of 4x *S. gourlayi*, 6x *S. oplocense* and 5x (*S. gourlayi – S. oplocense*) hybrids

Plant Material		No. buds pollinated	No. styles or pistils analyzed	Pollen tubes reaching ovary[a]	No. fruits	No. seed/fruit ( ) No. of fruit
	No. plants selfed					
a. Selfing						
4x grl	29	70	38	+++	13	80-95
6x opl	22	84	40	++;+++	32	22-230
5x (opl X grl)	13	100	51	0;+	14	0(7);1;5;8(2);9(3)
5x (grl X opl)	2	14	0	–	0	–
	No. interspecific combinations					
b. Crossing						
6x opl X 4x grl	480	1900	1870	0;+	0	–
4x grl X 6x opl	480	1680	1650	+++	3	0(2);1
c. Backcrossing						
5x (opl-grl) X 4x grl	18	59	14	0;+;++	19	0(5);1;7;8;9;17;31;44; 50(2);51;62;70;77;78
5x (opl-grl) X 6x opl	48	101	20	0;+;++	12	1(2);4;5(2);7;8;11;17; 27;35;40
4x grl X 5x (opl-grl)	20	80	59	0;+;++;+++	4	10;31;44;45
6x opl X 5x (opl-grl)	22	87	66	0;+;++;+++	6	0;7;11(2);27;30

[a] 0 = none; + = a few; ++ = 1/4-1/2; +++ = most

Selfing

1) 4x grl and 6x opl
A large number of pollen grains germinated following self-pollination of 4x grl and 6x opl. Most of the pollen tubes reached the ovaries and effected fertilization. The number of plump seed/fruit ranged from 80 to 95 in 4x grl, with a mean of 85, and from 22 to 230 in 6x opl, with a mean of 85.5. Low seed set in a few fruits, probably due to environmental effects, greatly decreased the value of the mean in 6x opl.

2) 5x hybrids
Pentaploid (opl × grl) and (grl × opl) hybrids, in contrast to their parental species, were difficult to self. Either none or a few of the pollen tubes observed in the upper portions of the styles reached the ovaries. Consequently, few fruits were obtained, even after treatment with a solution of 2-4D applied to promote ovarian growth. Some of the fruits obtained were parthenocarpic, others had one to nine seeds each.

Interspecific crosses

Six to ten plants from each introduction of 6x opl were reciprocally crossed to four to five plants from each introduction of 4x grl.

1) 6x opl × 4x grl
Three sites of the cross-incompatibility reaction were observed following 6x opl × 4x grl crosses; 1) on the stigma (pollen grains did not germinate), 2) in the first one-third of the style, 3) in the first two-thirds of the style (pollen tubes bunched, occasionally a few reached the ovaries). Only two exceptions to this crossing behavior were observed. Fruits were not obtained either in the greenhouse or in the field, as expected from the microscopic observations.

2) 4x grl × 6x opl
A very large number of pollen grains (usually ≥ 100 and ≤ 500) germinated following the reciprocal 4x × 6x crosses. Most of the pollen tubes reached the ovaries and were seen growing among the ovules. Some pollen tubes attached to individual ovules were also observed. Only six exceptions to this crossing behavior were found, out of more than four hundred crosses analyzed. No fruits were obtained in the greenhouse, though two fruits with aborted seeds plus one fruit with one plump seed in addition to aborted ones were obtained in the field.

Backcrosses

1) 5x (opl-grl) × 4x grl and 5x (opl-grl) × 6x opl
Six pentaploid (opl-grl) hybrids were backcrossed as females to three plants of 4x grl. Either none, a few or approximately one-half of the pollen tubes growing in the upper portions of the styles reached the ovaries. Nineteen fruits with 0 to 78 seeds were obtained, as expected from these microscopic observations. The chromosome numbers of a sample of seedlings from these backcrosses were found to be approximately 48.

Twelve pentaploid (opl-grl) hybrids were used as females in backcrosses to four plants of 6x opl. Twelve fruits were obtained. The number of plump seed per fruit ranged from one to 40. This was in agreement with expectations based on microscopic observations, since either none, a few or approximately one-third of the pollen tubes seen close to the stigmata reached the ovaries. A sample of seedlings from these backcrosses had approximately 60 chromosomes.

2) 4x grl × 5x (opl-grl) and 6x opl × 5x (opl-grl)
Pentaploid (opl-grl) hybrids were backcrossed as males to plants of 4x grl and 6x opl in forty-two different combinations. The behavior of the pentaploids in backcrosses to either parental species was very similar. Three of these backcrosses were fully compatible, therefore, most of the pollen tubes seen in the upper portion of the styles reached the ovaries. Seventeen backcrosses were partially compatible, since 25 to 70% (or up to 45 pollen tubes) reached any one ovary. In addition, complete or almost complete incompatibility, with three sites of reaction similar to those described for 6x × 4x crosses, were observed in the remaining backcrosses. The number of plump seeds per fruit obtained from pollinations in the field confirmed these observations.

Discussion

Two different kinds of relationship between pollen and pistil, leading to a restriction in hybridization, have been described; incompatibility, which results either from the identity of alleles at one or more specific incompatibility loci in both pollen and pistil, or from the existence of variations in floral structure such as anther height, pollen wall sculptures, pollen grain size, stylar length and stigmatic surface (Frankel and Galun 1977), and it occurs within and between closely related cross-fertilizing species, and incongruity, which results from the lack of information in one partner about some character in the other (Hogenboom 1973), and this is a corollary of evolutionary divergence.

The suggestion that pollen-style interspecific incompatibility, at least in related species, could have a genetic base common to the S-gene multiallelic gametophytic incompatibility system was obtained from the phenomenon of 'unilateral hybridization' in *Anthirrinium* (Harrison and Darby 1955). Lewis and Crowe (1958) pointed out the common occurrence of this phenomenon in flowering plants, and applied the term 'unilateral incompatibility' to the inhibition of pollen tube growth in SI × SC pollinations. Later, one-way crossability was found to occur not only in crosses between SI and SC species, but also in crosses between two SC or two SI ones. The term 'unilateral relation' was then proposed by Abdalla and Hermsen (1972) to qualify any inhibition other than the one observed in either SI × SC or SC × SI crosses.

Many authors, including Mather (1943), Bateman (1943), Lewis and Crowe (1958), Martin (1968) and Pandey (1964, 1968, 1969 a,b) accepted the dual function of the S-alleles as a basis for explaining both self-incompatibility and interspecific incompatibility. Grun and Radlow (1961) were the first to suggest that interspecific barriers in diploid Solanums were completely independent of the S-system, and Grun and Aubertin (1966) postulated that this barrier to hybdridization was due to the action of dominant genes. Hogenboom (1973) broadened the basis of this theory in his model for incongruity in intimate partner relationship. Abdalla (1970) and later Abdalla and Hermsen (1972) postulated a 'two-power competition' hypothesis, based on interactions of self-incompatibility (SI) genes in pollen grains and unilateral incompatibility (UI) genes in styles, that satisfactorily explains all examples reported in the literature of crossing between SC and SI diploid species of flowering plants with the one-locus gametophytic incompatibility system. Abdalla and Hermsen's 'two-power competition' hypothesis, in contrast to the 'dual function' hypothesis, is not overloaded with assumptions.

Development of the Cross-incompatibility System

It is apparent from the combined microscopic observations and crossing results that a pollen-pistil incompatibility system is operating between populations of 4x grl and 6x opl. A testable hypothesis regarding the genetic basis of this system is proposed. According to this hypothesis, each popyploid population would possess a variable number of cross-incompatibility (CI) genes that when present in the pistil in the dominant condition, and upon cross-pollination, would prevent fertilization by pollen grains carrying specific complementary dominant genes. It seems reasonable to assume that during their evolution sympatric populations of 4x grl and 6x opl developed complementary genic systems to prevent hybridization, since their continued existence would have been threatened in proportion to the freedom of interbreeding between them. Thus, any time a new mutation leading to the formation of a new specific complementary gene occurred in a population of a species, a new CI gene preventing fertilization by pollen grains carrying the newly formed gene would have developed in the sympatric population of the other species. In this way, a CI gene-specific complementary gene system would have originated, that is comparable to the gene-for-gene system proposed by Flor (1955) for host-parasite interactions in flax, and to the system later postulated by Abdalla and Hermsen (1972) to explain Unilateral Incompatibility (UI) and Unilateral Relation (UR) in diploid flowering plants.

Tetraploid grl and hexaploid opl are self-compatible species. This self-compatibility is due to 'competition interaction' between different alleles at the S-locus, and to the fact that the species do not possess CI genes against their own specific complementary genes. Occasionally, pentaploid hybrids are formed. Since each parental species is well adapted to the ecological niche that it normally occupies, most of the opportunities for the establishment of this hybrid progeny in their region of contact would be for genotypes that approach one parent or the other in their physiological characters. If pentaploid (opl-grl) hybrids could self, a large number of genotypes that would not be adapted to any one environment would be formed. The pentaploid hybrids, however, are self-incompatible. They would, therefore, carry CI genes in their pistils against specific complementary genes present in their pollen grains. They can backcross either as males or females to their parental populations, depending on their genotype for CI genes and specific complementary genes, and give rise to plants with a balanced or near balanced number of chromosomes. These backcross progenies, as Anderson (1949) has pointed out, would most likely have the requisite ecological preferences and would, thus, be probably favored by the existing environmental conditions.

Support for the hypothesis put forward is found in nature. Backcrosses of pentaploid interspecific hybrids such as those derived from the crosses (2x *S. infundbuliforme* × 6x *S. oplocense*) and (4x *S. tuberosum* Gp. Andigena × 6x *S. oplocense*) to 2x *S. infundibuliforme* and to 4x *S. tuberosum* Gp. Andigena, respectively, might have given origin to tetraploid (*S. infundibuliforme* × *S. oplocense*) and (*S. tuberosum* Gp. Andigena × *S. oplocense*) hybrids that have been collected in nature (Okada 1974, 1979). Furthermore, pentaploid plants found in populations of 6x opl (Hawkes 1979) could be the result of backcrosses of pentaploid hybrids derived from crosses between 6x opl and other diploid or tetraploid species to 6x opl.

Gene exchange between sympatric populations can, thus, take place, without threatening the identity of either species. Backcrosses of pentaploid hybrids to their diploid or tetraploid parental populations, i.e. 2x ifd, 4x grl, 4x adg, would result in introgression of 6x opl into the latter. Also, if pentaploid hybrids occasionally produce 3x gametes, introgression of tetraploid species into 6x opl would occur.

How the Cross-incompatibility System Works

Three sites of cross-incompatibility reaction in 6x × 4x crosses and one site in 4x × 6x crosses have been observed.

Four specific complementary dominant genes in pollen grains, each of them interacting with one dominant gene for CI in pistils are proposed to explain these observations. The number of CI genes and complementary genes, however, may vary in any population, and different genes may have the same phenotypic expression.

The results of reciprocal crosses between one plant (genotype) of 4x grl and three different plants (genotypes) of 6x opl, and of backcrosses of this plant of grl, as male and female, to two pentaploid interspecific hybrids are used to exemplify how the CI system works.

1. Cross	6x opl$_1$ X 4x grl
Site of CI reaction	on stigma
Genotype	--CI$_A$-- X --A--
Progeny (if any)	--- CI$_A$ A---
2. Cross	6x opl$_2$ X 4x grl
Site of CI reaction	in first 1/3 of the style
Genotype	--CI$_B$-- X --AB--
Progeny (if any)	--- A CI$_B$ B ---
3. Cross	6x opl$_3$ X 4x grl
Site of CI reaction	in first 2/3 of the style
Genotype	--CI$_C$-- X --ABC--
Progeny (if any)	--- ABCI$_C$C ---
4. Cross	4x grl X 6x opl$_{1,2,3}$
Site of CI reaction	in ovary
Genotype	---ABC CI$_D$-- X --D--
Progeny (if any)	--- ABC CI$_D$ D---
5. Cross	4x grl X 5x (opl-grl)
Site of CI reaction	none
Genotype	---ABC CI$_D$-- X --B--
Progeny (if any)	---ABC CI$_D$- B-
6. Cross	5x (opl-grl) X 4x grl
Site of CI reaction	in first 2/3 of the style
Genotype	--CI$_C$-- X --ABC CI$_D$--
Progeny (if any)	---ABCI$_C$C CI$_D$---

The CI reaction takes place on the stigma in cross no. 1, between a plant of 6x opl used as female and one of 4x grl used as male. According to the hypothesis postulated, pollen grains of that plant of 4x grl would carry a specific complementary gene A, that interacts with a CI$_A$ gene present in the pistils of 6x opl$_1$. In cross no. 2, the CI reaction occurs in the first one-third of the style. This indicates that 4x grl would carry, in addition to the A gene, a specific complementary gene B, that interacts with the CI$_B$ gene present in the pistils of 6x opl$_2$. Hybrids are not expected from these two crosses because either pollen grains do not germinate or pollen tubes do not reach the ovaries. In cross no. 3, the CI reaction occurs in the first two-thirds of the style; a few pollen tubes occasionally reach the ovaries and effect fertilization. A specific complementary gene C in pollen grains of 4x grl, interacting with a CI$_C$ gene in pistils of 6x opl$_3$, is postulated to explain these observations.

In the reciprocal 4x x 6x crosses, the CI reaction invariably occurs in the ovary. Thus, 6x opl$_1$, 6x opl$_2$ and 6x opl$_3$, would carry a specific complementary gene D in addition to the CI$_A$, CI$_B$, and CI$_C$ genes. This D gene would interact with the CI$_D$ gene present in the pistils of 4x grl, resulting in a CI reaction in the ovary. The plant of 4x grl used in these crosses is assigned the genotype --- A B C CI$_D$ ---, according to its crossing behavior with the three different plants of 6x opl.

If F1 hybrids are occasionally formed from cross no. 3, they would be of genotype ---A B C CI$_C$D CI$_D$------. They would self only if pollen grains homozygous recessive for both the C and D loci are produced, which has a low probability. This probability would be greatly reduced as the number of CI genes that the pentaploids possess increases above two. These pentaploids can be backcrossed to their parental species. They can also be backcrossed to their own parents if they produce pollen grains homozygous recessive for only one specific complementary gene (either C or D, depending on the parent).

Cross no. 5 is fully compatible. This indicates that the CI genes in 4x grl and the specific complementary genes in 5x (opl-grl) do not match. In cross no. 6 the CI reaction can be complete, as described for cross no. 3, and only occasionally progeny would be formed. However, the same cross can be partially compatible if 4x grl segregates for the C locus. In this instance, a variable number of pollen tubes would reach the ovaries and effect fertilization.

In any interspecific cross between two SC species several barriers may be involved, which are expected to affect crossability and the function of male and female gametes (Abdalla and Hermsen 1972). These barriers can also function in the segregating generations and in backcrosses. These considerations, together with the modifying effects of minor genes and the environment, may cause deviations from any theoretical explanation in any investigation. The hypothesis postulated, nevertheless, seems to offer a simple explanation for the phenomenon of cross-incompatibility between 4x grl and 6x opl, and for the presence of SI plants among hybrids derived from SC x SC crosses.

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