

CRYPTIC SELF-INCOMPATIBILITY IN THE WALLFLOWER : *CHEIRANTHUS CHEIRI* L.

A. J. BATEMAN

British Empire Cancer Campaign Fellow, Christie Hospital and
Holt Radium Institute, Manchester

Received 26.i.56

I. INTRODUCTION

FROM extensive studies in self-incompatibility in the Cruciferae (Bateman, 1955) there appeared to be a strong correlation between the breeding system of a species and the conspicuousness of its flowers. These two characters were related in such a way that self-compatible species generally had small and inconspicuous flowers, whereas self-incompatible species achieved conspicuousness. This they did either by the large size of the individual flowers or by their being arranged in conspicuous inflorescences, as in Sweet Alyssum (*Lobularia maritima* L., Desv.).

The correlation is best shown by considering genera containing both breeding systems (table 1). A plausible explanation is that autogamous species have no need to attract insects for their immediate

TABLE 1

Genus	Self-fertile		Self-sterile	
<i>Brassica</i>	<i>juncea</i>	O	<i>campestris</i>	O
	<i>napus</i>	O	<i>oleraceus</i>	O
<i>Matthiola</i>	<i>incana</i>	O	<i>nigra</i>	O
	<i>suffruticosum</i>	O	<i>bicornis</i>	O
<i>Erysimum</i>	<i>cheiranthoides</i>	X	<i>asperum</i>	O
	<i>bursa-pastoris</i>	X	<i>concinus</i>	O
<i>Capsella</i>	<i>alyssoides</i>	X	<i>grandiflora</i>	O
	<i>campestre</i>	X	<i>argenteum</i>	O
<i>Cardamine</i>	<i>hirsuta</i>	X	<i>saxatile</i>	O
	<i>hirsuta</i>	X	<i>pratensis</i>	O
<i>Arabis</i>	<i>officinale</i>	X	<i>albida</i>	O
	<i>irio</i>	X	<i>pinnatifidum</i>	O

The correlation between breeding system and flower conspicuousness in genera containing both self-fertile and self-sterile species. O, flowers conspicuous. X, flowers inconspicuous.

survival, but self-incompatible ones are entirely dependent for seed production on some pollinating agent. However, one must not overlook the fact that visually attractive flowers and abundant nectar would in themselves constitute an outbreeding mechanism, albeit a weak one if not reinforced by some barrier to self-fertilisation.*

* The author is not sufficiently familiar with other families to produce a similar table for Rosaceae, Leguminosae or Compositae. However, since these families have diverse additional outbreeding mechanisms based on flower structure, monoecy, apomixis, etc., one would not expect the correlation to be so high.

Among a few striking exceptions to the above rule is the Wall-flower, with its self-fertility and very conspicuous flowers; but as I propose to show, in this species at any rate, the exception is only apparent.

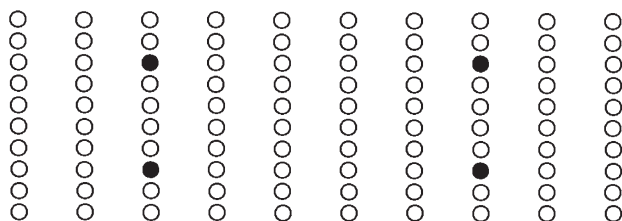


FIG. 1.—Arrangement of plants within one open-pollinated plot.
○ = red plant. ● = yellow plant.

Note: the plants are spaced so as to make the plot square.

2. OPEN POLLINATION

Self-pollination of flowers of this species regularly produces a full seed set. Yet casual observation of any bed of Wallflowers in bloom, or even when still only vegetative, discloses a large measure of variation, some of which (such as flower colour), is almost certainly hereditary. This indicates the presence of an outbreeding mechanism of some kind.

The outbreeding was confirmed in experiments in which open-pollinated seed was obtained from single plants of a yellow-flowered variety ("Cloth of Gold") exposed in a bed of red-flowered ones ("Vulcan"). In this material red proved dominant to yellow flowers. Square plots of 100 plants were grown, 10 rows of 10 plants, at three planting densities, the distances between plants being 6 in., 1 ft. and 2 ft. in plots numbered 1, 2 and 3. Planting out was in the autumn. Each plot contained 96 plants of Vulcan and 4 plants of Cloth of Gold, arranged as in fig. 1. It will be seen that each yellow-flowered plant is separated from similar plants by at least four reds and from the outside of the plot by at least two. The proportion of red seedlings in the progeny of such yellow plants will give a good estimate of the degree of natural outcrossing. It will in fact be a minimal estimate, because the following factors will tend to inflate the amount of natural selfing.

Firstly, there will inevitably be a small amount of crossing between yellows (much less than 3 per cent. of the total outcrossing). Secondly, it has been shown (Bateman, 1951) that the behaviour of pollinating insects is such that flower-colour differences between varieties act as isolating mechanisms, so that there would be selective pollination of yellow by yellow. Thirdly, any difference between the varieties in flowering period, or even in the distribution of flowering within the same period, would be an isolating factor.

The three spacings were introduced because the farther apart the individual plants, and the larger they are (size is assumed to be

promoted by wider spacing), the greater will be the ratio of pollinations between flowers on the same plant (geitonogamy) to pollinations between plants.

Owing to late sowing, flowering was not as free as desired, and one of the four yellows in plot 3 did not bloom. At harvesting the fruiting stems of each plant were separated into inner and outer branches. The inner branches should show most geitonogamy. It was found possible to score the progeny at the seedling stage, as the hypocotyls of selfed yellow were acyanic and the hybrids showed purple anthocyanin. Growing-on of a proportion of the seedlings to flowering in the next season confirmed the correctness of the scoring at the seedling stage. One hundred and eight seedlings were scored for each sample, or 216 per plant. The data are presented in table 2.

TABLE 2
*Percentage of outcrossing of single yellow Wallflower plants in
a plot of red ones*

	Plant no.	1	2	3	4	Mean
Plot 1 (6 in. spacing)	Inner branches .	80.6	80.6	72.2	68.5	75.5
	Outer branches .	89.8	80.6	82.4	51.9	76.2
	Mean . .	85.2	80.6	77.3	60.2	75.8
Plot 2 (1 ft. spacing)	Inner branches .	76.9	75.0	73.1	not	75.0
	Outer branches .	61.1	81.5	75.9	separated	72.8
	Mean . .	69.0	78.3	74.5	72.8	73.7
Plot 3 (2 ft. spacing)	Inner branches .	64.8	72.2	71.3	no	69.4
	Outer branches .	66.7	72.2	64.8	seed	67.9
	Mean . .	65.8	72.2	68.1	...	68.7

Analysis of variance merely confirmed what is apparent on inspection: that position on the plant and planting density are without effect. Although a slight trend in the expected direction appears with increasing spacing, this is only of the same magnitude as the intra-plot variation between plants. The main object of the experiment, however, was to estimate the degree of natural outcrossing. For this the minimal estimate is over 70 per cent. This is remarkably high for a species which, apart from the large flowers and strong scent, seems unadapted for cross-pollination and is self-fertile. Whatever the out-breeding factor may be it is evidently strong enough to swamp completely any effect of geitonogamy.

3. THE DETECTION OF SELF-INCOMPATIBILITY

It occurred to me that in spite of the full seed set on selfing there might be a weak incompatibility reaction which would only show when self pollen had to compete with foreign pollen on its own style, as under open pollination. Such a situation had been anticipated on theoretical grounds (Bateman, 1952). The incompatibility would be detectable only by accurate measurements of pollen tube growth or by mixed pollinations using self and foreign pollen.

The following test was made using only three plants, but its complete explanation of the field data warrants confidence in its validity. Plants numbered 1 and 2 were yellow-flowered, number 3 was red-flowered. Emasculated flowers of plant 1 were pollinated with what we endeavoured to make up as fifty-fifty mixtures of pollen

TABLE 3
Results of mixed pollinations

Pollination type	No. of pollination	No. of flowers pollinated	Progeny		Percentage crossed to red
			Red	Yellow	
$1 \times (2+3)$	1	3	33	72	31
	2	6	37	150	20
	3	4	17	74	19
	Total . .	13	87	296	22.7
$1 \times (1+3)$	4	5	88	11	88
	5	2	56	6	90
	6	5	168	9	95
	7	5	170	15	92
	Total . .	17	482	41	92.2

In column "pollination type," 1 and 2 represent different yellow plants; 3 one red plant.

from two plants. The mixtures were of two kinds: (a) plants 1 and 3 and (b) plants 2 and 3. It is difficult to be sure that any one mixture is properly balanced, but each pollination number in table 3 represents a separate mixture. As earlier, seedlings were classified on hypocotyl colour as red or yellow flowered.

There is a most striking contrast between a deficiency of red progeny when the mixed pollens were both from plants other than the seed parent and the great preponderance of red progeny when the yellow pollen was self pollen. Whatever might be the cause of the deficiency of red in the first series (genetic isolation between varieties?) it makes the excess in the second series all the more striking. This excess is greater than the outcrossing observed in the field. This is probably due to the spatial and temporal advantage of self

over foreign pollen under natural pollination. The magnitude of this advantage would be expected to vary with the activity of the pollinating insects and thus to be very sensitive to the local insect fauna, competing forage crops, and the weather, and also on the number of simultaneously open flowers per plant.

These results have an obvious moral for the plant breeder. It is dangerous to expect self-fertility in the field, merely because in the glasshouse plants give a full seed set on selfing. This danger is likely to be greatest for species which are members of families known to contain much self-incompatibility. Thus cauliflowers are alleged to be self-fertile, but they are suspected of being very prone to contamination by cross-pollination when being grown for seed.

4. SUMMARY

The Wallflower is an apparent exception to the rule in the Cruciferae that conspicuous flowers are associated with self-sterility. The Wallflower gives a full seed set on being artificially selfed.

However, in the field individual plants show outcrossing of more than 70 per cent.

Experiments with mixed pollinations show that this is because self pollen, though fully capable of fertilisation, cannot compete with foreign pollen, which when present in equal amounts, is responsible for over 90 per cent. of the seed set. There must be a weak self-incompatibility reaction, which under field conditions is still capable of functioning as a moderately efficient outbreeding mechanism.

Note.—The experiments were carried out at the John Innes Horticultural Institution, Hertford.

5. REFERENCES

- BATEMAN, A. J. 1951. The taxonomic discrimination of bees. *Heredity*, 5, 271-278.
 BATEMAN, A. J. 1952. Self-incompatibility systems in Angiosperms. I. Theory. *Heredity*, 6, 285-310.
 BATEMAN, A. J. 1955. Self-incompatibility systems in Angiosperms. III. Cruciferae. *Heredity*, 9, 53-68.