

IDENTIFYING POLLINATORS AMONG AN ARRAY OF FLOWER VISITORS, AND THE CASE OF INADEQUATE CASHEW POLLINATION IN NE BRAZIL.

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ABSTRACT

Cashew (*Anacardium occidentale*) is a andromonoecious tree native to NE Brazil. It is of considerable economic importance to the region for its nut, oil and cashew apple production, though crop yields are disappointingly low from commercial orchards. Cashew's flower form and presentation suggest that it is pollinated by insects, particularly bees, though other agents, namely wind and ant, have been cited as its pollinators. Our experiments incorporating the bagging of flowers confirmed that wind was not important as a pollinator. Numerous insects visited cashew flowers, though only bees did so regularly. By observing the visits of individual bees to virgin flowers in cashew's natural habitat, we defined the 'single-visit pollination efficiency' of two frequent flower visitors: honey bees (*Apis mellifera*) and a native oil bee (*Centris tarsata*), in terms of their (i) pollen removal from anthers, (ii) pollen deposition on stigmas, and (iii) initial fruit set. Though both performed well, *C. tarsata* was generally a superior pollinator compared to *A. mellifera*. In commercial orchards, *A. mellifera* was the only regular cashew flower visitor whilst *C. tarsata* was absent. Hand pollination experiments in this agricultural setting demonstrated a need for cross-pollination of commercially grown cashew strains, and inadequate pollination as an important cause of low nut set. To improve cashew crop yields, serious consideration needs to be given to both the conservation and management of its recognised, efficacious pollinators (*C. tarsata* and possibly *A. mellifera*) and also the design of orchards with appropriate mixes of compatible cashew strains.

INTRODUCTION

Cashew and its importance

The cashew tree (*Anacardium occidentale* L.) is andromonoecious, presenting male and hermaphrodite flowers (Fig. 1) in the same panicle. Both types of flowers produce pollen and nectar and both have five white petals at anthesis that gradually become red over a period of five days before withering. Each flower has 6-10 pollen-bearing structures, one (the stamen) being much longer than the others (staminoids). In the hermaphrodite flower, the style assumes the same position as the stamen of male flowers, and its own stamen is shorter than its style (Fig. 1). The ovary bears one single ovule and is rudimentary in male flowers (Northwood 1966; Free 1993; Freitas 1995). Panicles last around 100 days in a flowering season that varies from 5 to 7 months, with each tree producing hundreds of panicles across the flowering season. The proportion of hermaphrodite flowers per panicle ranges from <0.5% to circa 25% (Madhava Rao and Hassan 1957; Damodaran *et al.* 1979; Barros 1988).

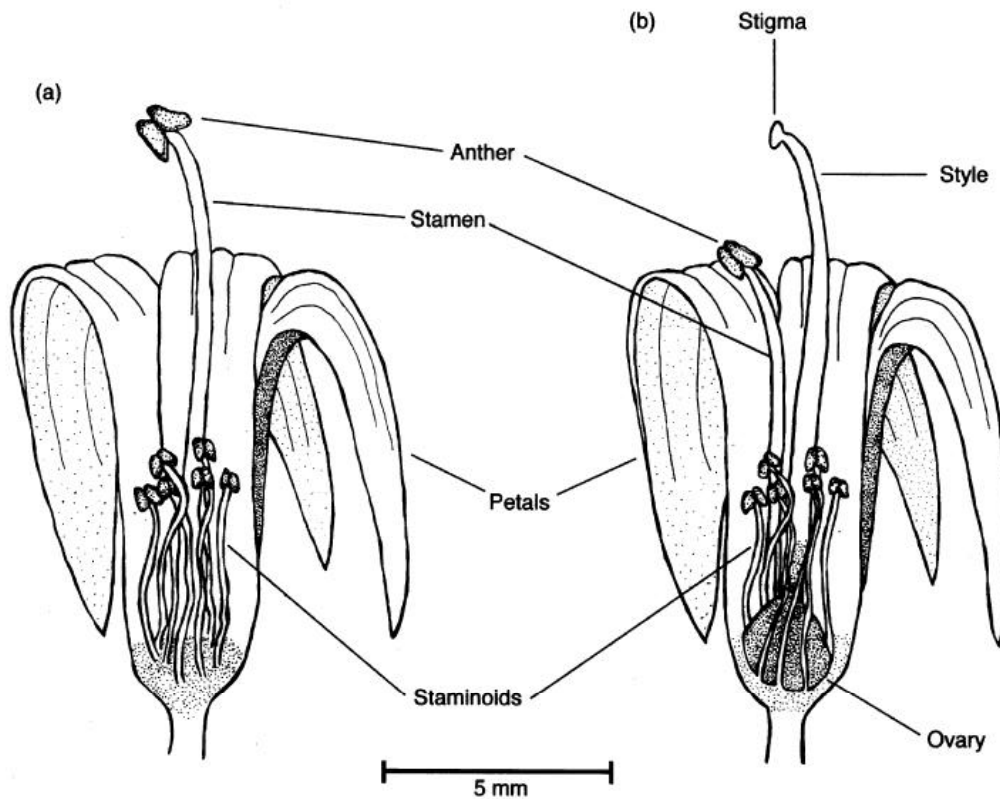


FIGURE 1. Cross-sectional diagram of a male (a) and an hermaphrodite (b) cashew flower, highlighting the relative positions of the stamen and staminoids of each and of the stigma of the hermaphrodite flower.

Cashew is native to coastal areas of Brazil (Fig. 2), especially the environmentally harsh sandy dunes in NE Brazil, where 40,000 to 50,000 ha of cashew trees are still found in the wild (Lopes Neto 1981; Freitas 1994). Before the arrival of the Portuguese to Brazil in 1500 and the subsequent spread of cashew around the world, cashew nuts were already cropped from the wild by native Indians; wild trees are still harvested by poor communities in NE Brazil nowadays. Besides extensive exploitation of wild trees, there are around 650,000 ha of cultivated cashew orchards in NE Brazil alone (Araújo and Silva 1995, cf Table 1).



FIGURE 2. Map of Brazil showing the natural distribution of *Anacardium occidentale* (light shaded), the major commercial cashew orchards (dark shaded), and the field sites where observations and experiments on cashew pollination took place (natural dune habitat at Frecheiras = F; commercial cashew orchards at Pacajus experimental station = P).

TABLE 1. Cashew and its estimated economic value to Brazil per year.

Total area of commercial cashew orchards	650,000 Hectares
Total annual yield of nuts	126,000 Tonnes
Value of exports (nuts only)	US \$ 135 million
(nut shell oil)	US \$ 91 million
Value of crop (nuts, oil and fruit) within Brazil	US \$ 54 million

Source: Sindicaju 1991, Freitas 1995, Araújo e Silva 1995

The cashew nut provides an edible kernel and industrial oil, both of value to local communities and many national economies, including that of Brazil (Morton 1961; Heard

et al. 1990; Reddi 1991, see Table 1). However, yields from cashew orchards have often been poor, circa 200 kg nuts/ha in Brazil when 1,300 kg nuts/ha could be expected (Araújo e Silva 1995), with blame being placed on under-pollination and the fall of immature fruits (Thankamma Pillai and Pillai 1975; Reddi 1987; Free 1993; Freitas and Paxton 1996). Earlier studies in orchards have suggested that wind and many insect species, such as ants, wasps and honey bees, are the pollinating agents of cashew (Bigger 1960; Damodaran *et al.* 1966; Free and Williams 1976; Reddi 1991; Freitas and Paxton 1996). However, their importance has not been critically determined. Indeed, only recently has attention been paid to the natural pollinators of cashew in its native range (Freitas and Paxton 1998).

Defining the role of specific flower visitors as pollinators

There are numerous reports documenting how to assess the pollination requirements of a plant with respect to its fruit, nut or seed set (Corbet *et al.* 1991; Free 1993; Roubik 1995). These incorporate manipulative experiments in which flowers pre-anthesis are bagged within insect-proof netting and to which pollen from varying sources (self, cross) may be added to stigmatic surfaces. For most of the world's Angiosperms, animals have been implicated as important pollen vectors, with insects, particularly bees (Hymenoptera, Apoidea), predominating (Proctor *et al.* 1996).

Plants that are pollinated by a taxonomically restricted set of animals often have similar floral traits, referred to as a pollination syndrome (Faegri and van der Pijl 1979; Proctor *et al.* 1996), and suggesting close coevolution between flower and vector, or at least convergence of floral traits across taxonomically disparate groups of Angiosperms. Mellitophily, the bee pollination syndrome, is typified by flowers with a sweet odour, having pollen and nectar as rewards, often protected in a shallow to moderately deep corolla (Faegri and van der Pijl 1979; Proctor *et al.* 1996). Cashew flowers have bright corollas which change colour with age, they produce nectar and an aroma, they have a reduced number of pollen grains and their staminoids presumably represent 'feeding anthers'. These traits would suggest cashew to be attractive to, and pollinated by, bees. However, the pollen and nectar in its flowers is readily accessible and so its flowers are conceivably attractive to a wide range of insects other than bees (Bigger 1960, Northwood 1966; Damodaran *et al.* 1966; Free and Williams 1976; Khoo *et al.* 1982; Reddi 1991; Dantas de Araujo 1994). Other crops of NE Brazil that require pollination to set seed vary in their floral traits, some apparently attracting a diversity of insects like cashew whilst others appear to conform to a pollination syndrome and attract and are presumably pollinated by a taxonomically restricted set of floral visitors (Table 2). Kevan has suggested that moths may be an important pollinators of cashew in the Costa Atlantica of Nicaragua (personal communication).

TABLE 2. Some crops grown in NE Brazil that require pollination for adequate fruit, nut or seed yield, ordered according to their floral traits and assumed pollination requirements.

Crop plant species	Common name	Presumed or known pollinators
<u>Floral traits suggest pollination not dependent upon one specialist visitor</u>		
<i>Anacardium occidentale</i>	cashew ^a	bees (this study)
<i>Mangifera indica</i>	Mango	bees, flies, beetles, butterflies (Free 1993)
<i>Persea americana</i>	Avocado	bees, possibly flies (Free 1993)
<u>Floral traits suggest pollination dependent upon a specialist visitor</u>		
<i>Malpighia emarginata</i>	West Indian cherry	oil bees, <i>Centris</i> (Freitas <i>et al.</i> 1999)

<i>Byrsonima verbascifolia</i>	murici ^a	oil bees, <i>Centris</i> (personal observation)
<i>Annona muricata</i>	Soursop	beetles, <i>Cyclocephala</i> (Aguar 1998)

^a: indigenous to NE Brazil

More recently, the concept of the pollination syndrome has been questioned (Waser *et al.* 1996). This is partly because of the circularity of reasoning that it introduces, as exemplified in our description of cashew as likely being bee pollinated. It is also partly because observations of floral visitors have indicated that many flowers supposedly adapted for pollination by a select group of animals are in reality visited by a much wider array of potential pollen vectors (Waser *et al.* 1996). However, it is crucial to distinguish between a mere flower visitor versus a pollinator, not only in order to shed light on this debate; when inadequate pollination is responsible for reduced crop yields, as may be the case for cashew in NE Brazil, it is also necessary to identify the importance of different flower visitors to the crop's pollination. This allows management aimed at augmenting pollinator numbers to be directed at the appropriate species.

Numerous methods to evaluate a flower visitor's role in the pollination of a plant species have been employed for a variety of crops and wild plants (Kendall and Smith 1975; Tepedino 1981; Dafni *et al.* 1987; Inouye *et al.* 1994), many providing only indirect estimates of a visitor's importance. A corollary is that the term 'pollinator efficiency' has been used in a multitude of senses. In an attempt to bring order and consistency among studies, Inouye *et al.* (1994) have suggested a standardised lexicon, to which we attempt to adhere in our studies on cashew pollination described below.

A direct method for evaluating the relative importance of different groups of flower visitors to a plant's pollination has been proposed by Spears (1983). The experimental paradigm involves allowing virgin flowers to be visited by one visitor and monitoring subsequent fruit, seed or nut set. Spears' (1983) single-visit pollination efficiency' index allows a pollinator's relative contribution to plant reproductive success from among a suite of flower visitors to be measured. Though this measure relates to a plant's reproductive success through only its female function, this may suffice for a number of agricultural crops where fruit, seed or nut yield (ie female function) is the focus of attention. We use this method to evaluate the importance of different pollinators in cashew pollination via a flower's female function.

Direct estimates of the importance of a pollinator to a plant's reproductive success via its flowers' male function have not been devised. We therefore adapt Spears' (1983) single-visit paradigm, recording pollen grains removed from a flower in a single visit, to obtain an indirect measure of the importance of different pollinators to cashew pollination via its flowers' male function.

Here we report on our researches upon cashew over its past six flowering seasons, 1993-1998 inclusive (and see Freitas 1994, 1997a,b; Freitas and Paxton 1996, 1998). These have been aimed, firstly, at defining cashew's pollination requirements, secondly, at evaluating the importance of different flower visitors in the pollination of cashew in native habitats where the plant is indigenous and, thirdly, at determining whether and why lack of pollination is a cause of inadequate crop yields in agricultural settings.

METHODS

In Brazil, cashew trees are grown commercially from clonal strains supplied by EMBRAPA, the national governmental agricultural research and support department. Limited selective breeding of clonal strains has been practised (Araújo and Silva 1995; EMBRAPA/CNPAT 1997) and, in flower form and presentation at least, wild and commercial cashew blossom is essentially identical.

Our fieldwork has been undertaken at two locations within the natural distribution of *A. occidentale*. At one location, Frecheiras, cashew grows wild in its natural dune habitat; at location Pacajus experimental station, clonal strains of cashew are grown (Fig. 2). A few clonal varieties are present in orchards at Pacajus, reflecting their use by EMBRAPA as experimental field sites. But each orchard contains only one clonal variety, as found in commercial orchards typical of NE Brazil.

To describe cashew flower form, presentation and phenology, we examined 400 each of male and hermaphrodite flowers at Pacajus across their entire period of bloom. Hand pollination experiments involved bagging flowers pre-anthesis in fine mesh netting (1 mm² mesh) and adding pollen from the same or another tree's flowers to the bagged stigmas when at peak receptivity (see Freitas and Paxton 1996 for further details).

Florescences were examined at Frecheiras and Pacajus to record the number of visits to them by different insect species, and their behaviour on individual flowers. To count the number of cashew pollen grains adhering to an insect's body, the insect was washed thoroughly in a solution of ethanol with detergent and dislodged cashew grains were counted under a haemocytometer (Freitas 1997a; Freitas and Paxton 1996). The 'single-visit pollination efficiency' (sensu Spears 1983) of *A. mellifera* and *C. tarsata* was evaluated at Frecheiras in terms of three components of relevance to cashew's pollination: pollen removal from anthers, pollen deposition on stigmas, and fruit set (Freitas and Paxton 1998). To do so, we compared the pollen removed, or deposited, or the fruit set by a single visit of a bee to a virgin flower (N = 50 flowers for each pollination component and bee species), as compared to that of permanently bagged flowers (N = 50 flowers for each pollination component) and that of flowers permanently open to floral visitors (N = 50 flowers for each pollination component; see Spears 1983; Freitas and Paxton 1998).

RESULTS

Cashew's need for pollination

Panicles consisted of approximately 10% hermaphrodite flowers to 90% male flowers (N = 500 panicles). Flowers of both types were white at anthesis with two pink stripes on each petal. They progressively acquired a pink coloration towards the end of the day, turning red by the third day and withering by the end of the fifth day after anthesis (see Free 1993; Freitas 1994).

Anthesis of male flowers started at 06:00 h and 82.2 ± 3.1% of flowers were open by 10:00 h (N = 500 flowers). In hermaphrodite flowers, anthesis and stigma presentation started around 10:00 h and 95.0 ± 2.3% of hermaphrodite flowers were open by 12:00 h, with only a few stigmas being first presented later in the day (N = 500 flowers). Anther dehiscence of stamens occurred mainly after 09:00 h for male flowers and 10:00 h for hermaphrodite flowers, but male flowers contributed proportionally most of the stamen-derived pollen available to insect visitors. Cashew stigmas were receptive up to 30 h

after anthesis (N = 300 stigmas), but stigma receptivity varied with age ($G^2 = 126.8$, $df = 9$, $P < 0.001$). Stigmas up to 4 h old were more receptive than older ones (N = 30 stigmas for 10 age cohorts from 0 h to 46 h; see Freitas and Paxton 1998).

Flowers excluded to insect visitation did not set any fruit and those open to floral visitors at Pacajus set 50.5% of their flowers (Table 3). Hand pollination of cashew stigmas using self- and cross-pollen grains gave an initial fruit set varying between 65.0 and 73.8% (Table 3) and did not differ significantly from each other ($\chi^2_1 = 1.441$, $P > 0.05$). There were no differences in pollination for pollen derived from male and hermaphrodite stamens (Freitas and Paxton 1996).

TABLE 3. Fruit set of cashew flowers either open to insect visitors (in a commercial orchard, Pacajus) or closed to insects and hand pollinated by pollen from male and hermaphrodite flowers.

Treatment of flower and origin of pollen, if bagged	No. of Flowers	No. of fruits set	% flowers that set fruit
Open to insect visitors	200	101	50.5
Bagged to insect visitors, no pollen	200	0	0
Bagged, stamen (cross)	80	59	73.8
Bagged, stamen (self)	80	52	65.0
Bagged, staminoid (cross)	80	2	2.5
Bagged, staminoid (self)	80	0	0

Other experiments caging a whole tree and capturing wind-blown pollen grains in cashew orchards (Freitas 1995a; Freitas and Paxton 1996) have indicated that wind and very small insects play little or no role in cashew pollination, contrary to previous assertions (Madhava Rao and Hassan 1957; Bigger 1960; Damodaran *et al.* 1966). Thus, initial fruit set in cashew seems to be from both self- and cross-pollination, effected by larger flower visitors. Pollination is likely restricted to the first day of anthesis, too. A delay in anther dehiscence of hermaphrodite flowers diminishes the chances of self-pollination. Yet despite this partial dichogamy, the great number of male flowers per tree may increase the level of geitonogamy (De Jong *et al.* 1993; Harder and Barret 1995).

The potential pollinators

A number of insect species have been recorded visiting cashew inflorescences in agricultural habitats, particularly ants, bees, butterflies and wasps (Freitas and Paxton 1996). In contrast, only an ant, *Camponotus* sp., and two bees, the honey bee *Apis mellifera* and the native oil bee *Centris tarsata* Smith, were recorded visiting cashew in natural sand dune habitats (Freitas and Paxton 1998).

We consider visitors of cashew inflorescences other than bees of little importance in pollinating its flowers. Either non-bee visitors made little or no contact with the flower's reproductive organs (eg ants, see Table 4). Alternatively, they did not discriminate between young flowers with fresh pollen or receptive stigmas and old ones (eg the butterfly *Aphrissa* sp.), or they visited flowers only when little viable pollen was available (eg the butterfly *Oanaus erippus* Cramer), or they did not show flower constancy to cashew (eg the butterfly *E. hegesra*) (Freitas and Paxton 1996).

TABLE 4. The average number of cashew pollen grains carried on the bodies of the principal visitors of cashew inflorescences and their abilities to touch the flower's reproductive organs. + = yes, - = no, oc = occasionally.

Type of insect visitor Common name	No. insects sampled	No. cashew pollen grains per insect	Touch	
			Anther	Stigma
APIS MELLIFERA honey bee ^a	20	1241 ± 56	+	+
<i>Camponotus</i> sp. an ant ^b	20	17 ± 6	-	-
<i>Centris tarsata</i> (pollen collector) an oil bee ^a	20	2271 ± 141	+	*
<i>Centris tarsata</i> (nectar collector) an oil bee ^a	20	1805 ± 182	+	+
<i>Polistes</i> sp. a social wasp ^b	20	25 ± 8	oc	oc
TRIGONA SPINIPES a stingless bee ^b	20	118 ± 20	oc	-

* Female *C. tarsata* collecting pollen visit only male cashew flowers; nectar collectors always touch the stigma of hermaphrodite flowers.

^a: insects collected in a natural habitat, Frecheiras, September 1994.

^b: insects collected in a commercial orchard, Pacajus, July-September 1993.

In contrast, bees appeared to be important to cashew pollination. The most frequent visitors of cashew flowers in natural habitats were *A. mellifera* and *C. tarsata* (Freitas and Paxton 1998). Both bee species showed foraging behaviour conducive to effective pollination; flower constancy, timing of visits in relation to hermaphrodite flower's anthesis, touching of anther and stigma in the same area of the body (Fig. 3), systematic movement between young flowers, and great numbers of cashew pollen grains on their bodies (Table 4). When both bee species visited cashew flowers, most cashew pollen grains were acquired in the ventral mesothorax of their bodies, an area in which the flower's reproductive organs usually touched the forager (Fig. 3). However, while *C. tarsata* bore between 52 and 118 cashew pollen grains per mm² in this body area, *A. mellifera* only carried only 5 cashew pollen grains per mm² of the same body area (Freitas 1997a), suggesting it might be a less efficacious pollinator of cashew flowers. Cashew pollen carried in the ventral mesothorax was however of equal germinability in the two bee species (Freitas 1997b).

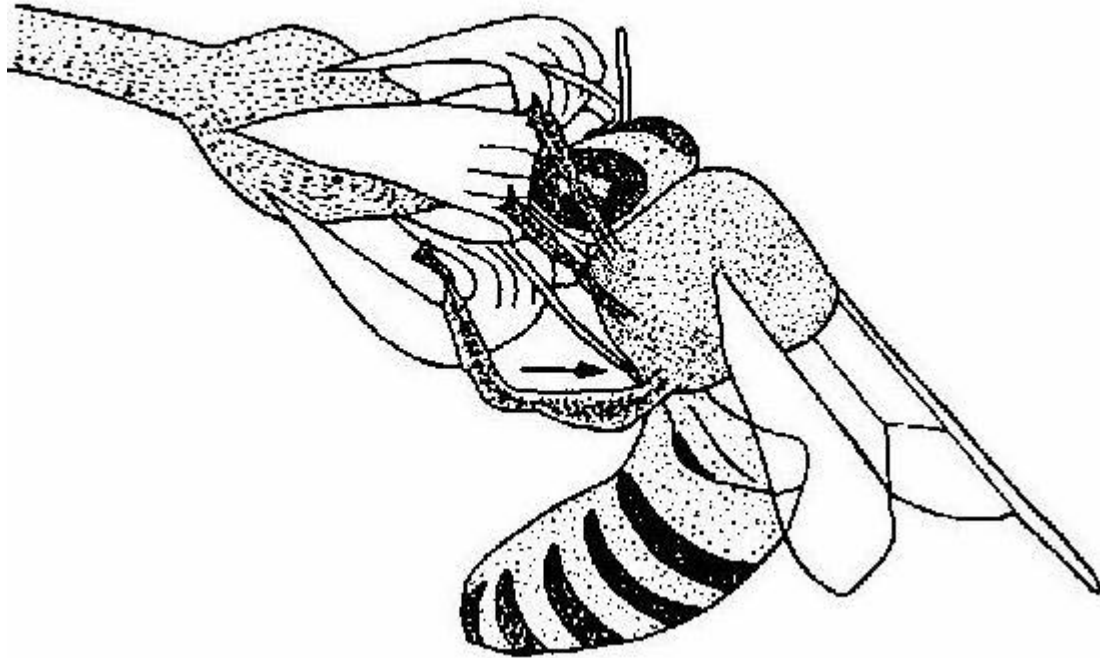


FIGURE 3. Schematic diagram of a honey bee (*Apis mellifera*) in its characteristic position when foraging for nectar on a cashew flower. Note that the stigma touches the bee's ventral thorax.

The importance of *A. mellifera* and *C. tarsata* as pollinators

We employed observations and experiments incorporating single visits by *A. mellifera* and *C. tarsata* to virgin cashew flowers growing at Frecheiras, a natural dune habitat, to evaluate the relative importance of these flower visitors in cashew pollination.

Firstly, the efficiency in removing pollen grains from stamens (ie viable pollen) differed significantly between the two bee species (Kruskal-Wallis ANOVA, $P < 0.001$; Table 5). In particular, flowers receiving single visits by female pollen collectors of *C. tarsata* removed most of the available pollen from a stigma in a single visit. Nectar collectors of *A. mellifera* and *C. tarsata* each removed approximately 67-68% of the available pollen (Table 5).

TABLE 5. Single-visit pollination efficiency measures for two bee species on cashew flowers at Frecheiras.

Single visit by	Efficiency of pollen removal from anther (\pm SEM)	Efficiency of pollen Deposition on Stigma (\pm SEM)	Efficiency of fruit set (\pm SEM)
<i>Apis mellifera</i> nectar collector	0.68 ^b \pm 0.05	0.24 ^b \pm 0.03	0.43 ^a \pm 0.10
<i>Centris tarsata</i> nectar collector	0.67 ^b \pm 0.05	0.48 ^a \pm 0.07	0.59 ^a \pm 0.08
<i>Centris tarsata</i> pollen collector	0.99 ^a \pm 0.04		

Means followed by the same letter within a column do not differ at $P < 0.05$

Honey bee foragers never actively collect pollen from cashew flowers, hence their absence from Table 5. The extent to which *C. tarsata* females switch between pollen collection (from male flowers only) and nectar collection (from male and hermaphrodite flowers) is not known, though nectar collectors usually carry some pollen in their scopal hairs, suggesting frequent switching. Further, we have merely measured the removal of pollen from anthers and not its subsequent fate; we have only recorded an indirect measure of a plant's reproductive success via its pollen export (see Queller 1997). Notwithstanding these limitations, our data suggest that *C. tarsata* is a more important pollinator than *A. mellifera* in terms of cashew's male reproductive function (Freitas and Paxton 1998).

Secondly, *A. mellifera* foragers deposited substantially fewer pollen grains on stigmas than did *C. tarsata* foragers during single visits to a hermaphrodite flowers (Mann-Whitney test, $P < 0.001$; Table 5). These data suggest that honey bees were of lesser importance than *C. tarsata* to pollination in terms of cashew's female reproductive function and its fruit and nut set. Despite initial fruit set through single visits by *A. mellifera* also being lower than those by *C. tarsata*, differences between the two species were not statistically significant (Table 5). Together, these data suggest that both bees may effect fruit set in cashew, with *C. tarsata* possibly a little superior to *A. mellifera* in terms of a cashew flower's female reproductive function (Freitas and Paxton 1998).

There is however a caveat to the interpretation of our data on fruit set. We have only recorded each species' single-visit pollination efficiency in terms of initial fruit set. For cashew, reproductive self-incompatibility may be manifest later in fruit development (see below). In this case, there is still a need to evaluate the relative importance of the two bees in terms of both the compatible pollen they carry and also the mature fruit and nuts to which their visits give rise.

Pollination in an agricultural setting

We have more recently re-examined the pollination requirements and fruit set of cashew within a commercial orchard setting at Pacajus, where a single clonal strain is typically

grown over a large area. To effect hand cross-pollination, different clonal strains of cashew were used as pollen donor and recipient. Though initial fruit set through hand cross- or self-pollination was high in 1998, there was great loss of self-pollinated fruit later in fruit development (Table 6), most fruit drop occurring 13-15 days after pollination (Holanda-Neto *et. al.* in preparation). Cashew fruit requires 56-60 days to mature following pollination. Microscopic examination of embryo development in young fruit suggests that pollination may stimulate preliminary fruit growth but that rarely does an embryo develop and a fruit complete development when pollination is by self-pollen (Holanda-Neto *et. al.* in preparation). Cashew, at least the clonal strains grown commercially in NE Brazil, appears to exhibit partial self-incompatibility.

TABLE 6 Fruit set of cashew grown in a commercial orchard, Pacajus, either open to insect visitors or closed to insects and hand pollinated. N = 100 flowers per treatment.

Treatment of flower ^a and origin of pollen, if bagged	1997	1998	
	No. fruits harvested	No. fruits remaining at given time after pollination	
		7 days	30 days
Open to insect visitors	2	75	2
Bagged to insect visitors, no pollen	0	0	0
Bagged, cross pollen ^b	17	89	31
Bagged, self pollen	5	89	4

^a: clone CCP-76; ^b: clone CC-12

A large amount of fruit drop following pollination was observed in commercially grown cashew, even when flowers were hand cross-pollinated (Table 6). However, for open pollinated flowers, levels of successful fruit and nut production were even lower, at only 2% in both 1997 and 1998 (Table 6). This was despite the addition of extra colonies of honey bees to the study orchard in 1998. These data reflect the complaints about low yields by commercial cashew producers in NE Brazil.

A compounding problem for cashew pollination in commercial orchards is that its flowers receive few visitors, the commonest being *A. mellifera* (Table 7). Honey bee foragers can effect initial fruit set in natural environments (Table 5). However, despite the fact that honey bee colonies are regularly brought into cashew orchards, *A. mellifera* frequently forages on the flowers of weeds growing beneath the cashew trees rather than from cashew blossom itself (Freitas 1994, 1995b). We have never recorded *C. tarsata* in cashew orchards despite several hundred hours of observation of blossom (eg Freitas and Paxton 1996). Given the apparent need of commercially grown cashew for cross-pollination, the restricted foraging range of individual *A. mellifera* foragers, often confined to one or a few adjacent fruit trees (Free 1993), may severely limit its ability to effect cross-pollination. In this regard, *C. tarsata* may effect greater cross-pollination as it flies rapidly between trees when foraging and deposits more pollen grains on a stigma per single flower visit than does *A. mellifera* (Table 5).

TABLE 7. The relative and absolute frequency of the principal floral visitors to cashew inflorescences (2400 inflorescences over a 3 month period) in a commercial orchard, Pacajus.

Insect species	Relative frequency on panicles (%) ^a	Mean No. of panicles with species present
<i>Apis mellifera</i> (honey bee)	28	6.25
<i>Camponotus</i> sp. (an ant)	24	5.25
<i>Polistes</i> sp. (a social wasp)	14	3.12
<i>Trigona spinipes</i> (a stingless bee)	12	2.50

^a: For additional species comprising the remaining 22%, see Freitas & Paxton 1996.

DISCUSSION

Which are the pollinators among the flower visitors?

lower visitor and pollinator are not synonymous terms. For any plant species whose reproduction is dependent upon pollination and where more than one potential vector is recorded visiting its flowers, it will be necessary to evaluate through manipulative experiments and observations the importance of each to the plant's reproductive output. Such an approach may also shed light on the debate over the validity of the pollination syndrome concept (Waser *et al.* 1996). For crops that are dependent upon pollination for fruit, nut and seed production, it is also important to identify the crop's pollinator or pollinators to ensure appropriate management of them. Despite earlier reports suggesting that cashew was pollinated by a wide range of insects (Northwood 1966; Free and Williams 1976; Khoo *et al.* 1982; Reddi 1991; Dantas de Araujo 1994), and even wind (Madhava Rao and Hassan 1957; Bigger 1960; Damodaran *et al.* 1966), it is clear from our results that only a few bees are the important vectors of cashew pollen.

Spear's (1983) index of 'single-visit pollinator efficiency' provides a direct measure of the importance of individual flower visitors to a plant's female reproductive function. For many crops dependent on pollination for adequate yields, and where crop yields are the focus of attention, determination of this index may be the most convenient and accurate means by which the relative importance of different flower visitors is evaluated.

Using this index in cashew fruit and nut production, we were easily able to compare the single-visit pollination efficiencies of two bees. We found that single visits by the indigenous *C. tarsata* led to slightly though not significantly higher initial fruit set than single visits by *A. mellifera* foragers. Our data also allowed us to state that both bees may provide an adequate pollination service to cashew.

Of course, the actual role of an insect species in effecting pollination in the field will be dependent not only upon its single-visit pollination efficiency but also on its relative and absolute frequency of visits to flowers. For example, several visits by *A. mellifera* foragers to a flower may compensate for fewer visits by *C. tarsata*. We also note that interacting flower visitors may compete for floral rewards such that one reduces the frequency of visits of the other to those flowers (Schaffer *et al.* 1979), or diminishes the duration of its flower visits with consequential effects on its pick-up from anther or deposition on stigma of pollen. Nevertheless, the single-visit pollination efficiency

paradigm may still be useful in providing an estimate of the theoretical importance of a flower visitor in pollination and crop production.

Inadequate pollination and poor cashew yields - the lack of pollinators

That cashew in NE Brazil is dependent upon bee pollination is clear from our work over the past six years. Cashew commercially grown in orchards also suffers from low crop yields, in large part due to inadequate pollination. There are two sides to this shortfall.

On the one side, there are few or no visits to orchard-grown cashew flowers by the appropriate bee species that are competent pollinators. One seemingly suitable pollinator, *A. mellifera*, does not readily visit cashew flowers even when brought into orchards in large numbers because it is attracted to competing weeds in bloom (Freitas 1995b). Methods are available to increase the pollination potential of honey bee foragers by directing them to visit specific crops in need of pollination (Jay 1986), theoretically overcoming this difficulty. However, commercially grown strains of cashew also seem to need cross-pollination. In this case, the flower constancy and narrow foraging range of individual honey bees (Free 1993) may limit further their role in cashew pollination and crop production. However, methods to enhance specifically the cross-pollination potential of honey bee foragers are available (Hatjina *et al.* 1999).

Another seemingly suitable cashew pollinator and one with higher single-visit pollination efficiency measures than those of the honey bee is *C. tarsata*, though it is not even found in commercial cashew orchards. In the natural dune habitats of cashew, cropping of wild trees does not use any sort of pesticides or agricultural practices that may harm its pollinators. However, in agricultural areas using the new dwarf strains of cashew, insecticide spraying and land ploughing have been widely practised. It has for long been recognised that insecticide spraying can be harmful for pollinating insects in general (eg Kevan 1975), and ploughing is particularly damaging because it may destroy nests of fossorial (ground-nesting) bee species such as those of *C. tarsata*. *Centris* bees nest in sandy ground beneath the bushes of *Byrsonimia verbascifolia*. Unfortunately there is a lack of direct information on the impact upon *C. tarsata* of insecticide spraying and ploughing, though the absence of the bee from commercial cashew orchards may in part be related to both forms of agricultural practice.

Inadequate pollination and poor cashew yields - the lack of compatible pollen

A second side to the shortfall in adequate pollination of commercially grown cashew is undoubtedly related to horticultural practices in which a partially self-sterile clonal strain is grown over large areas without thought being given to the need for compatible sources of pollen. This problem is exacerbated as more and more cultivated areas are being planted or replanted with dwarf clones (Freitas 1994; Araújo and Silva 1995). One obvious solution is to intercalate trees producing compatible pollen within main cropping strains. Hand-pollination experiments carried out in Australia and Brazil have identified types or strains of cashew, crossing among which produced higher yields (Wunnachit *et al.* 1992; EMBRAPA/CNPAT 1994, 1997). However, it will still be necessary to consider management of bees within commercial cashew orchards because they will be needed as the vectors of the compatible pollen.

An alternative approach is to introduce colonies of honey bees with 'hive inserts' to cashew orchards requiring pollination, those hive inserts containing pre-collected compatible pollen which foragers departing their colony pick up and subsequently transfer onto the stigmas of the flowers they visit (Jay 1986). The efficacy of hive inserts as a means of promoting cross-pollination has been called into question (Hatjina 1998);

the method requires a source of pre-collected pollen which may be difficult to acquire, and it is likely impractical for a crop like cashew that blooms over a 5-7 month period.

CONCLUSIONS

Cashew requires pollination for fruit and nut set; commercially grown strains are partially self-incompatible. Though a native bee, *Centris tarsata*, and the introduced honey bee *Apis mellifera*, appear to provide adequate pollination in cashew's natural habitats, orchard crops suffer low crop yields through inadequate pollination. To improve crop yields, attention needs to be paid to (i) pollinator management, to ensure that sufficient numbers of pollinators are present during flowering, and (ii) horticultural practices, to ensure cashew strains with compatible pollens are grown in the vicinity of each other. Widespread use of pesticides and intensive horticultural management may be detrimental to profitable cashew yields, in part because these practices are associated with the decline or extermination of pollinators, both native and introduced.

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