Insects facilitate wind pollination in pollen-limited *Crateva adansonii* (Capparaceae)

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Abstract. Low fruit-set in obligately outbreeding plant species is attributed to a variety of reasons that can be ascertained from reproductive studies. In the present work, the causes of poor natural fruit-set in *Crateva adansonii* DC. were investigated. Floral biology, the role of wind and insects in pollination and the breeding system of the species were studied in two natural populations for three consecutive seasons (2006–08). The flowers exhibited traits conducive to a mixture of wind and insect pollination (ambophily). Although a variety of insects visited the flowers, they were ineffective in pollinating. Nevertheless, active foraging by the honeybees (*Apis dorsata*, *A. mellifera* and *A. cerana indica*) facilitated enhanced pollen dispersal in the air and resulted in indirect pollination by wind. Airborne pollen grains pollinated the plants only up to 10 m. Fruit-set from open pollination was comparable to wind-pollinated flowers. Supplemental pollination treatments established the occurrence of strong self-incompatibility (SI) (index of SI = 0.14). Spontaneous autogamy was prevented by pronounced herkogamy. Low natural fecundity in *C. adansonii* is due to pollination failure, pollen limitation (pollen limitation index = 0.98) and the sparse distribution of the conspecifics; partial SI may partly ensure reproductive assurance through geitonogamy. In the absence of a pollinator wind appears to act as a secondary mode of pollination.

Introduction

Sexual reproduction in outbreeding plants usually involves a predominant biotic mode, or to a minor extent, yet widespread, abiotic mode of pollination (Richards 1986; Kearns *et al*. 1998; Sarma *et al*. 2007). The two modes are generally considered exclusive and the concept of pollination syndromes is often employed to predict the possible mode or the kind of vector involved in the pollination system (Faegri and van der Pijl 1979); the concept has its usefulness in designing the field experiments (Fenster *et al*. 2004). However, consideration of floral features alone to predict the pollination mechanism could be misleading (Waser *et al*. 1996; Johnson and Steiner 2000; Tandon *et al*. 2003). Further, several plant species that notionally conform to either anemophily (wind pollination) or entomophily (insect pollination) may exhibit ambophily, which involves a mixture of both wind and insect pollination (Culley *et al*. 2002; Lázaro and Traveset 2005; de la Bandera and Traveset 2006; Qu *et al*. 2007). Thus, for establishing the pollination system, it becomes imperative to ascertain the functional floral morphology and the efficacy of pollination mode in relation to breeding system of a species.

In the tropics, a great majority of plant species exhibit biotic pollination, mutualistic specialisation and varying levels of self-incompatibility (Bawa 1974, 1990; Kress and Beach 1994). Although biotic pollination ensures a relatively targeted pollen deposition on stigmas, zoophilous species may frequently suffer from low fecundity due to a variety of reasons including pollen or pollinator limitation (Burd 1994; Larson and Barrett 2000), low

densities of conspecifics (Antonovics and Levin 1980; Ågren 1996) and habitat fragmentation (Aizen and Feinsinger 1994). The effects of pollination failure are compounded in wind-pollinated species occurring in the open habitats, as the concentration of airborne pollen may decline with distance (Lemen 1980; Allison 1990; Ågren 1996; Kunin 1997).

The Garlic pear tree or the Caper tree, *Crateva adansonii* DC. (Capparaceae), occurs in the open and dry-deciduous areas of northern India. Like many other deciduous tree species in the region (Yadav and Yadav 2008), *C. adansonii* exhibits seasonal flowering during the leafless period (between March and May). The leafless canopies facilitate wind pollination or enhance the mass floral display to attract the biotic pollinators. Incidence of insect or wind pollination is known in some Capparaceae members. For example *Capparis* sp., *Crateva tapia*, are pollinated by bees and sphignids moths, respectively, while *Forchhameria* sp. is pollinated by wind (Bullock 1995). Interestingly, the floral features of *C. adansonii* indicate the possibility of a mixture of both insect and wind pollination. Features such as synchronous flowering in completely defoliated canopies, lack of fragrance in the flowers, numerous long and flexible stamens with extrorsely presented anthers, production of copious, dry and small pollen grains and the placement of the ovary on a long gynophore that may aid in capturing airborne pollen by the papillate and sticky stigma, are indicative of anemophily. Conversely, large, generalised and showy flowers, a sequential change in the colour of petals and stamens, nectar production and foraging by a variety of insects

(butterflies, bees and wasps) indicate the possibility of entomophily. However, poor natural fruit-set (~0.50%) in the species implies that mating success is limited by pollination failure. Therefore, floral biology, pollination mechanism and the breeding system of *C. adansonii* were investigated to identify the cause(s) of poor natural fecundity.

Materials and methods

Study species and sites

The taxonomic status of the genus *Crateva* has been reviewed by Jacobs (1964), according to which *C. adansonii* DC. subsp. *odora* Jacobs. (hereafter *C. adansonii*) is considered in the present work. This species is distributed in the regions of strongly seasonal climates of Africa, East Asia and China. In India the species occurs in Delhi, Haryana, Rajasthan and Uttar Pradesh. The trees can attain a height up to 15 m.

Field studies were performed for three seasons (2006–08) at two protected locations – (i) North Delhi Forest Reserve (between 28°36′–28°37′N and 77°10′–77°11′E), and (ii) Central Delhi Ridge Forest (between 28°40′–28°41′N and 77°12′–77°13′E) on the northern-most spur of the Aravalli Range. Trees of *C. adansonii* are part of the natural population; the average inter-tree distance was 44.3 ± 3.7 m. Twenty trees of *C. adansonii* were marked in each population for detailed studies.

Phenology and floral biology

Phenoevents comprising leaf senescence and flushing, onset and duration of flowering and fruiting were recorded at the population level. The onset of flowering was considered when more than 50% of the trees in the population began to bear the inflorescence primordia.

As with other species of *Crateva*, the flowers of *C. adansonii* are open from a very young developmental stage (Jacobs 1964). The flowers mature acropetally; maturity of flowers is indicated by the change in colour of petals from greenish-white to white, accompanied by production of nectar and dehiscence of anthers. Therefore, we considered the time of anther dehiscence as floral anthesis time, rather than referring to the time of opening of flowers.

Four developmental stages of the flower (C1–C4) were recognised on the basis of their morphological features, the time of anther dehiscence and onset of stigma receptivity (Table 1). The morphometric details of stamens and the pistil were measured from 20 flowers from each population. The production of stamens, pollen grains and ovules in a flower

was determined by random sampling of flowers from 10 trees in each population (total flowers = 20). Pollen production was determined using a haemocytometer (Kearns and Inouye 1993). Pollen viability was ascertained at 0, 24 and 48 h after anther dehiscence with a fluorochromatic reaction test (Heslop-Harrison and Heslop-Harrison 1970). *In vivo* pollen germination and tube growth were examined using the decolourised aniline blue fluorescence method (Linskens and Esser 1957). The onset of stigma receptivity was ascertained by localising the non-specific esterases (Mattson *et al*. 1974) and phosphatases on the stigma surface (Scandalios 1969). Five pistils representing each of the four floral stages (Table 1) were used for every treatment. Nectar was quantified using microcapillary tubes (5-µl Drummond Microcaps, Sigma, St. Louis, MO, USA). The concentration of sucrose equivalents was determined by using a hand-held refractometer (Sigma, 0–80%). The production of flowers in an inflorescence, and that of stamens, pollen, ovule and the volume of nectar in a flower were compared between two populations using a two-sample *t*-test.

Wind pollination

The density of airborne pollen at different distances from the tree canopy was determined by capturing pollen on glycerine jelly-coated microslides (2.5 × 7.5 cm). The coated slides (*n* = 20 slides each) were placed for 24 h at three distances – at 0 m (within the canopy) and at 5 and 10 m (on wooden planks) from the canopy of five isolated trees.

Temporal details of airborne pollen were determined by computing pollen captured on two coated slides placed at each distance that were exposed for a 3-h block period. Thus, pollen count of eight separate sampling periods beginning from the time of anther dehiscence (at 1900 hours) until 24 h were recorded for each of the three distances; fresh slides were kept for each of the sampling period. The experiment was conducted thrice during the peak time of flowering. The pollen on the slides from the above two experiments were counted under a microscope; the values were expressed as the number of pollen grains cm^{-2}.

To establish the role of wind in pollination, previously bagged flowers (*n* = 30 flowers at C1 stage) were replaced with mosquito-net bags (at C2 stage) to prevent insect visits to flowers, but allowing access to airborne pollen. The flowers were subsequently observed for fruit formation. Some of the flowers (*n* = 30, each population) were used to determine stigmatic pollen loads after 24 h following a method used earlier (Tandon *et al*. 2001a).

Table 1.   **Characteristics of four developmental stages of flower recognised for controlled pollinations**

Floral stage (petal colour)	Pollen viability [time (h) before (–) or after (+) attaining stigma receptivity]	Non-specific esterases/ phosphatases activity	Stigma orientation and receptivity
C1 (greenish-white)[A]	Anthers undehised (–24 h)	+/0	Gynophore drooping; stigma facing downward and not receptive
C2 (white)[B]	Anthers dehisces (1900 hours), 97% viability (0 h)	+++/++	Gynophore erect stigma facing; upward and stigma receptive
C3 (yellowish-white)	70% (+12 h)	++/+	As above
C4 (yellowish-orange)	48% (+24 h)	0/0	Gynophore erect; stigma non-receptive

[A]Stage used for emasculation.
[B]Stage used for pollination treatment.

Insect pollination

The role of insects in pollination was analysed by recording the type of insects, their foraging behaviour, flower handling time and pollen load. Five trees at suitable locations in full bloom were selected at each population. Initially, the activity of floral foragers was monitored at regular intervals of 30-min duration over a period of 24 h during the peak time of flowering on three occasions. For night-time observations, we used a hand-held battery-operated torch. Due to the absence of nocturnal foragers on the tree, observations were subsequently confined between 0500 and 2200 hours (total period of observation = 118 h). Insect types were recorded during the peak time of flowering, trapped using a net and preserved following the procedure described by Kearns and Inouye (1993). The collected insects (n = 7–13 of each type) were analysed for pollen deposition on their body parts and the total amount of pollen load was determined following a methods described by Dafni and Calder (1987). The flower handling period of each insect (n = 20) was recorded using a digital stop watch. The foraging frequency of each insect type was computed by recording their visits over 3–4 h staggered over 6 days in each season; the data were pooled.

Breeding system

The fruit-set data from open pollinations were used as a Control. For this, we randomly tagged 30 racemes in each population, counted the number of flowers on each raceme and monitored the number of fruits that developed at the end of the reproductive phase. As the stigmas were naturally exposed from the younger stages, there was a likelihood of pollen deposition before the attainment of stigma receptivity. Therefore, flowers were bagged at C1 (stigma facing downward) and the bags were removed on the days of pollination treatments (C2, characterised by erect gynophore and stigma facing upward) between 1700 and 1900 hours.

To establish the breeding system, supplemental self- and cross pollinations were done on emasculated flowers by pollinating stigmas with pollen from the flowers of the same and different trees, respectively. For this, 10 trees at each population were randomly selected in each season. Only one flower in an inflorescence was used for pollination. Spontaneous autogamy was tested by bagging unpollinated flowers without emasculating them. Apomixis was ascertained by emasculating unpollinated flowers and then bagging them. Paper bags were used to prevent wind pollination. The bags were partly opened 48 h after the pollination treatments and flowers were monitored for fruit formation. The difference of fruit-set between supplemental self- and cross pollination was ascertained through two-way ANOVA, where populations and pollination treatments were considered as fixed factors. Three-way ANOVA was performed to analyse the effects of pollination treatments [open pollination (Control) versus cross pollination], in two populations and 3 years on fruit-set; populations years and the treatment were considered as fixed factors.

An index of self-incompatibility (ISI) was computed as the ratio of the percentage of fruit-set resulting from supplemental self-pollination to cross pollination (Zapata and Arroyo 1978).

A pollen limitation index (PLI) was computed as 1 – (open fruit-set/cross fruit-set) (Larson and Barrett 2000).

All data analyses were undertaken using SPSS 12.0 package (SPSS Inc., Chicago, IL, USA). Normal distribution of data was ascertained for the suitability of parametric tests. Percent data were root square arcsine-transformed to achieve homoscedasticity (Sokal and Rohlf 1995). Data were pooled for the observations, which did not differ among the two populations. Means with ± s.e. are presented.

Results

Floral biology

The peak flowering period was between the third and fourth week of April (Fig. 1*a*). An inflorescence produced 17.27 ± 5.0 (n = 300 racemes) flowers without any significant difference among the two populations (t = –0.492, d.f. = 38, P > 0.05). The flowers remain in a drooping condition until the day the stigma becomes receptive (Fig. 1*c*). With the onset of stigma receptivity petals became white, filaments purple and anthers yellow (Table 1, Fig. 1*d*). During the post-receptive stages petals turned yellow (Fig. 1*e*), stigmas became black and the filaments wilted. Mature flowers exhibited herkogamy (Fig. 1*b*); the ovary (n = 20) is placed ~0.51 ± 0.1 cm above the anthers. Stigmas were capitate and belonged to the wet-papillate category (Heslop-Harrison and Shivanna 1977). Receptive stigma showed intense staining for non-specific esterases (Fig. 1*f*) and phosphatases (Table 1).

On average, flowers (n = 20) had 19.7 ± 2.5 stamens and each flower (n = 20) produced 26 693.9 ± 403.5 pollen grains. Neither the production of stamens [$t(38)$ = 0.80, P > 0.05] nor pollen [$t(38)$ = 0.10, P > 0.05] differed between the two populations. Each ovary (n = 20 pistils) developed 109.7 ± 12.1 ovules; and the two populations did not differ in the production of ovules (t = 1.33, d.f. = 38, P > 0.05). The pollen to ovule ratio and the outcrossing index (OCI) were 243.2 and 4, respectively. The anthers were bilobed, extrorse and dehisced longitudinally. Pollen grains were dry, tricolporate with microreticulate exine (Fig. 2*a*) and measured 20.1 ± 1.3 μm (n = 50) in diameter. Pollen viability assessed from freshly dehisced anthers (between 1900 and 2000 hours) was 97%, which declined to 48% after 24 h and pollen became completely non-viable after 48 h (Table 1).

The receptacle forms a horse shoe-shaped groove at the base of the flower (Fig. 2*b*, *c*) and produced 1.56 ± 0.72 μl of nectar (n = 40 samples) of ~47% concentration. The quantity of nectar produced among the two populations was not different (t = –1.47, d.f. = 38, P > 0.05). The duration of nectar secretion coincided with the time of anther dehiscence (~1900 hours).

Insect pollination

Insects were the only foragers and there was no difference in their types in both populations. Invariably, all the insects showed preference for flowers with white petals. Both pollen grains and nectar constituted the floral rewards. While the pollen grains were openly presented, nectar was partly concealed in a nectary groove (Fig. 2*b*, *c*). Nectar could be consumed only from an opening that is present on the adaxial side of the receptacle (Fig. 2*b*).
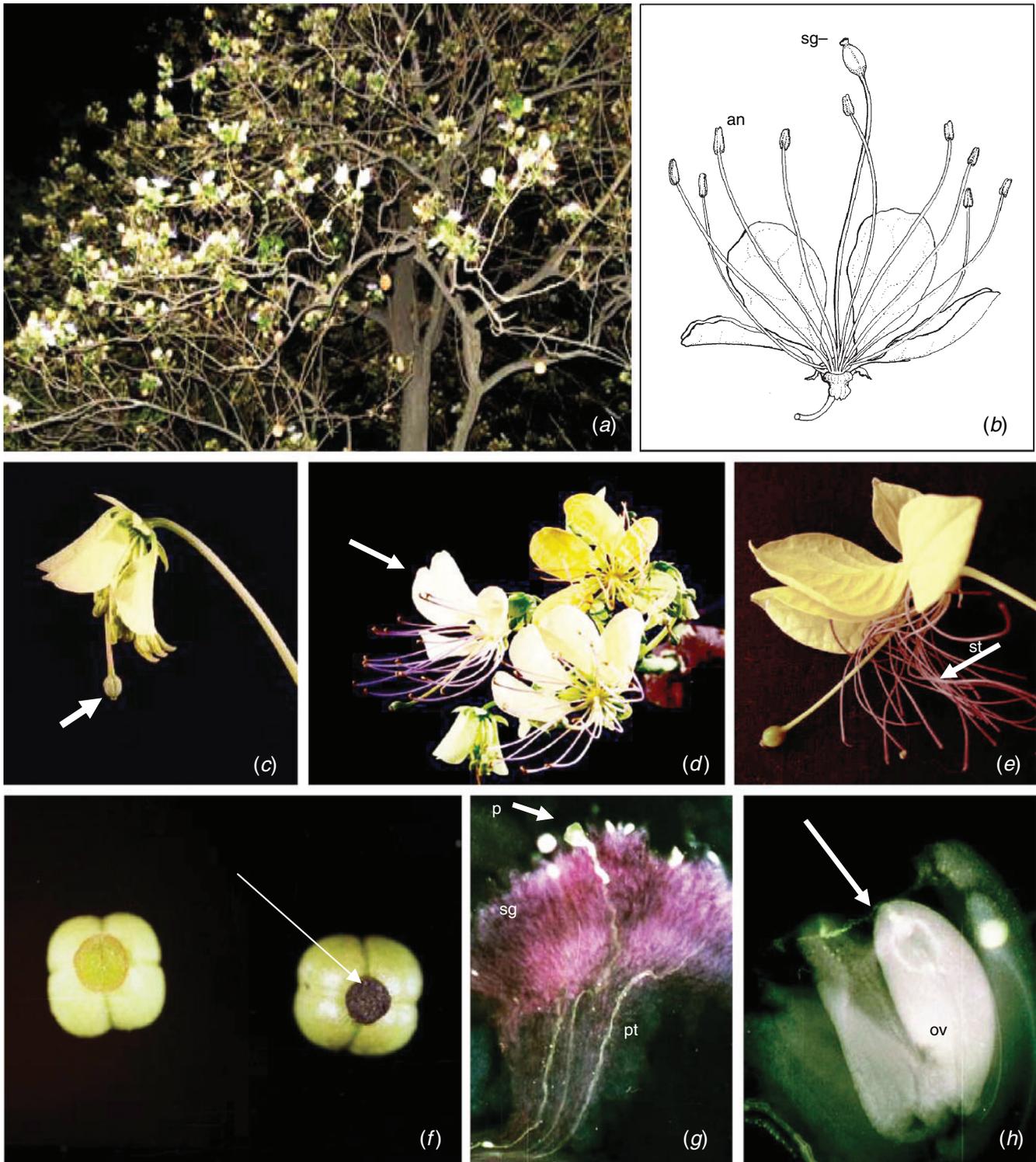
Fig. 1.　Floral biology of *Crateva adansonii*. (*a*) Canopy of a flowering tree. (*b*) A line diagram of a flower showing the placement of stigma (sg) and anthers (an). Only a few anthers are shown for clarity. (*c*) A young flower (C1 stage) showing the drooping floral parts, the stigma in the initial stages is facing downward (arrow). (*d*) An inflorescence with white and receptive flowers (C2 stage, arrow). Note the orientation of stamens and the pistil. (*e*) A flower at C4 stage with wilted stamens (st). (*f*) Polar view of the pistil showing localisation of non-specific esterases (arrow); on the left is Control. (*g, h*) Fluorescence micrographs of wind-pollinated pistil showing germinating pollen grains (p) on the stigma (sg), pollen tube (pt), growth and pollen tube entry into the ovule, ov (*h*).

Fig. 2. Features conducive to wind- and insect-pollination in *Crateva adansonii*. (*a*) Scanning electron micrograph of a pollen showing microreticulate exine (ex). (*b*) Receptacle of the flower forms a nectary groove at the base of flower with an adaxial opening (arrow). (*c*) Receptacle of a fresh flower cut longitudinally to show nectar drop (arrow) at the base of the groove. (*d*–*f*) Insects foraging the floral rewards. *Apis dorsata* at the base of flower (*d*), *Apis mellifera* (arrow) consuming nectar from outside the flower (*e*) and the syrphid fly harvesting the pollen from a dehisced anther (*f*).

Among the recorded insects (Table 2), honeybees (*Apis* spp.) were the most abundant and frequent. Insects began visiting soon after anther dehiscence in the evening around 1900 hours. *Apis dorsata* and *A. cerana indica* foraged at the flowers between 1900 and 2000 hours also, although they were more frequent in the morning (0530–1000 hours). The moth (*Aletia* sp.) foraged for nectar between 1900 and 0130 hours, but visits were infrequent (Table 2). No other nocturnal insect visited the flowers.

Among the observed insects, the syrphid fly (*Platycheirus* sp.) exclusively foraged for pollen (Fig. 2*f*) and exhibited a longer handling time (Table 2). The bees and other insects mostly foraged for nectar. While butterflies inserted their proboscis to

**Table 2.   The foraging period and pollen load of various flower visitors of *Crateva adansonii***

Floral visitor	Pollen load	Body parts with pollen	Frequency (individuals/h)	Flower handling time (sec) ($n = 20$)
Lepidoptera (butterflies and moths)				
Danaus chrysippus alcippoides	42.02 ± 12.39 ($n = 10$)	Wings	0.52 ± 0.12	3.25 ± 0.44
Hebomoia glaucippe	37.58 ± 8.54 ($n = 10$)	Wings	0.33 ± 0.10	3.10 ± 0.29
Percis almana almana	19.8 ± 2.94 ($n = 13$)	Wings	0.39 ± 0.09	1.65 ± 0.15
Aletia sp.	14.75 ± 4.7 ($n = 11$)	Wings	1.37 ± 0.29	3.0 ± 0.16
Hymenoptera (bees and wasps)				
Apis cerana indica	268.38 ± 81.46 ($n = 12$)	Wings, head	3.16 ± 0.49	4.5 ± 0.31
Apis dorsata	294.2 ± 46.69 ($n = 13$)	Wings, head	3.85 ± 0.56	5.7 ± 0.37
Apis mellifera	136.9 ± 16.46 ($n = 9$)	Wings, head	3.33 ± 0.66	5.9 ± 0.35
Polystes hebraeus	42.29 ± 14.77 ($n = 7$)	Wings, head	0.31 ± 0.08	1.8 ± 0.18
Diptera (flies)				
Platycheirus sp.	300 ± 33.6 ($n = 12$)	Wings, ventral part of the mid thorax, legs	1.12 ± 0.2	5.75 ± 0.36

consume nectar, bees and other diurnal insects landed from the front or from the back side of flowers (Fig. 2*d, e*) and crawled along the base of the gynophore and stamens several times to access nectar; their movement in the flowers caused trembling of stamens and anthers. The moths invariably perched from the lateral sides of the receptacle to consume nectar.

All the insects had pollen on different body parts, although the amount of pollen loads varied among them (Table 2). Except for the syrphid fly, the ventral body surface of other insects lacked pollen. In spite of the profuse foraging activity, none of the recorded insects came in contact with stigmas. Importantly, the frequency of visitation by insects positively influenced the dispersal of pollen grains in the air (Fig. 3).

Wind pollination

The density of airborne pollen within the canopy was 5.1 ± 4.1 grains cm^{-2} and gradually declined to 0.9 ± 1.3 at 5 m and to 0.6 ± 1.2 grains cm^{-2} at 10 m away from the canopy. Pollen dispersal was more pronounced during the morning hours and 9 h after the dehiscence of anthers (Fig. 4). The amount of pollen deposited on open-pollinated stigmas (pollination efficiency) was 9.8 ± 1.2 grains per stigma and the values among two population did not differ significantly (one-way ANOVA, $F = 1.91$, d.f. = 1, 29, $P = 0.117$).
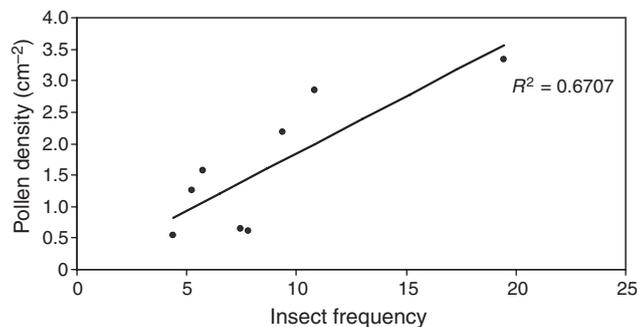
Fig. 3. Scatter plot of relation between frequency of insects in 8 batches of 3-h block periods and the density of airborne pollen in the corresponding durations. Solid line represents the best fitting regression of relation between the two sets of events.
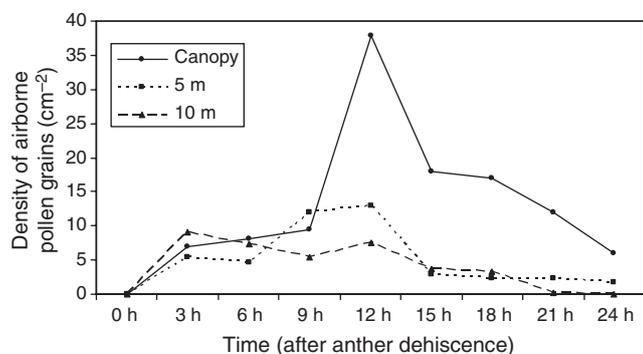
Fig. 4. Density of airborne pollen grains determined at regular intervals of 3 h, within and away from the canopy. There was increased availability of pollen in the air between 9 and 12 h after anther dehiscence.

The bagged flowers that excluded both insects and wind produced no fruits. By contrast, flowers bagged with mosquito nets to exclude insects showed successful pollen germination leading to fertilisation (Fig. 1*g, h*) and produced ~0.6% fruits, thus indicating that wind pollination resulted in fruit-set. The difference between fruit-set through wind pollination and open pollination was not significant (two-way ANOVA, $F = 0.01$, d.f. = 1, 55, $P > 0.001$).

Breeding system

Natural fruit-set in the trees was 0.53%. Invariably, each infructescence had only one fruit and only the lower branches of tree canopies developed fruits in nature. Flowers bagged ($n = 300$ each) to ascertain spontaneous autogamy and apomixis did not form fruits. Supplemental pollinations involving self- or cross-pollination treatments resulted in greater fruit-set than the open-pollinated flowers (Control) (Fig. 5). The trees were partially self-incompatible and self-pollinations ($n = 745$) yielded 5.14% fruits. Fruit-set from cross pollination was significantly greater than that from self-pollinations (two-way ANOVA, $F = 223.8$, d.f. = 1116, $P = 0.001$). The ISI was 0.14 and the PLI was 0.98. The OCI was 4. Three-way ANOVA showed that fruit-set following cross pollinations was significantly greater than open pollination ($F = 152.3$, d.f. = 2, 95, $P = 0.0001$). All other interactions including the three-way interaction were not significant ($F = 0.034$, d.f. = 2, 95, $P = 0.967$).

Discussion

Like several other seasonally flowering and dry deciduous tree species occurring in the Aravalli range, such as *Acacia senegal* and *Butea monosperma* (Tandon *et al.* 2001*b*, 2003), a partial self-incompatibility in *C. adansonii* suggests the possibility of natural selfing. Occurrence of predominant outbreeding in the
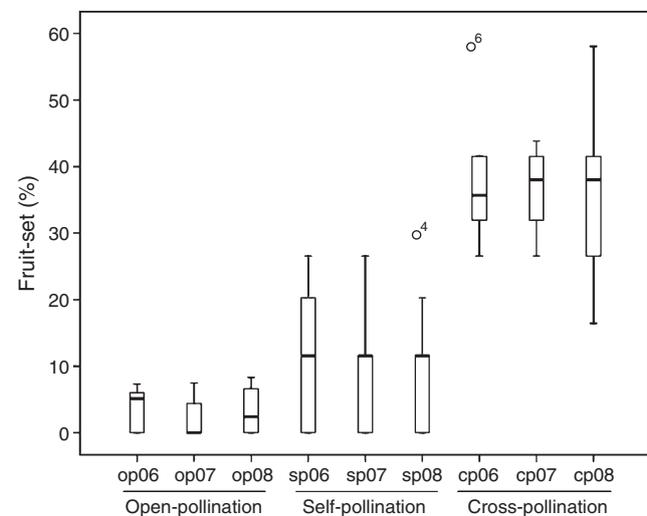
Fig. 5. Box plots of fruit-set obtained from different pollination treatments – open pollination (op), self-pollination (sp), cross pollination (cp) in three seasons (2006–08). The central horizontal bar indicates the median and the box represents the interquartile range. Circles with number indicate the outliers.

species is also consistent with many tropical trees of the dry regions with bisexual flowers (Bawa 1974). A relatively strong self-incompatibility, floral architecture and the lack of spontaneous autogamy indicates that *C. adansonii* is most likely an outcrossing spcies. Interestingly, the pollen to ovule ratio (~243) is rather low for an outcrossing species, which has an OCI of 4 (Cruden 1977).

As spontaneous or facilitated autogamy in the trees of *C. adansonii* was completely impeded by herkogamy, geitonogamy remains the only means for fruit-set. Since the airborne density of pollen grains was greater within the canopy, the pollen grains were likely to be captured by the flowers on the lower branches of the same tree, resulting in geitonogamous fruits. This was evident, as open-pollinated fruits were primarily formed on the lower branches of the canopies of trees. Although geitonogamy incurs fitness cost through pollen and ovule discounting (Galen *et al*. 1989; de Jong *et al*. 1993; Harder and Routley 2006), prevalence of selfing in *C. adansonii* at the genet level appears to serve as, partially if not completely, means of reproductive assurance under pollen-limited and pollinator-depauperate environment (Eckert *et al*. 2006). It is also likely that due to an increased availability of self-pollen in a short duration within the canopy and their simultaneous deposition on the pistils within the genets (geitonogamy), the trees may experience higher incidence of competing selfing (Friedman and Barrett 2009) and result in greater progeny vigour through increased gametophytic selection (Mulcahy and Mulcahy 1987).

Syrphid flies belonging to the *Melanostoma–Platycheirus* group constitute a major category of anthophilous insects that visit wind-pollinated plants (Stelleman 1984; Leereveld *et al*. 1991). However, unlike *C. adansonii*, in these species flowers are compactly grouped and frequent interfloral movement by the insects facilitates pollen transfer. Also, as a prerequisite, effective pollination requires the presence of pollen load on appropriate body parts that should come in contact with the stigma. In our study, *Apis* spp. and the syrphid fly (*Platycheirus* sp.) were most efficient in pollen collection and exhibited longer time in foraging the flowers, but they never contacted the stigmas. Among these insects, only syrphid flies collected pollen on the ventral surface of body parts (sternotribic collection). Inability of the remaining larger insects (butterflies, bees, wasps and moths) to access pollen from anthers could be due to their failure to perch on the anthers that are supported on long flexible filaments. This was evident because of the presence of pollen load on inappropriate places of the body parts (here nototribic collection) including the dorsal surface of the wings. Thus, non-legitimate foraging (equivalent to robbery of rewards) and the inability of the insects to contact stigmas rendered the receptive stigmas in *C. adansonii* with poor pollen load.

Species that lack effective insect pollinators are assumed to exhibit selfing through wind pollination (Anderson *et al*. 2001). In the absence of successful biotic-pollination, stigmatic pollen loads (~10 pollen grains per stigma) in both the populations (present work) was likely the outcome of pollen dispersed in the air. The pollen capture experiment on the coated slides showed that the density of airborne pollen was greater during the phase of increased foraging activity in the flowers. The shaking of flowers to dislodge pollen grains has been demonstrated in *Urginea*

maritima (Dafni and Dukas 1986), although in this species wind directly disperses the pollen from the flowering twigs. In some ambophilous species also, wind directly aids in the dispersal of pollen grains (Qu *et al*. 2007). However, the possibility of insect-facilitated dispersal of pollen into the air that leads to successful natural pollination in *C. adansonii* has not been previously reported. Occurrence of dry pollen with microreticulate exine in the species also indicates wind-mediated pollination (Bullock 1994; Hu *et al*. 2008).

The natural fruit formation in *C. adansonii* is limited due to the lack of sufficient xenogamous pollen and the sparse distribution of partially self-incompatible conspecifics adds to pollination failure. This is consistent with many SI plant species (Ågren 1996; Larson and Barrett 2000). Absence or loss of a legitimate forager from the populations could be another possible reason for pollination failure in trees at the study sites (Wilcock and Neiland 2002). Pollen limitation leading to low fruit and seed set is often linked with complete absence or decline in pollinator abundance (Kearns *et al*. 1998; Cunningham 2000; Larson *et al*. 2002). In the absence of a legitimate pollinator wind is now acting as a minor secondary mode of pollination in *C. adansonii*.

The presence of ambophilous floral features in *C. adansonii* does not guarantee that both the pollination modes will equally contribute to fruit formation. This is demonstrated in *Salix* spp. that has a combination of anemophilous and entomophilous floral traits, but the pollination success is exclusively attributed to either wind (Tamura and Kudo 2000) or insects (Sacchi and Price 1988; Peeters and Totland 1999). As in many other species of Capparaceae (Nelson 1994), nectar production in *C. adansonii* (low volume, high concentration) is typical of insect pollination, but the timing of production indicates suitability of pollination by nocturnal rather than diurnal insects as observed in hawk moth-pollinated *C. tapia* (Bullock 1995).

Acknowledgements

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