Sexual Selection in Plants: The Process, Components and Significance

TEJASWINI¹, K N GANESHAIAH*²,³ and R UMA SHAANKER²,³
¹Indian Institute of Horticultural Research, Bangalore 560 089
²Department of Plant Genetics and Breeding, ³Department of Crop Physiology,
University of Agricultural Sciences, GKV, 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 polyclads 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 posses 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 (Ganeshaiah & 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, Bernis 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 & Ellstrand 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 & Ratchetke 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 Bail 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 Shaaneker & 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 fruiticosa (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 Lepidopteran 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, Nilsson 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.png)  
**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 moschatus* (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 & Ganeshiah 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; Geneshiah 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 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 (Ganeshiah et al. 1986, Ganeshiah & Uma Shaanker 1988a, Uma Shaanker & Ganeshiah 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* (Ganeshaiah & 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 & Ganeshaiah 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 Jenesen et al. (1983) proposed a hormonal one. Genetical (Hinata & Okazaki 1986) as well as biochemical (Neelam Sharma & Shivanna 1986) signals are also known to 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 Shaaneker & 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 & Bazzaz 1982), in about 13 species of Fabaceae (Bawa & Buckley 1989) and in many species of Pinaceae (Lloyd 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 Shaaneker & 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 Shaaneker 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 Shaaneker 1988b, Uma Shaaneker & 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 Shaaneker & 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


Baker H G and Baker J 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 Mucahy and E Ottaviano (New York: Elsevier Biomedical)

Barnnes D K and Cleveland R W 1963 Pollen tube growth of diploid alfalfa in vitro; Crop Sci. 3 291-295


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


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

Ganeshaiah 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


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


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)

and _____ 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


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

Lloyd 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 1988 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 male choice in wild radish: evidence for selective seed abortion and its mechanisms; Am. Nat. 131 739-756


and Mulcahy D L 1983 Ecological aspects of gametophytic competition in Dianthus chinesis; Pollen: Biology and Implication for Plant Breeding pp 419-424 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 vigor in two distylosous species; in Biotechnology and Ecology of Pollen pp 443-448 eds D L Mulcahy, G B Mulcahy and E Ottaviano (Berlin: Springer Verlag)


Mulcahy D L 1979 The rise of the angiosperms: a genealogical factor; Science 206 20-23


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


Nillsson A L, Rabakonandriana E and Pettersson B 1992 Tracking of pollinia transfer in Ageratins ellisis; Nature 360 666-668

Pfarler P L 1967 Fertilization ability of maize pollen grains. II. Pollen genotype, female sporophyte and pollen storage interaction; Genetics 57 513-521


Ramseter J and Mulcahy D L 1988 Consequences of pollen competition for Auroelaria 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. 4126-131

Sari-Gorla M C, Ottaviano E and Bellintani R 1976 Competitive ability of maize pollen interaction between genotypes of pollen and stigmatic 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 pp 323-328 eds D L Mulcahy and G B Mulcahy (Amsterdam: Elsevier)


Sexual Selection in Plants

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 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 Winsor J A 1986 Lotus corniculatus regulates offspring quality through selective fruit abortion; Evolution 40 453-458


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

Tojaswini 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


Udovic D 1981 Determinants of fruit set in Yucca whipplei: reproductive expenditure vs. pollinator availability; Oecologia 46 389-399

Uma Shaanker R and Ganeshayah K N 1984 Age-specific sex ratio in a monoecious species, Croton bonplandianum Baill.; New Phytol. 97 523-531

____ and ____ 1988 Stylar 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 Prthonon Publishing group

____ and ____ 1997 Conflict between parent and offspring in plants: Predictions, processes and evolutionary consequences; Curc. 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


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 Incorp 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