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Genetics of Self Incompatibility in Diploid *Ageratum houstonianum* Mill.*

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Summary. Diallels and backcrosses among self-incompatible (SI) clones and progeny of *Ageratum houstonianum* Mill. could be organized into intra-incompatible classes. Four of 5 progenies segregated in expected ratios of S genotypes. *Ageratum* expressed a one-locus incompatibility system of the sporophytic type with a linear dominance series of multiple alleles and complete allelic dominance in both pollen and stigma. In the second part of the study, a high percentage of self-seed set was observed during the first flowering of a progeny from a pseudo-self compatible (PSC) seed source. Six progenies were derived from the PSC seed source. Five of the 6 segregated PSC : SI plants, 4 of which fit a 3 : 1 ratio of PSC : SI plants. All plants of the sixth progeny were SI. Two F_1 progenies with the same PSC pollen parent produced significantly different segregations of PSC : SI plants. It appeared that PSC acted as a major gene when the most recessive *S* allele was also present, but PSC was not expressed when the most dominant *S* allele was present. Clones propagated from PSC plants were SI and cross incompatible with a related *S*-allele tester. Thus, PSC was transient in that it was apparent in seed-propagated plants but not in plants clonally propagated from the PSC individuals.

Key words: Self incompatibility – Pseudo-self compatibility – *Ageratum*

Introduction

Self incompatibility (SI) is a natural barrier to self fertilization in many plant species. Self and cross incompatibility prevent fertilization when there is a matched *S* identity in pollen and pistil. Sporophytic SI is a system in which the *S* specificity or identity is determined by the sporophyte. The incompatibility reaction occurs on or near the stigma surface (Gerstel and Riner 1950), and is usually controlled in diploid plants by a single locus with multiple alleles and potential allelic interaction ranging from independence to complete dominance (Gerstel 1950; Hughes and Babcock 1950; Crowe 1954).

Several members of the Asteraceae have been shown to possess a sporophytic SI system (Gerstel 1950; Hughes and Babcock 1950; Crowe 1954; Habura 1957; Brewer and Parlevliet 1969; Imrie and Knowles 1971; Drewlow et al. 1973; Eenink 1981). *Ageratum houstonianum* Mill. is a member of this family, and is the only composite that is currently in commercial hybrid seed production using incompatibility for pollination control. The genetics of SI have never been established in ageratum or any other member of the Eupatorium tribe, although unpublished data of Reimann-Philipp (1965) suggested that ageratum probably had a sporophytic SI system. Thus, we were interested in characterizing the incompatibility system. We were also interested in the relationship between SI and pseudo-self compatibility (PSC), for 2 reasons. First, bud pollination is not a workable inbreeding technique with composites (Gerstel and Riner 1950), so some other form of inbreeding is necessary. Second, SI ageratum are inbred using apparent self-compatible parents, which segregate SI progeny. We wanted to know whether there was an interaction between SI and the apparent self compatibility.

Materials and Methods

1 Cultural Conditions and Crossing Technique

Cuttings of 3 unrelated diploid SI inbred clones[1], currently used to produce commercially available F_1 hybrids, were rooted in a peat-vermiculite medium under intermittent mist

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[1] Courtesy of Bodger Seeds Ltd., El Monte, Calif.

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for a 2 week period, transferred to 10 or 12 cm pots, and grown to flowering in a glasshouse at air temperatures of 17 °C night, 20 °C day. Seeds from crosses were germinated under mist and otherwise treated like rooted cuttings.

Inflorescences were trimmed to a terminal capitulum or flower head of buds when pigment formation was most intense, but before opening of the first corolla tube. Each peduncle was tagged and the capitulum covered with a glassine bag. Five to 10 days elapsed between trimming and first pollination, depending on weather conditions. Pollinations were then performed every other day until all rings of florets were open, receptive, and pollinated. Three pollinations were usually required for each cross. In preliminary tests, this pollination procedure resulted in the maximum seed set for time spent pollinating, when the cross was compatible. No emasculation was performed because of the small size and large number of florets, coupled with the fact that the anthers never appeared above the corolla tube. In addition, inflorescences used as the pollen sources were covered before anthesis to protect them from air-borne contamination.

Self pollinations on offspring of PSC parents were generally performed by bagging 3 capitula at once when in the bud stage, and tapping the bag lightly every other day to distribute pollen on the style branches. Terminal inflorescences were covered on the first flowering cycle of progenies 9AG28, 80-731, and 80-839. One capitulum on the terminal inflorescence and 2 on the side branches were covered during the first flowering cycle of progenies 80-38, 80-310 and 80-357.

Seeds were collected about 2 weeks after the last pollination when the floral parts above the achenes could be removed without disturbing any of the embryo-filled or empty achenes. Also at this time, the compatibility of the cross could be estimated visually. The entire capitulum with achenes attached to the receptacle was placed in a coin envelope and allowed to dry for several days to a week, after which the capitulum was shelled, and achenes were counted unter a 5× magnifying glass with fluorescent light. Filled achenes were black or opaque and distinguishable from empty achenes, which were translucent and collapsed under light pressure. Both kinds were counted. Data were reported as a percentage of potential achene set, that is, the number of filled achenes divided by the total number of achenes. Achene and seed set are used interchangeably, since each achene contains 1 seed. Achenes and chaff from a cross were all sown in germination medium, providing a check on the accuracy of the count. At no time did the number of germinated seeds exceed the achene count.

Plants from progenies were selected for crossing based on vigor and pollen-producing ability. Selections were cloned so that some plants of a clone could be used as seed parents, while other plants of the same clone could be used as pollen parents.

Table 1. A summary of crosses used to study the inheritance of self incompatibility and pseudo-self compatibility in ageratum

Inbred clonal diallel among BB-4, MB-3, and 22-2		
F_1 full sib diallels and backcrosses		
BB-4 (♀) × MB-3 (♂)	BB-4 (♀) × 22-2 (♂)	
↓	↓	
79-5	79-2	
17 siblings were:	10 siblings were:	
selected and 1. crossed in diallel 2. reciprocally backcrossed to each parent		
Backcross progenies		
BB-4 (♀) × 79-5-11 (♂)	BB-4 (♀) × 79-5-7 (♂)	
↓	↓	
79-539	80-2	
12 sibs were selected and crossed as ♀ to BB-4 and 79-5-11	10 sibs were selected and crossed as ♀ to BB-4 and 79-5-7	
F_2 progenies		
79-5-11 × 79-5-4	79-5-7 × 79-5-11	79-5-11 × 79-5-7
(♀) ↓ (♂)	(♀) ↓ (♂)	(♀) ↓ (♂)
79-632	80-158	80-268
8, 20, and 20 siblings, respectively, were all crossed to $S_{1.3}$, $S_{2.3}$, and $S_{3.3}$ pollen sources.		
Crosses involving a pseudo-self compatible seed source		
Inbred progenies	F_1, F_2, and backcross progenies	
'White Cushion'	BB-4 × 9AG28-3	22-2 × 9AG28-3
↓ ⊗	(♀) ↳ (♂)	(♀) ↳ (♂)
89AG23-1	88-357	80-310
↓ ⊗	80-357-17	
9AG28	1. selfed → 80-731	
9AG28-3	2. crossed as ♂ to BB-4 → 80-839	
↓ ⊗		
80-38		

2 Description of Crosses

The 3 original SI clones were crossed in diallel. From the compatible crosses, 2 F_1 progenies were generated. Each F_1 was crossed in a full sib diallel and the progeny backcrossed to both parents. Three F_2 progenies were generated from F_1 siblings that were cross compatible, and 2 backcross progenies were generated from compatible crosses of an F_1 plant to the female parent. These progenies were testcrossed to known S-genotype testers. A commercial diploid PSC source[1] was used to generate an I_2, and I_3, 2 F_1s, an F_2, and a BC generation. Again, all SI plants generated and used in crosses were test-crossed to known S genotypes or unrelated plants as a check on male and female fertility.

Each plant, with the exception of the clonal inbred parents, is identified by 3 numbers: the year in which the cross was made, the sequential cross number, and the plant number within the cross. A summary of crosses used in this study is presented in Table 1.

3 Analysis

The criterion for deciding whether a cross was compatible or incompatible was based on the distribution of seed sets in a frequency histogram. The separation between the high seed-set mode and the low seed-set mode was the dividing line between a compatible and an incompatible cross. Fifteen percent seed set and less was usually designated as an incompatible self or cross, and 16% seed set and greater was designated as a compatible self or cross. Because MB-3 was partially female sterile, 5% seed set and less was used as the criterion dividing an incompatible from a compatible cross when MB-3 was the seed parent. Compatible crosses or selfs were designated as "+" and incompatible as "–" in diallels. Each "+" or "–" was the average of 2–3 crosses.

The genetic control of SI was deduced from the compatibility classes present in the clonal and F_1 diallels and backcrosses. Chi-square tests were performed on S-genotype ratios in backcross and F_2 progenies to test the hypothesis and the assumption of random transmission of *S* alleles. Chi-square tests were also used to check goodness-of-fit ratios in I_2, I_3, F_1, F_2 and BC progenies and interaction between PSC and the *S* locus in 2 F_1 progenies.

Two single-gene markers, flower color and pappus scale length, were used to insure that SI parents were not producing selfed contaminants in crosses and that PSC parents were not producing apomictic seeds.

Results and Discussion

1 Self Incompatibility

Among crosses of the clonal inbreds, MB-3 and 22-2 were reciprocally incompatible. BB-4 was reciprocally compatible with both of the other clones. All 3 clones were strongly SI. In the 79-5 F_1 full sib diallel and backcrosses, there were 2 intra-incompatible, but reciprocally inter-compatible classes (Table 2). One class, containing 79-5-1, 2, 4, 5, 7, 9, 13, 15, and 17 was reciprocally cross compatible with the female parent BB-4, but was reciprocally cross incompatible with the

Table 2. Compatibility patterns in the 79-5 full sib diallel and reciprocal backcrosses to both parents. Incompatible crosses yielded 15% seed set and less, and compatible crosses yielded 16% seed set and greater, except when MB-3 was used as seed parent, in which case 5% seed set divided incompatible from compatible crosses. Blanks are crosses that were not made

♀ \ ♂	79-5-																			
	1	2	4	5	7	9	13	15	17	3	6	8	10	11	12	14	16	MB-3	BB-4
−1	–	–	–	–	–	–	–			+	+	+	+	+	+	+	+	–	+
2	–	–	–	–	–	–				+	+	+	+	+				–	+
4	–	–	–	–	–	–				+		+	+	+				+	+
5	–	–	–	–	–	–	–			+	+	+	+	+	+	+	+	–	+
7	–	–		–	–	–	–			+	+	+	+	+	+	+	+	–	+
9	–		–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	–	+
13	–			–	–	–	–	–	–	+	+	+	+	+	+	+	+	–	+
15					–	–	–	–	–			+	+	+	+	+	+	+	+
17							–	+	–				+	+	+	+	+	–	+
3	+	+	+	+	+	+	+			–	–	–	–	–				+	+
6	+	+	+	+	+	+	+			–	–	–	–	–	–	–	–	+	+
8		+	+	+	+	+	+			–	–	–	–	–	–	–		+	+
10	+	+	+	+	+	+	+	+			–	–	–	–	–	–	–	+	+
11	+	+	+	+	+	+	+	+	+		–	–	–	–	–	–	–	+	+
12	+			+	+	+	+	+	+		–	–	–	–	–	–	–	+	+
14	+			+	+	+	+	+	+		–	–	–	–	–	–	–	+	+
16	+			+	+	+	+	+	+		–	–	–	–	–	–	–	+	+
MB-3	–	–	–	–	–	–	–	–	–	–	+	–	+	+	+	+	+	–	+
BB-4	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–

Table 3. Compatibility patterns in the 79-2 full sib diallel and reciprocal backcrosses to both parents. Incompatible crosses yielded 15% seed set and less, and compatible crosses yielded 16% seed set and greater

♀ \ ♂	1	2	3	4	6	7	9	11	15	19	22-2	BB-4
79-2-1	–	–	–	–	–	–	–	–	–	–	–	+
2	–	–	–	–	–	–	–	–	–	–	–	+
3	–	–	–	–	–	–	–	–	–	–	–	+
4	–	–	–	–	–	–	–	–	–	–	–	+
6	–	–	–	–	–	–	–	–	–	–	–	+
7	–	–	–	–	–	–	–	–	–	–	–	+
9	–	–	–	–	–	–	–	–	–	–	–	+
11	–	–	–	–	–	–	–	–	–	–	–	+
15	–	–	–	–	–	–	–	–	–	–	–	+
19	–	–	–	–	–	–	–	–	–	–	–	+
22-2	–	–	–	–	–	–	–	–	–	–	–	+
BB-4	+	+	+	+	+	+	+	+	+	+	+	–

Table 4. Assignment of S alleles in clonal and F_1 diallels, and backcrosses, assuming a single-locus sporophytic self-incompatibility system with a linear dominance series, where $S_1 > S_2 > S_3$ in both pollen and stigma

Clonal inbred diallel

♀ \ ♂	MB-3 $S_{1.2}$	22-2 $S_{1.1}$	BB-4 $S_{3.3}$
MB-3 $S_{1.2}$	–	–	+
22-2 $S_{1.1}$	–	–	+
BB-4 $S_{3.3}$	+	+	–

79-5 sib diallel & backcrosses

♀ \ ♂	$S_{1.}$	$S_{2.3}$	$S_{1.2}$	$S_{3.3}$
$S_{1.3}$	–	+	–	+
$S_{2.3}$	+	–	+	+
$S_{1.2}$	–	+		
$S_{3.3}$	+	+		

79-2 sib diallel & backcrosses

♀ \ ♂	$S_{1.3}$	$S_{1.1}$	$S_{3.3}$
$S_{1.3}$	–	–	+
$S_{1.1}$	–		
$S_{3.3}$	+		

male parent MB-3, with 2 exceptions. The other class, including 79-5-3, 6, 8, 10, 11, 12, 14, and 16, was reciprocally cross compatible with both male and female parents MB-3 and BB-4, with 2 exceptions. All exceptions were near the dividing line between a compatible and an incompatible cross. Pseudo compatibility and sterility were judged responsible for these exceptions. The 79-2 F_1 full sib diallel and backcrosses yielded just 1 fully intra-incompatible class (Table 3). Each sib was reciprocally compatible with female parent BB-4, but reciprocally incompatible with male parent 22-2.

At this point, we established a working hypothesis. We proposed that incompatibility was based on a single-locus sporophytic system that operated with multiple alleles arranged in a linear dominance series, and that S_1 was dominant to S_2, which was dominant to S_3 in both pollen and stigma. According to this hypothesis, the preceding results could be explained in the following way. Two of the inbred clones were S-genotype homozygotes and 1 clone was an S-genotype heterozygote. In particular, clone 22-2 was $S_{1.1}$, BB-4 was $S_{3.3}$, and MB-3 was $S_{1.2}$ (Table 4). The 3 clones had a total of 3 S alleles. The 79-5 F_1 full sib diallel

Table 5. Chi-square test of *S*-genotype ratios in backcross progenies 79-539 and 80-2, and F_2 progenies 79-632, 80-158, and 80-268

Backcrosses	Observed			Expected			p
	$S_{1.-}$	$S_{2.3}$	$S_{3.3}$	$S_{1.-}$	$S_{2.3}$	$S_{3.3}$	
79-539	0	4	8	0	6	6	0.500 – 0.250
80-2	6	0	4	5	0	5	0.750 – 0.500
F_2s	$S_{1.-}$	$S_{2.3}$	$S_{3.3}$	$S_{1.-}$	$S_{2.3}$	$S_{3.3}$	
79-632	8	0	0	4	2	2	0.025 – 0.010
80-158	8	3	9	10	5	5	0.250 – 0.100
80-268	14	3	3	10	5	5	0.250 – 0.100

consisted of 2 classes: 1 class was $S_{1.3}$, and the other class was $S_{2.3}$. The 79-2 F_1 full sib diallel consisted of just 1 class, which was $S_{1.3}$. BB-4 may have had another *S* allele, which could have been concealed if it were recessive to the first 3 alleles, but no evidence was found to support the existence of an S_4 allele among these plants. We performed a chi-square test of S-genotype ratios from backcross and F_2 progenies to test the hypothesis outlined above (Table 5). Under the assumption of random transmission of *S* alleles, the observed S-genotype ratio differed significantly from the expected ratio in the 79-632 progeny only. In this case, all genotypes were $S_{1.-}$ whereas $S_{2.3}$ and $S_{3.3}$ genotypes were expected as well. Since the original cross was $S_{2.3}$ (♀)×$S_{1.3}$ (♂), it appeared that only S_1 pollen tubes penetrated the stigma. However, backcrosses 79-539, $S_{3.3}$ (♀)×$S_{2.3}$ (♂), and 80-2, $S_{3.3}$ (♀)×$S_{1.3}$ (♂), showed no evidence that either S_1 or S_2 alleles had a selective advantage over the S_3 allele. The exceptional progeny 79-632 may have been significant. However, we have found no explanation other than that the progeny size was too small to detect the other *S* genotypes.

Since no reciprocal differences in incompatibility were detected, allelic dominance was complete in both pollen and stigma. However, our conclusions were based on plant material from a narrow genetic base, and probably should not be applied to the species as a whole. Pollen-only dominance or stigma-only dominance may occur in other samples of ageratum germplasm.

There was no apparent difference in the strength of the SI reaction relative to homo- or heterozygosity at the *S* locus in the 3 original clones. Two of the clones, MB-3 and 22-2, had the dominant S_1 allele in common. These clones came from different commercial sources (Drewlow, personal communication), which confirms the plant breeder's common knowledge that unrelated breeding material should be tested for identical *S* alleles.

2 Pseudo-self Compatibility

2.1 Inheritance

Among crosses with a common PSC parent, a frequency distribution of percent self-seed set in I_2, I_3, 80-357 F_1, F_2, and BC progeny histograms showed that 4 of the progenies exhibited more than 2 frequency peaks, and thus could not be assumed to be bimodal (Fig. 1). However 4 of the 5 progenies had a frequency peak in the area from 0–15% seed set that corre-

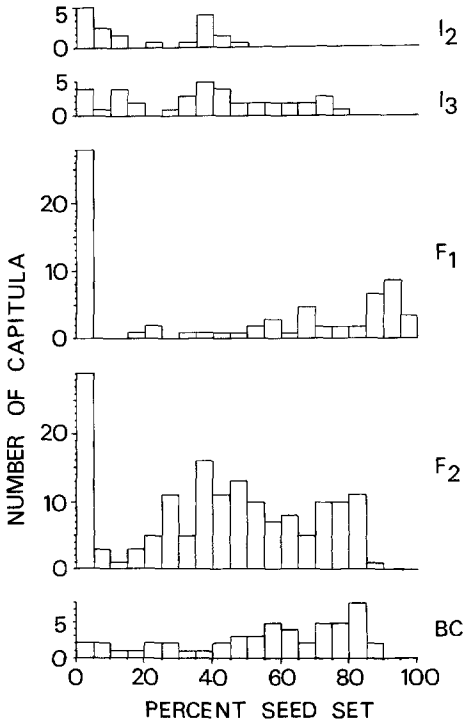

Fig. 1. Frequency histogram of percent self-seed set from the 9AG28 I_2, 80-38 I_3, 80-357 F_1, 80-731 F_2, and 80-839 BC progenies

Table 6. Segregation of pseudo-self compatible (PSC): self incompatible (SI) plants in 6 related progenies and chi-square tests of a 3 : 1 PSC : SI offspring ratio. Incompatible selfs are classified as having 0 – 15% seed set, compatible selfs having greater than 15% seed set

Parentage	Cross number	Generation	Number of plants		p
			PSC	SI	
8AG23-1 selfed	9AG28	I_2	3	4	0.050 – 0.025
9AG28-3 selfed	80-38	I_3	16	3	0.500 – 0.250
80-357-17 selfed	80-731	F_2	42	11	0.750 – 0.500
BB-4×80-357-17	80-839	BC	15	2	0.250 – 0.100
22-2×9AG28-3	80-310	F_1	0	46	< 0.005
BB-4×9AG28-3	80-357	F_1	17	7	0.750 – 0.500
		F_1 total	17	53	
			d. f.	X^2	
		F_1 total	2	138.22	< 0.005
		pooled	1	96.02	< 0.005
		inter.	1	42.2	< 0.005

sponded closely with the frequency peak of incompatible selfs and crosses from the 79-5 SI sib diallel. Therefore, 0–15% seed set was interpreted as being SI in these 5 progenies. Four of the 5 progenies had more than 1 frequency mode in the high self seed area from 16–100% seed set that we have called the PSC-class area. (The term PSC is used to describe the high level of self-seed set encountered in these progenies because a fully functional SI system was later found in all individuals tested from all progenies except the BC progeny, which was not tested for *S* activity). Even though several modes were found in the PSC-class area of these progenies, all these offspring were included in the PSC class for 2 reasons. First, low sample size may have obscured a real single peak in the PSC class. Second, there may be quantitative inheritance for seed yield. For example, a few individuals typically contributed to each frequency peak in percent seed set within the PSC-class area, suggesting that there were genotypic differences among individuals of a progeny that were unrelated to their classification as PSC individuals.

Of the progenies derived from crosses with a PSC parent, 5 of the 6 showed a mendelian segregation. A chi-square test showed that I_3, F_1 80-357, F_2, and BC progenies fit a 3 : 1 ratio of PSC : SI plants (Table 6). This ratio would be expected in all segregating progenies if the parents of each progeny were heterozygous for a dominant, single-gene PSC trait. The I_2 progeny contained only 7 plants, so low sample size may have accounted for the significant difference between observed and expected. If BB-4 was PSC at one time, the BC and 80-357 F_1 progenies also should have segregated in a 3 : 1 ratio of PSC : SI plants. Under this assumption, the expected ratios fit the observed data. The PSC : SI segregations suggested that PSC was inherited as a single-gene trait.

The 80-310 F_1 progeny did not segregate; all plants were SI (Table 6). Furthermore, all plants were cross incompatible with an $S_{1,3}$ pollen source, indicating that all were $S_{1,3}$ genotypes. Both 80-310 and 80-357 F_1 progeny totals from the PSC and SI classes were pooled and a highly significant interaction chi-square term was produced. Apparently, PSC was expressed when the genotype was $S_{3,-}$ but not expressed when the genotype was $S_{1,-}$.

In this study, SI offspring were found in all progenies from PSC parents. Reports from breeders suggest that this is a general rule with sources of PSC from open-pollinated cultivars of ageratum (Drewlow, personal communication). PSC is a valuable trait for inbreeding ageratum to produce SI clonal parents for F_1 hybrid production, as long as it is not linked to specific *S* alleles. It seems reasonable that this trait may also be present in other ornamental composites that are not now being produced as F_1 hybrids, or are being produced using more expensive methods of pollination control.

2.2 Transience of PSC

After the original PSC parent 9AG28-3 was cloned, diallel crosses revealed that it was SI and reciprocally cross incompatible with BB-4, yet reciprocally compatible with 22-2. Furthermore, all offspring of the PSC F_1 80-357 progeny were apparently SI after cloning

Table 7. Compatibility patterns between the 80-357 F_1 seedling progeny and the SI parent during the first flowering cycle and after cloning

	♂ / ♀	80-357-														
		2	9	10	12	16	17	23	3	11	14	18	21	22	6	7
1st flo. cycle	⊗	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–
	BB-4	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–
	$S_{1.3}$														+	+
After cloning	⊗	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	BB-4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	$S_{1.3}$	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
After cloning	♀ / ♂	80-357-														
		2	9	10	12	16	17	23	3	11	14	18	21	22	6	7
	BB-4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	$S_{1.3}$	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

(Table 7). All were fully male and female fertile and all were reciprocally cross incompatible with the $S_{3.3}$ tester, BB-4. Two SI 80-357 F_1 offspring were tested and continued to be SI and cross incompatible with BB-4, as before. It should be noted that each cross reported in Table 6 was incompatible after the respective parents were cloned, except 80-310, which was always compatible.

Two F_2 offspring, 80-731-149 and -170, were found to differ in their ability to maintain PSC in the first flowering from seed. One of the plants, 80-731-149, was PSC from the terminal inflorescence to the fifth node. Thereafter, some nodes contained PSC flowers and other nodes contained SI flowers. The other plant, 80-731-170, was PSC on flowers at the terminal inflorescence, but was SI on flowers at the fifth to basal nodes.

True self compatibility has been defined as a loss of function of the *S* locus, whereas pseudo-self compatibility has been defined as a condition in which a plant retains expression of some part of the *S* locus even though the plant will set seeds following self pollination (Ascher 1976). Many plants in the I_2, I_3, F_1, F_2 and BC generations exhibited self-seed set comparable to that which would be expected if they were self compatible. However, all plants from these progenies retained full expression of the *S* locus sometime after the first flowering cycle. The transition to SI was observed in the 80-357 F_1 offspring that were backcrossed to BB-4 in the first flowering cycle: about half had made the transition when pollen was collected from apparently SI side branches, and were cross incompatible with BB-4; the other half were pseudo compatible with BB-4, probably because pollen used was PSC (Table 7). Even though no controlled environments were tested, no obvious environmental effect was noticed, and no reversion to PSC was observed. Other PSC sources may not be transient in expression, but if BB-4 arose from such a source, it would explain the 3 : 1 PSC : SI segregations in BC and 80-357 F_1 progenies (section 2.1). This study shows that PSC can be transient in expression.

Cross pollination did not stimulate self pollen to grow in PSC plants. One of the PSC F_1 plants, 80-357-9, which was apparently SI after cloning and heterozygous dominant for blue flowers and long pappus scales (BbPp), was testcrossed to a pollen source which was bbPP (homozygous for white flowers and long pappus scales). The progeny, 81-692, segregated 28 blue: 29 white-flowered plants, and all had long pappus scales, which suggested that at the time of the cross, 80-357-9 was strongly SI. Nearly 25% of 80-357-9 selfs should have been white-flowered or exhibited short pappus scales, if 80-357-9 was PSC. If apomixis was prevalent, most plants should have been blue-flowered.

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