

## NOTES AND COMMENTS

SELF-INCOMPATIBILITY IN *LINARIA*

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## 1. INTRODUCTION

IN the family Scrophulariaceae, the following species have been shown to have a gametophytic system of self-incompatibility with a single multiallelic gene: *Veronica syriaca* (Filzer, 1926; Lehman, 1926), *Antirrhinum glutinosum* (Gruber, 1932), *Nemesia strumosa* (Riley, 1935; Docherty, 1982), *N. versicolor* and *N. capensis* (Docherty, loc. cit.). Sirks (1926) working with *Verbascum phoeniceum* made observations which were at variance with the "Nicotiana" type of system, and explained his results on a modified S-scheme. Lawrence (1930) pointed out however that *V. phoeniceum* is probably allotetraploid and explained Sirks' results by assuming duplicate S-genes derived from the two ancestral species.

Brüun (1937), reported that several species in the genus *Linaria* are self-sterile, and Valdés (1970a) found that in a number of *Linaria* species no seed was obtained from artificial self-pollinations while viable seed was generally produced from cross-pollinations between different plants. These reports indicate that many species of *Linaria* are self-incompatible. The genetic basis of incompatibility however, has not been determined in these species. In this study, 13 species of *Linaria* and six interspecific hybrids have been tested for self-incompatibility. In five of these species and three hybrids, the self-incompatibility system has been studied in detail.

## 2. MATERIAL AND METHODS

With the exception of two acquisitions (*L. vulgaris* V/74A and *L. pedunculata* PE/74 in each of which plants were collected from the wild), seed was supplied by Botanical Gardens. In many of the species two or three acquisitions were used, a minimum of four plants being tested for each species. The interspecific hybrids tested were produced by the author from crosses between some of the species tested. For observation of pollen-tube growth, gynaecia were softened in sodium hydroxide and stained with aniline blue (Martin, 1959 modified).

## 3. RESULTS

Each species was tested for self-incompatibility by seed-setting and pollen-tube growth. In compatible pollinations, pollen tubes grew into the ovary and fertilised all the ovules. In incompatible pollinations the pollen tubes stopped growing 0.9–1.2 mm into the style (approximately  $\frac{1}{6}$ – $\frac{1}{4}$  of

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the style length) and callose plugs were usually formed at the tips of incompatible pollen tubes. The results from the seed-setting and pollen-tube growth tests were in complete agreement; the following species were all self-incompatible: *L. bipartita*, *L. genistifolia* subspecies *genistifolia* and *dalmatica*, and the subspecies hybrid *genistifolia* × *dalmatica*, *L. maroccana*, *L. purpurea*, *L. reticulata*, *L. spartea*, *L. supina*, *L. triornithophora* and *L. vulgaris*, and four species were self-compatible: *L. alpina*, *L. pedunculata*, *L. repens*, and *L. triphylla*.

The interspecific hybrids were tested for self-incompatibility by seed-setting (table 1).

TABLE 1

*Results from self-pollinations in interspecific hybrids*

Interspecific hybrid	Breeding system
<i>L. bipartita</i> × <i>L. reticulata</i>	Self-incompatible
<i>L. bipartita</i> × <i>L. spartea</i>	Self-incompatible
<i>L. genistifolia</i> subsp. <i>genistifolia</i> × <i>L. vulgaris</i>	Self-incompatible
<i>L. spartea</i> × <i>L. reticulata</i>	Self-incompatible
<i>L. genistifolia</i> subsp. <i>genistifolia</i> × <i>L. repens</i>	Self-incompatible (4 plants tested)
<i>L. vulgaris</i> × <i>L. repens</i>	Self-incompatible/weakly self-compatible

TABLE 2

*Summary of the results from the dialleles, showing the incompatibility relationships of plants in the F<sub>1</sub> families*

A. Intraspecific				
Species	Reference of F <sub>1</sub> family	No. of plants	No. of groups*	No. of plants in the diff. groups
<i>L. bipartita</i>	21/75A (x × y)	15	4	5, 5, 3, 2
<i>L. bipartita</i>	21/75A (y × z)	12	2	7, 5
<i>L. genistifolia</i> subsp. <i>genistifolia</i>	74/73	12	4	5, 3, 2, 2
<i>L. genistifolia</i> subsp. <i>genistifolia</i> × subsp. <i>dalmatica</i>	74/74A × 72/74	14	4	6, 4, 3, 1
<i>L. reticulata</i>	70/74	11	4	5, 3, 2, 1
<i>L. supina</i>	78/74	14	2	9, 5
<i>L. vulgaris</i>	V/74	16	4	6, 5, 3, 2
B. Interspecific				
<i>L. bipartita</i> × <i>L. reticulata</i>	21/75B × 70/74	14	4	5, 3, 3, 3
<i>L. bipartita</i> × <i>L. spartea</i>	21/75B × 31/75	16	4	6, 4, 4, 2
<i>L. genistifolia</i> subsp. <i>genistifolia</i> × <i>L. vulgaris</i>	74/74A × V/74A	12	4	5, 3, 2, 2

\* Groups are intra-incompatible and inter-compatible.

To determine the genetic basis of incompatibility in each of five species and three interspecific hybrids found to be self-incompatible, an F<sub>1</sub> progeny was produced by crossing together two of the plants previously tested for self-incompatibility. Where possible, the two plants used were from different sources. The mating behaviour of each F<sub>1</sub> family was analysed in a diallel cross. In one of the species, *L. bipartita*, two families (x × y) and

( $y \times z$ ) were produced using plants  $x$ ,  $y$ , and  $z$  as parents, and two subspecies of *L. genistifolia* were tested *i.e.*, subsp. *genistifolia* and subsp. *dalmatica*.

The results from the crosses show that in every progeny examined, the  $F_1$  plants like their parents were strictly self-incompatible. In each  $F_1$  progeny examined the plants can be arranged either into four or into two different breeding groups. Each plant is reciprocally compatible with plants in the same group and reciprocally incompatible with plants in the other breeding groups. No reciprocal differences were observed in any of the combinations. The results are summarised in table 2.

The breeding relationships of the plants within the  $F_1$  family ( $x \times y$ ) of *L. bipartita* were tested by (i) seed setting and (ii) pollen-tube growth. As identical results were obtained by the two methods in this family, the mating behaviour of plants in all the other  $F_1$  families has been analysed only by the more convenient method of seed-setting.

In some of the crosses of *L. bipartita*, there is 100 per cent pollen-tube growth into the ovary (fully compatible). Using stigmata of the same genotype with different male parents, a large number of pollen-tubes (presumed about half) stop in the style and callose plugs are formed.

#### 4. DISCUSSION

Nine of the 13 *Linaria* species examined are self-incompatible. This is comparable with the results of Brüun (*loc. cit.*) who also found that there is a predominance of self-incompatible species in this genus. Some authors have reported (Brüun, *loc. cit.*; Dilleman, 1948; Clapham, Tutin and Warburg, 1962; Stace, 1975) that *L. repens* is self-sterile. In the present study it was noted that some plants of *L. repens* set very little seed in self-pollinations, while others were highly self-compatible. Also, no seed was produced by any of the plants unless self-pollen was deposited on the stigma (with a pair of forceps). The above authors may have not ensured that self-pollen was deposited on the stigma of the flowers tested. A more likely explanation however is that *L. repens* has a versatile incompatibility system with plants ranging from complete self-incompatibility to complete self-compatibility which would account for the differences in the results. Further investigations in this species and its hybrids could prove interesting.

With a maximum of four mating types in any of the  $F_1$  families examined, a one-locus self-incompatibility system is postulated. The absence of reciprocal differences, the site of pollen-tube inhibition in the style and the differential behaviour of the pollen from the male parents in certain crosses are indications of gametophytic control of pollen specificity.

In the five species examined, there are indications of a large number of alleles for the incompatibility gene. In *L. reticulata*, *L. vulgaris* and *L. genistifolia* four different alleles are present in the two parent plants used to produce the  $F_1$  progeny. In *L. supina* only two mating groups in the  $F_1$  progeny indicates that the parent plants must have a common allele. In *L. bipartita*, crosses between the mating groups of the two  $F_1$  families showed that the four groups of family ( $x \times y$ ) were different from the groups of family ( $y \times z$ ). There is therefore a total of five different *S*-alleles in the three parent plants.

Despite the diversity of outbreeding systems in the Angiosperms, the genetic basis for self-incompatibility is usually similar in closely related

groups (Crowe, 1964). The results from this study support this view, adding to the number of species in the Scrophulariaceae found to have the one-locus gametophytic homomorphic system of self-incompatibility.

The incompatibility system in the species examined is not disturbed by hybridisation. All the hybrids between two self-incompatible species were found to be fertile but self-incompatible. They do not set seed unless they are cross-pollinated with plants of a different mating specificity. Therefore reports that some interspecific hybrids of *Linaria* are sterile (e.g., Valdés, 1970b, reported that 58 different hybrids he obtained from crosses between *Linaria* species were all sterile) are probably based on insufficient analysis. The results from this study show that in a genus like *Linaria* where several self-incompatible insect-pollinated species hybridise readily and self-incompatibility is inherited in the hybrids, careful tests are necessary to find whether a failure to set seed in the hybrids is due to sexual sterility or self-incompatibility.

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## 5. REFERENCES

- BRÜUN, H. G. 1937. Genetical notes on *Linaria*. *Hereditas*, 22, 395–400.
- CLAPHAM, A. R., TUTIN, T. G., AND WARBURG, E. F. 1962. *Flora of the British Isles*, 2nd edition, Cambridge University Press.
- CROWE, L. K. 1964. The evolution of outbreeding in plants. I. The Angiosperms. *Heredity*, 19, 435–457.
- DILLEMAN, G. 1948. Remarques sur l'hybridation spontanée des *Linaires* dans les jardins Botaniques. *Bull. Mus. natn. Hist. nat., Paris*, 20, 546–547.
- DOCHERTY, Z. 1982. Self-incompatibility in *Nemesia*. *Heredity*, 48, 137–138.
- FILZER, P. 1926. Die Selbsterilität von *Veronica syriaca*. *Z. indukt. Abstamm.-u. Vererb. Lehre*, 41, 137.
- GRUBER, F. 1932. Über die Verträglichkeitsverhältnisse bei einigen selbsterilen Wildsiffen von *Antirrhinum* und über eine selbstfertile Mutande. *Z. indukt. Abstamm.-u. Vererb. Lehre*, 62, 429–462.
- LAWRENCE, W. J. C. 1930. Incompatibility in polyploids. *Genetica*, 12, 269–294.
- LEHMAN, E. C. 1926. The heredity of self-sterility in *Veronica syriaca*. *Mem. hort. Soc. N. Y.*, 3, 310–320.
- MARTIN, F. W. 1959. Staining and observing pollen tubes in the style by means of fluorescence. *Stain Technol.*, 34, 125–128.
- RILEY, H. P. 1935. Self-sterility and self-fertility in species of the genus *Nemesia*. *Amer. J. Bot.*, 22, 889–894.
- SIRKS, M. J. 1926. Further data on the self- and cross-incompatibility in *Verbascum phoeniceum*. *Genetica*, 8, 345–351.
- STACE, C. A. 1975. *Hybridization and the Flora of the British Isles*. Stace, C. A. (ed.) Academic Press, London and New York.
- VALDÉS, B. 1970a. Taxonomía experimental del género *Linaria*-IV. Reproducción sexual: autogamia y polinización intraespecífica. *Boln R. Soc. esp. Hist. nat.*, 68, 79–89.
- VALDÉS, B. 1970b. Taxonomía experimental del género *Linaria*-V. Hybridación Inter-específica. *Acta Phytotaxonomia-Barcinomensis*, 4, 5–24.