CYTOGENETICS OF CULTIVATED BOUGAINVILLEAS

II. Pollination Mechanism and Breeding System

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In *Bougainvillea* cultivars, while floral morphology together with coincidence of stigma receptivity and anther dehiscence suggests a self-pollinating mechanism, the presence of coloured bracts and nectariferous flowers points towards a cross-pollinating mechanism. Our studies have shown that about 80 per cent of garden bougainvilleas are both male and female sterile. The fertile forms do not set seed on selfing, but do so readily on crossing. Simultaneous cytokinesis during pollen formation, trinucleate pollen, and inhibition of pollen germination upon selfing suggest a sporophytic system of self-incompatibility; this is corroborated by retention of incompatibility in induced tetraploids.

Introduction

The knowledge of natural mode of pollination helps in understanding the mating system and breeding procedures that need to be followed to obtain desired results. The mode of propagation and maintenance of the ensuing type deserves an equal attention, which in turn depends upon the breeding objective itself. In seed propagated species, methods have to be adopted which would not impair the fertility of the new type, while in vegetatively propagated plants, where a single superior individual is the goal, one is free to choose a method which may or may not impair the sexual potency. Ornamental shrubs which can be multiplied and maintained by vegetative means fall in the latter category.

The type of pollination is usually correlated to floral morphology, relative length of style and stamens, time of anther dehiscence, and receptivity of stigma. Other features which affect pollination mechanism include the colour of flowers and bracts.

Observations

In *Bougainvillea* (Nyctaginaceae) flowers are borne in groups of three subtended by coloured and prominent bracts. The flower is tubular; the lower half of the tube is rather dilated, the upper half is funnel-shaped and opens out as a conspicuous 5-rayed cream-coloured star. From the base of the tube arises a single carpel. Encircling the ovary is a cup-shaped nectary; from its rim the stamens arise (Fig. 1).

A survey of relative lengths of stigmas and stamens of some species and cultivars of *Bougainvillea* reveals that the stigma is placed lower than the anthers (Fig. 4a–f)

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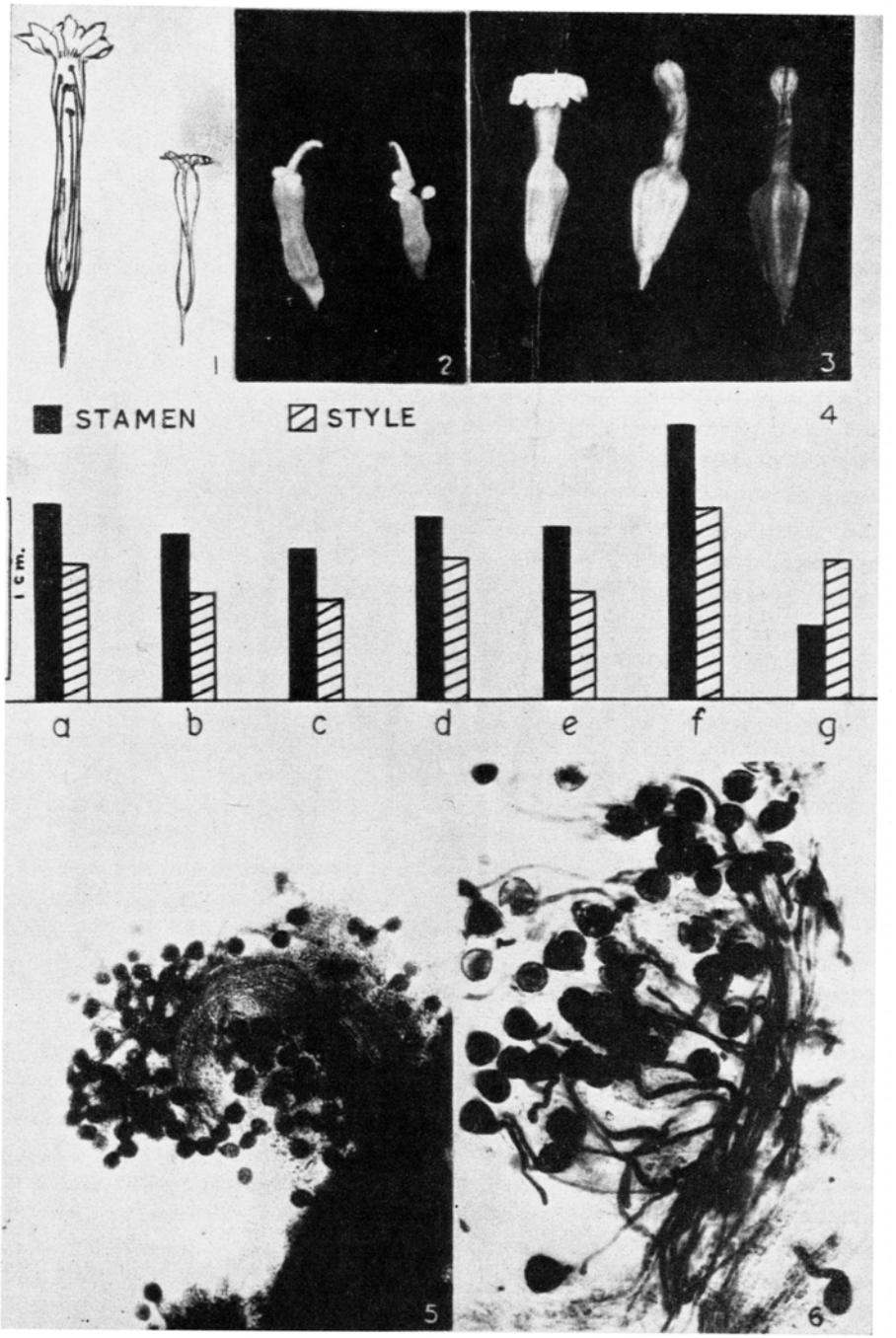

FIGS. 1–6. 1, L.S. flower showing position of style and stamens (left) and perfect flower tube (right). × 2 and × 1 respectively. 2, Imperfect flower tubes of *B.* × *buttiana* 'Scarlet Queen' × 2.5. 3, Twisting of flower tube × 1.5. 4, Relative lengths of style and stamens in (*a*) *B. spectabilis* 'Mrs. Chico', (*b*) *B. peruviana* 'Princess Margaret Rose', (*c*) *B. glabra* 'Dream', (*d*) *B.* × *buttiana* 'Mrs McClean', (*e*) *B.* × *specto-glabra* 'Sanderiana', (*f*) *B.* × *specto-peruviana* 'H.C. Buck', (*g*) *B.* × *buttiana* 'Scarlet Queen' (average of 25 flowers each) 5, 6, Whole mounts of part of stigma subsequent to self-pollination (2× self) and cross-pollination (2*x* × 4*x*), respectively; note absence of pollen germination upon selfing. Fig. 5 × ca. 200, Fig. 6 × ca. 250.

except in a few cultivars of *B.* × *buttiana* group in which the flower tube is imperfect and not star-shaped, and the filaments are considerably shortened, but the style length is not affected. Consequently the stigma protrudes from the tube and the anthers cluster around the base of style (Figs. 2, 4g, *see also* Zadoo *et al.* 1975).

Under the climatic conditions of Lucknow, in bougainvilleas the flowers open around 10.00 hr (earlier on warmer days) followed by dehiscence of anthers, which in turn coincides with the receptivity of stigma. The following day the upper part of flower tube becomes twisted (Fig. 3).

In their home in South America, bougainvilleas are visited by humming birds for nectar (Holttum 1955). In Singapore skipper butterflies and other kinds of butterflies have been seen visiting the flowers, but whether they effect pollination is not known (Holttum 1955). In Teneriffe (Canary Islands) the flowers are visited by *Convolvulus* hawk moth which also pollinates *Plumbago capensis* (*see* Holttum 1955). In Bombay (India) sun birds, *Leptocoma asiatica*, *L. zeylonica*, *L. minima* and *Aethopyga siparaga-vigrosi* (Ali 1932) are reported to regularly visit the flowers; the birds probe their bills deep into the flower tube and sip the nectar.

In Lucknow butterflies have been seen to visit the flowers during April-May. They land on the flower tube and introduce their proboscis into it to reach for the nectar. In doing so they transfer pollen grains, to stigma of same flower or of other varieties growing in proximity, if they happen to visit. We have noticed ample seed set in two varieties—'Mrs Chico' and 'Dream'—growing adjacently and that were constantly visited by butterflies, but when one of the varieties was removed, the other ceased to set seed although the butterflies did visit its flowers. This prompted us to study pollen cytology, pollen viability, and pollen germination following self-pollination, cross-pollination and bud-pollination.

Our studies have shown that in the pollen mother cells cytokinesis is simultaneous and the pollen is shed at trinucleate condition.

A survey of 50 cultivars including the basal species (*Bougainvillea glabra* Choisy, *B. peruviana* Humb and Bonp., and *B. spectabilis* Willd.) for pollen viability as determined by stainability in 1 : 1 acetocarmine-glycerine solution showed that only 12 cultivars produced approximately 22—90 per cent viable pollen (Table I). Hence the compatibility studies were restricted to these 12 cultivars. None of these cultivars set seed on selfing; however, they set seed readily upon cross pollinaton. That selfing is infructuous has earlier been observed by Lancaster (1934), W. N. Sands (*see* Holttum 1955), and East (1940).

Pollen germination seldom occurred after self-pollination (Fig. 5). A few grains that germinated issued short pollen tubes which failed to penetrate the style. This is in contrast to normal pollen germination and pollen tube growth subsequent to cross-pollination (Fig. 6). Bud-pollination also did not result in seed set, neither did self-pollination after excision of stigma.

Discussion

The relative position of stigma and anthers, their simultaneous maturity and the twisting of floral tube, the day after anthesis, suggest a self-pollination mechanism in *Bougainvillea*. But the presence of coloured bracts in most of the cultivars points toward an adaptation for attracting insects or birds for cross-pollination. Unless such a

TABLE I

Pollen viability in some cultivars of Bougainvillea

Cultivar	Pollen viability (%)
Dream	90.0
Mrs. Chico	85.5
Pradhan's Profusion	84.7
Lilicina	76.9
Princess Margaret Rose	69.7
Lord Willingdon	65.5
Jennifer	60.8
Formosa	57.0
Splendens	56.0
Magnifica	37.6
Sanderiana	22.4
Perfection (3×)	89.0

case is otherwise studied it would not be possible to recognize its pollination mechanism.

The floral adaptations for cross pollination in *Bougainvillea* are less marked because the insect or bird visitors in their attempt to reach for nectar at the base of the ovary are more likely to transfer the pollen to the stigma of the same flower. Some cultivars of *Bougainvillea* × *buttiana* group which are of bud sport origin have the stigma exserted. This could be viewed as an adaptation for outcrossing; however, such flowers are not visited by insects. Furthermore, all cultivars of *B.* × *buttiana* group are both pollen and ovule sterile.

The development of coloured and showy bracts is characteristic of only cultivated bougainvilleas (Standley 1931). In the wild species a feature which could attract pollinators is the presence of nectary. This renders the role of colourful and showy bracts in the cultivated taxa secondary. This is further substantiated by the white bracted cultivars of the genus which are regularly visited by pollinators.

Nyctaginaceae are characterized by the occurrence of cleistogamy or autogamy (East 1940). The related families Amaranthaceae and Chenopodiaceae are outbreeders but nevertheless self-compatible. Being a woody perennial, *Bougainvillea* is characterized by cross-pollination and self-incompatibility. Owing to perennial habit such genera do not have an immediate problem of ensuring their survival by self-compatibility or apomixis (Stebbins 1950, 1958).

In self-incompatible taxa the difference in the timing of pollen maturity and stigma receptivity, or the inability of pollen to germinate acts as barrier to fertilization (Solbrig 1970). Of these the former can be discounted in *Bougainvillea* as its flowers are bisexual and show perfect coincidence of pollen maturity and stigma receptivity. Its floral architecture does not suggest any mechanism which could be effective in preventing self-fertilization, thus leaving only pollen germination for consideration. Since the control is at the level of pollen germination, it indicates a barrier governed by self-incompatibility(S) alleles. The homomorphic flowers, simultaneous cytokinesis,

trinucleate pollen, and inhibition of pollen germination upon selfing suggest the self-incompatibility type in *Bougainvillea* to be sporophytic (*see* Brewbaker 1957, Pandey 1960). This is further substantiated by the fact that there was no breakdown of incompatibility in colchicine tetraploids (*see* Lewis 1954).

The nature of pollination system in the wild species of *Bougainvillea* is not known although their floral morphology and lack of showy bracts would suggest the prevalence of self-compatibility. Then the development of showy bracts and the institution of self-incompatibility could be subsequent features in the evolution of bougainvilleas. Self-sterility is a recent innovation in the reproductive process (East 1940). Accordingly, self sterility which ensures cross-pollination is an important factor in producing variability and perpetuating heterozygosity. Both these are of evolutionary value in angiosperms. However, according to Stebbins (1957) self-incompatibility is a primitive condition in most taxa and probably self-compatibility is a derived condition in angiosperms. That self-fertilized species present a more specialized morphology than their self-incompatible and cross-fertilized relatives, and that many self-fertilized species possess structures that are generally of value in cross-pollination support such a contention.

In view of the foregoing discussion the breeding system of *Bougainvillea* can be understood only after studying the wild species. There is only a passing reference that bougainvilleas do not set seed in the wild (Holttum 1938); this could be due to self-incompatibility, or absence in their vicinity of individuals having different incompatibility alleles, or some other factor.

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