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The Inheritance of Pseudo-Self-Compatibility (PSC) in *Nemesia strumosa* Benth.*

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Summary. Pseudo-self-compatibility (PSC) in *Nemesia strumosa* was determined by recessive modifying genes which interferred with the normal stylar incompatibility reaction. The PSC levels ranged from none or low to amounts resembling full self-compatibility. PSC within a progeny could be maintained at low or high levels by selecting parents either high or low in PSC. Pollen from plants of any PSC level failed to produce seed when placed on other incompatible styles bearing the same *S* alleles.

Introduction

Self incompatibility, determined by a single gene, the *S* gene, prevents seed set after self pollination even though a plant has functional ovules and pollen. In the gametophytic system of self incompatibility (East and Mangelsdorf 1925), matching identity between the *S* allele in the haploid pollen tube with either of the two in the diploid style inhibits normal growth of that pollen tube. When there is no match between *S* alleles, the pollen tubes grow normally and insure fertilization.

The self-incompatibility system poses a barrier to inbreeding; much work has been done studying ways to overcome it. Pollen-part (Lewis 1951, 1961; Lewis and Crowe 1954) and stylar-part (Lewis and Crowe 1954; Pandey 1956) mutants are two types of genetic changes within the *S*-locus which theoretically prevent its activity and allow plants bearing them to produce full complements of seed after self-pollination. The presence of S_f alleles (East 1929; Williams and Williams 1947; Takahashi 1973) which override the *S*-gene has been reported and similarly results in full seed set after selfing.

Another means of procuring some self seed is by pseudo-self-compatibility (PSC). PSC is a phenomenon in which plants with a functional incompatibility system produce self seeds in amounts ranging from an occasional few to levels approaching true self-compatibility. Large variation in the amounts of self typifies a pseudo-self-compatible plant.

Freely segregating modifying genes which interfere with normal *S*-gene activity have been proposed to explain PSC (Atwood 1942; Denward 1963; Mather 1943; Takahashi 1973; Williams and Silow 1933). In some cases these genes seemed subject to environmental interaction (Denward 1963) and sometimes were additive in effect (Atwood 1942). Environmental effects have often been considered a major factor in the expression of PSC (Leffel 1971; Stout 1938). Differential self pollen tube growth rates have been associated with different *S* allele combinations in the style; the fastest growth rates occurred when the PSC levels were the highest (East 1934; Takahashi 1973). Interspecific crosses of a self-incompatible and a self-compatible species resulted in a progeny with PSC (Mather 1943). Polygenes from the self-compatible species apparently interferred with the polygenic background of the self-incompatible species leading to various degrees of PSC. In general, inbreeding has not been a successful means of increasing PSC levels (Denward 1963; Duncan *et al.* 1973; Taylor *et al.* 1970; Townsend 1965).

Nemesia strumosa, a cool season annual in the Scrophulariaceae with a strong gametophytic self-incompatibility system (Riley 1933), is a good plant for genetic studies of self incompatibility. The plants flower in 10-12 weeks from seeding. Flowers are borne on indeterminant racemes which bloom for several weeks. The flowers are easy to emasculate and pollinate after which the sepals close over the style providing a barrier to foreign pollen. Rapid development of seed cap-

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sules enables one to determine the success or failure of a pollination within a few days and in 2-4 weeks seed capsules are ripe and ready for harvest. The presence of a single seed preserves the seed capsule until maturity so small seed sets, resulting from rare mutations in the *S* gene or low levels of PSC, can be detected and rescued. We had planned to use *Nemesia* in irradiation experiments to obtain pollen-part mutants but the consistent occurrence of PSC often made the plants under study difficult to characterize. Detailed studies of the genetics of PSC - within a single species expressing levels of PSC - from none or low, to those approaching true self compatibility are scarce, so we began to study the genetics of PSC in *Nemesia*.

Materials and Methods

Growing the Seedlings and Testing for PSC

Nemesia seeds were soaked overnight on filter paper moistened with 100 ppm gibberellic acid and transferred to finely milled sphagnum moss. Germination occurred within 4-5 days. Seedlings were placed under approximately 1200 ft-cd. of constant lighting from incandescent and fluorescent bulbs to speed initial growth. At the four leaf stage young plants were potted in 2-inch plastic pots in a mixture of equal parts peat moss, perlite and soil. They were repotted into 4-inch and finally 5 or 6 inch pots. Plants nearing flowering were moved to greenhouse sections held at 13° C nights. Pollination was begun when all the plants in a progeny were flowering and in a vigorous state of growth. Crossing was done during the fall, winter and spring seasons to avoid hot summer weather and its possible effects on self seed set (Campbell and Ascher 1972). In place of the standard diallele, used to determine *S* genotypes, individual plants were studied using selfing and a series of tester crosses. The type of tester crosses and their purposes were: 1. Crossing as female with a plant having at least one *S* allele different (to determine the maximum seed setting ability); 2. Crossing reciprocally with incompatible plants of the same *S*-genotype (to look for lack of pollen or stylar activity or new *S* specificities); 3. Crossing as female with plants homozygous for the *S* alleles each plant contained (to check for differing activity between *S* alleles in the style); and, 4. Crossing as male in a compatible combination (to test for the production of fertile pollen). Most plants were self pollinated 5-7 times or more and tester crosses, if possible, were made at least twice and often 5-7 times or more. The same pollination on any one plant was not made more than twice in the same day to average the effects of environmental variation on seed set. Flowers were emasculated and pollinated on the day of anthesis with any unused ones removed to avoid contamination. Initially, all stigmas were washed before pollination with a pipe cleaner wetted in tap water, but this practice was eventually discontinued for selfing, and later for all crosses, as no evidence of contamination was encountered in the screened greenhouses. Seed counts from all pollinations were recorded and the means computed. The percent PSC (% PSC) of a plant was determined by dividing its mean self seed set by its average seed set from tester crosses as female in compatible combinations. Histograms were used to show the distribution of % PSC among the members of a progeny. Each diagram lists the progeny code, the cross which gave the population and the overall mean % PSC for the progeny.

Seed Source and Types of Crosses

Three seedlings, 69NG1 ($S_{3.4}$), 69NG2 ($S_{1.2}$) and 69NG3 ($S_{2.3}$), were selected from a partial diallele involving 39 plants grown from seed purchased from the Harry E. Saier Seed Company of Diamondale, Michigan. These plants each produced a few seeds from only one of several self pollinations. *S* alleles were determined and arbitrarily numbered by diallele tests of self and intercross progenies (Campbell and Ascher 1972). The selfed progeny of 69NG3 and the progeny of 69NG1 × 69NG2 were ancestral to all succeeding generations of nemesias used in this study (Fig. 1). Seedlings were numerically coded with the 1st two numbers representing the population code and the last number the seedling number. For example, plant 73-20-24 refers to the 24th seedling from population 73-20.

Individual mean self and compatible cross seed sets, % PSC and *S* genotype of the parental plants are listed (Table 1). In general, three main types of crosses were made to study the inheritance of PSC in *Nemesia*:

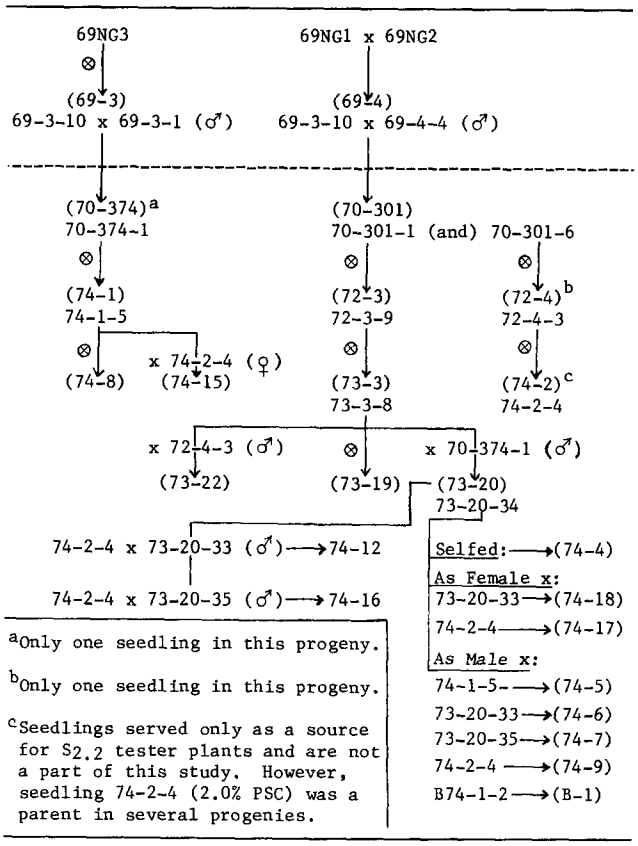

Fig. 1. A lineage of nemesias used studying the inheritance of pseudo-self-compatibility (PSC) in *Nemesia strumosa*

Table 1. The *S*-genotype, percent pseudo-self-compatibility (PSC), mean self, cross, and tester-cross seed sets of *Nemesia* seedlings used as parents in crosses to study the inheritance of PSC

Seedling	*S*-Genotype	% PSC	Type of Pollination			
			Self	Compatible Cross as Female	$S_{2.2}$ Tester as Male	$S_{3.3}$ Tester as Male
70-301-1	2.3	3.3	2.2	67.0	---	---
70-301-6	2.3	1.1	0.8	70.1	---	---
72-3-9[a]	2.3	---	22.8	---	---	---
73-3-8	2.3	100.0	24.4	21.8	15.3	23.2
70-374-1	3.3	0.1	0.4	69.9	---	---
72-4-3	2.2	1.0	0.4	41.8	---	---
73-20-34	2.3	100.0	41.5	39.9	20.7	28.8
74-1-5	3.3	75.0	40.2	53.6	---	12.0
73-20-33	3.3	0.0	0.0	39.0	---	---
73-20-35	3.3	45.1	31.1	69.0	---	3.7
74-2-4	2.2	2.0	0.8	40.6	0.4	---
B74-1-2[b]	---	0.0	0.0	61.3	---	---

[a] Compatible cross seed set data lacking for this plant
[b] *S*-alleles not determined but can be labeled as $S_{x.y}$

1. Low level PSC plants (0.0-3.3 %) were selfed and intercrossed;
2. Highly PSC plants (75.0-100.0 %) were selfed and intercrossed;
3. Highly PSC plants were crossed with plants low in PSC. Several crosses of each type were made.

Results

Inbreeding

The four seedlings in I_0 population 70-301 (Fig.2) had an overall mean PSC level of 2.0 %. Seedling 70-301-1, 72-3-9 and 73-3-8 yielded I_1 (72-3), I_2 (73-3) and I_3 (73-19) progenies respectively in which the overall mean PSC level went from 19.3 % to 34.8 % to 70.1 % (Fig.1 and 2). In I_3 progeny 73-19, 7 of 14 seedlings were above 90.0 % PSC while the other 7 ranged between 0.0 % and 70.0 % PSC. Due to loss of vigor, plant size and an approximate 50.0 % or more reduction in maximum seed setting ability in the I_3's, an I_4 progeny was not grown.

High × Low and Low × Low Crosses

A 100.0 % PSC I_2 plant (73-3-8) crossed with an 0.1 % plant (70-374-1) gave 31 seedlings (population 73-20) with an overall mean PSC level of 14.5 % and when crossed with a 1.0 % PSC plant (72-4-3) gave 11 seedlings (population 73-22) with 6.9 % PSC (Fig.3). This was a dramatic drop in PSC compared to the I_3 progeny (73-19) from 73-3-8 (Fig.2). In the progenies

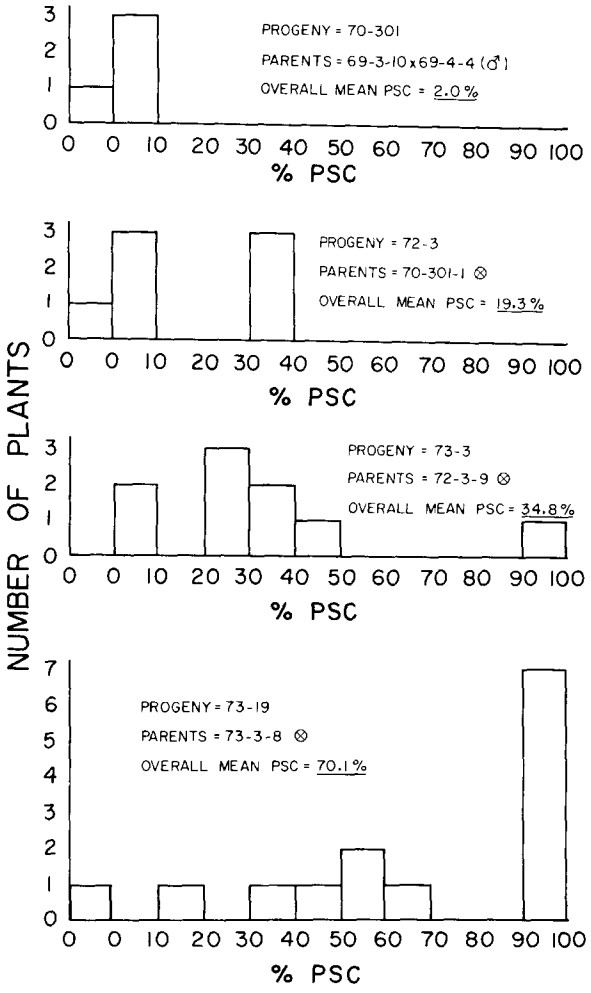

Fig.2. Frequency distribution of % PSC in four populations of *Nemesia strumosa* representing I_0 (70-301), I_1 (72-3), I_2 (73-3) and I_3 (73-19) generations

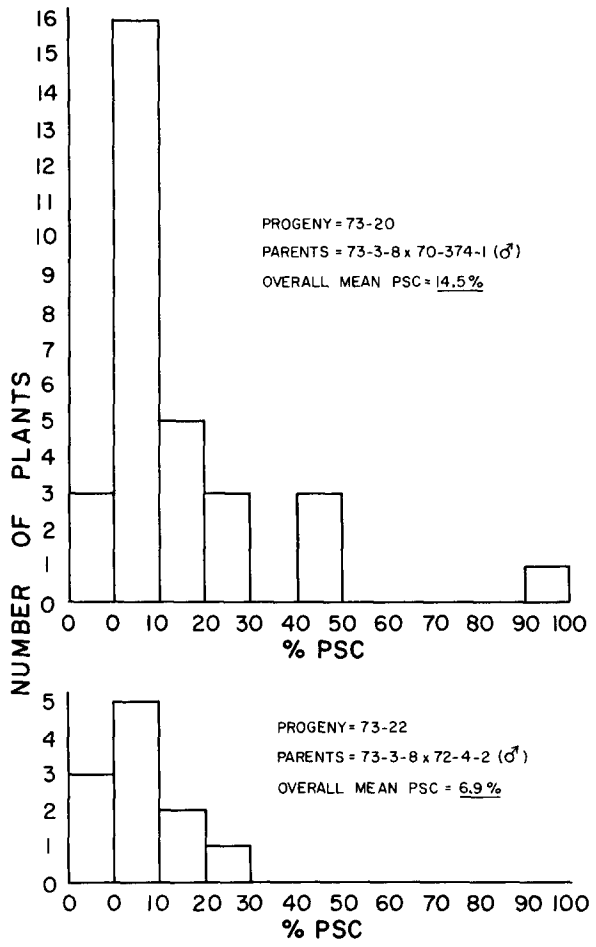

Fig.3. Frequency distribution of % PSC in two populations of *Nemesia strumosa* from crosses of a 100.0 % PSC plant (73-3-8) with a 0.1 % PSC plant (70-374-1) and a 1.0 % PSC plant (72-4-3)

from selfing 70-374-1 and 72-4-3 (Fig.4), the overall mean PSC was 14.1 % and 4.2 % respectively. When these two plants were intercrossed, 70-374-1 as female, 19 seedlings (progeny 73-21) yielded a mean PSC value of only 4.6 % (Fig.4 and Table 2). Four of the inbreds from 70-374-1 had PSC levels greater than 20.0 % but none occurred above this level when 72-4-3 was selfed (Fig.4). Similarly none of the offspring in population 73-22 or 73-21 were above 30.0 % PSC but four such plants were present in population 73-20 (Fig. 3 and 4). When crossing a plant low in PSC with one high, or another low, the majority of the offspring were in the 0.0-10.0 % PSC class.

High × High Crosses

Selfing a 100.0 % PSC plant (73-20-34) produced population 74-4 consisting of 39 seedlings with an overall mean PSC level of 83.3 % (Fig.5 and Table 3). The 14 seedlings of population 74-8, obtained by selfing a 75.0 % PSC plant (74-1-5), averaged 71.4 % PSC overall (Fig.5 and Table 3). Intercrossing these two plants, 74-1-5 as female, gave 42 seedlings (progeny 74-5) which had an overall mean PSC value of 84.2 % (Fig.6 and Table 3). Only one plant in populations 74-4, 74-5 and 74-8 had a level of PSC less than 40.0 %. Also, the majority of seedlings in progenies 73-19, 74-4, 74-5 and 74-8, highly PSC plants either selfed or intercrossed, were in the 90.0-100.0 % PSC class.

Table 2. The overall mean percent pseudo-self-compatibility (% PSC), self and tester-cross seed sets in eight populations of *Nemesia* resulting from crossing or selfing plants low (3.3 % or less) in PSC

Population	*S*-Genotype	No. Plants	Self	Compatible Cross as Female	$S_{2.2}$ Tester as Male	$S_{3.3}$ Tester as Male	$S_{2.3}$ Tester as Male	Overall % PSC
70-301	2.3	4	1.1	56.8	---	---	---	2.0
74-1	3.3	18	6.7	48.1	---	3.1	---	14.1
74-2	2.2	8	0.8	26.8	2.3	---	---	2.7
73-21	2.3	19	2.8	62.6	1.3	4.1	3.6	4.6
72-3[a]	---	7	11.1	59.8	---	---	---	19.3
73-3[b]	---	9	9.0	26.1	---	---	---	34.8
74-12	2.3	6	2.8	61.2	---	---	3.3	4.2
74-16[c]	2.3	12	7.3	72.8	---	---	2.9	9.5

[a] *S*-genotype of all seedlings not determined but either $S_{2.2}$, $S_{3.3}$ or $S_{2.3}$

[b] % PSC of the parent plant (72-3-9) of this population not determined

[c] % PSC of the male parent plant (73-20-35) was 45.1 %

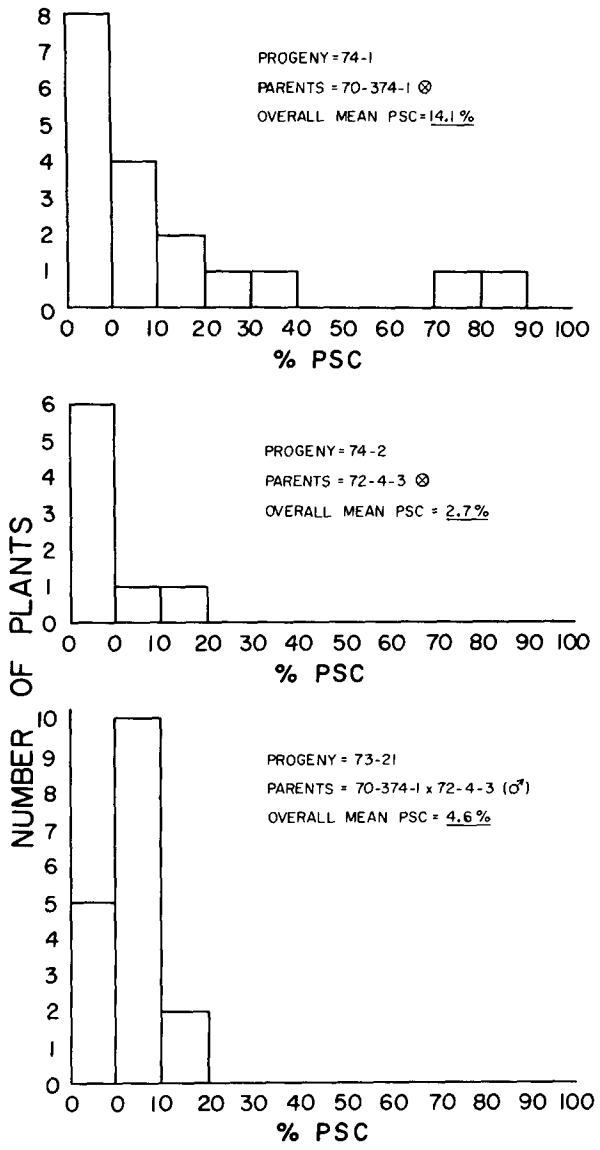

Fig. 4. Frequency distribution of % PSC in three populations of *Nemesia strumosa* from selfing and intercrossing a 0.1 % PSC plant (70-374-1) and a 1.0 % PSC plant (72-4-3)

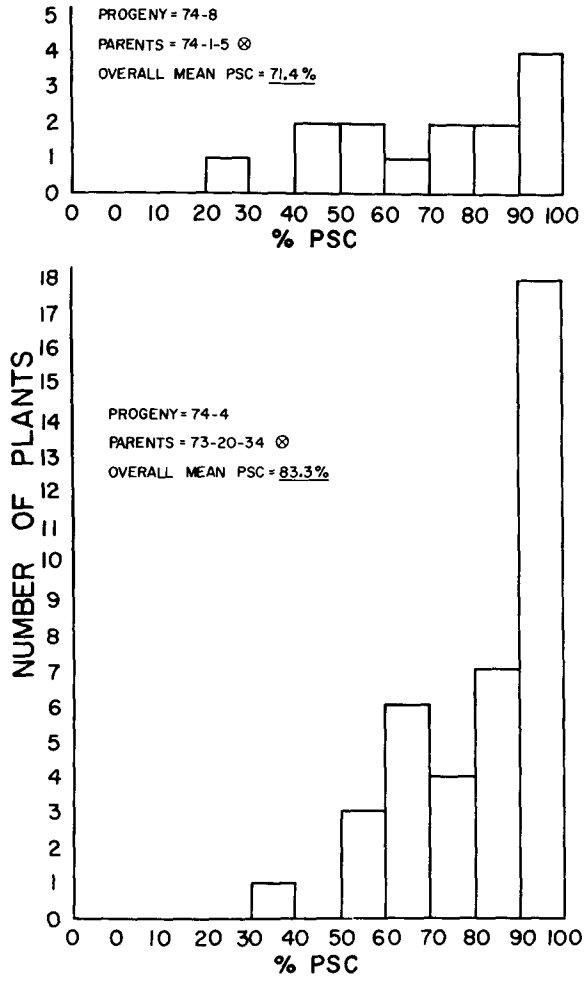

Fig. 5. Frequency distribution of % PSC in two populations of *Nemesia strumosa* from selfing a 75.0 % PSC plant (74-1-5) and a 100.0 % PSC plant (73-20-34)

Table 3. The overall mean percent pseudo-self-compatibility (% PSC), self and tester-cross seed sets in four populations of *Nemesia* resulting from crossing or selfing plants high (75.0 % +) in PSC

Population	*S*-Genotype	No. Plants	Self	Compatible Cross as Female	$S_{2.2}$ Tester as Male	$S_{3.3}$ Tester as Male	$S_{2.3}$ Tester as Male	Overall % PSC
73-19[a]	---	14	15.1	19.0	---	---	---	70.1
74-4	2.2	6	27.7	42.3	13.1	---	---	64.8
"	3.3	15	39.6	46.7	---	43.9	---	83.6
"	2.3	18	38.4	40.7	21.8	35.6	35.4	89.2
Total	---	39	39.0	43.5	---	---	---	83.3
74-5	2.3	42	48.4	56.6	27.6	38.2	36.3	84.2
74-8	3.3	14	41.8	59.6	---	37.7	---	71.4

[a] *S*-genotype of all seedlings not determined but are either $S_{2.2}$, $S_{3.3}$ or $S_{2.3}$

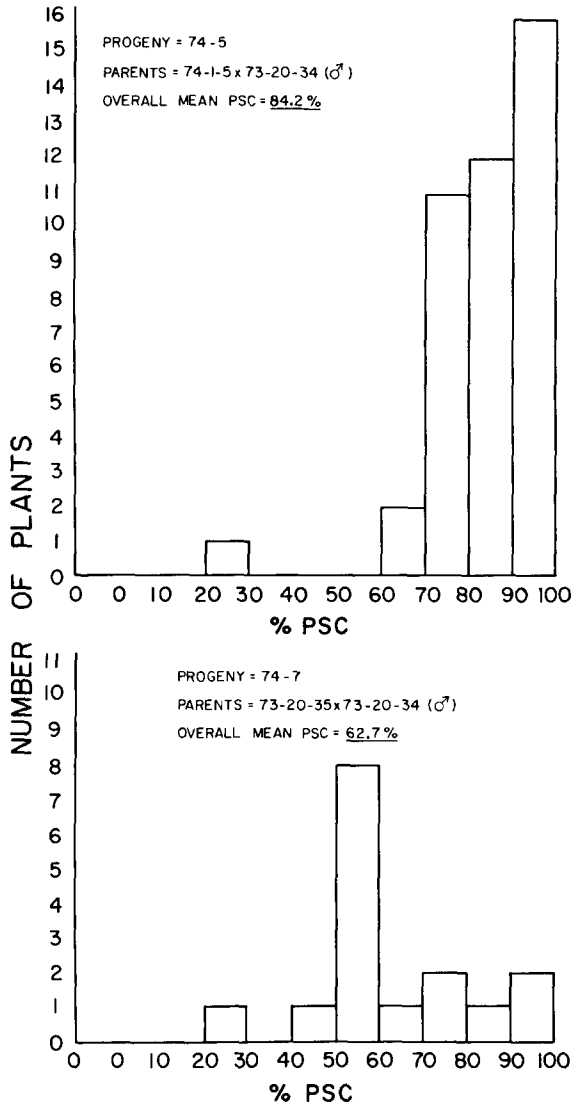

Fig.6. Frequency distribution of % PSC in two populations of *Nemesia strumosa* resulting from crosses of a 100.0 % PSC plant (73-20-34) with a 75.0 % PSC plant (74-1-5) and a 45.1 % PSC sib (73-20-35)

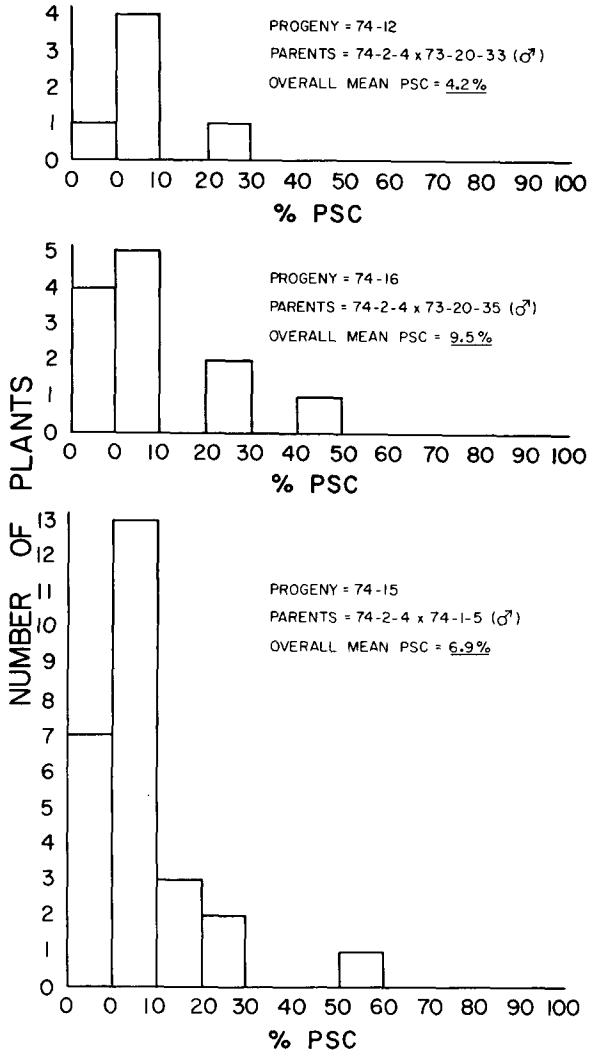

Fig.7. Frequency distribution of % PSC in three populations of *Nemesia strumosa* from crossing a 2.0 % PSC plant (74-2-4) with a 0.0 % PSC plant (73-20-33), a 45.1 % PSC plant (73-20-35) and a 75.0 % PSC plant (74-1-5)

Sib Crosses

Crossing a 100.0 % PSC plant (73-20-34) with a 0.0 % PSC sib (73-20-33) yielded 37 seedlings (population 74-6) which averaged 36.8 % PSC overall (Fig.9 and Table 5). In a broad distribution, 19 seedlings were less than 30.0 % PSC while 18 were greater than 40.0 % PSC (Fig.9). The reciprocal cross produced 17 offspring (population 74-18) with an overall mean PSC level of 50.0 % (Fig.9 and Table 5). Also, 73-20-34 as male in a cross with a 45.1 % PSC sib (73-20-35) gave 16 seedlings (population 74-7) which had an overall mean PSC value of 62.7 % (Fig.6 and Table 5).

These three sibs, 73-20-33, 73-20-35 and 73-20-34, when crossed as male with a 2.0 % PSC plant (74-2-4), produced three progenies: 1. Progeny 74-12 with an overall mean PSC level of 4.2 % (Fig.7 and Table 2); 2. Progeny 74-16 with an overall mean PSC level of 9.5 % (Fig.7 and Table 2); and, 3. Progeny 74-9 with an overall mean PSC level of 14.4 % (Fig.8 and Table 4). A 75.0 % PSC plant (74-1-5) also crossed as male with 74-2-4, yielded 26 offspring (population 74-15) with an overall mean PSC value of 6.9 % (Fig.7 and Table 4). No plants had a PSC level over 50.0 % in populations 74-9, 74-12, 74-16 or 74-17 whereas one plant in progeny 74-15 exceeded 50.0 % PSC.

Table 4. The overall mean percent pseudo-self-compatibility (% PSC), self and tester-cross seed sets in five populations of *Nemesia* resulting from crossing plants highly PSC (75.0 % +) with plants low (2.0 % or less) in PSC

Population	*S*-Genotype	No. Plants	Self	Compatible Cross as Female	$S_{2.2}$ Tester as Male	$S_{3.3}$ Tester as Male	$S_{2.3}$ Tester as Male	Overall % PSC
73-20	3.3	25	6.2	50.2	---	4.5	---	11.5
"	2.3	6	11.8	44.7	3.4	9.8	14.2	26.9
Total	---	31	7.3	49.1	---	5.5	---	14.5
73-22	2.2	6	3.6	63.4	0.5	---	---	5.5
"	2.3	5	6.5	61.9	4.7	7.6	11.5	8.5
Total	---	11	4.9	62.7	2.4	---	---	6.9
74-9[a]	2.3	17	16.0	67.6	3.7	13.8	10.1	23.1
"	2.3	14	2.1	61.1	---	---	1.2	3.9
Total	---	31	9.8	64.7	---	---	2.8	6.9
74-15[b]	2.3	19	7.0	74.8	4.0	7.0	3.7	9.2
"	2.3	7	0.4	70.0	---	---	0.5	0.6
Total	---	26	5.2	73.5	---	---	2.8	6.9
74-17	2.3	10	12.3	61.8	2.2	7.6	3.3	22.1
"	2.2	19	7.4	76.8	3.2	---	---	9.5
Total	---	29	9.1	71.6	2.8	---	---	13.9

[a] Only 17 of 31 seedlings tested with homozygous tester plants
[b] Only 19 of 26 seedlings tested with homozygous tester plants

Other Tester Cross Results

All seedlings, regardless of their degree of PSC, essentially yielded no seeds when crossed as male with incompatible tester plants of identical *S* genotype. For example, the 42 seedlings in population 74-5 averaged 48.4 seeds per self pollination overall (Table 3). Those same seedlings, when tested as male on an incompatible $S_{2.3}$ plant averaged only 0.02 seeds per pollination in over 200 tester crosses. In some cases a few seeds were produced but only at levels consistent with the small degree of PSC sometimes present in the different tester plants used. Similar results were obtained for all plants tested in this study.

As would be expected, the reciprocal of these crosses yielded seed in amounts that approximated the level of self seed set. However, the amounts were often

Table 5. The overall mean percent pseudo-self-compatibility (% PSC), self and tester-cross seed sets in three populations of *Nemesia* resulting from intercrossing three sibs (0.0 %, 45.1 % and 100.0 % PSC) from population 73-20. Also included is the data from population B-1; a cross of a 100.0 % PSC plant (73-20-34) and a 0.0 % PSC plant (B74-1-2), from a commercial source unrelated to the initial populations

Population	*S*-Genotype	No. Plants	Self	Compatible Cross as Female	$S_{2.2}$ Tester as Male	$S_{3.3}$ Tester as Male	$S_{2.3}$ Tester as Male	Overall % PSC
74-6	2.3	37	17.9	47.4	---	---	11.9	36.8
74-7	2.3	16	36.2	59.3	---	36.7	35.9	62.7
74-18	3.3	8	23.3	49.8	---	20.2	---	39.6
"	2.3	9	28.4	49.7	6.6	18.7	13.1	59.3
Total	---	17	26.0	49.7	---	19.4	---	50.0
B-1[a]	---	19	0.8	78.1	---	---	---	0.9

[a] *S*-genotypes not determined but are either $S_{2.x}$, $S_{3.x}$, $S_{2.y}$ or $S_{3.y}$

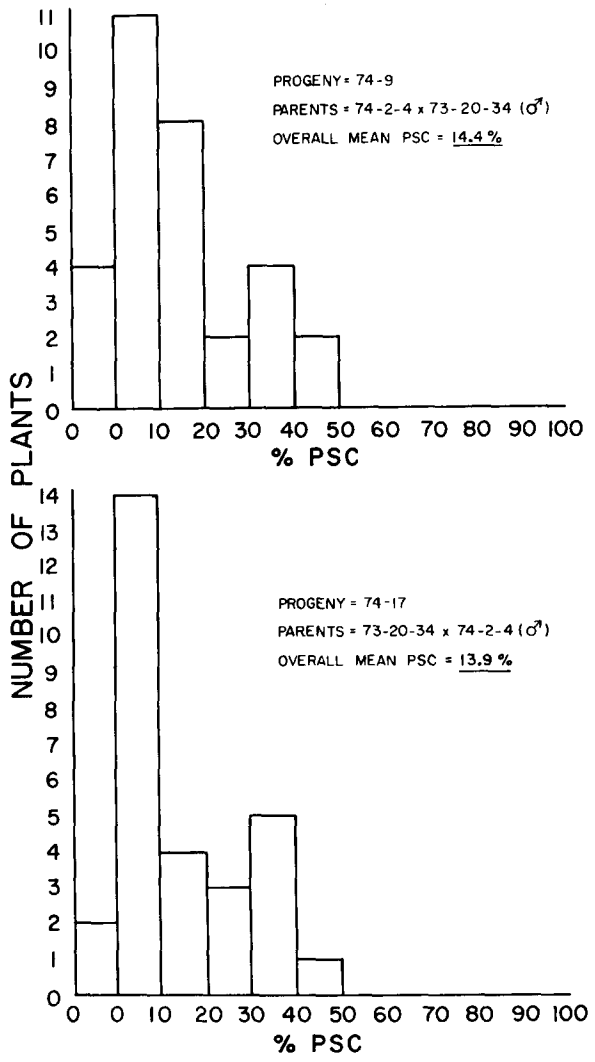

Fig. 8. Frequency distribution of % PSC in two populations of *Nemesia strumosa* resulting from reciprocal crosses of a 100.0 % PSC plant (73-20-34) and a 2.0 % PSC plant (74-2-4)

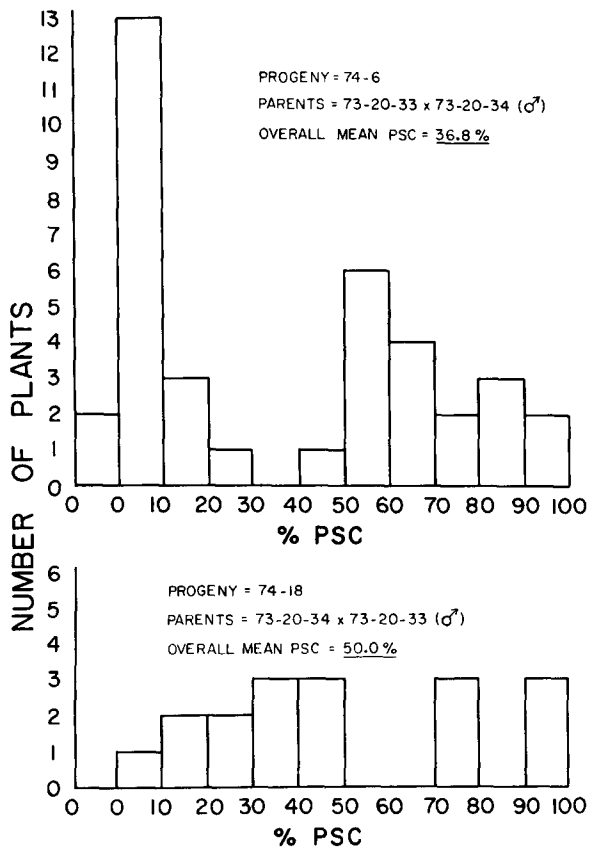

Fig. 9. Frequency distribution of % PSC in two populations of *Nemesia strumosa* resulting from reciprocal crosses of a 100.0 % PSC plant (73-20-34) with its 0.0 % PSC sib (73-20-33)

less (Henny and Ascher 1976). Again, in population 74-5, where the overall mean self seed set was 48.4 seeds, pollen from an $S_{2.3}$ tester averaged only 36.3 seeds overall (Table 3). Pollen from $S_{2.2}$ and $S_{3.3}$ tester plants averaged 27.6 and 38.2 seeds respectively. In other progenies, when testers homozygous for S alleles were used as male, the overall mean seed sets were almost always less than the mean self seed set (Tables 1-5). Pollen from $S_{2.2}$ plants always yielded less seeds than pollen from $S_{3.3}$ and (except in population 74-15) $S_{2.3}$ tester plants, whenever such comparisons could be made.

Seedlings 73-20-35 and 74-1-5, each $S_{3.3}$, averaged 31.1 and 40.2 seeds per self pollination and yet only 3.7 and 12.0 seeds when pollen from other incompatible $S_{3.3}$ plants was used. Both of these seedlings were crossed as female with 73-20-34 ($S_{2.3}$). The 58 seedlings from the two crosses, 16 from 73-20-35 and 42 from 74-1-5, were all $S_{2.3}$ indicating that the S_3 allele from the male parents did not effect fertilization.

Pollen sterility was not a problem. Although some plants produced pollen only sporadically, it proved to be fully fertile when used in compatible cross combinations.

S Genotpyes

Populations 70-301, 73-21, 74-5, 74-6, 74-7, 74-9, 74-12, 74-15 and 74-16 were composed of only $S_{2.3}$ plants. Progenies 74-1 and 74-8 were all $S_{3.3}$ plants while 74-2 had only $S_{2.2}$ individuals. There were 19 $S_{2.2}$ and 10 $S_{2.3}$ seedlings in population 74-17, 8

$S_{3.3}$ and 9 $S_{2.3}$ seedlings in progeny 74-18, 6 $S_{2.2}$ and 5 $S_{2.3}$ seedlings in progeny 73-22 and 25 $S_{3.3}$ and 6 $S_{2.3}$ seedlings in population 73-20. The 39 plants in progeny 74-4 consisted of 6 $S_{2.2}$, 15 $S_{3.3}$ and 18 $S_{2.3}$ individuals. It was not possible to determine all the S genotypes in populations 73-2, 73-3 or 73-19 from the available data. However, those three populations contained only the S_2 and S_3 alleles.

Discussion

No evidence was found for the presence of pollen-part or stylar-part mutants or S_f genes in the *Nemesia* seedlings tested. Such genotypes, if present, would be expected to yield discrete segregations composed of totally self-compatible or self-incompatible plants. Depending on the cross and the S genotype of the individuals carrying the mutant genes or the S_f alleles, a minimum of one-half of the offspring would be totally self compatible.[1] None of the offspring from crosses involving one self-compatible parent (100.0 % PSC) and one self-incompatible parent (2.0 % PSC or less), were totally self compatible. In fact, rarely was a seedling with greater than 50.0 % PSC recovered. The distribution of PSC among *Nemesia* progenies was continuous instead of discrete and requires a quantitative rather than a qualitative genetic base.

To be better able to detect the occurrence of new S specificities, or possible contamination from a foreign pollen source, we limited the total number of S alleles in this study to four and actually confined the majority of work to the S_2 and S_3 alleles. The generation of new S specificities following inbreeding has been reported in various crops (Denward 1963; de Nettancourt and Ecochard 1971; Pandey 1970). However, in *Nemesia*, no new S specificities were uncovered following inbreeding or crossing closely related individuals.

Pollen from plants of any PSC level failed to produce seed when placed on incompatible plants of the same S genotype, indicating that it reacted normally in the incompatibility response. Therefore, PSC was due to either partial or total lack of stylar activity. The blockage of stylar activity was not linked with any particular S allele. A highly PSC plant containing two distinct S alleles allowed pollen tubes containing either allele to induce seed set. However, the presence of the S_3 allele in the style seemed to increase the level of PSC compared to S_2. Similar results have been shown in other plants (East and Yarnell 1929; East 1934) where various S alleles could be associated with different activity levels in the style.

The increase to high levels of PSC in three generations of inbreeding and the maintenance of these levels by selfing or by intercrossing highly PSC plants implies that a relatively small number of loci conferring PSC were involved. The drastic reduction in overall PSC levels found when crossing a highly PSC plant with one low in PSC suggests the recessive nature of these loci. Yet, PSC was not totally eliminated in crosses when one or both parents were low in PSC. As all the plants in these populations can be traced to three original parents, it is likely that each plant had the genetic potential (some recessive alleles for PSC) favorable to the eventual expression of PSC. A cross of a highly PSC plant with incompatible plants from a genetic source where these genes for PSC may be uncommon or lacking should limit the PSC level in the offspring to amount S less than found with such crosses within our own narrow genetic base. We crossed seedling 73-20-34 (100.0 % PSC) with an incompatible plant (B74-1-2; 0.0 % PSC) obtained from a commercial source (unrelated to our initial parents) and tested the offspring for PSC. In progeny B-1, PSC was the lowest of any population tested with only 6 of 19 seedlings producing any self seed (Fig. 10 and Table 4). F_2 or inbred plants from B-1 have not yet been tested for PSC, however, the levels should become much higher in those populations.

If homozygous recessive alleles are needed at a critical number of loci before expression of PSC (a threshold effect), then various plants, low in PSC, could differ in their capacity to produce highly PSC seedlings. For example, a seedling low in PSC but having one highly PSC parent, may be expected to yield a few highly PSC offspring from a cross pollination. Another seedling, also low in PSC but with no highly PSC relatives, when used as the non-recur-

[1] In the case of a stylar-part mutation one exception should be noted here. If an $S_{2.3^+}$ ($3^+ = S_3$ allele being mutated) plant was crossed as male with an incompatible female bearing S_3, the offspring would all be incompatible, since, the pollen from a plant with a stylar-part mutation acts normally in the incompatibility reaction, and the mutated S_{3+} allele would not be transmitted.

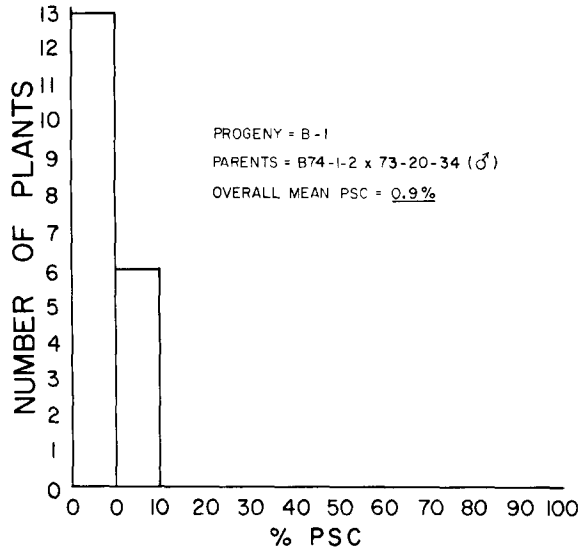

Fig. 10. Frequency distribution of % PSC in one population of *Nemesia strumosa* from crossing a 100.0 % PSC plant (73-20-34) with a 0.0 % PSC plant (B74-1-2). Seedling B74-1-2 was unrelated to the other nemesias in this study

rent parent in the same cross should produce fewer highly PSC seedlings. This difference was realized in reciprocal sib- and non-sib crosses of one highly PSC plant (73-20-34) with plants (73-20-33 and 74-2-4) both low in PSC. The sib-crosses produced progenies (74-6 and 74-18) with an approximately three times higher overall mean level of PSC than the non-sib crosses (progenies 74-9 and 74-17).

In *Petunia* (Takahashi 1973) self pollen tube growth rate steadily increased as the % PSC increased but never reached that of compatible tubes. Our results (populations 74-5 and 74-7; Tables 3 and 5) support those findings. Here, highly PSC $S_{3.3}$ parents, used as female in crosses with an $S_{2.3}$ male produced only $S_{2.3}$ offspring. Apparently pollen tubes with the S_3 allele did not compete in the $S_{3.3}$ style of even a highly PSC plant, with pollen tubes carrying the compatible S_2 allele.

On the basis of one model (Ascher 1966), incompatible pollen tube growth results when a functional dimer repressor is formed by the combination of stylar and pollen components produced by S alleles of matched identity. The functional dimer inhibits a fast growth operon in the pollen tube thereby allowing only a slow growth system to operate. Incompatible tubes continue the slow growth (being unable to metabolize available stylar products) and fail to reach the ovary before floral senescence. Compatible tubes begin the fast rate of growth (upon assimilation of stylar substrates) and reach the ovary in the same time the incompatible tubes are only halfway down the style. This model allows for both pollen- and stylar-conditioned PSC.

Pollen-conditioned PSC would result from a lack of sufficient pollen repressor due to environment or mutations reducing the activity of genes which produce the substrates necessary for the pollen S allele to use in construction of the repressor. Stylar-conditioned PSC could occur from: 1. Inadequate formation of stylar repressor due to lack of sufficient stylar substrates or synthesis machinery; 2. Inhibition of the activity of the stylar repressor to various degrees; or, 3. Inefficient transport of the stylar repressor substance so that it cannot reach the pollen tube. Each of these four situations could conceivably cause various levels of PSC, although in *Nemesia*, a lack of sufficient pollen repressor substance is not likely since the pollen reacted normally on incompatible styles bearing the same S alleles.

With or without the presence of the repressor, proper membrane permeability and the energy for transport must be present in the style so that normal secretion occurs and pollen tubes can utilize the stylar products needed for compatible growth. Abolition of the stylar secretory system should not result in PSC, but rather uniform incompatibility (Ascher 1975). Of the stylar related problems, a lack of formation of the stylar repressor substance seems the most probable explanation for the PSC we observed. The incompatibility substance may be composed of either dimers (Ascher 1966) or tetramers (Lewis 1965), presumably made of smaller molecules (subunits). Most models of incompatibility derive S specificity from the particular arrangement of these subunits with the self-incompatibility reaction requiring matching of identical halfrepressor molecules from the pollen tube and style. Limited amount of substrates in the style could lead to errors during half-repressor formation as well as to partially synthesized molecules and this in turn to decreased activity levels of the half-repressor. In this sense formation and activity would be linked. It seems more natural to explain formation, and to a degree activity, of the stylar repressor on a quantitative basis. The synthesis of each of the half-repressor molecule subunits could be controlled by one or more genes.

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