

## **S gene polymorphism in *Nicotiana***

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### 1. INTRODUCTION

The study of closely linked integrally organized gene systems called 'super-genes' (Mather & de Winton, 1941; Darlington & Mather, 1947) is ideal for unravelling the processes of gene organization and gene evolution, for the processes occurring at the super-gene and finer-gene structure levels must be essentially similar. The phenomenon of genetic polymorphism (Mather, 1955; Ford, 1965), an inevitable consequence of the evolution of super-genes, has recently attracted a good deal of attention, particularly with reference to animals. But these have been mostly concerned with gene ecology rather than gene structure and gene evolution (Thoday, 1964; Sheppard, 1964; Dobzhansky, 1964; Kettlewell, 1965).

In higher plants, well-known cases of genetic polymorphism include sexual polymorphisms—dioecism (Godley, 1955), gynodioecism (Lewis & Crowe, 1956; Godley, 1964) and heteromorphic incompatibility (Stebbins, 1950; Baker, 1954, 1966; Dowrick, 1956)—and polymorphism in hydrogen cyanide production (Dawson, 1941; Corkill, 1942; Daday, 1958).

The *S* gene, with its large number of alleles controlling self-incompatibility in homomorphic plants, has been investigated for its involvement in intraspecific and interspecific incompatibility (Lewis, 1954*a*; Stebbins, 1957; Lewis & Crowe, 1958; Crowe, 1955, 1964; Pandey, 1957, 1960*a*, 1962*a*, 1962*c*; Lundqvist, 1964), its mutability, and its structural complexity (Lewis, 1954*a, b*, 1960, 1963; Pandey, 1956, 1962*b*, 1967). Genetic studies have suggested that self-compatible species have generally arisen through mutation of the *S* gene in the originally self-incompatible species, and that there are at least two forms of self-compatibility genes present in the natural population. Pollen containing one form of the self-compatibility gene ( $S_c$ ), presumably of relatively recent origin, is compatible on styles of a species having the usual self-incompatibility alleles, whereas pollen containing the other gene ( $S_C$ ), presumably of ancient origin, is incompatible on such styles. These two forms of self-compatibility gene, however, usually occur, in different species.

Until recently it was believed that all self-incompatibility alleles ( $S_I$ ) in homomorphic species were normally only of one kind. That this is not the case has been shown in a detailed study of the *S* alleles in *Nicotiana alata* (Pandey, 1964). Approximately 50% of the plants of this species contained at least one allele which was not

identical to the usual  $S_I$  class of alleles. Styles of plants having the unusual self-incompatibility allele, called  $S_{FI}$ , rejected pollen carrying the gene  $S_f$  (a variant of the  $S_c?$ ), from a related self-compatible species *N. langsdorffii*, whereas those having only  $S_I$  alleles accepted it. The recognition of the two classes of self-incompatibility genes, the  $S_I$  and the  $S_{FI}$ , in *N. alata* was the first definite indicated of  $S$  gene polymorphism in homomorphic plants. The present study reveals genetic polymorphism on a large scale, and throws light upon the complex structure of a super-gene of great antiquity and significance in the evolution of flowering plants.

## 2. MATERIALS AND METHODS

Plants of *N. alata*, *N. 'Sanderac'*, *N. langsdorffii*, *N. glutinosa* and the usual self-compatible form of *N. glauca* (N) were grown from seed obtained from various botanical gardens and research institutes (Pandey, 1964). The seed of the unusual, self-incompatible strain of *N. glauca* var. *lateritia* (M) was obtained from Instituto de Botanica Agricola, Castelar, Argentina, and those of *N. noctiflora* and *N. bonariensis* from U.S.D.A., Beltsville, Maryland, U.S.A.

Different homozygous  $S$  genotypes of *N. alata* were produced through bud-pollination (Pandey, 1963). These genotypes were actually extracted from plants of hybrid origin involving *N. alata* and *N. langsdorffii*. They were perfectly normal with regard to fertility and the expression of incompatibility alleles but conveniently had flowers about one-half to one-third the size of *N. alata* flowers.

The compatible crosses usually produced high seed sets. All crosses which failed to produce seed were examined for pollen-tube growth (Pandey, 1964). In a cross where the male parent had a considerably shorter style than the female parent, the cross was considered compatible if, within 48 hours, the pollen-tubes were at least equal to the stylar length of the pollen parent. Usually, however, such crosses showed much greater pollen-tube penetration (1.5 to 2.5 times the stylar length of the pollen parent). Where the male parent had a considerably longer style than the female parent, incompatibility was still usually distinguished from compatibility by the partial penetration of the style by pollen-tubes.

## 3. RESULTS AND DISCUSSION

In the previous study of  $S$  alleles in *N. alata* it was assumed that the  $S_{FI}$  gene, like the  $S_I$  gene, has a large number of alleles and the difference between the genes lay only in their relationship with the  $S_f$  of *N. langsdorffii* (Pandey, 1964). Studies of a total of thirty plants all having the  $S_{FI}$  gene, and derived from three different sources, have shown only two types of the  $S_{FI}$  gene, namely  $S_{FI10}$  (eighteen) and  $S_{FI11}$  (twelve). A further examination of five  $S_{FI}$ -containing plants of the artificial species *N. 'Sanderac'* (of hybrid origin from *N. alata* and *N. forgetiana*) showed that the  $S_{FI}$  alleles in these plants also were either  $S_{FI10}$  (two) or  $S_{FI11}$  (three). Thus it appears that there are only two alleles of the  $S_{FI}$  gene in the natural population.

The yellow-flowered self-compatible species of *N. glauca*, usually has the  $S_C$  gene. However, there is a report by Goodspeed (1954) of the occurrence in Argentina of a bright red-flowered strain (var. *lateritia*) which is self-incompatible. Of fifty plants grown from fresh seeds obtained from this region one plant (M) was found to be of this strain, others being of the normal type. As expected, this plant was conspicuously red-flowered and was fully self-incompatible. It was also female-incompatible but male-compatible with the plants of the usual self-compatible form (N). The close linkage of the self-incompatibility gene with the bright flower-colour gene (Murty *et al.*, 1962) in *N. glauca* is a striking example of the evolution of a super-gene and resultant genetic polymorphism.

These examples of *S* gene polymorphism in homomorphic plants of *Nicotiana* led the author to investigate two further self-incompatible species of this genus, *N. noctiflora* and *N. bonariensis*. Plants of these species were reciprocally crossed with most of the nine testers grouped as follows:

- (i) Self-compatible species *N. langsdorffii* ( $S_I$ ) and *N. glutinosa* ( $S_C$ ).
- (ii) The two forms, self-incompatible M and self-compatible N ( $S_C$ ) of *N. glauca*.
- (iii) Two  $S_{FI}$  genotypes ( $S_{F10}S_{F10}$  and  $S_{F11}S_{F11}$ ), two  $S_I$  genotypes ( $S_1S_1$  and  $S_3S_3$ ), and one genotype ( $S_1S_{F11}$ ) having both types of alleles, of the self-incompatible species *N. alata*.

Table 1. *Results\* of crosses of N. noctiflora plants with testers*

Pl. No.	<i>N. langsdorffii</i>		<i>N. glutinosa</i>		<i>N. glauca</i>		<i>N. alata</i>		<i>N. alata</i>		<i>N. alata</i>		<i>N. alata</i>	
			N		$S_{F10}S_{F10}$		$S_{F11}S_{F11}$		$S_1S_1$		$S_1S_{F11}$		$S_3S_3$	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	-	+	-	+	+	-	+	+	+	-	+	-	+	+
2	-	+	-	+	+	-	+	+	+	-	+	-	+	+
3	-	+	-	+			+	+						
8	-	+	-	+	+	-	+	+	+	-	+	-	+	+
4	+	+	-	+	+	-	+	+	+	-	+	-	+	+
5	+	+	-	+	+	-	+	+	+	-	+	-	+	+
6	+	+	-	+	+	-	+	+	+	-	+	-	+	+
7	+	+	-	+	+	-	+	+	+	-	+	-	+	+
9	+	+	-	+	+	-	+	+	+	-	+	-	+	+

\* - Incompatible; + Compatible.

In *N. noctiflora* only nine plants, all fully self-incompatible, were available. The results of their crosses with testers are given in Table 1. With the exception of *N. langsdorffii* as male parents, crosses with testers gave uniform results; all nine plants were either compatible or incompatible. As females they were all compatible with all *N. alata* genotypes and incompatible with *N. glauca* N, and *N. glutinosa*; as males they were all compatible with *N. alata* genotypes  $S_{F11}S_{F11}$  and  $S_3S_3$ , *N. glauca* N, *N. glutinosa*, and *N. langsdorffii*, and incompatible with *N. alata* genotypes  $S_{F10}S_{F10}$ ,  $S_1S_1$  and  $S_1S_{F11}$ .

The behaviour of *N. noctiflora* plants with *N. glutinosa* and *N. glauca* N was as expected of crosses between any self-incompatible species and a self-compatible species having the  $S_C$  allele (Lewis & Crowe, 1958; Pandey, 1962*a, b*). The behaviour of the different genotypes of *N. alata*, however, was most unexpected. Not only was there a distinction between the two  $S_{FI}$  alleles, the  $S_{F11}S_{F11}$  being reciprocally compatible whereas the  $S_{F10}S_{F10}$  was compatible only as male, but there was also a difference between the two  $S_I$  alleles tested; like  $S_{F11}S_{F11}$  the  $S_3S_3$  was reciprocally compatible, whereas like  $S_{F10}S_{F10}$  the  $S_1S_1$  was compatible only as male. As expected on the behaviour of the  $S_1S_1$  genotype, the styles of  $S_1S_{F11}$  plants, because of the presence of the  $S_1$  allele, rejected *N. noctiflora* pollen. Of two further  $S_I$  alleles,  $S_2$  and  $S_6$ , examined in this respect, both, like  $S_1$ , rejected *N. noctiflora* pollen. Again, as expected, *N. noctiflora* pollen was rejected by styles of the genotype  $S_2S_{F11}$ .

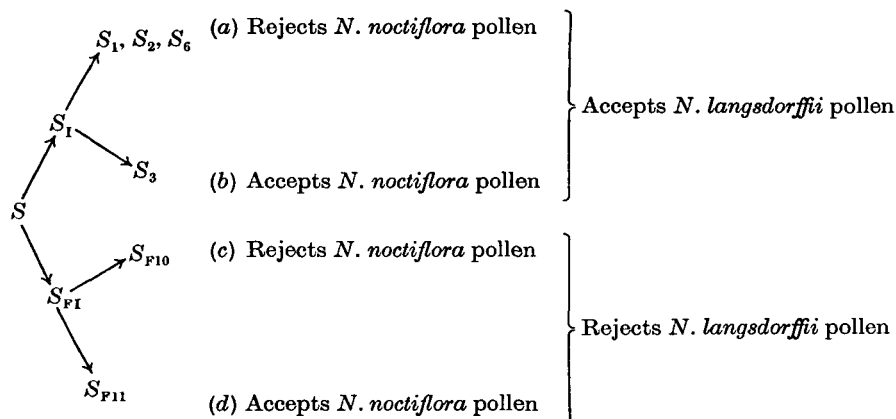
Table 2. Results of crosses of *N. noctiflora* plants between themselves

	Plants incompatible with <i>N. langsdorffii</i> (♂)				Plants compatible with <i>N. langsdorffii</i> (♂)				
	1	2	3	8	4	5	6	7	9
1	—	—	—	—	+	+	+	+	+
2	—	—	—	—	+	+	+	+	+
3			—						
8	—	—	—	—	+	+	+	+	+
4	+	+		+	—	—	—	—	—
5	+	+		+	—	—	—	—	—
6	+	+		+	—	—	—	—	—
7	+	+		+	—	—	—	—	—
9	+	+		+	—	—	—	—	—

The cross-compatibility relationship of *N. noctiflora* with *N. langsdorffii* is unique. Whereas, as males, all plants of *N. noctiflora* were compatible with this species, as females they fell into two groups: Four plants (Nos. 1, 2, 3 and 8—group I) were incompatible and five (Nos. 4, 5, 6, 7 and 9—group II) compatible. The significance of this behaviour was further heightened when the cross-compatibility relationships of the *N. noctiflora* plants among themselves were examined (Table 2). The two groups of plants determined through compatibility among themselves on the one hand and through compatibility with *N. langsdorffii* (♂) on the other, were identical. The five plants which were compatible and four plants which were incompatible with *N. langsdorffii* formed two respective groups of intra-incompatible and inter-compatible plants.

These results suggest that (1) the incompatibility genes in *N. noctiflora* are not all alike and belong at least to two classes differentiated by their stylar reactions with *N. langsdorffii* pollen; one, like  $S_I$  genes, accepts the *N. langsdorffii* pollen, while the other, like the  $S_{FI}$  genes, rejects them. Their pollen reaction, however, is uniform.

(2) The intraspecific incompatibility and the interspecific incompatibility with *N. langsdorffii* (♂) are controlled by the same genes. (3) In *N. alata*, in the limited material studied, there are at least four classes of self-incompatibility genes differentiated by interspecific compatibility relationships:



The above conclusions are further supported by the work in *N. bonariensis*.

In *N. bonariensis* forty plants were studied. Most of these were highly self-incompatible, only five plants showing varying degrees of self-compatibility. The results of crossing twenty-nine plants with certain testers, which included the two phenotypic groups I (Plant 2) and II (Plant 5) of *N. noctiflora*, are given in Table 3. The following results were obtained: (1) As males, all *N. bonariensis* plants behaved alike with all testers, they were compatible. (2) As females, they behaved alike with *N. glauca* N, all crosses being incompatible; and with the genotypes *S<sub>FI10</sub>S<sub>FI10</sub>* and *S<sub>FI11</sub>S<sub>FI11</sub>*, all crosses being compatible. (3) As females, however, with respect to *N. langsdorffii* on the one hand, and with *N. glauca* M and the *N. noctiflora* phenotypes I and II on the other, they fell into three groups, the pollen of the latter testers behaving alike as a group:

- (i) Plants incompatible with *N. langsdorffii* (six out of forty).
- (ii) Plants incompatible with *N. glauca* M, and the two *N. noctiflora* phenotypes I and II (seventeen out of twenty-nine tested)
- (iii) Plants compatible with both groups of testers (six out of twenty-nine tested).

When twelve plants of *N. bonariensis*, composed of four plants selected from each of the above three groups, were intercrossed, the results were again striking (Table 4). They formed three respective intra-incompatible and inter-compatible groups.

Two plants, Nos. 3 and 21, which were partly self-compatible also showed varying degrees of partial cross-compatibility in incompatible combinations. But this reaction showed only when they were used as females; as males they behaved normally. This type of self- and cross-compatibility showing change of reaction in one direction only is reminiscent of induced mutants of the *S* gene when mutation occurred mostly either in the pollen-governing or the stylar-governing units of the *S* complex (Lewis, 1954, 1960; Pandey, 1956, 1967). While in certain cases effects of genes other than *S*, or polygenic differences, could bring about similar reactions, it is

Table 3. *Results of crosses of N. bonariensis plants with testers*

<i>N.</i> <i>bonariensis</i> Pl. No.	<i>N.</i> <i>langsdorffii</i>		<i>N.</i> <i>noctiflora</i> Pl. 2		<i>N.</i> <i>noctiflora</i> Pl. 5		<i>N.</i> <i>glauca</i> M		<i>N.</i> <i>glauca</i> N		<i>N.</i> <i>alata</i> $S_{F10}S_{F10}$		<i>N.</i> <i>alata</i> $S_{F11}S_{F11}$	
	♂ ♀		♂ ♀		♂ ♀		♂ ♀		♂ ♀		♂ ♀		♂ ♀	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	-	+	+	+	+	+	+	+	-	+	+	+	+	+
3	-	+	+	+	+	+	+	+	-	+	+	+	+	+
13	-	+	+	+	+	+	+	+	-	+	+	+	+	+
17	-	+	+	+	+	+	+	+			+	+	+	+
36	-	+	+	+	+	+	+	+			+	+	+	+
37	-	+	+	+	+	+	+	+			+	+	+	+
2	+	+	-	+	-	+	-	+	-	+	+	+	+	+
5	+	+	-	+	-	+	-	+	-	+	+	+	+	+
6	+	+	-	+	-	+	-	+	-	+	+	+	+	+
15	+	+	-	+	-	+	-	+	-	+	+	+	+	+
22	+	+	-	+	-	+	-	+	-	+	+	+	+	+
23	+	+	-	+	-	+	-	+	-	+	+	+	+	+
24	+	+	-	+	-	+	-	+			+	+	+	+
26	+	+	-	+	-	+	-	+	-	+	+	+	+	+
27	+	+	-	+	-	+	-	+	-	+	+	+	+	+
29	+	+	-	+	-	+	-	+			+	+	+	+
30	+	+	-	+	-	+	-	+			+	+	+	+
32	+	+	-	+	-	+	-	+	-	+	+	+	+	+
33	+	+	-	+	-	+	-	+	-	+	+	+	+	+
34	+	+	-	+	-	+	-	+	-	+	+	+	+	+
35	+	+	-	+	-	+	-	+	-	+	+	+	+	+
39	+	+	-	+	-	+	-	+	-	+	+	+	+	+
40	+	+	-	+	-	+	-	+	-	+	+	+	+	+
8	+	+	+	+	+	+	+	+	-	+	+	+	+	+
21	+	+	+	+	+	+	+	+	-	+	+	+	+	+
25	+	+	+	+	+	+	+	+	-	+	+	+	+	+
28	+	+	+	+	+	+	+	+	-	+	+	+	+	+
31	+	+	+	+	+	+	+	+	-	+	+	+	+	+
38	+	+	+	+	+	+	+	+			+	+	+	+

more likely that clear-cut reactions of this kind are due to mutation of the pollen- or stylar-regulator units of the *S* complex. Once, however, such a mutation has occurred, the varying expression of self- and cross-compatibility will depend upon the polygenic background of the individual plants involved. This varies greatly although, in normal circumstances, it is adjusted to the proper functioning of the incompatible state of the regulator units (Pandey, 1959, 1960*a*, *b*)—an idea first propounded by Mather & de Winton (1941) in their classical elucidation of the 'switch-concept' of super-genes. This conclusion is strongly supported by the detailed study of certain pollen-part mutants of the *S* gene in *N. alata* (Pandey, 1967) which, while themselves remaining self-incompatible, behaved exactly as the pollen-part mutants in crosses with other plants of their original genotype.

Although final judgement must be reserved till the details of the genetic systems of incompatibility have been studied, the perfect relationship between the *S* gene polymorphism and the intra-incompatible and inter-compatible groups in both the species indicates that the occurrence of the breeding groups may not be fortuitous. If this is true, then the two groups of *N. noctiflora* and three groups of *N. bonariensis* may be considered reminiscent respectively of dimorphic and trimorphic incompatibility systems in heteromorphic plants.

Table 4. *Results of crosses among twelve N. bonariensis plants composed of four plants from each of the three groups determined by crossing with testers*

	1	3	36	37	21	25	28	31	22	24	26	33
1	—	—	—	—	+	+	+	+	+	+	+	+
*3	⚭	⚭	⚭	⚭	+	+	+	+	+	+	+	+
36	—	—	—	—	+	+	+	+	+	+	+	+
37	—	—	—	—	+	+	+	+	+	+	+	+
*21	+	+	+	+	⚭	⚭	⚭	⚭	+	+	+	+
25	+	+	+	+	—	—	—	—	+	+	+	+
28	+	+	+	+	—	—	—	—	+	+	+	+
31	+	+	+	+	—	—	—	—	+	+	+	+
22	+	+	+	+	+	+	+	+	—	—	—	—
24	+	+	+	+	+	+	+	+	—	—	—	—
26	+	+	+	+	+	+	+	+	—	—	—	—
33	+	+	+	+	+	+	+	+	—	—	—	—

\*These two plants were partly self-compatible and also partly cross-compatible as female parents in incompatible crosses (⚭).

The present work undoubtedly proves the complex nature of the *S* gene, evidence for which has been accumulating for some time from mutation experiments and from the study of intra- and inter-specific incompatibility reactions. Differences in the ability of different *S<sub>I</sub>* alleles to complement the same female-part mutation, as found in *S* gene mutation studies in *N. alata* (Pandey, 1967), may be due to variations in the genetic elements composing these alleles. This conclusion is supported by the present finding that the different *S<sub>I</sub>* class of alleles, e.g. *S<sub>1</sub>* and *S<sub>3</sub>*, differ in their interspecific incompatibility reactions when tested against appropriate genotypes.

Within a species the pollen reaction in interspecific crosses is similar for all alleles, the allelic variability being confined to the stylar reaction. The differences in crossability with other genotypes between male and female reactions of otherwise similar alleles show that the genetic elements responsible for the two reactions are, from the points of view of mutation and recombination, independent entities, each in itself composed of several elements. The theory of *S* gene structure as outlined by the author (1962) has, therefore, been essentially substantiated.



The present study lays the foundation for genetic re-examination of a considerable amount of published data on intra- and inter-specific incompatibility relationships. It demonstrates a very interesting and, presumably, very widespread case of genetic polymorphism in higher plants and offers unique material for the elucidation of gene structure, gene regulation and gene organization.

#### SUMMARY

Interspecific crosses between different genotypes and species of *Nicotiana* have revealed *S* gene polymorphism on a large scale. In the usually yellow-flowered self-compatible species *N. glauca* a strain occurs that has a self-incompatibility gene which is tightly linked with the bright-red corolla colour gene. In self-incompatible species, there are two kinds of self-incompatibility alleles,  $S_I$  and  $S_{FI}$ , distinguished on the basis of the acceptability of *N. langsdorffii* pollen. The  $S_I$  form has a large number of alleles whereas the  $S_{FI}$  form has only two,  $S_{FI10}$  and  $S_{FI11}$ . The  $S_I$  alleles are again divisible into two groups on the basis of the acceptability of *N. noctiflora* pollen and, on the same criterion, the two  $S_{FI}$  alleles,  $S_{FI10}$  and  $S_{FI11}$ , also are distinguishable. *N. noctiflora* and *N. bonariensis* plants could be divided into two and three groups respectively on the basis of interspecific compatibility relationships. When plants of each species were crossed among themselves, they formed two and three intra-incompatible and inter-compatible groups respectively, identical with those found on the basis of interspecific compatibility relationships. The significance of this observation is at present not fully understood.

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