Reproductive Biology of *Faidherbia albida* (Del.) A. Chev.

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Phenology, flowering and fructification were studied in 5 natural populations of *Faidherbia albida* in a semi-arid zone in Senegal. In this species, the inflorescence acts as the reproductive unit; the basal flowers, opening first, have a low rate of fertilisation; the maximum rate of fertilisation (65%) was obtained in the apical flowers.

Stigmatic receptivity, tested by esterasic reaction, was maximal immediately after anthesis. Stigmata of *F. albida* can bear simultaneously 2 or 3 polyads. Controlled pollination revealed that allogamy is the dominant reproductive system (ISI = 0.2) in natural populations of *F. albida*. Intra-specific variability in selfing (ISI ranging from 0 to 0.54) was also observed. Despite of the complete reproductive mechanism during flowering, only a small number of ripe pods (1.25%) is produced, and an average of 70% of the ovules per carpel are fertilized.

Keywords *Faidherbia albida*, flowering, fructification, polyad, allogamy, selfing
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1 Introduction

Faidherbia albida (Del.) A. Chev. Mimosaceae is widely spread in Africa (Nongonierma 1978, CTFT 1989). The inverse phenological rhythm of the species is an important reason for the use of *Faidherbia albida* in traditional agro forestry systems because of the lack of competition between tree and crops during the rainy season. The persistent foliage during the dry season is an important source of fodder. *Faidherbia albida* presents a great genotypic and phenotypic diversity (Joly 1992, Wood 1992).

Development of any programme of tree breeding needs study of the pollination strategy naturally developed by species. To determine the principal features in the organization of genetic diversity in natural populations, knowledge on reproductive biology is essential. In many African, Australian and Asiatic species belonging to the genus *Acacia* (Dnyansagar 1975, Milton 1987, Vanstone and Paton 1988, Kenrick and Knox 1989a, Kenrick and Knox 1989b, Sedgley et al. 1992, Diallo 1994), studies revealed the variability and the flexibility of the reproductive system. Reproductive biology of some tropical

forest species, *Balanites aegyptiaca* (N'Doye 1999), *Borassus aethiopium* (Thione 2000), *Anacardium occidentale* (Niang 2001), have been investigated to find an optimal management system of genetic diversity in dry lands forest ecosystems. In *F. albida*, there are few studies on the reproduction system (Guinet 1969, Wickens 1969, Tybirk and Jorgensen 1994).

The aim of the present study was, based on 2 years of observations on phenology, to investigate the flowering, breeding system, pod and seed yields in five natural populations of *F. albida*.

2 Materials and Methods

The study was carried out in Dakar region (14°43'N, 17°26'W) in Senegal. The climate is Sahelian influenced by maritime trade winds alleviating high temperatures and low moisture during dry season; the mean annual temperature is 24°C and rainfall 300 mm.

The study was done on 5 natural populations of *Faidherbia albida* growing in a radius of 15 km around Dakar: ORSTOM (ORS); University (UNI); Hann village (HAN); Dalifort (DAL); Foire (FOR).

Surface photographs of floral organs were obtained after fixation and dehydratation in acetone, passing to critical point and coating in a fine pellicle of metal for scanning microscopy (Jeol JMS 35CF). Material for electron microscopy was fixed in 1.5% glutaraldehyde in 0,05M phosphate buffer pH 7.2 during six hours and post-fixed in 1% OsO_4 in the same buffer for two hours, followed by a thorough rinsing in the same buffer. After dehydratation in ethanol series and in two baths of propylene oxide, the tissues were embedded in epon. Thin sections obtained using glass knives were mounted on copper grids, and post-stained with uranyl acetate.

Flowers were collected at different times from the opening of the flower bud to the withering. Pollen grain were collected by sieving on a fine mesh (200 μm) and viability estimated using two methods:

1) FCR test (fluorochromatic reaction; Heslop-Harrison et al. 1984). When dipped in a solution of fluorescein di-acetate (0.2 mg/ml), viable pollen grains send out fluorescent light, which can be detected with fluorescent microscope at 420 nm. The viability is estimated by intensity of fluorescence emitted by pollen grains.
2) Germination of pollen grains. Pollen stored in Petri dishes at 25°C is allowed to germinate on a drop of Brewbaker and Kwack (1963) medium supplemented with sucrose (20 g/l) and solidified with phytagel (2g/l). Pollen was incubated in darkness at 30°C under high humidity.

The receptivity period of stigma was determined by esterasic test with the substrate naphtyl acetate (Kenrick and Knox 1981).

Slides with adhesive bands (double face) were randomly placed on trees and maintained near inflorescences; 24 hours later, pollen of *Faidherbia albida* transported by wind was identified and quantified.

For controlled pollination, eight trees fully covered with flowers, were identified on two sites (Université, Foire) and marked; young buds and open buds were removed and only apical and median floral buds close to anthesis were maintained. They were kept in fine nylon mesh pockets that did not affect the air temperature and humidity. Three days after placing the pockets, all flower buds were removed and opened flowers were hand pollinated with fresh pollen.

Five tests were set in this experiment:

- Reference: flowers only bagged
- Flowers bagged and regularly slightly shaken to allow pollen movement, furthering self-pollinisation (*sensu stricto*)
- Flowers bagged and pollinated with auto-pollen collected on the same tree (geitonogamy)
- Flowers bagged and pollinated with allo-pollen collected on different trees
- Flowers not bagged and pollination open to wind and insects

Young pods were counted after one month. The index of self incompatibility (ISI) was subsequently estimated (Zappata and Arroyo 1978). Flower parameters and reproduction data were submitted to analysis of variance using Fischer LSD test at 95%.

3 Results

3.1 Phenology

The phenological study was followed during two years in natural populations at the five sites; leaves begin to flush late in October; during February, March and April, all tree crowns are foliated. The process of defoliation starts in July and ends in October; in November about 50% of trees begin flowering, and flowering peak is found in February-March; pods mature and seed setting is effective during the rainy season (June to September).

3.2 Flowering and Reproductive Mechanism

The inflorescence of *Faidherbia albida* is a 8–10 cm long spike, opening progressively during 72 hours from basal to apical flowers.

The mean number of inflorescences per branch is 4.5; 75 to 120 flowers are formed in each inflorescence. The style is 6 to 7 mm long and the saucer shaped stigma is approximately 150 μm in width (Fig. 1A).

The bottom ovary contains 18 to 24 parietal and campylotropous ovules (Fig. 1B) arranged in two rows in the ovarian cavity. Stamens (35–55 in number), joined at their bottom, are extended by anthers containing eight clusters of pollen grains; the polyad (80 to 100 μm of diameter) is formed by two to three crowns of 32 monads (Fig. 1C). The number of polyads per flower (Table1) indicates the male effort during one pollination event. The monad/ovule ratio ranged from 1.2 to 1.5.

Thin sections of the monad showed four layers as follows (Fig. 1D):

- The inner and thin layer of intin revealing at apertures many vesicles and microtubules contributing to further pollen tube development.
- The nexin with a dense and lamellar structure.
- The heterogeneous sexin presents a granular structure with many vesicles and granules.
- The outer, most superficial layer, the tectum, is a callused wall developing very early at meiosis; the callose is hydrolysed in spaces between the monads but persistent in free and outer spaces.

3.3 Reproduction

Quality and Viability of Pollen

The pollen quality and viability tested during 120 hours (five days after collecting) indicated that polyads present variable degrees of intensity in fluorescence emitted. At bud break, the esterasic activity is very high in 50% of the monads, revealed by a high level of fluorescent activity. In comparison, 31% of monads show a moderate fluorescence and 14% are completely extinguished.

During storage of flower buds at room temperature, 70% of the monads maintained viability for five days. When pollen was extracted from flowers and stored at room temperature, the viability of pollen grains was reduced after 72 hours and completely lost after five days exposure to laboratory conditions.

In vitro germination tests showed that maximal rate of germination (87%) was obtained in

Table 1. Characteristics of floral organs in 5 populations of *Faidherbia albida* (each measured variable concerns 30 observations).

Population	Flowers/ sike	Anthers/ flower	Polyads/ spike	Ovules/ flower	Monads/ polyad	Monads/ ovule
ORS	90.42	34.12 b	24681	19.25 a	30.66 a	1.59
UNI	87.51	52.00 a	36404	20.57 a	31.89 a	1.55
HAN	76.50	51.41 a	31462	22.09 a	31.73 a	1.44
DAL	110.6	52.30 a	46275	19.52 a	25.05 b	1.28
FOR	92.57	52.50 a	38879	22.00 a	24.87 b	1.13

Population codes indicating studied sites: ORS (ORSTOM); UNI (University); HAN (Hann village); DAL (Dalifort); FOR (Foire).
Data followed by the same letter are not significantly different at 95%.

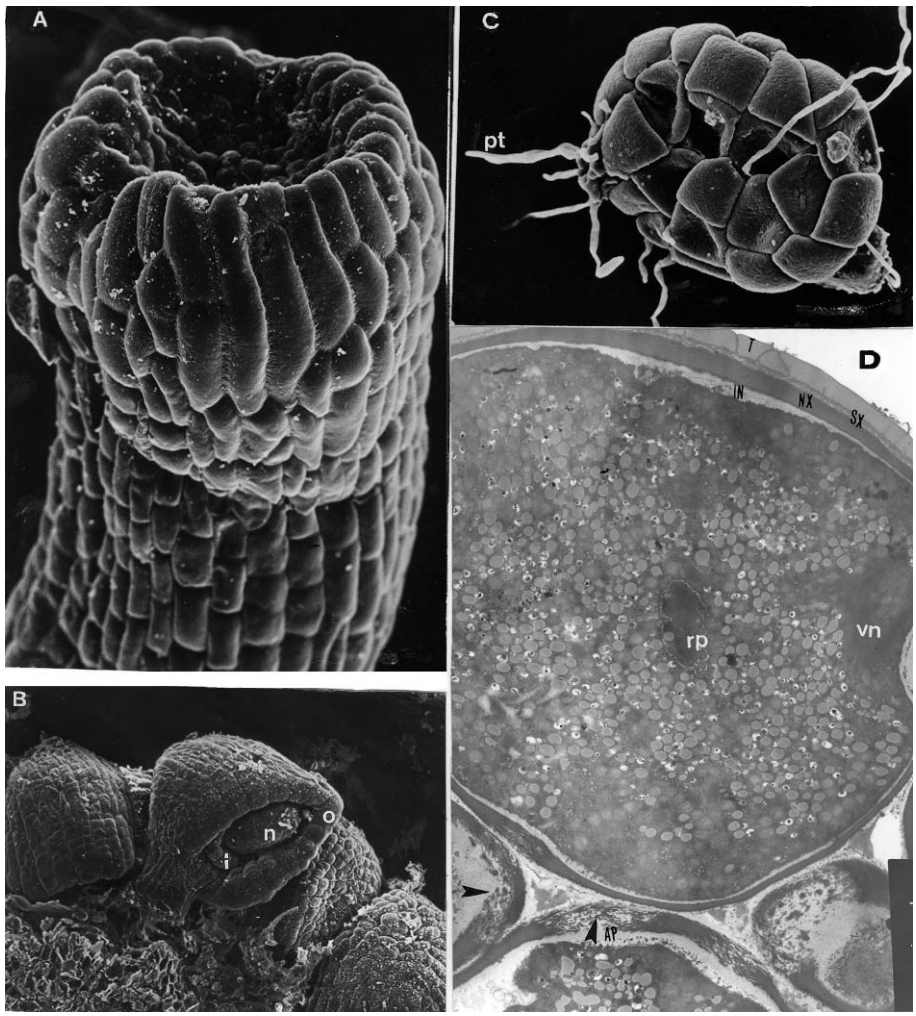

Fig. 1. Scanning electron micrographs showing morphological and anatomical details of floral organs in *Faidherbia albida*. **A**. Saucer shaped stigma of *F. albida* (4800 x). **B**. Parietal and campylotropous ovules showing inner (i), and outer (o) teguments and nucellus (n) (4800 x). **C**. Polyad of *F. albida* comprising aggregated monads in germination. Note pollen tubes (pt) emerging from apertures (4800 x). **D**. Ultrastructure of the monad showing intin (in), nexin (nx), sexin (sx) and tectum (t) partially hydrolysed. The lamellar structure of nexin is evident at apertures (ap, arrows).Two multilobed reproductive cells (rp) and the dense vegetative nucleus (vn) are present in the mature monad (8000 x).

fresh pollen. The average number of pollen tubes developing per polyad was 12. After 48 hours of conservation, the germination rate was stable. Viability of pollen seems to be affected only after 72 hours as indicated by a reduction of germination rate (41%) and the number of pollen tubes produced (7.19). Five days later, all polyads had lost their germination capacity.

Table 2. Pod and seed yields studied on 5 populations of *Faidherbia albida* (each measured variable concerns 30 observations).

Population	Heads/ raceme	Pods/ head	Rate of fertilization (%)	Seeds/ pod	Ovule/ flower	Lack of fertilization (%)
ORS	4.53 a	1.31 a	1.44	14.35 a	19.25 a	25.45
UNI	5.12 a	1.11 a	1.27	14.25 a	20.57 a	30.72
HAN	3.23 b	2.01 b	2.63	15.04 a	22.09 a	31.91
DAL	4.51 a	1.29 a	1.16	15.30 a	19.52 a	21.62
FOR	3.11 b	1.20 a	1.29	12.35 b	22.00 a	43.86

Population codes indicating studied sites: ORS (ORTOM); UNI (University); HAN (Hann village); DAL (Dalifort); FOR (Foire).
Data followed by the same letter are not significantly different at 95%.

Stigmata Receptivity

At anthesis, 65.5% of stigmata were intensively colored red; the stigmatic receptivity was maintained until withering. The style extended just before anthesis, and exuded abundant mucus at the centre of the stigma, allowing adhesion of pollen grains. 75 to 80% of stigmata observed after anthesis bore only one polyad, and 16 to 25% bore two.

Fructification

Flowers are sessile and only effectively pollinated flowers remain on the inflorescences; they maintain a long and turgescent style that is easily identified, among withered organs. Median flowers and almost apical flowers are the most receptive ones (65% of fruit efficiency was found in apical flowers, 25% in median flowers and only 11% in basal flowers). The fruit began to develop with the enlargement of an ovary turning to green and growing to a mature pod within two months.

The mean number of pods per inflorescence ranged from 1.1 to 2.0 (Table 2). Fertility rate at the level of one inflorescence was very low (1.2 %). The mean number of seeds/pod varied from 12.35 to 15.30. *Faidherbia albida* presents a low degree of carpel filling; it varied from 21.62% to 43.86%.

Table 3. Determination of self and cross pollination yields in eight trees of *Faidherbia albida* (index of self incompatibility (ISI) equalled 0.272)

Method	Spikes	Flowers	Pods initiated	Yields/spike
A	52	4550	6 c	0.115 c
B	33	2887	3 c	0.091 c
C	45	3850	6 c	0.136 c
D	50	4628	25 b	0.500 b
E	63	8747	45 a	0.722 a

A: Reference : flowers only bagged
B: Flowers bagged and regularly slightly shaken to allow pollen movement, for self-pollination (*sensu stricto*)
C: Flowers bagged and pollinated with auto-pollen collected on the same tree
D: Flowers bagged and pollinated with allo-pollen collected on different trees
E: Flowers not bagged and pollination open to wind and insects
Data followed by the same letter are not significantly different at 95%.

Breeding System

On double face slides placed near the inflorescences, the mean number of polyads stuck on an area of 10 cm^2 of adhesive tape was 134; these polyads were transferred by wind, thus showing that *F. albida* is partly anemophilous.

Crossing experiments to define ratio between allo and auto fertilization in natural populations of *F. albida* (Table 3) showed that

1) Control inflorescences bagged without manipulation produced pods with a fertilization rate of 0.115. Compared with bagged inflorescences regularly slightly shaken to allow pollen movement, and inflorescences pollinated with auto-pollen collected on the same tree, the rates of fertilization slightly increased but were not significantly different.
2) When stigmas were pollinated with allo-pollen, the rate of fertilization was higher (0.50) but still sig-

nificantly different from the yield of 0.722 obtained in natural pollination by wind and insects.

The Index of Self-Incompatibility (ISI) for all trees studied was 0.272. Nevertheless, there was a great intra-specific variability at the individual level where ISI varied from 0 to 0.54 (Table 4).

Our results suggested that *F. albida* is mainly an auto-incompatible species, with great variability at individual level, and genotypes partially self-compatible.

Table 4. Determination of individual index of self-incompatibility values (ISI) per tree pollinated.

Population	Tree	Rate of fertilization Crossing	Selfing	ISI value
UNI	Tree 1	0.5	0.14	0.28
	Tree 2	0.61	0.28	0.46
	Tree 3	0.11	0.06	0.54
	Tree 4	0.5	0.00	0
FOR	Tree 1	0.66	0.00	0
	Tree 2	0.33	0.00	0
	Tree 3	1.5	0.00	0
	Tree 4	0.40	0.00	0

Population codes indicating studied sites: UNI (University); FOR (Foire).

5 Discussion

The inflorescence in *Faidherbia albida* functions as a reproductive unit with the basal flowers attractive to pollinators because of pollen reward. Apical flowers open more slowly and produce more pods than the basal and median ones. Basal flowers that open first attract the pollinators; apical flowers are well situated to receive pollen from surrounding trees. The same trend has been observed in *Acacia tortilis* with well-shaped inflorescence (Tybirk 1993).

In *Faidherbia albida*, the monad/ovule ratio is 1.5, while in *Acacia nilotica* the ratio is close to one (Tybirk 1989). In many species of Mimosaceae and Asclepiadaceae, the pollen/ovule ratios are generally low (1.0 to 1.5). A low ratio indicates an efficient pollen vector system. The monad package is a minimal investment delivered during one trip of the insect (Cruden 1977): when all monads present on the polyad are simultaneously transferred on the stigmata and pollinate all the ovules, the reproductive gain is maximised and the resources used optimally. However, in *Faidherbia albida* all monads in a polyad are not viable at dispersal of pollen; only 85% of monads present viability. In *A. retinodes* (Kenrick and Knox 1983) only 70% of the monads are viable.

The fertility rate in *Faidherbia albida* is low and similar to many Australian species of Acacia in which only about 1.0 % of flowers bear fruit (Milton 1981). Pollination in *F. albida* is both anemophilous and entomophilous with wasps and butterflies (Tybirk 1993).

Differences between the rates of allo fertilization by hand or by wind or insects showed that the bag introduces a barrier to pollen transferred by wind and by insects. The significant difference between auto and allo-pollination shows that in *Faidherbia albida* the main and dominant reproductive system is allogamy.

A genetic study on natural populations of *F. albida* based on isoenzymes revealed a deficit of heterozygoty (Joly et al. 1992) compared to values expected in open allo fertilization; our results confirm this partial selfing in *F. albida*.

Faidherbia albida presents, as many African and Australian species of Acacia a great variability in their reproductive systems from strict auto-incompatibility to selfing with many intermediate types (Kenrick and Knox 1989a, Moncur et al. 1991), variability being related to genetic mating system (Lloyd 1980, Bawa and Webb 1984) or to ecological factors (Levri 1998).

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