

Sexual Selection in Plants: The Process, Components and Significance

TEJASWINI¹, K N GANESHAIAH^{*2,4} and R UMA SHAANKER^{3,4}

¹Indian Institute of Horticultural Research, Bangalore 560 089

² Department of Plant Genetics and Breeding, ³ Department of Crop Physiology,
University of Agricultural Sciences, GKVK, Bangalore 560 065

⁴Jawaharlal Nehru Centre for Advanced Scientific Research, Jakkur, Bangalore 560 064

(Received on 11 September 2001; Accepted after revision on 7 October 2001)

Darwin (1859) proposed the theory of sexual selection to explain the evolution of sexually dimorphic characters in animals. He observed that in animals the bulk of the reproductive investments in to the offspring are made by females. This, he suggested results in (a) female choice - where females choose the best fit males and, (b) male competition - where males compete among themselves to mate with the females.

In the late 1980s a few laboratories including ours have attempted to extend the theory of sexual selection to plants. These attempts have shown that though plants 'neither sing nor dance', they do exhibit female choice and male competition as intensely as animals do. In this paper we review the conceptual developments in the area of sexual selection in plants with an emphasis on the work carried out at our laboratory over the last two decades. These studies have shown that a number of plant reproductive features, such as the pollen-ovule ratios, floral sex ratio, evolution of polyads etc., that hitherto have been treated as "sterile" botanical issues may indeed have evolved as a consequence of intense sexual selection in plants.

Key Words: Sexual selection, Female choice, Male-male competition, Pollen loads, Stigmatic inhibition, Gamete selection

Sexual Selection

In forwarding the theory of natural selection, Darwin faced several challenges. One of them was the difficulty he faced in explaining the evolution of sexually dimorphic characters such as peacock feathers or tusks of the male elephants or elaborate antlers in the male ungulates etc., He found that his theory of natural selection can not explain their evolution. Almost all such sexually dimorphic characters are energetically costly to produce and do not contribute to the survival of the bearer of these traits. The bizarre traits, being conspicuous, are likely to render their bearers more vulnerable for the predators, than if the animals did not possess them. Thus these traits seemed to be an unnecessary burden for the organisms bearing them and hence, natural selection is expected to act against them. Darwin resolved this problem by proposing an alternate process of selection called sexual selection.

The theory of sexual selection proposes that males compete among themselves to gain access to females during reproduction and in the process of such competition, those males that either physically defeat other males and/or those that 'appeal' better to the females succeed in mating and hence reproduce more of themselves. Darwin proposed that for this reason, males are selected to become stronger and or conspicuous to the females such that the females can exercise a choice to select them. Males thus may evolve secondary sexual traits such as weapons, e.g., horns of beetles or antlers of ungulates that help them in the male-male competition or bizarre traits such as peacock feathers that help them 'appeal' to the female during their mating dances. In the last three to four decades, the concept of sexual selection has significantly expanded both conceptually and empirically; the details of which are beyond the scope of this paper.

^{*}Corresponding author : E-mail: kng@vsnl.com, Tel: 91-80-3636276

For a long time, plants, unlike animals, were considered passive in the process of sexual selection. However, it was realised that just as in animals, severe competition could occur among pollen gametes for fertilising ovules, the female gametes. Following this sexual selection has been sought by several workers to explain the evolution of numerous morphological and adaptive characters in plants (Willson 1977, Charnov 1979, Mulcahy 1979, Queller 1983, Uma Shaanker & Ganeshiah 1997). In this paper we briefly review the major developments in translating the components of sexual selection to, and identifying them in, plants. We also discuss the present understanding of the role of sexual selection in the evolution of several plant reproductive traits.

Do Plants Meet Necessary Conditions for the Operation of Sexual Selection?

Darwin's suggestion for the operation of sexual selection in animals rested on an important assumption that females invest relatively more than males in an offspring. Accordingly, he proposed that it would be in the interest of the female to ensure that her offspring is sired by the most competitive male parent. While females can exercise choice over the males actively and directly, they could also ensure selection of the fit males by allowing them to compete amongst themselves. Obviously sexual selection can be expected to operate in plants only if an asymmetry exists among the maternal and paternal parents in resource investment to the offspring; this is indeed true to a large extent. Almost all of the resources for the development of the seed, the offspring in plants, are contributed by the maternal parent and the contribution by the male is limited to energy contained in a pollen grain. Further, females also expend a lot of resources to attract the pollen grains through insect vectors in the form of conspicuous features such as showy flowers and or by producing more flowers than actually develop into fruits (Willson 1977, Willson & Price 1977; Udovic 1981) and by expending energy in stigmatic structures that enhance trapping of pollen in the wind (Ganeshiah & Uma Shaanker 1982) or water pollinated flowers. Though such asymmetries are hard to be recognised in hermaphroditic or bisexual flowers, these differences are at least very clear in the dioecious

and monoecious species (Sutherland & Delph 1984, Sutherland 1986). The energy for either endosperm production, seed coat development, as well as, packing of seed in pod are essentially invested by the female. Thus there is a clear asymmetry in the investment of resources; females spend invariably more and are hence selected to be selective or choosy over males while males spend less and are hence selected to be competitive to produce as many males as possible.

Male-Male Competition

Do males compete to access the females among plants? And if they do what strategies they adopt? These questions are particularly important in the background of the general view that plants are inactive, less dramatic and perhaps are incapable of exhibiting behavioural features as animals do. Competition among male gametes can take several forms in plants and two major strategies are described below.

Gamete Inundation

In natural populations, genetically diverse pollen grains in numbers far exceeding the number of ovules are known to be present on stigma of a flower (Levin & Berube 1972, Mulcahy et al. 1983, Stephenson & Bertin 1983). This can be expected to result in severe competition among male gametes to gain access to and fertilise the ovules, akin to that found among the males in animals. Data from paternity analysis of seeds of wild radish (Ellstrand 1984), *Chamelirium luteum* (Meagher 1986) and *Asclepias* (Broyles & Wyatt 1990) indicate that seeds within a fruit are differentially sired by pollen donors. For instance as early as 1939, Iyengar and in 1958, Bemis have shown, in cotton and lima bean respectively that application of mixture of pollen grains from diverse genetic sources on to stigmatic surface resulted in non-random fertilisation of the ovules. Such non-random siring of the ovules within a fruit has been demonstrated in a number of plant species such as Douglas fir (Apait et al. 1989), *Hibiscus moscheutos* (Snow & Spira, 1991), Norway spruce (Cheliak et al. 1987), Onion (Currah 1981), *Vigna unguiculata* (Radha et al. 1993), and *Raphanus sativus* (Marshall & Ellstarand 1986, Marshall 1991). Thus essentially, in plants as well, males do compete and result in differential siring of the offspring, an immediate consequence expected from the intra-sexual competition.

The genotypes that inundate the gametes on the stigmatic surface leave behind more offspring sired by them increasing their reproductive success. Hence, the processes that favour this would obviously be selected for, and in fact, competition can be visualised among the plants to ensure a greater representation of their pollen pool in the habitats. This could perhaps explain the "far more than needed" pollen to ovule ratios even in otherwise predominantly self-pollinated plants (Miller 1982). Swamping the pollinating space or environment of the plant with more number of pollen grains is one of the strategies adopted by plants to enhance the probability of success in finding a female. Several species are known to produce more number of flowers (Willson 1977, Willson & Price 1977, Willson & Ratchke 1974, Udovic 1981) than actually sustain till development into fruits. This strategy of over production of flowers increases pollen donation and /or reception and attracts more number of pollinators there by enhancing transfer of high pollen load (Willson & Price 1977, Udovic 1981).

Plants can even make temporal shifts in sex ratio so as to represent their pollen loads at the appropriate times. For instance in *Croton bonplandianum* Baill the ratio of male to female flowers is high in early stages of the plant when the fitness gained through the pollen grains is higher. At later stages of the plant growth when the fitness accrued through the pollen is less and that through ovule is higher and assured, plants allocate more resource towards female flowers (Uma Shaanker & Ganeshiah 1984, figure 1). As a fine tuning strategy, plants are even known to maximise their resource allocation to males, in top relative to bottom end of inflorescences and to plants located at higher than lower altitude as observed in case of *Acalypha fruticosa* (Vasudev et al. 1987).

Besides number, shape and size of flowers, even the internal chemistry of pollen grains of some species appear to have evolved as a strategy of inundating their gametes. For instance flowers of certain plant species pollinated by birds and Lepidopeteran insects are starch rich (Baker & Baker 1983) and thus ensure the attraction of their respective pollinators and in turn transfer of pollen grains. Packing pollen grains in masses like pollinia and polyads or clumps of pollen grains (Kenrick

& Knox 1982, Nillsson et al. 1992, Cruden & Jensen 1979) is also viewed as an evolutionary consequence of competition among plants to represent their gamete pools on the stigmatic surfaces.

Gamete Exclusion and Pre-empting Strategies
Swamping the atmosphere with more number of pollen grains does not alone ensure the reproductive success. Male-male competition may continue even after deposition of pollen grains on stigmatic surface. In the game of gametic war, a plant may gain success (reproductive fitness) by recruiting overwhelmingly more number of soldiers (gametes) or by few strong gametes that strategically exclude the other competitors on the stigmatic surface. For instance the pollen grain that bear most vigorous pollen tubes may pre-empt the fertilisation of ovules (Stephenson et al. 1988, Rocha & Stephenson 1991, Radha et al. 1993).

Success of a gamete is a combined effect of germination percentage and rate of tube growth. For instance, when pollen from different individuals are competing on a stigmatic surface, that individual having faster tube growth would succeed in siring the progeny. Thus in multi-ovulated species genotypes with higher germination percentage can sire more progeny. Several studies have shown significant differences in germination ability of pollen grains among different clones or individuals and among different varieties within a species (Radha et al. 1993, Pfahler 1997, Tejaswini 1999).

Competitive ability of different donors to sire seeds is correlated with the tube growth rate of their

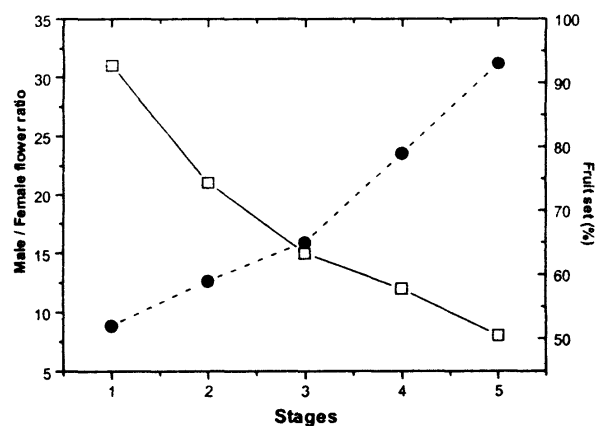


Figure 1 Floral sex ratio in *Croton bonplandianum* with stage of plant. Note that the allocation to the female flower increases with increase in the reproductive success (as measured by increase in seed and fruit set).

pollen grains (Snow & Spira 1991, Radha et al, 1993). As in case of germination percentage, variation also exists for pollen tube growth rate among different genotypes within a species. For instance in *D. caryophyllus* and *D. chinensis* (Tejaswini 1999), *Hibiscus moschetus* (Snow & Spira 1991), wild radish or *Raphanus sativus* (Marshall & Ellstrand 1986) and in *Zea mays* (Sari Gorla et al. 1983) intra-specific variation in pollen tube growth rate has been reported.

Abundance of one type of pollen grain could physically exclude or physiologically inhibit another type of pollen from the stigma (Wasser 1978, Sukhada & Jayachandra 1980, Thompson et al. 1981). In *Macadonia*, pollen tube outgrows after fertilising an ovule and disrupts the otherwise normally functional ovule (Sedgley 1981, 1989). An extreme form of sexual competition among mates is seen in case of *Klenhovia hospita* (Uma Shaanker & Ganeshaiiah 1988). In this species, pollen grains that germinate early would modify the stigma such that the germination and tube growth of pollen grains that arrive late are inhibited (figure 2).

Female Choice

As discussed in earlier section, since females expend more resources in the offspring, she is selected to ensure that the offspring she bears is of genetically superior quality and capable of gaining higher fitness to her. She can not afford to risk the asymmetrically greater resources she spends on the offspring whose genetic potentiality is not ensured. Therefore selection favours female to exercise care in choosing the partner who would sire her offspring. Thus, females are selected to be "choosy".

In animals this female choice is expressed in a range of intriguing ways. She often creates competitive conditions where males are incited to compete such that the best of the male is by default selected to mate with her. This kind of 'Swayamvara' is seen in a number of forms ranging from dance competition among males (e.g., in fruitflies and peacocks) to tug of horns (e.g., in ungulates) and perhaps to the competition of archery skills in human beings (as it is claimed to have occurred in mythical narration of the Swayamvara of Seetha and Draupadi; Geneshaiiah 1998). It has been shown that in plants as well, this female choice might occur in equally unique but ways distinct from that seen in

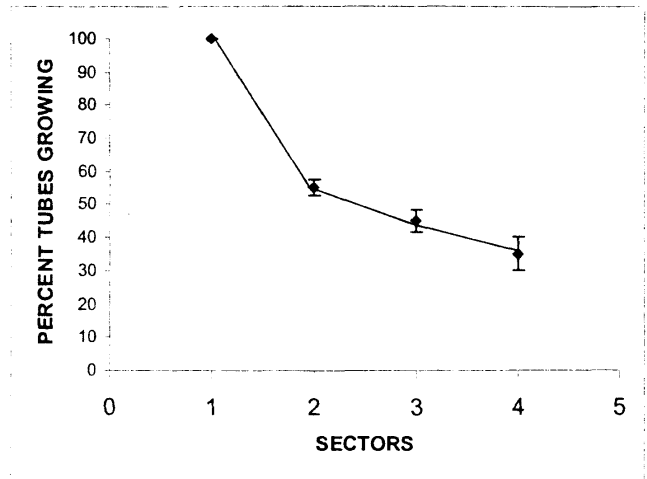


Figure 2 Stylar plugging in *Kleinhovia hospita*. Growth of the first germinating pollen grains through the stylar tissue progressively inhibits the germination and growth of the succeeding pollen grains and tubes. This mechanism is akin to the vaginal plugging reported in several animal systems, especially reptiles.

animals. Existence of various stylar and stigmatic mechanisms ensuring intense competition among pollen grains so that the best among them fertilise the ovule are interpreted to represent female choice (Ganeshaiiah et al. 1986, Ganeshaiiah & Uma Shaanker 1988a, Uma Shaanker & Ganeshaiiah 1990). There are other conditions where the stigmatic tissue is known to recognise the pollen donor and accordingly either facilitates or inhibits germination (Dumas & Gaude 1981).

Besides recognition, female plants often use certain strategies to incite male competition. The strategies adopted by species may be different starting from attracting the insects (to receive more pollen grains than actually she can sire), exhibiting wide and long stigmatic surface and extended period of stigma receptivity (a large amount of pollen grains can settle on stigmatic surface), having a long style (so that the pollen grains have to race among themselves to succeed in reaching the few ovules available) etc.

Inciting Competition to choose the Best Mate

In several ornamental plants e.g., in pinks, carnation, hippeastrum and hibiscus, the style is very long and has an extended period of stigma receptivity (Unpublished observations). While the prolonged receptivity favours deposition of more and diverse pollen grains, the long stylar and stigmatic structures enhance the intensity of competition for the already

competing pollen grains. Both the strategies ensure that the best of the pollen pool fertilise the ovules. In some populations of *Talinum mengesii*, germination of pollen grains was delayed up to two hours in order to generate enough variability of pollen genotypes on the stigma (Murdy & Carter 1987).

Perhaps one of the most uniquely interesting phenomenon of inducing the competition among pollen grains has been reported in *Leucaena leucocephala* (Ganeshiah & Uma Shaanker 1988a, figure 3). Stigmas of *Leucaena leucocephala* have a pouch containing a viscous fluid maintained at pH 5.0. Pollen grains are deposited into this pouch. Pollen grains less than a critical number (less than the mean ovule number per ovary; 20-25) in the pouch do not germinate. A proteinaceous inhibitor that is active at stigmatic fluid pH of 5.0 regulates the pollen grain germination. Pollen grain number greater than twenty-five can additively raise the stigmatic fluid pH to 6.0. This change in pH inactivates the inhibitor and thus allows all the pollen grains to germinate at once. In effect, this mechanism ensures an intense competition among the pollen grains such that the best among them fertilise the ovules. Similar mechanism has also been reported in *Moringa* (Uma Shaanker & Ganeshiah 1990). Similarly, pollen competition or pre-pollination mechanism of male-male competition was reported to be a common phenomenon occurring in *Hibiscus moscheutos* (Spira et al. 1992).

Strategy of Preferential Selection

Styles serve as filters for selecting the superior male. It is interesting to note that even after males ensure early pollen germination the female exerts her secondary round of selection process. Self-incompatibility is a clear manifestation of cellular recognition between the pollen and the sporophytic tissues of the pistil. Because of this female regulation, pollen from different donors grows at different rates (Barnes & Cleveland 1963, Schemske & Fenster 1983). Female regulates pollen tube growth through the supply of nutrient and or chemical signals (Pfahler 1967, Sari-Gorla et al. 1976, Linskens & Pfahler 1977). Linskens and Spanjers (1973) proposed an electrical signal while Jensen et al. (1983) proposed a hormonal one. Genetical (Hinata & Okazaki 1986) as well as biochemical (Neelam Sharma & Shivanna 1986) signals are also known to

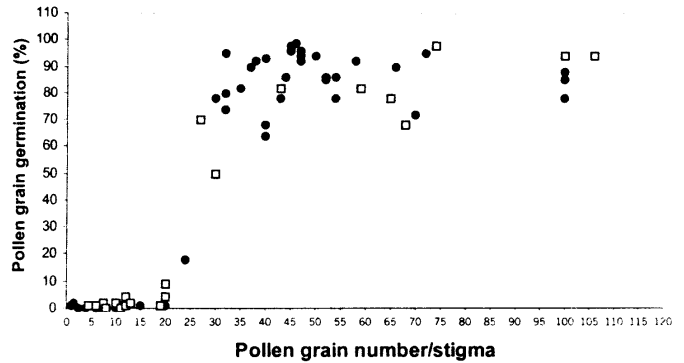


Figure 3 Relation between the pollen grain load in the stigmatic pouch and per cent pollen grain germination in *Leucaena leucocephala*. The relation is typical of an end-point reaction. As mentioned in the text, the germination of the pollen grain is finely regulated by a proteinaceous inhibitor that is active at pH 5.0 (at which the pollen grain germination is inhibited).

be transmitted between style and growing pollen tube in order to ensure selection process of female.

Consequences of Sexual Selection

Sexual selection has played an important role in evolution of plants. Angiosperms are characterised by closed carpels i.e., the presence of pistils and thus differ from the gymnosperms, which have naked carpels, meaning that they lack pistils (Mulcahy 1979). It is hypothesised that development of pistils, in particular the styles and stigmas, acted as filters and contributed to an intensified competition among micro-gametes and lead to the pre-eminent position of angiosperms in the present world flora (Mulcahy 1979).

In the course of evolution, sexual selection has favoured the correlation between the pollen gametophyte with the resulting sporophyte progeny. The correlation between gametophyte and the resulting sporophyte is due to a large overlap in gene expression between the gametophytic and sporophytic stages of the life cycle. A large portion of the microgametophyte genome is transcribed and translated and a vast majority of genes expressed by pollen are also expressed in the sporophyte (Tanksley et al. 1981, Willing & Mascarenhas 1984).

In natural populations, seedling establishment, progeny vigour and its performance are important parameters of reproductive success that are dependent on the parentage of the seeds (McKenna & Mulcahy 1983). Importance of pollen load size in seedling establishment in natural population is well

established. Pollen competition as ensured by increased pollen load is positively correlated with progeny performance in several plant species such as apple and pear (Visser & Verhaegh 1988, Janse & Verhaegh 1993), *Aureolaria flava* (Ramstetter & Mulcahy 1988), *Cassia fasciculata* (Lee & Hartgerink 1985), *Cucurbita pepo* (Quesada et al. 1996), *Cucurbita texana* (Johanson & Stephenson 1997), Lotus (Schlichting et al. 1987), Maize (Frascaroli & Landi 1991), Petunia (Mulcahy et al. 1975) and *Turnera ulmifolia* L. (McKenna 1985).

Sexual Selection or Selection of Superior Genotypes?

Male competition and female choice do not seem to end once the fertilisation process is over. Rather the process of selection by eliminating the non-fit ones continues even after fertilisation, through abortion of seeds and fruits.

Abortion of those fruits with few seeds is found to be higher than those fruits with greater number of seeds (Martin et al. 1961, Lee 1984, Stephenson & Winsor 1986). It is hypothesised that this pattern of fruit abortion benefits plants through the mechanism of intense pollen competition (Lee 1984). Fruits with a less than full complement of seeds are those produced without pollen tube competition. Differential or selective abortion of such fruits would lead to the selection of genetically superior offspring. In fact it has been well established that fruit abortion in plants is strictly due to mate choice, and not due to resource limitation (Stephenson 1984, Stephenson & Winsor 1986).

In multi-ovulated species sexual selection may also be manifested after the fertilization process in the form of zygotic competition or as seed abortion in developing fruits (Uma Shaanker & Ganeshaiah 1990). Non-random seed abortion in several species of plants is clearly related to the paternity of the seeds and in turn to the process of sexual selection (Marshall & Ellstrand 1988, Marshall 1998). In fact seed abortion has been considered as a possible maternal strategy to cull the inferior offspring resulting from siring by genetically poor paternal parents. In *Cassia fasciculata* (Lee & Bazazz 1982), in about 13 species of Fabaceae (Bawa & Buckley 1989) and in many species of Pinaceae (Llyod 1979) and in *Phaseolus* spp. (Weins 1984, Lee 1984, Nakamura 1986)

seed abortion is reported to occur as a maternal strategy of removing the inferior offspring.

Contrary to this maternal strategy, embryo abortion is also viewed as a result of sibling rivalry and parent-offspring conflict (Uma Shaanker & Ganeshaiah 1997). With sufficient empirical evidences they argue that the evolution of a number of plant reproductive features are manifestations of strategies and counter strategies of the offspring and maternal parent towards ensuring their respective interests.

Seed abortion can occur as a consequence of sibling rivalry for several reasons such as dispersal advantage, post-dispersal competition, to avoid predation and to gain resources (Ganeshaiah & Uma Shaanker 1988b). From the point of offspring it is advantageous to be a lone survivor and in such situations developing embryos resort to sibling rivalry and fratricide (Ganeshaiah & Uma Shaanker 1988b, Uma Shaanker & Ganeshaiah 1988). However, the sibling rivalry can also be viewed as a consequence of sexual selection or mate choice as sibling rivalry is found to be a function of genetic relatedness among the offspring developing in a fruit (Uma Shaanker & Ganeshaiah 1988). Evidence for this argument was also provided in *Vigna unguiculata* (Radha 1990) where the extent of resource allocation to a seed was influenced by competing sibling genotypes.

In conclusion all these post-zygotic selection raises the question of sexual selection merging with the selection of superior genotype. Plants produce more flowers than it can sustain till full development in to fruits. Similarly in a multi- ovulated species, each flower has more ovule than it can sustain till full development into seeds. Abortion of seeds or fruits is non-random and since, it depends on the paternal genotype, mate choice at the early stage turns to be maternal selection and sibling rivalry at the later stages. In other words, through the various processes (ranging from inundating with the pollen grains, male-male competition, female choice etc), it appears that sexual selection can be viewed as ensuring the selection of superior genotypes.

Acknowledgements

The work reported from our laboratory has been supported by grants from the Department of Science and Technology, Government of India.

References

- Apait V J, Nakamura R R and Wheeler N C 1989 Differential male reproductive success in douglas-fir; *Theor. Appl. Genet.* 77 681-684
- Baker H G and Baker I 1983 Some evolutionary and taxonomic implications of variation in the chemical reserves of pollen; in *Pollen: Biology and Implications for Plant Breeding* pp 43-52 eds D L Mulcahy and E Ottaviano (New York: Elsevier Biomedical)
- Barnes D K and Cleveland R W 1963 Pollen tube growth of diploid alfalfa *in vitro.*; *Crop Sci.* 3 291-295
- Bawa K S and Buckley D P 1989 Seed-ovule ratios, selective abortion and mating systems in Leguminosae; in *Advances in Legume Biology* eds C H Stinson and J L Aarucchi; *Miss. Bot. Gard. Monogr. Syst. Bot.* pp 243-262
- Bemis W P 1958 Selective fertilisation in Lima beans; *Genetics* 44 555-562
- Broyles S B and Wyatt R 1990 Paternity analysis in a natural population of *Asclepias exaltata*: multiple paternity, functional gender, and the pollen donation hypothesis; *Evolution* 43 318-334
- Charnov E L 1979 Simultaneous hermaphroditism and sexual selection; *Proc. Natl. Acad. Sci. (USA)* 76 2480-2484
- Cheliak W M, Skroppa T and Pitel J A 1987 Genetics of the polycross.1. Experimental results from Norway spruce; *Theor. Appl. Genet.* 73 321-329
- Cruden R W and Jensen K G 1979 Viscin threads, pollination efficiency and low pollen-ovule ratios; *American J. Botany* 66 875-879
- Currah L 1981 Pollen competition in onion (*Allium cepa* L.); *Euphytica* 30 687-696
- Dumas C D and Gaude T 1981 Stigma-pollen recognition and pollen hydration; *Phytomorphology* 31 191-201
- Ellstrand N C 1984 Multiple paternity within the fruits of the wild radish, *Raphanus sativus*; *Am. Nat.* 123 819-828
- Frascaroli E and Landi P 1991 Pollen and plant characteristics of maize populations derived from gametophytic selection; *Agricultura mediterranea* 121 130-134
- Ganeshiah K N 1998 Love games that insects play; *Resonance* 3 36-46
- _____ and Uma Shaanker R 1982 Evolution of reproductive behaviour in the genus *Eleusine*; *Euphytica* 31 397-404
- _____ and _____ 1988a Regulation of seed number per pod and female incitation of mate competition by pH-dependent proteinaceous inhibitor of pollen grain germination in stigmatic fluid in *Leucaena leucocephala*; *Oecologia* 75 110-113
- _____ and _____ 1988b Seed abortion in wind dispersed pods of *Dalbergia sissoo*: maternal regulation or sibling rivalry? *Oecologia* 77 135-139
- _____, _____ and Shivashankar G 1986 Stigmatic inhibition of pollen grain germination - its implication for frequency distribution of seed number on pods of *Leucaena leucocephala* (Lam) de Wit; *Oecologia* 70 568-572
- Hinata, K and Okazaki K 1986 Role of stigma in the expression of self-incompatibility in Crucifers in view of genetic analysis; in *Biotechnology and Ecology of Pollen* pp185-190 eds D L Mulcahy, G B Mulcahy and E Ottaviano (New York: Springer-Verlag)
- Iyengar N K 1939 Pollen tube studies in *Gossypium*; *J. Genet.* 37 69-106
- Janse J and Verhaegh J J 1993 Effects of varying pollen load on fruit set, seed set and seedling performance in apple and pear; *Sexual Plant Reproduction* 6 122-126
- Jensen W A, Ashton M E and Beasley C A 1983 Pollen tube-embryo sac interaction in cotton; in *Pollen: Biology and Implication for Plant Breeding* 67-72 eds D L Mulcahy and Ottaviano E Elsevier
- Johanson M H and Stephenson A G 1997 Effects of pollination intensity on the vigor of the sporophytic and gametophytic generation of *Cucurbita texana*; *Sexual Plant Reproduction* 10 236-240
- Kenrick J and Knox R B 1982 Function of the polyad in reproduction of Acacia; *Annals of Botany* 50 721-727
- Lee T D and Hartgerink A P 1985 Pollination intensity, fruit maturation pattern and offspring quality; in *Cassia fasciculata (Leguminosae) Biotechnology and Ecology of Pollen* pp 417-422 eds D L Mulcahy, G B Mulcahy and E Ottaviano (New York : Springer-verlag)
- _____ 1984 Patterns of fruit maturation: a gametophytic competition hypothesis; *Am. Nat.* 12 427-432
- _____ and Bazzaz F A 1982 Regulation of fruit maturation pattern in an annual legume *Cassia fasciculata*; *Ecology* 63 1374-1388
- Linskens H F and Pfahler P L 1977 Genotypic effects on the amino acid relationship in maize (*Zea mays* L) pollen and style; *Theor. Appl. Genet.* 50 173-177
- _____ and Spanjers A W 1973 Changes of the electrical potential in the transmitting tissue of *Petunia* styles after cross and self pollination; *Incomp. News Let.* 3 81-85
- Levin D A and Berube D E 1972 *Phlox* and *Colius*: The efficiency of a pollination system; *Evolution* 26 242-250
- Llyold D G 1979 Parental strategies of angiosperms, *N Z J. Bot.* 17 595-606
- Marshall D L 1991 Non-random mating in wild radish: variation in pollen donor success and effects of multiple paternity among one to six donor pollination; *Am. J. Bot.* 78 1404-1418

- Marshall D L 1998 Pollen donor performance can be consistent across maternal plants in wild radish (*Raphanus sativus*, Brassicaceae): A necessary condition for the action of sexual selection; *Am. J. Bot.* 85 1389-1397
- _____ and Ellstrand N C 1986 Sexual selection in *Raphanus sativus*: experimental data on non-random fertilisation, maternal choice and consequences of multiple paternity; *Am. Nat.* 127 446-461
- _____ and _____ 1988 Effective mate choice in wild radish: evidence for selective seed abortion and its mechanisms; *Am. Nat.* 131 739-756
- Martin D, Lewis T L and Cerny J 1961 Jonathan Spot - three factors related to incidence: Fruit size, breakdown and seed numbers; *Aust.J.Agric.Res.* 12 1039-1049
- Mc Kenna M A 1985 Heterostyly and microgametophytic selection: the effect of pollen competition on sporophytic vigor in two distylous species; in *Biotechnology and Ecology of Pollen* pp 443-448 eds D L Mulcahy, G B Mulcahy and E Ottaviano (New York: Springer-verlag)
- _____ and Mulcahy D L 1983 Ecological aspects of gametophytic competition in *Dianthus chinensis*; *Pollen: Biology and Implication for Plant Breeding* pp419-424 eds D L Mulcahy and E Ottaviano (Amsterdam: Elsevier Science Publishers)
- Meagher T R 1986 Heterostyly and microgametophytic selection The effects of pollen competition on sporophytic vigour in two distylous species; in *Biotechnology and Ecology of Pollen* pp443-448 eds D L Mulcahy, G B Mulcahy and E Ottaviano (Berlin: Springer Verlag)
- Miller D P 1982 Maize pollen: Collection and enzymology; in *Maize for Biological Research* pp279-293 ed F Sheridan *Plant Mol. Biol. Assoc.*, Washington, D C
- Mulcahy D L 1979 The rise of the angiosperms: a genealogical factor; *Science* 206 20-23
- _____, Curtis P S and Snow A A 1983 Pollen competition in a natural population; in *Handbook of Experimental Pollination Biology* pp330-337 eds C E Jones and R J Little (New York: Scientific and Academic Editions)
- _____, Mulcahy G B and Ottaviano E 1975 Sporophytic expression of gametophytic competition in *Petunia hybrida*; in *Gamete Competition in Plants and Animals* pp227-232 eds D L Mulcahy, (The Netherlands, Amsterdam: North-Holland Publishing Co)
- Murdy W H and Carter M E B 1987 Regulation of timing of pollen germination by the pistil in *Talinum mengesii* (Portulacaceae); *Am. J. Bot.* 74 1888-1892
- Nakamura R R 1986, Maternal investment and fruit abortion in *Phaseolus vulgaris*; *Am. J. Bot.* 73 1049-1057
- Sharma, Neelam and Shivanna, K R 1986 Self-incompatibility: Recognition and inhibition in *Nicotiana glauca*; in *Biotechnology and Ecology of Pollen* pp179-184 eds D L Mulcahy, G B Mulcahy and E Ottaviano (New York: Springer-Verlag)
- Nilsson A L, Rabakonandrianina E and Pettersson B 1992 Tracking of pollinia transfer in *Aerangis ellisii*; *Nature* 360 666-668
- Pfahler P L 1967 Fertilization ability of maize pollen grains. II. Pollen genotype, female sporophyte and pollen storage interaction; *Genetics* 57 513-521
- _____, Pereira M J and Barnett R D 1997 Genetic variation for *in vitro* sesame pollen germination and tube growth; *Theor. Appl. Genet.* 95 1218-1222
- Queller D C 1983 Kin selection and conflict in seed maturation; *J. Theor. Biol.*, 100 153-172
- Quesada M, Winsor J A and Stephenson A G 1996 Effects of pollen competition on the reproductive performance in Cucurbita hybrids (Cucurbitaceae): F1 and backcross generations; *Can. J. Bot.* 74 1113-1118
- Radha M R 1990 Components of sexual selection in *Vigna unguiculata* (L.) Walp., M Sc (Ag) Thesis, Department of Genetics and Plant Breeding, University of Agricultural Sciences, GKVK, Bangalore
- _____, Vasudeva R, Hegde S G, Ganeshiah K N and Uma Shaanker R 1993 Components of male gametophytic competition in *Vigna unguiculata* L. (Walp); *Evolutionary Trends in Plants* 7 29-36
- Ramsetter J and Mulcahy D L 1988 Consequences of pollen competition for *Aureolaria flava* seedlings; *Bull. Ecol. Soc. Amer. Suppl.* 69 269-270
- Rocha O J and Stephenson A G 1991 Order of fertilisation within the ovary of *Phaseolus coccineus* L (Leguminosae); *Sex. Plant Reprod.* 4:126-131
- Sari-Gorla M C, Ottaviano E and Bellintani R 1976 Competitive ability of maize pollen Interaction between genotypes of pollen and stilar tissues; *Maydica* 21 77-80
- _____, Frova C, Ottaviano E and Soave C 1983 Gene expression at the gametophytic phase in maize; in *Pollen Biology and Implications for Plant Breeding* pp323-328 eds D L Mulcahy and G B Mulcahy (Amsterdam: Elsevier)
- Schemske D W and Fenster C 1983 Pollen-grain interactions in a neotropical *Costus*: Effects of clump size and competitors; in *Pollen: Biology and Implication for Plant Breeding* pp405-410 eds D L Mulcahy and E Ottaviano (Amsterdam: Elsevier Science Publishers)
- Schlichting C D, Stephanson A G, Davis L E and Winsor J A 1987 Pollen competition and offspring variance; *Evol. Trends Plants* 1 35-39

- Sedgley M 1981 Early development of the *Macadonia* ovary; *Aust.J.Bot.* 29 185-193
- _____ 1989 Ovule and seed development in *Eucalyptus woodwardii* Maiden (Symphomyrtus); *Bot.Gaz.* 150 271-280
- Snow A A and Spira T P 1991 Differential pollen tube growth rates and non random fertilization in *Hibiscus moscheutos* (Malvaceae); *Amer. J. Bot.* 77 671-676
- Spira T P, Snow A A, Whigham D F and Leak J 1992 Flower visitation, pollen deposition, and pollen-tube competition in *Hibiscus moscheutos* (Malvaceae); *Am. J. Bot.* 79 428-433
- Sutherland S 1986 Patterns of fruit set: What controls fruit-flower ratios in plants? *Evolution* 40 117-128
- _____ and Delph L F 1984 On the importance of male fitness in plants : patterns of fruit set; *Ecology* 65 1093-1104
- Stephenson A G 1984 The regulation of maternal investment in an indeterminate flowering plant (*Lotus corniculatus*); *Ecology* 65 113-121
- _____ and Bertin R I 1983 Male competition, female choice and sexual selection in plants; in *Pollination Biology* ed L Real) (New York : Academic Press)
- _____ and Winsor J A 1986 *Lotus corniculatus* regulates offspring quality through selective fruit abortion; *Evolution* 40 453-458
- Stephenson A G, Winsor J A and Schlichting C D 1988 Evidence for non random fertilisation in the the common zucchini, *Cucurbita pepo*; in *Sexual Reproduction in Higher Plants* pp 333-338 eds M Cresti, P Gori and E Pacini (New York: Springer-Verlag)
- Sukhada D K and Jayachandra 1980 Pollen allelopathy - A new phenomenon *New Phytol.* 84 739-746
- Tanksley D S, Zamir D and Rick C M 1981 Evidence for extensive overlap of sporophytic and gametophytic gene expression in *Lycopersicon esculentum*; *Science* 213 453-455
- Tejaswini 1999 Gametophytic selection as a plant breeding tool to develop disease resistant and vigorous plants: Testing the feasibility in *Dianthus* spp. *Ph.D Thesis*, Department of Genetics and Plant Breeding, University of Agricultural Sciences, Bangalore
- Thompson J D , Andrews B J and Plowright R C 1981 The effect of a foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae); *New Phytol.* 90 777-783
- Udovic D 1981 Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability; *Oecologia* 48 389-399
- Uma Shaanker R and Ganeshaiyah K N 1984 Age-specific sex ratio in a monoecious species, *Croton bonplandianum* Baill; *New Phytol.* 97 523-531
- _____ and _____ 1988 Styler plugging by fertilised ovules in *Kleinhovia hospita* (Sterculiaceae) – a case of vaginal sealing in plants? *Evolutionary trends in plants* 3 59-64
- _____ and _____ 1990 Pollen grain deposition patterns and stigma strategies in regulating seed number per pod in multi ovulated species; in *Reproductive Biology of Tropical Forest Plants* pp 165-178 eds K S Bawa and M Hadley UNESCO and Prthenon Publishing group
- _____ and _____ 1997 Conflict between parent and offspring in plants: Predictions, processes and evolutionary consequences; *Curr. Sci.* 72 932-939
- _____, _____ and Bawa K S 1988 Parent - offspring conflict, sibling rivalry and brood size patterns in plants; *Ann. Rev. Ecol. Syst.* 19 177-205
- Vasudev R, Vinayak K, Ganeshaiyah K N and Uma Shaanker R 1987 Sex ratio variations in *Acalypha fruticosa* Frosk along plant height and altitude; *Proc. Indian Acad. Sci.* 97 11-15
- Visser T and Verhaegh J J 1988 The influence of double pollination and pollen load on seed set and seedling vigour of apple and pear In: *Sexual Reproduction in Higher Plants* pp 369-374 eds M Cresti, P Gori and E Pacini (New York : Springer-Verlag)
- Wasser N 1978 Competition for hummingbird pollination and sequential flowering in two native Colorado wildflowers; *Ecology* 59 934-944
- Weins D 1984 Ovule survivorship, brood size, life history, breeding systems and reproductive success in plants; *Oecologia* 64 47-53
- Willing R P and Mascarenhas J P 1984 Genes active during pollen development and the construction of cloned cDNA libraries to mRNAs from pollen; *Plant Cell Incomp Newslett.* 16 11-12
- Willson M F 1977 Sexual selection in plants; *Am. Nat.* 113 777-790
- _____ and B J Ratchke 1974 Adaptive design of the floral display in *Asclepias syriaca* L; *Amer. Midl. Nat.* 92 47-57
- _____ and Price P W 1977 The evolution of inflorescence size in *Asclepias* (Asclepiadaceae) *Evolution* 31 495-511