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Self Compatibility in Garden *Chrysanthemum*: Occurrence, Inheritance and Breeding Potential*

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Summary. Self compatibility (SC), which was found to occur only rarely in the normally self-incompatible (SI) hexaploid garden chrysanthemum, *Chrysanthemum morifolium* Ramat., was studied by making a series of self and cross pollinations in progenies of 3 different SC sources. SC was transmitted without exception in 15 F_1 progenies from crosses between SC and SI plants. No maternal effects were noted in 10 F_1 progenies from reciprocal crosses between SC and SI plants. Selfing or intercrossing of SC plants did not produce any large, uniformly SC progenies. Initial intercrosses between SC and SI plants suggested that SC might be controlled by a single dominant factor. Further crosses suggested that the inheritance of SC was more complex and could be associated with more than 1 gene or be modified by other genes such as the S-genes. Seed yield following self pollination in some progenies gave evidence of a clear separation into SC and SI classes while in other progenies the separation was not so distinct. The condition of pseudo-self-compatibility was evident in progenies derived from selfing SC plants or crossing between SC plants. SC was used to produce large quantities of inbred seed which is now available for producing both I_1 and I_2 generations. By using SC parents, the combined self and cross compatibility was increased as compared to compatibility in progenies derived from SI-SI matings.

Introduction

Homomorphic sporophytic self incompatibility (SI) was first described by Gerstel (1950) and Hughes and Babcock (1950) in two different members of the Compositae. Since the initial description of this type of SI, it has come to be recognized as characteristic of the Compositae, Cruciferae and Convolvulaceae families.

Drewlow, Ascher and Widmer (1973) reported that *Chrysanthemum morifolium* (Compositae) exhibited typical sporophytic SI characteristics including pollen inhibition at the stigmatic surface and reciprocal differences in crosses. The high frequency of cross incompatibility in full sib matings suggested that the SI system might involve more than one locus, a situation that would not be unreasonable in a hexaploid crop purportedly derived from 3 SI diploids. SI was found to be highly uniform with only 1 spontaneous self compatible (SC) plant occurring in about 50 tested. This single plant, with a selfed seed yield of 24 seeds per head, was found in a second generation inbred family derived from inbreeding a clone which had shown a high frequency of cross compatibility in full sib matings.

There is general acceptance of the theory that SC species have been derived from SI species by a process of human or natural selection (Stebbins, 1957). While occasional naturally occurring SC plants have been reported in most normally SI species, mutagenic treatments, particularly those using radiation, have produced numerous SC plants (Lewis, 1949; de Nettancourt, 1969). Self-fertility (S_f) mutations at the incompatibility (S) locus are generally the basis of SC in plants possessing gametophytic control of pollen specificity.

SC, in plants possessing sporophytic control of pollen specificity, has been studied most thoroughly in *Brassica* (Cruciferae) where it has been associated with a major dominant gene unrelated to the S-locus (Thompson and Taylor, 1966, 1971). This type of SC was affected by the dominance of S-alleles and was also influenced by other modifying genes. Lloyd (1967) made crosses within and between natural SC and SI populations of *Leavenworthia* (Cruciferae) and found that each population was true breeding and that SC was recessive.

In the only reported study of a hexaploid species with sporophytic homomorphic incompatibility, Martin (1972) concluded that SC in sweet potato (Convolvulaceae) was neither dominant nor recessive, was probably controlled by more than one gene and was closely associated with loss of pollen S-allele activity. Martin (1973) in further studies of progenies of SC plants, found that severe inbreeding depression hindered the elucidation of SC. Selfing of SC plants produced few SC progeny and he concluded that this character was controlled by rare combinations of many genes acting epistatically.

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Genetic mechanism controlling SC in the sporophytic system are complex and have not been clearly elucidated in most families. We sought to determine the occurrence of SC and to study its transmission in normally SI hexaploid garden chrysanthemums. The high frequency of self and cross incompatibility in chrysanthemum suggested the possible value of SC as a means to increase seed yield, permit inbreeding studies and improve techniques for genetic analysis, particularly of recessive characteristics.

Materials and Methods

Standard compatibility testing procedures were used throughout the study. Self pollinations were tested on 4 flower heads. Cross pollinations were made on 1 or 2 carefully emasculated flower heads. All flowers were pollinated at least twice within a 1 wk period to assure adequate pollination. Six weeks after pollination, flower heads were removed from the plant, dried and threshed.

Proper classification of compatible and incompatible matings is difficult in a multi-flowered inflorescence such as chrysanthemum. Low seed yield of 1-2 seeds per head may occur in many pollinations as a result of pseudo-self-compatibility (PSC) or contamination. The number of flowers per inflorescence also varies as a result of genotypic and environmental effects. To separate true compatibility from other effects, seed yield was averaged and only those self and cross pollinations yielding 10 or more seeds per head were identified as compatible.

Two precautions were taken to avoid confounding sterility with SI. Plants were visually examined for good pollen production prior to use in selfing or crossing. In addition, test crosses were also made as a check on male and female fertility.

All crossing was done in a greenhouse, over a 3 yr period, in which temperatures were maintained as closely as possible to 16° C N and 21° C D. These temperatures were considered optimal for plant growth, pollen production and seed development.

The frequency of SC plants was determined by selfing 21 selections and cultivars and 49 partially inbred clones in the University of Minnesota chrysanthemum breeding project. The parents of all 49 clones were known to be SI but the same information was not available for all of the other 21 clones.

Three available SC clones (7207, 71D-30-10 and 70D-113-1) were used initially in crosses to study SC. Clone 7207, which yielded 20-50 selfed seeds per head, originated from a cross between two SI plants at the Morden Research Station, Morden, Canada. This clone with its semi-double flowers and excellent pollen production was widely used in crosses. Clones 71D-30-10 and 70D-113-1, which yielded 20 and 24 selfed seeds per head respectively, both traced to 67-111-42 a clone which, although SI, exhibited a high frequency of cross compatibility in full sib matings. Limited pollen production on clone 71D-30-10 and loss of clone 70D-113-1 restricted crossing with these 2 sources of SC. Clone 72R-289-6, a SC plant from a cross between 71D-30-10 and a SI (71D-13-23) plant, and clone 72D-189-4, a SC plant from a progeny of 70D-113-1 selfed, were used in several crosses to represent these 2 SC sources.

Fifteen F_1 progenies totalling 190 plants from crosses involving the 3 SC sources and unrelated SI plants, all from the University of Minnesota chrysanthemum project, were tested for SC. Five F_1 progenies from crosses between the unrelated SC sources were similarly tested. Plants from reciprocal crosses between 7207 and 71-27-24 (SI) were reciprocally backcrossed to their parents to determine the frequency of compatibility and to test for a pollen or stylar loss of specificity in SC plants. Reciprocal backcross and sib matings were also made in a progeny of 71D-30-10 (SC) x 71D-13-23 (SI). Three F_1 progenies from sib matings and backcross of one SC source (7207) were evaluated to determine whether progenies homozygous for SC might be recovered. A single F_1 progeny of a SI plant originating from a SC x SI mating, backcrossed to its SI parents, was tested to determine whether SC had recessive characteristics.

Progenies from self pollination of 7207 and 70D-113-1 (1 plant) flowered and were tested for SC. Ten selfed progenies were grown from derived F_1 SC plants of the 7207 source to compare the segregation ratios with those of 7207 selfed and to search for progenies that might be all SC.

Diallel matings among 8 unrelated plants and sib matings in 15 other progenies were made to observe the effects of genetic source and the SC status of parents on the frequency of combined self and cross compatibility. An outline of self and cross pollinations made to study the genetic control of SC in garden chrysanthemum is shown in Fig.1.

Chi-square values were calculated for F_1 progenies of crosses between SC and SI plants.

Results

Occurrence of SC

A very low frequency of plants were found to be SC (Fig.2). Only 2 of the 21 selections yielded more than 10 seeds per head and only one of these produced a large quantity of seed (46 seeds per head). Two plants out of 49 clones, the parents of which had been determined to be SI, yielded more than 10 seeds per head (17 and 20 seeds per head). One of these plants (71D-30-10) was used in subsequent crosses to study SC. Most of the 70 plants yielded fewer than 2.0 seeds per head, indicating that PSC was not a significant factor in these chrysanthemums.

Intercrosses of SC and SI Plants

Transmission of SC occurred in all 15 F_1 progenies from crosses between SI plants and the 3 sources of SC (Tables 1 and 2). The combined segregation ratio for the 150 plants in the 10 progenies of 7207 was 85 SI:65 SC plants. Chi-square values for all terms of the 10 7207 progenies gave an acceptable fit to a 1:1 ratio at the 5 % level. A total of 36 plants in 4 71D-30-10 progenies segregated 27 SI:9 SC plants. Three of these progenies gave an acceptable fit to a 1:1 ratio while 1 of the progenies and the total term were closer to a 3:1 segregation. One small progeny involv-

1. Three SC sources (7207, 71D-30-10 and 70D-113-1) were crossed to 8 unrelated SI clones (66-17-15, 71-27-24, 71-35-58, 67-111-42, 71-27-25, 7105, 71D-13-23, and 70D-121-3), of the University of Minnesota chrysanthemum project, and 190 F_1 plants in 15 progenies. were evaluated for SC (Tables 1 and 2).

2. a. 7207 (SC) and 71-27-24 (SI) were reciprocally backcrossed to their SC and SI offspring in progenies 72R-310 (71-27-24 X 7207) and 72R-311 (7207 X 71-27-24) to determine cross compatibility (Figs. 4 and 5).

   b. 71D-30-10 (SC) and 72R-289-6 (SC) = 71D-30-10 X 71D-13-23 (SI) were reciprocally backcrossed to SI offspring and sibs respectively (72R-289-1, -2, -4, -5, -7, and -8) to determine cross compatibility (Fig. 6).

3. Original or derived plants (72R-289-6 (SC), (72D-189-4 (SC) = 70D-113-1 (SC) selfed) were intercrossed and the 54 plants in 5 progenies were evaluated for SC (Table 3).

4. 72R-310-5 (SC) and 72R-310-7 (SC) were sib mated and backcrossed to their SC parent (7207) and the 31 plants in 3 progenies were evaluated for SC (Table 4).

5. 72R-311-7 (SI) was backcrossed to its SI parent (71-27-24) and the progeny was evaluated for SC (Table 4).

6. The original SC sources were self pollinated. Two progenies of 7207 and 1 plant of 70D-113-1 flowered and were tested for SC (Table 5). Ten SC plants, from crosses between 7207 and unrelated SI plants, were selfed and 10 progenies were evaluated for SC (Table 5).

7. Combined self and cross compatibility frequency was determined for 1 diallel involving 8 unrelated clones (71-27-24, 67-111-42, 'Purple Star', 71D-30-10, 'Gala Gold', 'Raspberry Sundae', Acc. 7215, and 7207) and for 14 other diallels varying in SC and genetic source (Table 6).

Fig. 1. Self and cross pollinations made to study the genetic control of SC in garden chrysanthemums

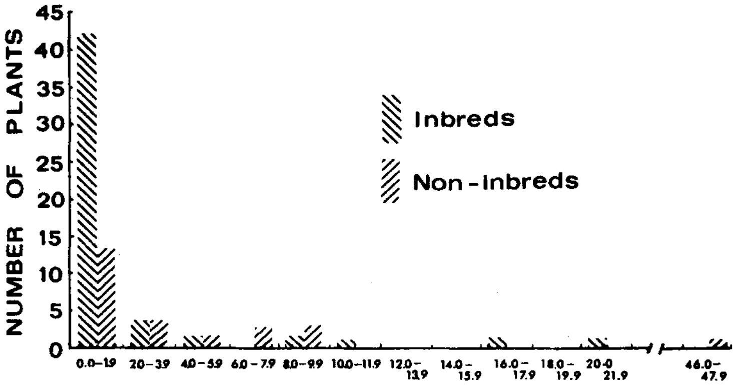

Fig.2. Frequency distribution for seed yield following self pollination of 49 partially inbred and 21 chrysanthemum clones

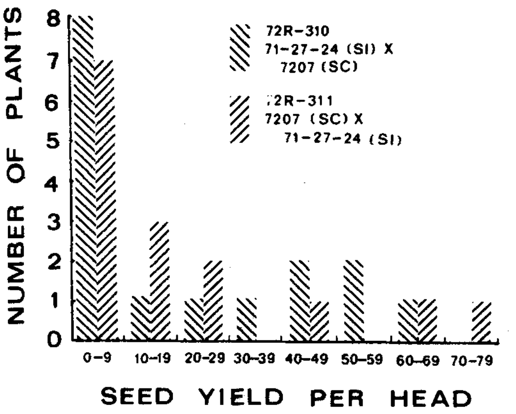

Fig.3. Frequency distribution of seed yield following self pollination of 31 plants in 2 progenies from reciprocal crosses between a SC and SI plant

Table 1. Segregation of self-incompatible (SI): self-compatible (SC) plants in 10 progenies from crosses between 7207 (SC) and SI plants

Parentage	Cross Number	Number of Plants		P
		SI	SC	
7207 X 66-17-15	72R-321	3	3	.99
7207 X 71-27-24	72R-311	7	8	.90-.75
7207 X 71-35-58	72R-322	1	2	.75-.50
7207 X 67-111-42	73R-2	16	11	.50-.25
7207 X 71-27-25	73R-3	7	4	.50-.25
Total		34	28	
	df	X^2		
Total	5	2.14		.90-.75
Pooled	1	.58		.50-.25
Interaction	4	1.56		.90-.75
66-17-15 X 7207	72R-312	4	3	.75-.50
71-27-24 X 7207	72R-310	8	8	.99
71-35-58 X 7207	72R-313	13	12	.90-.75
67-111-42 X 7207	73R-8	19	9	.10-.05
7105 X 7207	72R-287	7	5	.90-.75
Total		51	37	
	df	X^2		
Total	5	4.09		.75-.50
Pooled	1	2.23		.25-.10
Interaction	4	1.86		.90-.75

ing the third 70D-113-1 SC source segregated 2 SI:2 SC plants.

There was no strong evidence to suggest maternal effects on SC transmission in 10 reciprocal crosses between SC and SI plants. Five crosses using 7207 and 71D-30-10 as females, segregated 34 SI:27 SC plants while the reciprocal crosses segregated 49 SI:35 SC plants. Most of the SI parent plants possessed different S-alleles as indicated by their cross compatibilities. The chi-square interaction term, which could indicate whether SC interacts with the different S-alleles of the SI plants, was not significant for the 10 7207 crosses.

A frequency distribution of seed yield after self pollination of 31 F_1 plants in 2 progenies (72R-310 and 72R-311), resulting from reciprocal crossing of 7207 (SC) and 71-27-24 (SI), indicates that selfed seed yield is distributed over many frequency intervals (Fig.3). The frequency curve tails to the right and, although there is some evidence for a bimodal distribution in the 72R-310 family, a like trend is not apparent in the 72R-311 family. The largest class of plants yielded fewer than 5 seeds per head; the remaining plants ranged upward to a high of 76 seeds per head.

A high frequency of cross compatibility was noted in backcross matings of 7207 (SC) and 71-27-24 (SI) with their SC and SI offspring (Figs.4 and 5). Parental clones were cross compatible as males with all but 2 of the SC and SI offspring. When crossed as females, 7207 was incompatible with 4 of its SC and 7 of its SI offspring while 71-27-24 was incompatible with 3 SC and 3 SI offspring. Significantly, cross incompatibility occurred in both sets of reciprocal crosses involving 7207 and its SC offspring indicating that SC plants may possess incompatibility reactions in some crosses. 71D-30-10 and 72R-289-6 were cross compatible as males with all SI offspring and sib plants (Fig.6). Reciprocal pollinations resulted in 2 incompatible matings involving each of the SC plants.

Intercrosses of unrelated SC Sources

Five F_1 progeny from crosses between the 3 related SC sources segregated 28 SI:26 SC plants with both types of individuals appearing in all 5 progenies (Table 3). Two of the largest progenies (73R-13 and 73R-11) segregated a majority of SC plants while the other progenies segregated equal or fewer SC plants. All plants in the 2 larger progenies yielded some seed following self pollination. This condition of PSC was particularly evident in the 73R-11 progeny where 4 of the 7 plants classified as SI yielded between 7.5 and 9.9 seeds per head.

Table 2. Segregation of self-incompatible (SI): self-compatible (SC) plants in 5 progenies from crosses between 71D-30-10 (SC) and 70D-113-1 (SC) with SI plants

Parentage	Cross Number	Number of Plants		P
		SI	SC	
71D-30-10 X 71D-13-23	72R-289	6	1	.10-.05
71D-30-10 X 71-27-25	73R-131	9	2	.05-.025
71D-30-10 X 71-27-24	73R-132	7	3	.25-.10
71-27-24 X 71D-30-10	73R-36	5	3	.50-.25
Totals		27	9	
		df	X^2	
	Total	4	10.13	.05-.025
	Pooled	1	9.00	$<.005$
	Interaction	3	1.12	.90-.75
70D-113-1 X 70D-121-3	72D-217	2	2	.99

a. SC	7207	71-27-24
72R-310-1	+	+
72R-310-2	+	+
72R-310-5	+	+
72R-310-7	+	+
72R-310-8	-	+
72R-310-9	+	+
72R-310-12	+	+
72R-310-16	-	-
72R-311-2	+	+
72R-311-3	+	+
72R-311-4	+	+
72R-311-6	+	+
72R-311-8	+	+
72R-311-11	+	+
72R-311-12	+	+
72R-311-15	+	-

b. SI	7207	71-27-24
72R-310-3	+	+
72R-310-4	+	+
72R-310-10	+	-
72R-310-11	-	+
72R-310-13	+	+
72R-310-14	+	+
72R-310-15	+	+
72R-311-1	+	+
72R-311-5	+	+
72R-311-7	+	+
72R-311-9	-	-
72R-311-10	+	+
72R-311-13	+	+
72R-311-14	+	+

Fig. 4. Determination of cross incompatibility using the 7207 (SC) and 71-27-24 (SI) parents as males in crosses to a. SC progeny and b. SI progeny (+ = compatible) (- = incompatible)

SI a. SC	72R-289-1	72R-289-2	72R-289-4	72R-289-5	72R-289-7	72R-289-8
71D-30-10	-	+	+	+	+	-
72R-289-6			-			-

SC b. SI	71D-30-10	72R-289-6
72R-289-1	+	
72R-289-2	+	
72R-289-4	+	+
72R-289-5	+	+
72R-289-7	+	+
72R-289-8	+	+

Fig. 6. Determination of cross incompatibility between two SC plants (71D-30-10, 72R-289-6) and their respective SI offspring and sib progeny. a. SC plants used as females in crosses, b. SC plants used as males in crosses (+ = compatible) (- = incompatible) (blank = cross not made)

a. SC	72R-310-1	72R-310-2	72R-310-5	72R-310-7	72R-310-8	72R-310-9	72R-310-12	72R-311-2	72R-311-3	72R-311-4	72R-311-6	72R-311-8	72R-311-11	72R-311-12	72R-311-15
7207	+	+	-	+	+	+	+	-	-	-	+	+	+	+	+
71-27-24	+	+	+	+	+	+	+	-	-	-	+	+	+	+	+

b. SI	72R-310-3	72R-310-4	72R-310-11	72R-310-13	72R-310-14	72R-310-15	72R-311-1	72R-311-7	72R-311-9	72R-311-10	72R-311-13	72R-311-14
7207	-	+	-	+	-	-	-	-	-	-	-	+
71-27-24	+	-	+	+	-	+	+	+	-	+	+	+

Fig. 5. Determination of cross incompatibility using the 7207 (SC) and 71-27-24 (SI) parents as females in crosses to a. SC progeny and b. SI progeny (+ = compatible) (- = incompatible)

Table 3. Segregation of self-incompatible (SI): self-compatible (SC) plants in 5 progenies from crosses between the original or derived plants of three SC sources

Parentage	Cross Number	Number of Plants SI	Number of Plants SC
7207 X 71D-30-10	73R-13	6	7
71D-30-10 X 7207	72R-316	5	5
72R-289-6 X 7207	73R-28	9	4
72D-189-4 X 7207	73R-11	7	9
72D-189-4 X 71D-30-10	73R-12	1	1
Totals		28	26

Table 4. Segregation of self-incompatible (SI): self-compatible (SC) plants in progenies from a cross between SC sibs (73R-24), from backcrosses between SC plants (73R-25, 73R-141) and from a backcross between SI plants (73R-142)

Parentage	Cross Number	Number of Plants SI	Number of Plants SC
72R-310-7 X 72R-310-5	73R-24	8	10
72R-310-7 X 7207	73R-25	1	3
72R-310-5 X 7207	73R-141	5	6
Totals		14	19
72R-311-7 X 71-27-24	73R-142	8	4

Table 5. Segregation of self-incompatible (SI): self-compatible (SC) plants in progenies produced by selfing the original or derived SC plants

Parentage		Cross Number	Number of Plants SI	Number of Plants SC
Cuttings				
7207	(selfed)	72R-309	3	3
"	"	73R-7	5	4
72R-310-1	"	73R-22	5	9
Subtotal			13	16
Seedlings				
72R-310-8	(selfed)	73R-88	4	0
72R-311-2	"	73R-93	0	1
72R-311-11	"	73R-95	11	4
72R-321-1	"	73R-104	6	0
72R-321-2	"	73R-105	4	0
72R-322-1	"	73R-100	5	3
72R-322-2	"	73R-101	3	1
72R-316-9	"	73R-116	3	0
73R-2-1	"	73R-138	1	1
73R-2-7	"	73R-139	8	2
70D-113-1	"	72D-189	0	1
Total			58	29

Intercrosses between related SC Sources

Three progenies produced by sib mating and backcrosses of SC plants from the 7207 source segregated a majority of SC plants (14 SI:19 SC) (Table 4). However, SI plants were recovered in all 3 progenies. High levels of PSC were apparent in the 73R-24 and 73R-141 families in which some seed was obtained on all plants following a self pollination.

Intercross of SI (SC × SI origin) × SI (SI × SI origin) Plants

This single backcross progeny segregated 8 SI: 4 SC plants (Table 4). Two of the 4 SC plants were highly SC yielding more than 30 seeds per head.

Selfed progenies of SC Plants

Progenies grown from selfed seed of SC plants exhibited no overall consistency for SI:SC segregation (Table 5). All 14 progenies, except for 2 single plant progenies, yielded SI plants; four progenies contained no SC plants. Two major problems were apparent in the selfed progenies. Weak growing plants often had poor flowers and many had limited pollen production, both of which may have significantly contributed to low seed yields. The lack of vigor evident in seedling progenies was somewhat reduced by repropagating the plants from cuttings. Three of the progenies (72R-309, 73R-7 and 73R-22) repropagated in this manner prior to testing for SC segregated 13 SI: 16 SC plants. This ratio is very close to the 14 SI: 19 SC ratio found for progenies from backcross and sib matings of SC plants from the same 7207 source, in which loss of vigor and poor pollen was not nearly as severe as in selfed progeny.

Diallels of 8 unrelated Plants and of full Sib Progenies

The combined self and cross compatibility of unrelated clones and of full sibs varied widely (Table 6). Compatibility among 8 unrelated clones was 71%. Reciprocal differences in cross compatibility were confirmed and individuals could be grouped into overlapping classes (Fig.7). When both parents were SI, 36 and 40% of the self and sib matings were compatible in 2 progenies. Eight progenies with 1 parent SC were tested for self and sib compatibility and ranged from a low of 37% to a high of 63% compatibility. Three progenies in which both parents were unrelated SC sources ranged from 57 to 68% compatibility. Compatibility in 1 of these families (73R-11) approached the level found among the 8 completely unrelated clones. Compatibility among families that were obtained by selfing or sib mating SC plants was reduced (45% and 31% respectively) compared to the SC × SC (unrelated cross) progenies.

Discussion

The infrequent occurrence of SC in both non-inbred selections and cultivars and the inbred plants indicates that genetic combinations controlling this factor are infrequent in these garden chrysanthemums. SC may arise rarely from intermating of fully SI plants as reported earlier (Drewlow, Ascher and Widmer, 1973) and confirmed in this study. Inbreeding, mostly by full sib mating, did not increase the frequency of SC as compared to the non-inbred selections and cultivars.

Since SC favors high self and cross seed yield it could be expected to be common in a breeding population in the absence of severe negative selection. Two factors associated with SC may combine to keep the frequency of SC at a low level in breeding materials: first, severe inbreeding depression indicated by a lack of vigor, and second, male sterility and slightly earlier

Table 6. Compatibility in diallel matings as related to the SC and genetic source of parents

Diallel Family	Compatibility of Parents	Number of Tests		Frequency of Compatibility
		Comp.	Incomp.	
Unrelated	6 (SI) 2 (SC)	42	17	71%
71D-12	SI X SI	10	5	40%
73R-45	SI X SI	9	16	36%
72R-289	SC X SI	11	19	37%
72D-217	SC X SI	7	8	47%
72R-321	SC X SI	9	11	45%
72R-311	SC X SI	22	23	49%
72R-322	SC X SI	5	4	56%
72R-310	SI X SC	32	19	63%
72R-313	SI X SC	31	34	48%
72R-287	SI X SC	13	19	41%
72R-316	SC X SC (unrelated)	17	13	57%
73R-13	SC X SC "	18	12	60%
73R-11	SC X SC "	26	12	68%
73R-24	SC X SC (related)	16	19	46%
73R-7	SC (selfed)	4	9	31%

♀ \ ♂	71-27-24	67-111-42	Purple Star	71D-30-10	Gala Gold	Raspberry Sundae	Acc. 7215	Acc. 7207
71-27-24 (SI)	-	+	+	+	+	+	+	+
67-111-42 (SI)	+	-	-	+	+	+	+	+
Purple Star (SI)	+	-	-	-		+	+	+
71D-30-10 (SC)	+	-	-	+		-		+
Gala Gold (SI)	+	+	-	-	-	-	+	-
Raspberry Sundae (SI)	+	+	+	-		-	+	+
Acc. 7215 (SI)	+	+	+	+	+	+	-	+
Acc. 7207 (SC)	+	+	+	+		+	+	+

Fig.7. Incompatibility patterns in crosses among 8 unrelated plants (6 SI and 2 SC)(+ = compatible)(- = incompatible) (blank = cross not made)

flower senescence. Both could lead to negative selection for biological and horticultural fitness.

Inheritance of SC in hexaploid chrysanthemum may not conform to any simple genetic explanation. All original SC sources arose from SI plants and can be expected to be heterozygous. Intercrosses with greenhouse chrysanthemums (Ronald and Ascher, 1975) support a similar genotype for 7207 and derived heterozygous plants produced by crossing 7207 to various SI plants. Several lines of evidence suggest that SC cannot be due to a single recessive gene. Consistent transmission of SC in progenies from crosses between SC and SI plants would not be expected unless all SI plants were heterozygous for SC, a proposition which is not supported by SI x SI crosses. The 1:1 segregation ratio in progenies of SC-SI crosses, even when using heterozygous SI plants as parents, would not be expected if SC is based on a recessive gene.

In the F_1 crosses between SC and SI plants, SC could be interpreted as behaving as a single dominant gene. With the exception of 1 progeny of 71D-30-10, all F_1 progenies of SC-SI crosses segregated in a relatively uniform 1 SI:1 SC pattern. The low frequency of SC transmission by 71D-30-10 and its backcross behavior suggest that this plant may have a different genetic basis for SC than in either of the other sources. On the basis of backcrossing alone, SC in 71D-30-10 appeared to be associated with a loss of pollen specificity (pollen-part mutation), however, in other crosses 71D-30-10 did exhibit cross incompatibility as a male. The action of a single dominant gene should result in 1 SI:3 SC ratios in progenies from selfing or intercrossing of SC plants carrying the same SC factor. Failure to find any consistent support for this ratio in progeny of 7207 raises doubt as to the validity of a single dominant gene basis for SC.

Qualitative genetic data is scarce in chrysanthemums. The hexaploid chromosome complement in chrysanthemum could support a digenic or multigenic basis for SC. Drewlow, Ascher and Widmer (1973) found evidence to suggest that SI was controlled by more than 1 locus. SC in hexaploid sweet potato was found to have a complex basis and Martin (1972, 1973), while unable to elucidate the genetic control, concluded that it must involve more than 1 gene. Crosses in chrysanthemum suggest that SC may involve more than 1 gene or at least involve a complex interaction of a single gene with 2 or more SI loci. The action of 2 complementing genes S should lead to a wide variation in segregation ratios in progenies of SC-SI crosses and should also result in variable ratios in SC selfed and SC-SC sib and backcross matings. Extensive progenies from SC-SI crosses, for the most part, segregated uniformly. Additional progenies from SC-SC crosses are needed before definite conclusions can be made regarding digenic behavior.

The effect of altering the criterion for SC was examined closely in all families. In the 72R-310 and 72R-311 families a criterion of 10 or more seeds per head for SC results in ratios of 8 SI:8 SC (72R-310) and 7 SI:8 SC(72R-31). If the criterion for SC is raised to 15 or more seeds per head the ratios become 9 SI:7 SC (72R-310) and 9 SI:6 SC (72R-311). Hypotheses explaining SC were not clarified by altering the criterion for SC.

Interpretations of inheritance patterns in chrysanthemums must consider the reported variable chromosome complement which ranges from 51 to 64 with a basic 6x number of 54 (Dowrick, 1953; Sampson et al., 1958; Dowrick and El-Bayoumi, 1966). Many of the flower color mutants that have been reported both naturally and as a result of radiation have been shown to result from a loss or gain of chromosomes. SC might similarly result from a change in the chromosome complement, perhaps from the loss of chromosomes carrying the incompatibility gene(s). Such a loss might account for the unusual breeding behavior of SC plants. In a normal diploid plant, differences would be expected in reciprocal crosses between a chromosome deficient plant and a normal plant. The buffering capacity of a hexaploid might well cover these differences.

Deviation from the expected segregation pattern could also be explained if SC operates only in the presence of heterozygous S-alleles at the S-gene(s). Intermating of related plants or selfing may produce partial S-allele homozygosity which could result in SI in the presence of the SC factor. This behavior could account for the higher levels of SI in selfed progenies of SC plants, as compared to progenies from SC-SC sib or backcross matings, since selfing should lead to the highest frequency of S-allele homozygosity. This behavior might also account for the release of SC in the cross of a SI (SC × SI) origin × SI (SI × SI origin) plant.

PSC, a condition which describes a low level of self seed yield which may not have clear genetic control, was evident in chrysanthemum. Lloyd (1967) found a similar condition in *Leavenworthia* following crossing between SC and SI natural populations. He did not, however, find any transmission of true SC in such crosses, a marked difference from the results of similar crosses in *Chrysanthemum*.

The occurrence of cross incompatibility in pollinations between SC plants and support for overlapping incompatibility classes in a diallel of 8 unrelated plants are both new to incompatibility. These events further underline the complexity of the self-incompatibility system in chrysanthemum.

Literature

de Nettencourt, D.: Radiation effects on the one locus gametophytic system of self-incompatibility in higher plants (a review). Theoret. Appl. Genet. 39, 187-196 (1969)

Dowrick, G.J.: The chromosomes of chrysanthemum. II. Garden varieties. Heredity 7, 59-72 (1953)

Dowrick, G.J.; El-Bayoumi, A.: The origin of new forms of the garden chrysanthemum. Euphytica 15, 32-38 (1966)

Drewlow. L.W.; Ascher, P.D.; Widmer, R.E.: Genetic studies of self incompatibility in the garden chrysanthemum, *Chrysanthemum morifolium* Ramat. Theoret. Appl. Genet. 43, 1-5 (1973)

Gerstel, D.U.: Self-incompatibility studies in guayule. II. Inheritance. Genetics 35, 482-506 (1950)

Hughes, M.B.; Babcock, E.B.: Self incompatibility in *Crepis foetida* (L.) subspecies *roeadifolia* (Biel) Schiz. et Keller. Genetics 35, 570-588 (1950)

Lewis, D.: Structure of the incompatibility gene. II. Induced mutation rate. Heredity 3, 339-355 (1949)

Lloyd, D.G.: The genetics of self-incompatibility in *Leavenworthia crassa* Rollins (Cruciferae). Genetica 38, 227-242 (1967)

Martin, F.W.: Inheritance of self-incompatibility versus self-fertility in the sweet potato. Incompatibility Newsletter 1, 17-19 (1972)

Martin, F.W.: Fertility, incompatibility and morphological abnormalities of sweet potato inbreds. Incompatibility Newletter 2, 29-31 (1973)

Ronald, W.G.; Ascher, P.D.: Transfer of self compability from garden to greenhouse strains of *Chrysanthemum morifolium* Ramat. (Manuscript for submission to J. Amer. Soc, Hort. Sci.)

Sampson, D.R.; Walker, G.W., Hunter A.W., Bragdo, M.: Investigations on the sporting process in greenhouse chrysanthemum. Can. J. Plant Sci. 38, 346-356 (1958)

Stebbins, G.L.: Self fertilization and population variability in the higher plants. Amer. Nat. 91, 337-354 (1957)

Thompson, K.F.; Taylor, J.P.: The breakdown of self-incompatibility in cultivars of *Brassica oleracea*. Heredity 21, 637-648 (1966)

Thompson, K.F.; Taylor, J.P.: Self-compatibility in kale. Heredity 26, 459-471 (1971)

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