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Elements of the *S*-gene complex

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1. INTRODUCTION

As pointed out by Dunn *et al.* (1962), 'the processes by which a genetic locus assumes diverse forms of expression are of interest both as sources of genetic variability on which evolutionary forces may act and as indicators of the potentialities of the locus in controlling metabolic and developmental processes'. Whilst the study of these processes is inherently much more difficult in higher plants and animals than in other biological groups, there are exceptions, notably the *S*-gene system controlling incompatibility. Potentially, this multi-allelic system meets all the requirements of a genetic, and ultimately biochemical, attack on gene structure and gene function.

The *S*-gene system is generally considered to have had a long evolutionary history which is reflected in its great diversity and spread in the angiosperms. Analytical studies have led to the recognition so far of six different systems of incompatibility (Lewis, 1949; Pandey, 1957; Kroh, 1956) and potentially four 'sub-units' of control (Lewis, 1954*a*; Pandey, 1962*a*). The search for new kinds of alleles, either natural or induced, in partly explored and unexplored genera and families, continues (Lewis, 1954*b*; Lewis & Crowe, 1958; Pandey, 1956, 1962*b*, *c*; Martin, 1961*a*). To this has been added the special study of exceptional alleles having a different expression from that of their near relatives. One such allele is the S_F gene (Anderson & de Winton, 1931).

The S_F gene or its equivalent has been reported only twice: in *Nicotiana alata* (Anderson & de Winton, 1931), and in *Petunia violacea* (Mather, 1943; Bateman, 1943), both of which are self-incompatible. Normally, strains of these species are reciprocally cross-compatible with their near relatives, *Nicotiana langsdorffii* and *Petunia axillaris* respectively, both of which are self-compatible. But in each case an exceptional strain, which carried an unusual allele named 'S_F' in *N. alata*, is compatible only as male, incompatible as female; in other words, the strains carrying the unusual allele reject not only their own pollen but also that of the opposed self-fertile species.

The present paper is concerned with the genetics of the allele S_F, which, as is evident from this study, is by no means uncommon, at least in *N. alata*. The results suggest that the S_F allele has two specificities in the style, one corresponding to its own specificity in the pollen and the other which is responsible for rejecting the

self-compatible pollen of *N. langsdorffii*, and confirm the findings of Anderson & de Winton (1931).

2. MATERIALS, METHODS AND NOTATIONS

Plants were grown from seed obtained from various Botanical gardens and research institutions as follows:

Nicotiana alata (i) University Botanic Garden, St. Andrews (A).
(ii) Institut Pflanzenbau, Geisenheim, Rheingau, Germany (G).
(iii) Instituto ed Orto Botanico dell'Universita, Modena, Italy (I).
N. langsdorffii Royal Botanic Gardens, Kew.

Compatibility was determined from pollen-tube growth. Usually four flowers were pollinated for each cross. They were then removed, placed in water, and incubated at 25°C. At 48 hours after pollination, the styles were crushed between slides, fixed in acetic alcohol (1:3) and stained in acid-fuchsin-light-green. The standard of measurement was that of the longest distance traversed by five or more pollen-tubes.

Selfed seeds (from pollinations between plants of the same S allelic constitution) were produced in self-incompatible plants by bud-pollination. Abundant seed-set occurred when stigmas of flower-buds, approximately half the size of mature flowers, were smeared with secretion from mature stigmas before pollination (Pandey, 1963).

Notation:

S_I: The common class of self-incompatible alleles (S_1, S_2, etc.).
S_f: The self-compatible allele in *Nicotiana langsdorffii*.
S_{FI}: The S_F class of incompatible alleles re-defined.
S_{F1}, S_{F2}, etc.: Different alleles in the S_{FI} system.
M: Plants containing an S_{FI} allele (*N. alata*).
N: Normal plants of that species.
S.C.: Self-compatible.
S.I.: Self-incompatible.

3. RESULTS

(i) *Frequency of M plants*

There were two kinds of plants in *N. alata*: the normal plants (N), which are reciprocally compatible with *N. langsdorffii* (East, 1929), and the exceptional plants (M) which reject the pollen of *N. langsdorffii* while the reciprocals are compatible. In the present study 50% of plants grown from seeds of three different sources were of M type which is in contrast to the single plant of this type reported earlier (Anderson & de Winton, 1931) (Table 1).

Table 1. *Pollen-tube growth in selfed M and N plants (measurements at 48 hours after pollination)*

N. alata		Selfed pollen-tube growth		Crossed with *N. langsdorffii* as	
Type	Source	mm.	(% of style)	♂	♀
M	G1	11·0	(15)	−	+
	G4	8·0	(13)	−	+
	G6	14·3	(25)	−	+
	G7	18·6	(27)	−	+
	G8*	34·3	(51)	−	+
	G10*	32·9	(50)	−	+
	G12	17·1	(26)	−	+
	G13*	22·9	(36)	−	+
	G16	12·9	(21)	−	+
N	G2	—		+	+
	G3	—		+	+
	G5	—		+	+
	G9	22·9	(37)	+	+
	G11	20·0	(31)	+	+
	G14	—		+	+
	G15	24·3	(34)	+	+
	G17	—		+	+
M	I3*	27·1	(36)	−	+
	I4	18·6	(22)	−	+
	I9	14·3	(17)	−	+
	I11	14·3	(19)	−	+
N	I1	22·9	(35)	+	+
	I2	22·9	(29)	+	+
	I5	22·9	(30)	+	+
	I6	20·0	(28)	+	+
	I7	21·4	(25)	+	+
	I8	27·1	(38)	+	+
	I10	21·4	(29)	+	+
	I12	21·4	(31)	+	+
M	A2	8·0	(12)	−	+
	A3	11·0	(17)	−	+
	A4	7·0	(10)	−	+
	A5	11·0	(15)	−	+
N	A1	11·0	(18)	+	+
Total:		34 (17 M + 17 N); Difference in pollen-tube growth between M and N plants highly significant ($P = 0{\cdot}1$).			

* These plants are partly- or fully self-fertile and have been excluded from calculations.

G: Germany; I: Italy; A: Scotland.

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(ii) *Genetics of M plants*

(*a*) *Hybrids with* N. langsdorffii

Three F_1 families were studied from crosses between *N. langsdorffii* (♀) and different *N. alata* M plants ($S_I S_{FI}$). The results are as follows:

(1) Each family contained two classes of genotypes, one self- and intra-compatible (S.C.), the other self- and intra-incompatible (S.I.) (Table 2).

Table 2. *Classification of genotypes in F_1 families*: N. langsdorffii (N.l.) × N. alata (N.a.) (*M*)

Cross ♀ × M ♂	Self-compatible intra-compatible $S_I S_f$	Self-incompatible intra-incompatible $S_{FI} S_f$
N.l. × *N.a.* A3	8	3
N.l. × *N.a.* A4	12	1
N.l. × *N.a.* G3	8	4
Total	28	8

On the basis of 1 : 1 $\chi^2 = 11{\cdot}11$; $P = < 0{\cdot}01$

(2) S.C. F_1 plants were compatible as females with both M and N classes of *N. alata*, and reciprocally compatible with *N. langsdorffii* (Fig. 1).

(3) S.I. F_1 plants behaved identically, as in *b*, with respect to *N. alata*, but were compatible only as males with respect to *N. langsdorffii* (Fig. 1).

These findings confirm and extend those of Anderson & de Winton (1931), and require only the assumption that M plants are heterozygous for an S_{FI} allele. Two genotypic classes in equal proportions are therefore expected in F_1, as follows:

$$S_f S_f \times S_I S_{FI} \longrightarrow \underset{\text{(S.C.)}}{1 S_I S_f} : \underset{\text{(S.I.)}}{1 S_{FI} S_f}$$

(The 1 : 1 expectation was not realized since there was a lack of S.I. plants in all families, particularly from the cross of *alata* A4 (Table 2). Observations on pollen-tube growth are relevant to this question and are discussed later.)

Plants of constitution $S_{FI} S_f$, from whatever source, thus have the common property of repelling both S_{FI} and S_f pollen; hence they are invariably S.I., and cross-incompatible as females with *N. langsdorffii*. In all other respects, they behave like plants with the common S_I alleles.

Two questions may now be asked:

(1) Are the S_{FI} alleles from *N. alata* identical in specificity?

(2) At the same time, is this specificity superimposed on the usual specificity which is the property of the common S_I class of alleles?

Experiments designed to answer these questions are described below.

(*b*) *M* × *M and M* × *N progenies*

Five pairs of M plants, and one pair involving M and N, were crossed reciprocally, and the F_1's tested against *N. langsdorffii* ♂. The results are presented in Table 3.

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Eight of ten M × M families produced four intra-incompatible inter-compatible groups of which three were cross-incompatible and one cross-compatible with *N. langsdorffii* ♂. Evidently four different alleles were involved in each cross, i.e. two kinds of S_I and two kinds of S_{FI}.

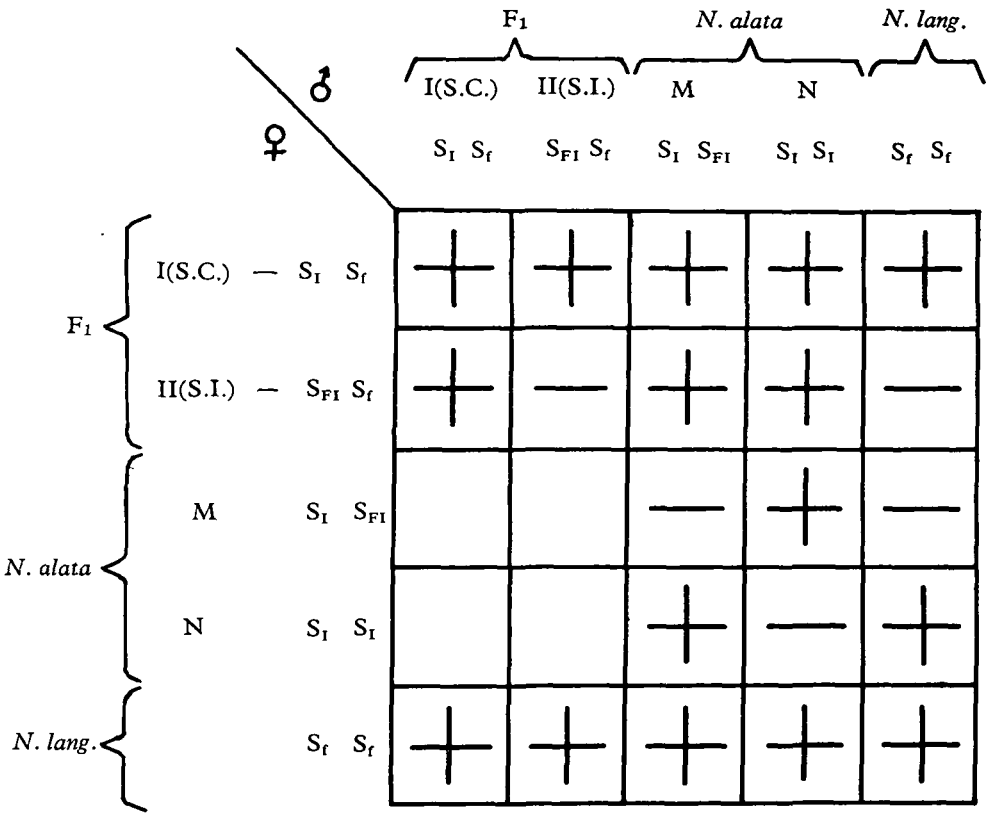

Fig. 1. Inter- and backcross relationships of the two groups, S.C. (self-compatible) and S.I. (self-incompatible) in the F_1 progeny of the cross *N. langsdorffii* (♀) × *N. alata* (M). *N. alata* plants used in backcrosses had different S_I alleles from those present in the original parents.

The remaining two M × M families produced only two such groups of which one was cross-incompatible and one cross-compatible with *N. langsdorffii* ♂. Here it must be presumed that the parents had an S_{FI} allele in common.

Reciprocal crosses between M and N also produced four groups, but in these, two groups were cross-incompatible and two cross-compatible with *N. langsdorffii* ♂.

The present experiments show, as before, the special character of the S_{FI} gene in heterozygotes: whether it is the same, or different from plant to plant, it invariably rejects S_f pollen. They also show that S_{FI} alleles of differing specificity do occur. Finally, they suggest that such alleles have a dual or composite specificity

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Table 3. *The behaviour of F_1 progeny in $M \times M$ and $M \times N$ families*

Cross	Family No.	F^1 Groups Crossed with *N. langsdorffii* ♂ Compat. (No. of plants)		Incompat. (No. of plants)	
$M \times M$					
I11 × G1	9112	1	(12)	1	(8)
recip.	9115	1	(12)	1	(8)
I11 × G11	9113	1	(8)	3	(5,4,3)
recip.	9121	1	(4)	3	(8,6,1)
I11 × G8	9114	1	(7)	3	(5,4,3)
recip.	9122	1	(4)	3	(7,6,3)
I4 × G1	J1(1)	1	(8)	3	(3,3,3)
recip.	9120	1	(5)	3	(5,5,5)
G1 × G8	9123	1	(4)	3	(3,8,5)
recip.	9124	1	(3)	3	(6,8,3)
$M \times N$					
G1 × I2	J1(2)	2	(6,5)	2	(5,2)
recip.	9125	2	(11,4)	2	(3,2)

in which one component is common to usual S_I alleles in general and an additional component gives them their special character. Further results support this view.

(*c*) F_2, *selfed and backcross families*

In this last group of experiments the immediate parents were consistently extracted from the same F_1 families, as follows (the designations + and − indicate compatible or incompatible reaction with pollen from *N. langsdorffii*): IX (+) and X (−) ex family 9112; III (+) and I, II, IV (all −) ex family 9113 (Table 3). Plants from these sources were (*a*) inter-crossed (Table 4); (*b*) selfed in the bud (Table 5); (*c*) backcrossed to *N. langsdorffii* ♀ (Table 6); and (*d*) all progenies uniformly tested against *N. langsdorffii* ♂.

The overall results are consistent with the assumption that M plants of *N. alata* contain an *S* allele which produces two kinds of specificity in the style, one responsible for the rejection of self-pollen, and the other responsible for the rejection of S_f pollen from *N. langsdorffii*. The genetic sub-units concerned must be very closely linked, for there was no evidence for their dissociation in the 599 plants studied. In the segregation of *S* alleles in different families all plants with any S_{FI} allele invariably rejected S_f pollen, while none of the segregants homozygous for S_I alleles ever rejected S_f pollen.

The possibility, however, suggested from the work of Martin (1961*b*) in *Lycopersicon* hybrids, that another locus, linked to the *S* locus, may be responsible for the interspecific inhibitions, must be considered. In the F_1, F_2 and backcross generations of the hybrids between the self-compatible *L. esculentum* and the self-incompatible *L. chilense* Martin found evidence for the segregation of a dominant gene from *L. chilense*, which affected the strength of the incompatibility reaction.

Similarly there were indications for the occurrence of two or more such genes in the *L. esculentum* genotypes. No genes affecting the incompatibility reaction were found in the present study of *Nicotiana* hybrids, as was also the case in hybrids between *L. esculentum* and *L. peruvianum* studied by McGuire & Rick (1954).

What is significant in all these crosses, mentioned above, is that in the original crosses between the species, the action of the *S* locus is paramount; the S_{FI} alleles in *N. alata* styles on the one hand, and the S_I alleles in *L. chilense* and *L. peruvianum* on the other, were all completely and unfailingly effective in inhibiting the S_f pollen from *N. langsdorffii* and *L. esculentum* respectively. Apparently there is no major gene strong enough to affect the action of the S_I and S_f alleles when they act in their own respective genetic backgrounds. The weakening of the *S* locus owing to the action of other major genes occurs only when there is a recombination between two genomes of distinct species. Thus it will be difficult to ascribe the regular rejection of the *S* pollen of *N. langsdorffii* by *N. alata* styles to anything but the S_{FI} allele.

The conclusion that S_{FI} and S_I are different forms of incompatibility alleles at the same locus is further strengthened from the fact that such a variability also exists in the self-compatibility alleles of the same complex. The self-compatibility alleles, the S_f in *N. langsdorffii* on the one hand and the S_f in *L. esculentum* and *N. glutinosa* (in this case renamed 'S_C') on the other, are not identical as is clearly shown from their reactions in pollinations between these species and a related self-incompatible species having S_I alleles (Lewis & Crowe, 1958; Pandey, 1962*a*).

(iii) *Rate of pollen-tube growth*

Plants homozygous or heterozygous for S_{FI} alleles are distinguished by their prompt inhibition of S_f pollen, which usually occurs within the stigmatic region. In the same plants, when incompatibly pollinated with S_I pollen, the inhibition occurs at about $\frac{1}{3}$ length of the style from the stigma.

Table 4. *The behaviour of F_2 progeny in inter-group crosses*

Genotypes		Family No.	F2 Groups Cross with *N. langsdorffii* ♂	
Parents	Progeny		Compat. (No. of plants)	Incompat. (No. of plants)
III × I				
$S_1S_2 \times S_2S_{F10}$	$\longrightarrow S_1S_{F10} + S_2S_{F10}$	9143	0	2 (8,12)
III × II				
$S_1S_2 \times S_{F10}S_{F11}$	$\rightarrow S_1S_{F10} + S_1S_{F11} + S_2S_{F11}$	9144	0	4 (4,8,5,3)
III × IV				
$S_1S_2 \times S_1S_{F11}$	$\longrightarrow S_1S_{F11} + S_2S_{F11}$	9145	0	2 (8,8)
IX × X				
$S_1S_3 \times S_3S_{F10}$	$\longrightarrow S_1S_{F10} + S_3S_{F10}$	9154	0	2 (11,9)
X × IX				
$S_3S_{F10} \times S_1S_3$	$\longrightarrow S_1S_3 + S_1S_{F10}$	9155	1 (10)	1 (10)

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Table 5. *The behaviour of selfed progeny of F_1 mating groups*

	Genotypes		Family	Progeny groups			
				Male compat.; female incompat.		Intercompat.	
	Parents	Selfed progeny	No.	Groups (No. of plants)	Cross with *N.l.* ♂	Groups (No. of plants)	Cross with *N.l.* ♂
(I)	S_2S_{F10}	$\longrightarrow S_2S_2+S_2S_{F10}+S_{F10}S_{F10}$	9150	1 (9)	−	2 (5,5)	+,−
(II)	$S_{F10}S_{F11}$	$\rightarrow S_{F10}S_{F10}+S_{F10}S_{F11}+S_{F11}S_{F11}$	9151	1 (10)	−	2 (2,7)	−,−
(III)	S_1S_2	$\longrightarrow S_1S_1+S_1S_2+S_2S_2$	9166	1 (7)	+	2 (4,9)	+,+
(IV)	S_1S_{F11}	$\longrightarrow S_1S_1+S_1S_{F11}+S_{F11}S_{F11}$	9153	1 (7)	−	2 (3,3)	+,−
(IX)	S_1S_3	$\longrightarrow S_1S_1+S_1S_3+S_3S_3$	9158	1 (11)	+	2 (4,5)	+,+
(X)	S_3S_{F10}	$\longrightarrow S_3S_3+S_3S_{F10}+S_{F10}S_{F10}$	9159	1 (9)	−	2 (8,2)	+,−

N.l. = *N. langsdorffii*; + = compatible; − = incompatible.

Table 6. *The behaviour of backcross progenies*: N. langsdorffii (N.l) ♀ × F_1 *Mating groups*

Genotypes		Family No.	Progeny groups			
			Self- and intra-compat.		Self- and intra-incompat.	
Parents	Progeny		Groups (No. of plants)	Cross with *N.l.* ♂	Groups (No. of plants)	Cross with *N.l.* ♂
N.l. × I						
$S_fS_f \times S_2S_{F10} \longrightarrow$	$S_2S_f + S_{F10}S_f$	9146	1 (12)	+	1 (8)	−
N.l. × II						
$S_fS_f \times S_{F10}S_{F11} \longrightarrow$	$S_{F10}S_f \times S_{F11}S_f$	9147	0	...	2 (11,7)	−, −
N.l. × III						
$S_fS_f \times S_1S_2 \longrightarrow$	$S_1S_f + S_2S_f$	9148	1 (19)	+	0	...
N.l. × IV						
$S_fS_f \times S_1S_{F11} \longrightarrow$	$S_1S_f + S_{F11}S_f$	9149	1 (8)	+	1 (8)	—
N.l. × IX						
$S_fS_f \times S_1S_3 \longrightarrow$	$S_1S_f + S_3S_f$	9156	1 (20)	+	0	...
N.l. × X						
$S_fS_f \times S_3S_{F10} \longrightarrow$	$S_3S_f + S_{F10}S_f$	9157	1 (9)	+	1 (11)	—

+ = compatible; − = incompatible.

The rate of pollen-tube growth differs significantly in selfed M and N plants (cf. Table 1). Penetration of the style at 48 hours ranges from 7·0 to 18·6 mm. (10–27 % of style length) in M plants, and from 11·0 to 27·1 mm. (18–38 %) in N plants; the corresponding means are 12·8 (18·5 %), and 21·5 (28 %). In compatible

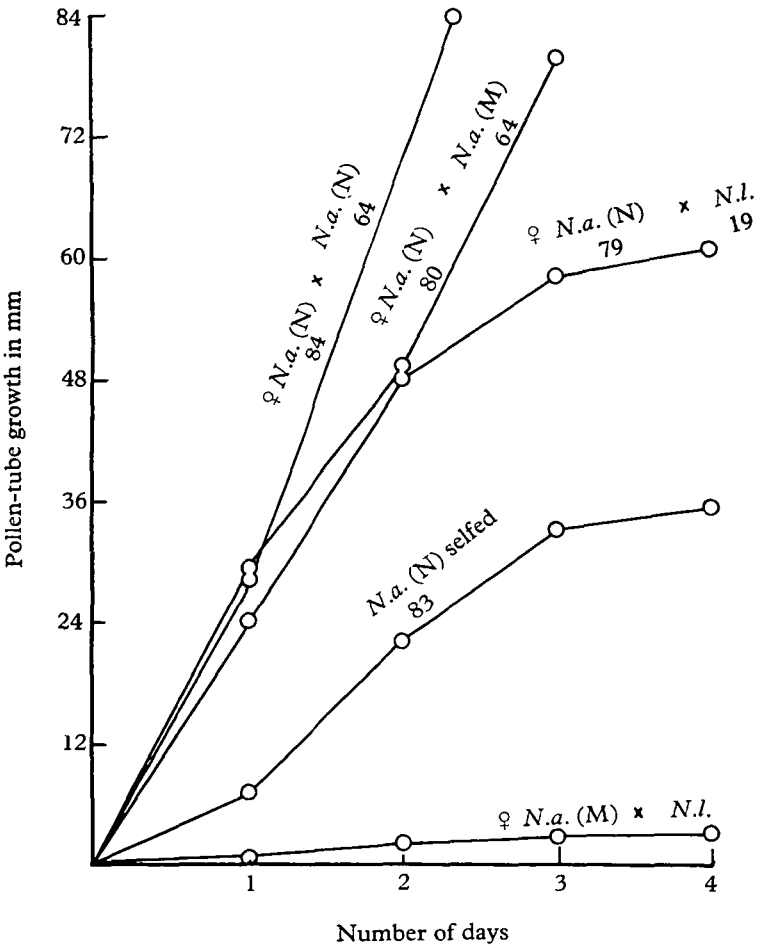

Fig. 2. Comparative rates of pollen-tube growth in styles of the two kinds of *Nicotiana alata* plants, M and N. Average length of styles is given below the names of parents; *N.a.* = *N. alata*, *N.l.* = *N. langsdorffii*.

crosses, N × N, and N × M ♂, full penetration of the style is achieved at 48 hours in the first group but at 72 hours in the second group. Thus, both in incompatible and in compatible pollinations M pollen-tubes grow more slowly than do N tubes.

This differential effect would be explicable on the assumption that the S_{FI} gene slows down pollen-tube growth, and that its action is such that it affects S_I pollen less than S_{FI} pollen. Such an action would suggest an element of sporophytic control somewhat reminiscent of that detected by Crowe (1955) in *Oenothera*.

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This would account for the observed deviation from a 1:1 expectation of S.I. to S.C. plants from crosses using $S_I S_{FI}$ as males (see Table 2 and Table 3, family 9125). Here, S_I pollen, even though it grew more slowly than in N plants (S_1S_2 etc.), would have an advantage with respect to S_{FI} pollen.

It is interesting to note the circumstances, outwardly similar, in which the two kinds of pollen, S_{FI} and S_I, apparently grew at comparable rates. When F_1 $S_I S_{FI}$ plants, derived from M × M crosses in which the parental plants came from different original sources, were used as males in backcrosses to *N. langsdorffii*, the progenies showed the expected ratio of 1 S.C.:1 S.I. (Table 6, families 9146, 9149, 9157). The most likely explanation is that the behaviour of the S_{FI} gene varies with a change in the genetic background. The change would be from a presumed degree of homozygosity in M plants from each of the cultivated sources to a degree of heterozygosity in the inter-crosses (Mather, 1943; Pandey, 1960). If this is so, it may happen that the more inbred the material the stronger the action of the S_{FI} alleles in retarding the growth of pollen-tubes.

4. DISCUSSION

(i) *The* S_{FI} *gene in natural populations*

The high incidence of S_{FI} alleles in cultivated plants from several sources suggests that they may be relatively common in natural populations. If this is so, their effect will be largely indistinguishable from that of the ordinary S_I alleles so long as the populations maintain their integrity as strictly outbreeding communities (S.I.). Under these circumstances, there would appear to be no reason why one class of allele should have a selective advantage over the other.

The situation will be different, however, if the S.I. population is exposed to the influence of the self-compatible allele S_f which (*a*) may arise by mutation either within the population or in a second overlapping population (also S.I.) with which the first can freely introgress; or (*b*), may intrude from a closely related sympatric species (S.C.). Under these conditions, plants carrying an S_{FI} allele, by rejecting new or 'old' self-compatible pollen, will dampen the spread of inbreeding and so be favoured by selection (Grun & Radlow, 1961; Pandey, 1962*b*).

(ii) *Primary and secondary specificity*

It has been suggested (Pandey, 1962*a*) that the *S*-gene complex has two sub-units for specificity: one of ancient origin and relatively simple organization which is common to all alleles and determines their basic or *primary specificity*; the other of complex organization, inherently variable, and thus a reservoir of many kinds of *secondary specificity*. Secondary specificity is thought to be superimposed on primary specificity. It is also believed that for each class of specificity there are respective stylar and pollen components.

The problem raised by the present study is that of the physiological inter-relationships of the two kinds of specificity, when (*a*) only one kind is expressed; and (*b*) both kinds are expressed at the same time.

The first question has been discussed before (Pandey, 1962*a*). In ordinary S_I alleles it was assumed that secondary specificity was superimposed on primary specificity and dominant to it; hence the latter was not expressed in both pollen and style. The loss of secondary specificity would then permit the expression of primary specificity at the site concerned, e.g., in S_f pollen of *N. langsdorffii*. In this instance, the expression of the two kinds of specificity is interdependent. An alternative assumption, not made before, is that primary specificity is inactivated in S_I alleles, so that even if secondary specificity were lost, no specificity at all would be expressed. The emphasis here is on an incipient independence of expression of the two kinds of specificity, and it is this concept, rather than one of interdependence, which is thought to lead directly to the second question.

The second question, that of the simultaneous expression of both primary and secondary specificity in the style, as demonstrated in M plants of *N. alata*, can presumably be resolved by a mutation which re-activates primary specificity. This would explain the origin of both the S_{FI} and S_f alleles; the latter would result when an allele which had developed the capacity to produce both primary and secondary specificity in the pollen (in the manner above), subsequently lost its ability to produce secondary specificity.

SUMMARY

Cultivated plants of *Nicotiana alata* are self-incompatible and are of two kinds: normal (N); and exceptional (M). N plants are reciprocally compatible with *N. langsdorffii*; M plants are compatible only as males. M plants contain an unusual allele, S_{FI}, which has a dual action in the style: it rejects both self-pollen, and S_f pollen from *N. langsdorffii*. The overall results agree with the assumption that the S_{FI} gene produces two kinds of specificity in the style: *primary* specificity, which is responsible for the rejection of S_f pollen; and *secondary* specificity, which is responsible for the rejection of self-pollen as in S_I alleles generally. The genetic sub-units concerned must be closely linked; there was no evidence for their dissociation in the 599 plants studied.

In both compatible and incompatible pollinations, S_{FI} pollen grows more slowly than S_I and, in addition, appears to depress the normal rate of growth of S_I pollen. In consequence, crosses $S_fS_f \times S_IS_{FI}$ ♂ yielded significantly fewer S.I. plants than the 50% expected. The two kinds of pollen grew at comparable rates, however, when F_1 (M × M) plants involving parents from different original sources were backcrossed to S_fS_f ♀. Progenies then showed the expected 1:1 ratio of S.I. to S.C. plants. These results are assumed to be due to differential behaviour of the S_{FI} allele according to its genetic background. The change in background would be from a degree of homozygosity, in plants from the same source, to a degree of heterozygosity, in crosses between plants from different sources.

The high incidence of the S_{FI} gene in *N. alata* is considered to be due to the advantage it confers on a self-incompatible population when it is overlapping with a related self-compatible population (having the S_f gene). Plants carrying an S_{FI}

allele, by rejecting the S_f pollen, will restrict the spread of inbreeding and so be favoured by selection.

The origin of the S_{FI} and S_f alleles are discussed in relation to the author's hypothesis of *S*-gene structure.

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