

Reproductive biology and evolution of the genus *Acacia*

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ABSTRACT

The basic pollination system in the family is unspecialized insect pollination; flower odour and high pollen reward for visiting insects are the major pollinator attractants in the genus *Acacia*. Moreover, the polyad and the multi-stigmatic flowering unit – the inflorescence – enhance pollen collection by visiting insects. This strategy has been successful in mimosoid genera in tropical and subtropical, semi-arid areas. The diversity of floral visitors to African acacias is high, with Hymenoptera the dominating group, followed by Lepidoptera, Coleoptera and Diptera. There is no clear difference in the frequency and diversity of visitors among species producing nectar and those without nectar. Pollination is efficient, between 30-60% of all stigmas receive polyads.

Acacia tortilis has a high degree of self-incompatibility which is probably a basal and important character in the relatively promiscuous pollination strategy of acacias. The fruit set per flower is low, typically less than 1%, but with a high ratio of seeds to ovules. The polyad is capable of fertilizing all ovules in one successful pollination event. Selective seed abortion has been indicated and the seed set per tree is highly variable.

Acacia seeds are spread mainly by wind or animals. African species are predominantly wind- or ungulate-dispersed, whereas seeds of Australian species are bird- or ant-dispersed. Adaptations of dispersal strategy seem rather rapid, compared to other evolutionary changes. Number of seeds per pod is correlated with the dispersal strategy in African acacias; wind-dispersed pods have a higher degree of seed abortions. The dispersal strategy is also correlated with susceptibility of attack by bruchid beetles and thus with the survival of seeds, as well as their germination under different conditions.

It is argued that the reproductive biology, including pollen movement, selection of progeny and dispersal of seeds of the genus, has had a great impact on the evolution and adaptation of the genus to various conditions.

INTRODUCTION

The understanding of evolutionary trends is one of the driving forces and primary challenges for biologists when studying the development, distribution and diversification of species of plants and animals. The age of the group, the diversity, the distribution, their specialization, their dominance in an ecosystem, may all be taken as indicators of the evolutionary adaptability of a group, but none of these factors alone is sufficient.

Apparently, the Leguminosae were quite widespread and already differentiated into the three subfamilies by the end of the Cretaceous, 65 million years ago, for pollen of Mimosoideae has been dated to this period (Guinet 1981). The genus *Acacia* was apparently widespread some 40-50 million years ago, but whether the ancestors of the genus were found in Africa or South- or Central America has been debated (Guinet and Vassal 1978, Pedley 1986). Without doubt, acacias were found on both continents rather early. The genus has been more widespread than

today, but probably the main speciation of the genus occurred during the last 15 million years, after acacias had arrived on the Australian continent (Pedley 1986).

This paper summarizes and discusses evolutionary perspectives of a number of recent pollination studies conducted by the author and other researchers on Mimosoideae. This is done by reviewing the main factors influencing the reproductive success of the genus *Acacia* and comparing it with the trends of closely related genera in the subfamily. This should provide an understanding of the importance of reproductive ecology in the evolution and success of the largest genus within the subfamily. Emphasis is given to three of the most important factors influencing the reproductive success of plants, namely, the movement of pollen, the selection of progeny and the dispersal of seeds.

POLLEN MOVEMENT

The transfer of pollen is an extremely important feature for the spreading of genes, and for the survival and evolution of plant species. Morphology of the flowers, the rewards available and the insects carrying out the event are important for survival and evolution of insect pollinated genera.

Flowers

The small, reduced flowers of most of the species in the subfamily Mimosoideae are united in dense inflorescences which attract pollinators. The unit of pollination is not the single flower but the inflorescence, a multi-stigmatic unit, rather flexible in size and with its "surface" consisting of densely exerted stamens. The occurrence of floral nectar is common and probably a basic character for the Mimosoideae but has been reduced or has disappeared independently in different (sub-) genera, as with *Acacia*, where it is only found in subgenus *Aculeiferum* (*sensu* Vassal 1972).

The phenology of the inflorescence has evolved differently in the three subgenera of *Acacia*. The Australian subgenus *Phyllodineae* (syn. subgenus *Heterophyllum*) has protogynous inflorescences, while the subgenera *Aculeiferum* and *Acacia* have synchronised opening of the individual flowers. Subgenus *Acacia*, with capitate inflorescences, has synchronised opening of the whole inflorescence during one night and the flowers wither the following afternoon, while the flowers of subgenus *Aculeiferum*, with spike shaped inflorescences, open in sequences during several days (Kenrick and Knox 1989, Tybirk and Jørgensen 1994).

The anther gland found in large parts of the Mimosoideae is an interesting character in an evolutionary perspective. The function of the gland is probably to produce odour shortly after opening of the flowers (Bernhardt 1989, Tybirk and Jørgensen 1994), but a detailed study of the occurrence and function of the gland in the Mimosoideae is needed.

The odour for attraction and pollen as the reward have become the most important factors in pollinator attraction in *Acacia*. Splitting of anthers with a fixed number of pollen grains per anther has been favoured. Pollen production per inflorescence is high and the unification of pollen in polyads increases the ease of pollen gathering by visiting insects.

The selective forces acting on the multi-stigmatic pollination unit are different from other mono-stigmatic legume flowers with free pollen grains. Undoubtedly the polyad is a derived character in Mimosoideae, and it is striking that the number of grains in the polyad is correlated with the number of ovules in the ovary, indicating a high degree of specialisation and an efficient system of pollination (Kenrick and Knox 1989, Tybirk 1989, Tybirk and Jørgensen 1994).

The evolution of female, sterile, proximal flowers functioning only as pollen donors is seen as a specialisation in subgenus *Acacia*. This tendency is further developed in the genera *Parkia* and *Dichrostachys* with flowers specialised for nectar production or visual attraction (Arroyo 1981). This has probably evolved due to the incapacity of the inflorescence to sustain the development of all the fruits in a single inflorescence, should all gynoecea be successfully pollinated.

Apparently the strategy of small flowers is advantageous in tropical and subtropical arid and semi-arid areas where genera with the least specialised flowers in the family (*Mimosa*, *Acacia*, *Prosopis*) include about half of all mimosoid species.

Pollination

The basic pollination system in Mimosoideae is unspecialised insect pollination, whereas pollination by bats (*Parkia*), birds and moths (in parts of *Inga* and *Calliandra*) has evolved from insect pollination comparatively recently. Also the bird pollination of some Australian acacias (Ford and Forde 1976) is without doubt a specialization derived from insect pollination. Bernhardt (1990) regards the pollination system of Mimosoideae as extremely diverse despite the stereotyped inflorescence architecture.

A similar pattern can be seen in Caesalpinioideae and Papilionoideae where bee pollination is most common, but other more specialised syndromes occur in different parts of these sub-families.

The inflorescences of acacias do not require any specialised technique for pollen collection or nectar search. Recent studies have shown that the diversity of visitors on African species is high, with 118 taxa from six orders of insects collected on four *Acacia* species. Hymenoptera is the dominating group (wasps slightly more frequent than bees), followed by Lepidoptera, Coleoptera and Diptera (Tybirk 1993). When *Acacia* diversified, Coleoptera, primitive Hymenoptera (most wasps) and Lepidoptera (many moths) existed, while more specialized butterflies and bees were not yet present (Michener 1979). This suggests that the acacias had a variety of insects as potential pollinators from the start.

A most interesting result of these pollination studies in an evolutionary perspective is that apparently no clear difference in the number and diversity of insects visiting *Acacia* species with and without nectar has been found. Many butterflies and carnivorous wasps, known only to feed on nectar as an energy source, commonly visit *A. tortilis* which has no nectary (Tybirk 1993). This can only be interpreted as deceit, and it is surprising that subgenus *Aculeiferum* maintains the floral nectar production, when apparently it is not advantageous.

In subgenus *Phyllodineae* (syn. subgenus *Heterophyllum*) in Australia, the floral nectaries have disappeared, but they maintain extra-floral nectar as a secondary reward for visiting bees.

Nectaries have also disappeared in the genus *Schrankia* suggesting that generalist melittophily without nectar has evolved independently several times within the Mimosoideae (Bernhardt 1989, 1990).

The stigmas of acacias are easily pollinated by pollen-collecting or nectar-searching insects visiting the inflorescence; 30-60% of all stigmas investigated of various species carry pollen (Tybirk and Jørgensen 1994). Again no clear difference has been found between species with and without a nectary. In summary, the transfer of pollen to the stigmas is efficient and the compatibility of the pollen is thus critical in determining the levels of fruit set.

SELECTION OF PROGENY

The selection of progeny is a field that has been rarely investigated in tropical woody species, probably due to difficulties in obtaining reliable data from the field and in testing the hypothesis in the laboratory.

Breeding System

Studies of the Australian acacias have shown that they are predominantly outcrossed, but with some variation between individuals, populations and species (Kenrick and Knox 1989, Moran *et al.* 1989). Although *A. nilotica* was found self-compatible in a study based on isozyme analysis (Mandal *et al.* 1994), *A. tortilis* in Senegal showed a high degree of self-incompatibility but apparently pod set was not limited by outcrossing (Tybirk 1993). Probably self-incompatibility is a basal and an important character in the relatively promiscuous pollination strategies of Mimosoideae and Caesalpinioideae. In Papilionoideae, however, 80% of the tested species are self-compatible, illustrating the relatively specialised pollination strategy of many herbaceous and temperate species of this subfamily (Arroyo 1981).

Studies have indicated that the individual trees of *A. tortilis* have quite different contributions, in terms of the male and female gender expression of the population. Some individuals in Senegal set many pods, while others flower profusely but develop no pods, suggesting that they only act as pollen donors (Tybirk 1993).

Fruit and seed set

The fruit-set per flower of Mimosoid species is low compared with other legumes. In acacias, typically less than 1% of the flowers result in a fruit, but with a high ratio of seeds to ovules. This is a consequence of the polyad being capable of fertilising all the ovules in the ovary by one successful pollination event. The acacias have an either/or strategy, primarily resulting in competition between the individual pods in an inflorescence, rather than between seeds in a pod, for many *Acacia* pods abort during the first weeks of development (Tybirk 1993). In contrast, Caesalpinioideae and Papilionoideae have higher fruit per flower ratio and lower seed to ovule ratio (Bawa and Buckley 1989). This implies that the selection is between seeds in the pod in these two subfamilies, while in most of Mimosoideae the selection is between the different pods in the infructescence.

For the Mimosoid genera with polyads, the seed to ovule ratio is expected to approach one. Full seed set is rare in acacias, however, and this is probably caused by reduced pollen viability and later seed abortions in the developing pod. Seed set is less than half the ovule number in the wind dispersed *Acacia senegal*, *A. polyacantha* and *A. ataxacantha* (Tybirk 1993). This results from a combination of lack of fertilization and later abortions of developing ovules. The latter may primarily be caused by developing bruchid (Coleoptera: Bruchidae) larvae in the fertilized ovules. Ungulate dispersed species have higher seed to ovule ratios (Tybirk 1993).

Studies of the position of seed abortions in the pods of acacias indicate a selective seed abortion as found in many legumes (Bawa and Webb 1984, Lee and Bazzaz 1986, Bawa and Buckley 1989). The acacias studied have a basipetal abortion pattern, showing a higher proportion of abortions in the proximal (closest to the basal end) ovules in the pod. This is supposed to be caused by competition between growing pollen tubes through the stigma. Superior male genotypes growing faster will arrive first in the ovary and fertilize the nearest ovules in the distal end of the ovary. Consequently the inferior male genotypes will arrive later and fertilize the "left over" basal ovules, resulting in less competitive ability in the development of the pod (Lee and Bazzaz 1986, Tybirk 1993). This selective abortion pattern of seeds in acacias with genetically quite homogeneous pollen grains is quite different from the selective forces acting on other legume species with individual pollen grains. Some *Acacia* species are able to screen their progeny by the incompatibility system and later fruit and seed abortions (Tybirk 1993). This has interesting, but little understood, implications for the competition between the progeny of the acacias and needs much more experimental work in the field and the laboratory.

SEED DISPERSAL

The movement of pollen and dispersal of seeds are key factors for plant species in spreading their genes. The seeds and the young plants represent the most vulnerable phase in the life of the acacias and the coexistence with dispersal agents and predators of seeds has probably been an important selective force in the diversification of the genus.

Dispersal strategies

Within Mimosoideae two main strategies predominate for seed dispersal: wind- and animal-dispersal. The latter can be subdivided into ungulate-, bird- and ant-dispersal. Adaptations for different dispersal strategies seem to be gained fairly easily and rapidly compared to other evolutionary changes (Augspurger 1989), so different adaptations of pods have apparently occurred several times independently in Mimosoideae, and parts of the subfamily are separated mainly by pod characters (Nielsen 1981).

Many African and New World acacias are wind-dispersed. This is an adaptation to the open and windy semi-arid savannas (Augspurger 1989), but in similar habitats many species are also ungulate dispersed in Africa. The bird-dispersal strategy in *Acacia hockii*, *A. seyal* and *A. ehrenbergiana* and water dispersal occurring as a secondary strategy in some species, are interesting exceptions (Tybirk 1991). In Australia, in similar semi-arid and open habitats, the absence of large ungulates has favoured the development of an arillus and corresponding bird- or ant-dispersal. The above-mentioned species with bird dispersal in Africa have pods that are

strikingly similar to some Australian species with the same dispersal strategy, but the African species lack the arillus.

Ungulate-dispersed African *Acacia* species have larger pods with more seeds per pod than wind dispersed species. This has probably evolved to give a high reward to the ungulate while thin and light pods favour wind dispersal (Tybirk 1993). Ungulate consumption also reduces the probability of predation after passage through the ungulate intestine and improves the germination of seeds adapted for this strategy (Miller 1994b).

Seed predation

The relationship between the seeds of Leguminosae and bruchid beetles is very close. These interactions have undoubtedly had a great impact on the evolution and speciation of both legumes and bruchids. The bruchids have adapted to feed on the otherwise toxic nitrogenous compounds produced by the legumes to protect the seeds against predation. This has developed into a certain degree of host specificity; a review of literature has shown that this is not very narrow with more than 20 species of bruchids attacking the seeds of some Sahelian acacias (Tybirk 1991).

The seed predation probably influences several factors. Dispersal in time and space is an efficient way to counteract attacks by bruchids. Nevertheless, the interactions of ungulate dispersal, seed predation, savanna fires, and germination of *Acacia* seeds on the savannas are indeed complex and still being debated (Coe and Coe 1987, Tybirk 1991, Tybirk *et al.* 1994, Hauser 1994, Miller 1993, 1994 a, b, c, Traveset 1992).

In Australia, the Bruchidae are poorly represented, but they have had and still have great importance on the evolution of species and as regulators of populations of many legume species in Africa and the Americas.

Germination

The large rounded seeds of the ungulate dispersed *Acacia* species have a very thick and impenetrable seed coat; this has evolved to sustain the chewing and mastication of the ruminants, enabling the seeds to pass undamaged through the alimentary canal, facilitating dispersal with low seed losses. The seeds develop seed dormancy if they are not stimulated to germinate while young and soft; older seeds can be stimulated to germinate by weakening the seed coat while passing through the ungulate alimentary canal. On the contrary, the wind dispersed *Acacia* species have a relatively thin seed coat and germinate with less stimulation (Coe and Coe 1987, Tybirk 1991, Miller 1994b). The development of dormancy has probably been evolved to spread the seeds through time, although the few seed bank investigations carried out have not confirmed this (Tybirk *et al.* 1994).

Germination is also interlinked in a complex way with the described dispersal strategy and predation. Fire in the ecosystem is another frequently occurring factor that may have influenced the evolution of dormancy and the subsequent breaking of dormancy. Hastening of the germination and selective killing by fire of developing bruchid larvae in the seeds has been reported (Sabiiti and Wein 1987, Tybirk 1991), but the fires may kill seeds if the temperature becomes too high.

Germination of the different species is closely adapted to the prevailing water availability of the soil in the distribution area of each species. Desert species may germinate when experimentally watered only every five days, while savanna species may need watering every day or even waterlogging to germinate (see review by Tybirk 1991). These factors show other aspects of the adaptability of acacias to different environments.

FLEXIBILITY

The reproductive strategy of the large and diverse genus *Acacia* has had a tremendous influence on the evolution and success of the genus. The key to understanding this is flexibility.

Compared with the rest of the legume family, the mimosoid and, in particular, the *Acacia* flowers are reduced to many small flowers but with high rewards for pollinators. The unspecialised flower combined with the highly specialised polyad and the multi-stigmatic inflorescence can seem contradictory, but reflects a highly flexible pollination system.

The broad spectrum of pollinators that can pollinate the genus has provided the basis for competitiveness in many habitats. Furthermore, the ability to pollinate all-in-one pollination event and later select between progeny by self-incompatibility and the selective seed abortion within the pod, all contribute to the adaptability and speciation of the genus. Finally, the variability in dispersal strategies, the co-evolution with bruchid beetles and adaptations for germination under different and variable conditions complete the fitness of these pioneer species able to withstand the extreme and variable conditions in semi-arid tropics.

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