Floral Biology and Breeding System of *Anaxagorea dolichocarpa* (*Annonaceae*), with Observations on the Interval between Anthesis and Fruit Formation

By

Marcus BRAUN*) and Gerhard GOTTSBERGER**)

With 3 Figures

Summary

BRAUN M. & GOTTSBERGER G. 2011. Floral biology and breeding system of *Anaxagorea dolichocarpa* (*Annonaceae*), with observations on the interval between anthesis and fruit formation. – Phyton (Horn, Austria) 51(2): 315–327, with 3 figures.

Floral biology, phenology, and fruit set of *Anaxagorea dolichocarpa* SPRAGUE & SANDWITH (*Annonaceae*) was studied in the Atlantic forest in Northeast Brazil. Herein, the thick petals form a floral chamber, which is accessible only to small insects. Flowers are protogynous, without overlap between the carpellate and the staminate phase. The anthesis starts in the afternoon (14.00–15.00 h), and the carpellate phase lasts until late morning of the next day. Pollen is released in the early afternoon (12.00–13.00 h) on the second day of flowering. The staminate phase ends between 14.45 and 15.45 h with the opening and shedding of the petals, which overlapped with the beginning of the carpellate phase of the next days' flowers. Both the carpellate and the staminate phase are accompanied by strong fruity scent and thermogenesis of up to 3.8 °C (carpellate) and 3.7 °C (staminate phase) above ambient temperature. Experiments showed that *A. dolichocarpa* is self-compatible, but pollinator-dependent for fruit set. Although stingless bees (Trigona sp.) regularly visit staminate phase flowers for pollen at the end of anthesis, only small nitidulid beetles (Colopterus spp.) were recorded as pollinators. They enter the floral chamber

*) Dr. Marcus BRAUN (corresponding author), Institute of Systematic Botany and Ecology, University of Ulm, 89081 Ulm, Germany; e-mail: marc.usbraun@web.de

**) Pens. Univ.-Prof. Dr. Gerhard GOTTSBERGER, Botanical Garden and Herbarium, University of Ulm, 89081 Ulm, Germany.

during the first hours of anthesis, feed on pollen during the staminate phase, and stay until the petals shed. Flowering is continuous and trees produce few flowers at a time. The beginning of visible fruit growth was delayed for a rather long period of up to nine months, varying strongly among single flowers. Seeds are dispersed by an autochorous mechanism.

Zusammenfassung

BRAUN M. & GOTTSBERGER G. 2011. Floral biology and breeding system of *Anaxagorea dolichocarpa* (*Annonaceae*), with observations on the interval between anthesis and fruit formation. [Blütenbiologie und Reproduktionssystem von *Anaxagorea dolichocarpa* (*Annonaceae*), mit Beobachtungen zum Zeitraum zwischen Anthese und Fruchtwachstum]. – Phyton (Horn, Austria) 51(2): 315–327, mit 3 Abbildungen.

Blütenbiologie, Blühphänologie und Fruchtansatz von *Anaxagorea dolichocarpa* SPRAGUE & SANDWITH (*Annonaceae*) wurden im Atlantischen Regenwald Nordost-Brasiliens untersucht. Die fleischigen Petalen bilden eine Bestäuberkammer, die nur für kleine Insekten zugänglich ist. Die Blüten sind protogyn und die weibliche und männliche Blühphase überlappen sich nicht. Die Anthese beginnt am Nachmittag (14.00–15.00 Uhr), die weibliche Phase dauert bis zum Morgen des folgenden Tages. Die Pollenabgabe beginnt am frühen Nachmittag (12.00–13.00 Uhr) des zweiten Blühtages. Die männliche Phase endet zwischen 14.45 und 15.45 Uhr mit dem Öffnen und anschließendem Abfallen der Petalen, was sich mit dem Beginn der weiblichen Blühphase der neuen Blüten des aktuellen Tages überschneidet. Beide Blühphasen werden von starkem, fruchtähnlichem Duft sowie Thermogenese begleitet, wobei die Blütentemperatur in der weiblichen Phase bis 3.8 °C und in der männlichen bis 3.7 °C über der Umgebungstemperatur liegt. Handbestäubungen zeigten, dass *A. dolichocarpa* selbstkompatibel, aber nicht selbstbestäubend ist. Ausschließlich Käfer der Gattung C o l o p t e r u s (N i t i d u l i d a e) wurden als Bestäuber festgestellt, obwohl auch stachellose Bienen der Gattung T r i g o n a am Ende der Anthese zu den Blütenbesuchern zählen. Die Käfer verbringen, einmal angelockt, die gesamte Blühzeit bis zum Abfallen der Petalen in der Bestäuberkammer und fressen regelmäßig Pollen während der männlichen Phase. Blüten werden während des ganzen Jahres in geringer Zahl produziert. Erst nach einem längeren und von Blüte zu Blüte unterschiedlichen Zeitraum von bis zu neun Monaten nach der Anthese beginnen die Karpelle zur Frucht auszuwachsen. Die Samen werden autochor ausgebreitet.

1. Introduction

The *Annonaceae* family is represented in the Neotropics by about 900 species (CHATROU & al. 2004). Its species diversity is high in tropical lowland rainforests of the New World, where members of *Annonaceae* are often numerous and structurally important in the understory and subcanopy (BURNHAM & JOHNSON 2004). The peculiar pollination biology of the family has received much attention in the last decades, especially in the Neotropics. Protogyny and cantharophily have been recognized as important characteristics (GOTTSBERGER 1970, 1989a, 1989b, SCHATZ 1987, SILBER-

BAUER-GOTTSBERGER & al. 2003), although some genera are pollinated by thrips (GOTTSBERGER 1999, SILBERBAUER-GOTTSBERGER & al. 2003) or bees (CARVALHO & WEBBER 2000, TEICHERT & al. 2008). Thermogenesis and scents consisting of relatively few aliphatic esters ("fruit esters") are important traits (WEBBER 1996, GOTTSBERGER 1999, JÜRGENS & al. 2000), shared with unrelated, beetle-pollinated plants such as in the aroid genus *Philodendron* (GIBERNAU & BARABÉ 2000), or in many *Arecaceae* (KNUDSEN & al. 2001).

Anaxagorea is considered to be the earliest derived extant genus within the family (DOYLE & LE THOMAS 1994, SAUQUET & al. 2003). It shares, among other ancestral characters, inner staminodes and a distinctive laminar stamen morphology with the *Magnoliales* outgroup (SCHARASCHKIN & DOYLE 2006). 22 species are found in Central and South America (MAAS & WESTRA 1984, 1985). Floral biology has been described for a few Neotropical species (WEBBER 1996, ARMSTRONG & MARSH 1997, TEICHERT 2007, 2008). About the most widespread species, *Anaxagorea dolichocarpa*, little is known with that respect (but see MAAS-VAN DE KAMER 1993, TEICHERT 2007). Data on fruit development time have not been published for any species of *Anaxagorea*, although TEICHERT 2008 hypothesized that fruit development of *A. prinoides* is slow and may take up to one year.

2. Materials and Methods

2.1 Study Site and Species

We conducted research on the São José sugarcane plantation (Usina São José S/A, subsequently: USJ) in the municipality of Igarassu, Pernambuco State, northeastern Brazil (07°41'–07°54'S, 34°54'–35°05'W). The USJ property covers an area of 247 km^2 and contains 106 forest fragments with a combined forest cover of 24% and a total area of 66 km^2 (TRINDADE & al. 2008). Surrounding areas are used for sugarcane production. The climate is tropical with a wet season between January and August and a drier season (less than 100 mm per month) between September and December. The mean annual temperature is 25.1 °C and mean precipitation is 1688 mm (meteorological data collected at Usina São José station between 1998 and 2006). The vegetation in the area is lowland rainforest with transition to semideciduous forest (VELOSO & al. 1991).

Anaxagorea dolichocarpa SPRAGUE & SANDWITH (*Annonaceae*) is a small tree of the forest interior, reaching heights up to 10–12 m at the study site. It is widespread in Amazonian, Guianan and East Brazilian humid forests (MAAS & WESTRA 1985). At USJ, the species is most often found near creeks in valleys, but also on steep slopes away from water. Its distribution is patchy and local.

Voucher specimens were deposited at ULM (Botanical Garden and Herbarium, University of Ulm, Germany) and IPA (Instituto Agronômico de Pernambuco, Recife, Brazil).

2.2 Flower Morphology, Breeding System and P/O Ratio

Ten flowers were dissected and the number and position of stamens, staminodes, carpels and ovules was determined. Pollen grains of 20 anthers (two anthers each of

ten flowers) were counted under a stereomicroscope. The mean pollen number per anther was multiplied with mean anther number for total pollen number per flower. P/O ratios were calculated following CRUDEN 1977. Breeding system experiments were carried out by placing fresh pollen on the receptive stigmas of pistillate phase flowers previously bagged with nylon mesh, and subsequently bagging the flower again. Flowers of the same plant individual were used as pollen donor for self-pollination (n=12), and those of trees nearby for outcross pollination (n=18). Fifteen flowers were bagged and excluded from pollinators to test for spontaneous selfing. Fruit set (fruits/flower ratio) was calculated for all treatments.

2.3 Flowering Phenology, Fruit Development and Natural Fruit Set

The number of a n t h e t i c f l o w e r s per tree was assessed for a total of 117 bud-bearing trees on ten survey days between February and December 2008 (one survey per month, except in Oct).

Fruit set from natural pollination was measured by tagging post-anthetic flowers (n=209), between April 2007 and August 2008. Tagged flower carpels were monitored for fruit set once per month until they either aborted or the fruit became ripe. For this purpose, fruit set is here defined as the process from the first visible swelling of carpels to fruit maturation. A distinction was made between i n i t i a l f r u i t s, which had still growing carpels and could be recognized, apart from smaller size, by a reddish to brownish coloration, and m a t u r e - s i z e d f r u i t s, which had stopped growing and had a bright lemon-green coloration. Initial fruits were taken as a measure of pollination success, and mature-sized fruits were used to measure the proportion that progressed through fruit ripening. On each survey, carpels were counted on initial and mature-sized fruits.

2.4 Anthesis, Thermogenesis and Flower Visitors

Fifteen flowers were observed to determine the important stages of anthesis: the first opening of slits between petals, beginning and end of scent production, stigma receptivity, pollen release, and dropping of petals. Flower visitors and their behavior were recorded on these flowers as well. Thermogenic activity was measured in five flowers from beginning to end of anthesis using a digital data logger and a thermocouple thermometer (Bioblock Scientific 16200, Illkirch, France). One simultaneous recording of flower and ambient temperature was taken every 10 min. Flower and ambient sensors were fully cross-calibrated to ensure data consistency. The flower sensor was placed in the tissue of one of the inner petals. All sensors were located permanently in natural forest shade.

3. Results

3.1 Flower Morphology and Breeding System

Flowers are produced on trunks and branches. They possess three leathery sepals, 7–9 mm long, and two whorls of cream-colored petals that are notably thick and fleshy (Fig. 1). All petals have a bright pinkish to scarlet spot at their inner bases. The outer petals (13–14 mm long, 6.6–8.7 mm wide) are longer and wider than the inner petals (11.3–12.5 mm
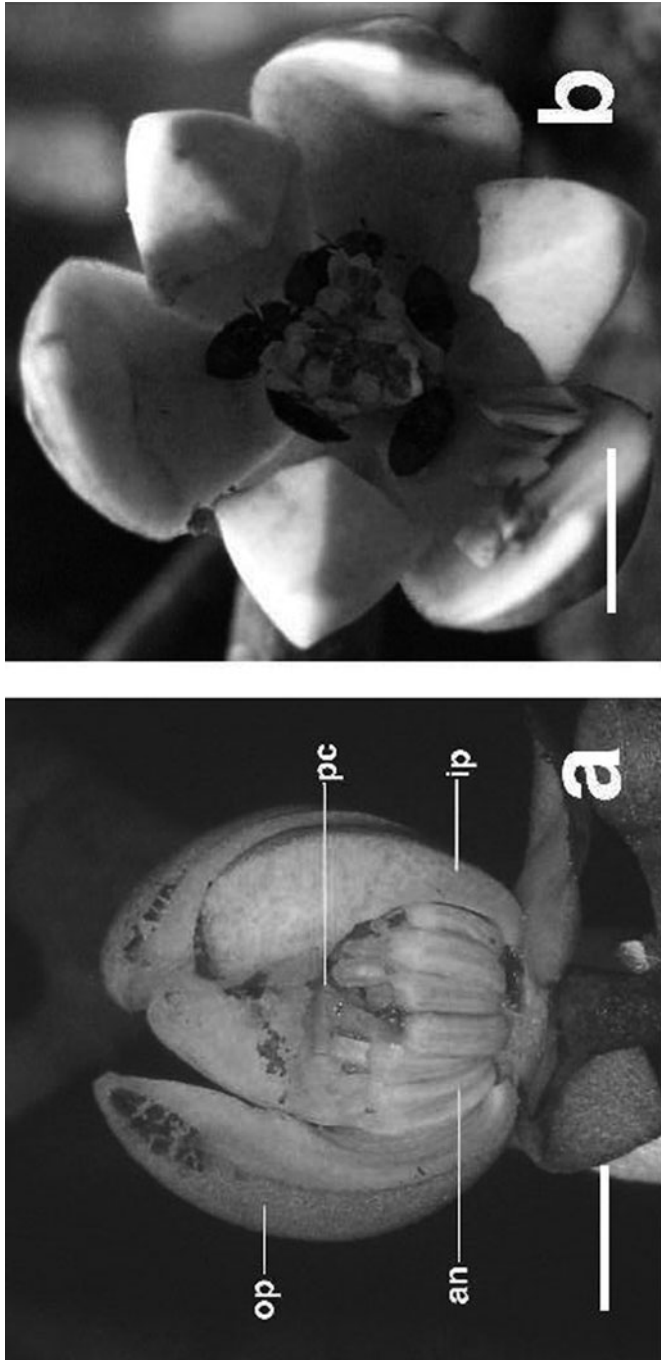
Fig. 1. Flower of *Anaxagorea dolichocarpa*. – a Carpellate phase (two petals removed). – **op** outer petal **ip** inner petal **an** anther **pc** pollination chamber: – b Staminate phase near end of anthesis with opened petals and C o l o p t e r u s spp. ingesting pollen grains. – Note persisting staminodes that partly cover the stigmatic plate. – Scale bars = 5 mm.

long, 5.8–6.4 mm wide). The inner petals are thickest distally, almost triangular in top view, and recess near their bases to form a cavity. This space is almost entirely filled with the numerous tightly-packed reproductive organs, consisting of a flat helix of 33 to 45 fertile, laminar stamens (4.5–5.5 mm long), 12–18 staminodes and 9–15 (–21) free carpels in a triangular ensemble of two whorls. The narrow space (2–3 mm) left between petals and reproductive organs forms a "pollination chamber", access to which is restricted by small gaps between the petals. The truncate stamens have extrorse anthers completely embedded within a laminar, tongue-shaped connective with an outward-bent apex. Carpels are short (5.0–5.5 mm), cylindrical, with one sessile stigma and two marginal ovules.

Flowers produce between 3200 and 7500 pollen grains (mean 4628; SD 1439) and a mean of 26.2 ovules (SD 6.6). The mean P/O ratio per flower was 184.6 (SD 33.8). Flowers are self-compatible, but need insects for pollen transfer (Table 1). The mean natural fruit set (fruits/flower ratio) was 31.1% for initiated and 15.3% for mature fruits. Initial fruit set was almost twice as high in both hand-pollination treatments, while mature fruit set through hand-pollination was only slightly higher than natural (Table 1). More than half of all fruits set following hand pollination experiments aborted.

Table 1. Fruit production of *Anaxagorea dolichocarpa* following pollination treatments. Bagged flowers: spontaneous self-pollination; self pollination conducted with pollen from neighboring flowers of the same tree; natural fruit set from flowers tagged in 2007 and 2008. N = number of flowers

Treatment	N	Initial fruits N (%)	Carpels mean $\pm$ SD	Mature fruits n (%)	Carpels mean $\pm$ SD
Bagged flowers	15	0	–	0	–
Manual self-pollination	12	7 (58.3)	4.3 $\pm$ 3.6	2 (16.7)	5.5
Manual outcross pollination	18	11 (61.1)	8.0 $\pm$ 3.5	4 (22.2)	4.8 $\pm$ 3.1
Natural fruit set	209	66 (31.6)	7.6 $\pm$ 4.1	32 (15.3)	3.2 $\pm$ 2.6

3.2 Anthesis and Flower Visitors

Anthesis is well-synchronized among flowers of different trees. Flowers are protogynous, with a long c a r p e l l a t e p h a s e and a short pollen-dispersing phase (Fig. 2). Anthesis spans two days: The petals open just slightly to narrow slits in the early morning. Emission of a fruity, banana-like odor starts between 14.00 h and 15.00 h, and lasts into the early evening hours. Odor is most intense between 16.00 and 18.00 h. The stigmas are covered with a gelatinous, translucent exudate. Scent emission lasts until 19.00–23.00 h. The pollinator attraction phase therefore lasts 4–9 h.

In this phase, three morphospecies of small (1–3 mm) beetles (Colopterus: Nitidulidae) were commonly and exclusively observed alighting on petals and entering the floral chamber, where they remain throughout anthesis. On the next morning the stigmatic exudate assumes a reddish color and slowly dries up, forming a dry plug on each stigma at 10.00–11.00 h. This ends the carpellate phase. The staminate phase begins with the release of pollen at 12.00–13.00 h. At the same time, the staminal connectives assume a reddish coloration. On some occasions, start of pollen release was somewhat earlier or later, but never overlapped the carpellate phase of the same flower. Between 13.00 h and 14.00 h scent emission starts accompanying the staminate phase, this time with a slightly more acrid, acetone-like note compared to the carpellate phase. Staminate phase flowers therefore start scent emission somewhat earlier than the carpellate phase flowers in the population. Nevertheless, the scented staminate flowers overlap the scent emission of the same days' new, carpellate flowers. The end of anthesis begins between 14.45 h and 15.45 h with the complete opening of the petals, a process that lasts c. 10 minutes. At this point the inner staminodes, hidden between the anthers and the carpels before pollen release, often lengthen and are bent over the stigmatic surface. Beetles commonly feed on pollen, but no feeding signs on petals and other flower organs were noticed. Beetles leaving the flowers are regularly covered with pollen on all body parts.

At the end of anthesis, while the petals spread, other flower visitors arrive: pollen collecting bees (Trigona cf. spinipes) and undetermined fruit flies, which make oviposition movements on the inner petals. Both play no role in pollination, since carpels were no longer receptive at that time. 20-30 minutes after opening the petals fall off in quick succession. The carpels remain in place, but unfertilized ones are abscised within one week.

Flower temperatures are above ambient temperatures during the first hours of the carpellate phase and the later stage of the staminate phase until petal spreading (Fig. 2). Thermogenesis lasts between 160 and 250 minutes in the carpellate phase, beginning 14.30–14.50 h, peaking 15.00–17.00 h and ending 17.10–19.00 h. In the staminate phase the duration is between 50 and 110 min, starting 13.30–14.50 h and ending 15.00–15.45 h. Mean and maximum peak differences between flower and ambient temperature are 3.5 °C (SD 0.3) and 3.8 °C, respectively, in the carpellate phase, and 2.4 °C (SD 1.1) and 3.7 °C in the staminate phase. In both phases an active increase of flower temperature was observed, but differences were also produced by falling ambient temperatures. Flower heating coincided with the beginning of scent production in both phases, scent being emitted for at least one hour longer than thermogenesis in the carpellate phase.

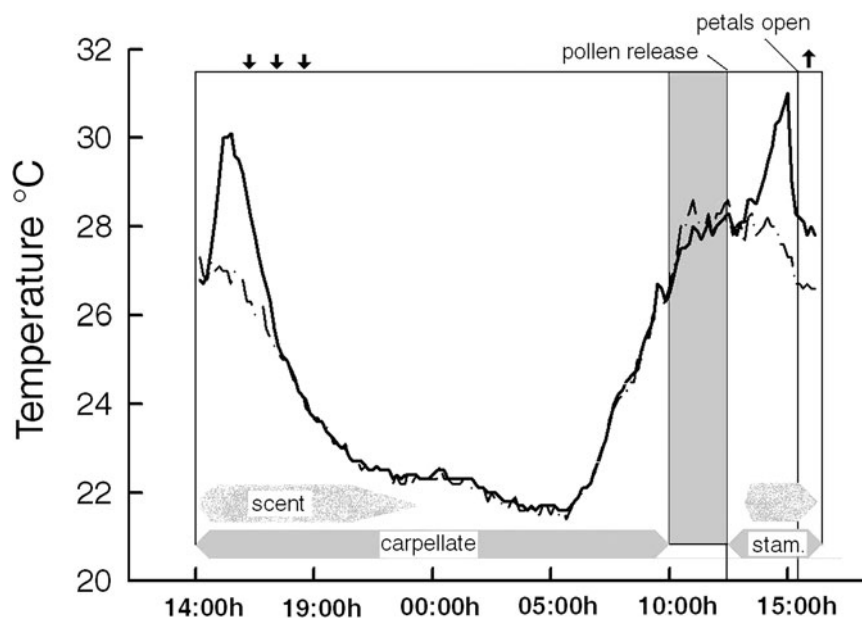For floral scent characteristics see JÜRGENS & al. 2000.

Fig. 2. Scent production, presence of beetles and thermogenesis during anthesis of *Anaxagorea dolichocarpa* (Nov 25–26, 2008). – Black line: flower temperature; dotted line: ambient temperature. – Arrows down: beetles arrive; arrow up: beetles leave. Gray bar denotes interim phase. Time (hours) given on X-axis.

3.3 Flowering Phenology

Buds and anthetic flowers were found at all times of the year. We counted a total of 192 flowers (carpellate and staminate) on 117 trees over 10 sampling dates. During the 10 days in 86 cases observations could not be made. Thus, instead of the theoretical 1170 observations only 1084 were realized. This corresponds to a mean of 0.18 flowers per observed tree and day. 13% of trees (15 trees) had one or more open flowers on any survey day. Of these, 21.5% (3 trees) had more than one anthetic flower on all survey days. The maximum number of simultaneous flowers per tree was five. Carpellate and staminate phase flowers were frequently observed together on the same tree. In average of the 10 days, 87% of the trees were found without flowers.

3.4 Interval Between Anthesis and Beginning Carpel Growth, Fruit Development Time, Seed Dispersal

In successfully pollinated flowers, there is always a time interval between anthesis and the beginning of carpel swelling, during which the carpels remain outwardly unchanged. This interval is variable among

flowers, lasting mostly between 3 and 6 months, but with extremes ranging from 1 to 9 months (Fig. 3a). The variability shows no seasonal pattern, i. e., at any time of the year, the interval of a given flower before fruit initiation is unpredictable (Fig. 3b). Then the carpels start swelling, and grow slowly at a rate of about 1 cm per week for 4–5 weeks, until reaching their final size (4–5 cm carpel length). At this point, carpels change color from reddish-brown to bright lemon green. They now remain without visible change for another 6-10 weeks before the ripe seeds are dispersed. The period from the first swelling of carpels to the release of seeds thus lasts for a total of 10–15 weeks. The total time span from anthesis to seed dispersal is between 7 and 10 months for most flowers, and could extend up to 13 months, depending on the delay between anthesis and the beginning of fruit growth. The mean carpel number of naturally pollinated, ripe fruits was 3.2 (SD 2.6; Table 1) and ranged from 1 to 15 (exceptionally 20). Seeds are dispersed by an autochorous mechanism. The process could be observed with ripe fruits (with leathery walls, opening at the ventral suture), which eject both seeds of a carpel simultaneously with high speed, and up to a distance of c. 5 m.

4. Discussion

Anaxagorea dolichocarpa has a specialized pollination system with nitidulid beetles as the only pollinating agents. Flowers display traits typical of beetle pollination, such as protogyny, fruity scent during both sexual phases, and a high degree of synchronization between flowers (e.g., SCHATZ 1987, GOTTSBERGER 1989a, 1989b, 1999, WEBBER 1996). Thermogenesis has been documented for several *Anaxagorea* species (KÜCHMEISTER & al. 1998, JÜRGENS & al. 2000, but see TEICHERT 2008). The timing of thermogenesis in *A. dolichocarpa* corresponds well with the timing of scent production, which is also the case in *Anaxagorea brevipes* and *Xylopia benthamii* (JÜRGENS & al. 2000). Peak thermogenesis coincides with the main pollinator attraction phase, but subsides soon afterwards. Flowers do not display elevated temperatures during most of the time spent by pollinators in the floral chamber. In contrast to our findings, flowers can maintain elevated temperatures over a much longer period during anthesis (RATNAYAKE & al. 2006, 2007), or even thermoregulate at a certain temperature for extended periods (SEYMOUR & GIBERNAU 2008). Thermogenesis has therefore been interpreted as a heat reward to pollinators, enhancing their activity (AZUMA & al. 1999, SEYMOUR & al. 2003). We suggest that thermogenesis in *A. dolichocarpa* may primarily serve pollinator attraction by enhancing scent emission through a "funnel effect". However, elevated temperatures during the staminate phase may also stimulate beetle flight activity and therefore serve as a heat reward as well.
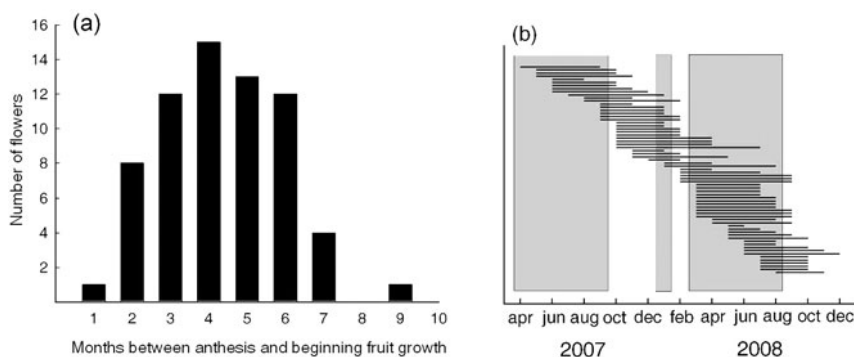
Fig. 3. Time intervals (in months) between anthesis and subsequent beginning of carpel swelling in 66 flowers of *Anaxagorea dolichocarpa*. – a Frequency distribution of flowers. – b Phenology between April 2007 and December 2008. Each horizontal bar denotes the interval between anthesis and beginning carpel swelling of a single flower. – Gray-shaded months had more than 100 mm rainfall.

Flowers display effective dichogamy, with virtually no incidence of self-pollination. Staminodes elongate and cover the stigmas at the end of the carpellate phase in several *Anaxagorea* spp. (MAAS-VAN DE KAMER 1993, WEBBER 1996). They may therefore act as a physical barrier to pollen transfer at the end of the carpellate phase (SAUNDERS 2010). Our observations were not consistent with this view, since staminodes do not elongate before pollen release. They do, however, provide some physical protection for the stigmatic surface against large flower visitors like pollen-robbing Trigona bees when the petals opened at the end of anthesis. Effective dichogamy is instead achieved through a strict temporal separation of the carpellate and staminate phases. Interestingly, we observed a much shorter duration of the staminate phase than MAAS-VAN DE KAMER 1993 in Guyana, where flowers released pollen several hours earlier than in the present study.

Trees display continuous flowering (GENTRY 1974, NEWSTROM & al. 1994) and produce few flowers at a time. A much higher flowering intensity was reported for *Anaxagorea crassipetala* (ARMSTRONG & MARSH 1997) and *A. prinoides* (TEICHERT 2008), both with a distinct flowering season. Flowers are unable to self-fertilize, but geitonogamous self-pollination is possible in self-compatible *A. dolichocarpa*. However, the low flowering intensity should result in high outcrossing rates, since in most cases pollinators will have to fly to another plant to find a new flower. In some *Annonaceae*, the same is achieved by heterodichogamy (WESTER 1910, TEICHERT 2008). Pollen flow is the main agent of gene flow in self-dispersing plants, and few flowers at a time can promote "overdispersal" of pollen (STACY & al. 1996) and thus prevent genetic structuring by self- and

near-neighbor pollination. The low P/O ratio is surprising in this context, as it suggests a higher rate of self-pollination (CRUDEN 1977). It may indicate that relatively small amounts of pollen are wasted during the pollination process.

Fruit set is often pollen-limited in animal-pollinated plants (BURD 1994). In this study, hand-pollinated flowers initiated more fruits than naturally pollinated ones, but did not produce more ripe fruits. Generally, many fruits were aborted during ripening, which indicates that *A. dolichocarpa* is probably resource- rather than pollen-limited at our study site.

Fruit production in *Annonaceae* can be a slow process (COATES-ESTRADA & ESTRADA 1988). We confirmed a long fruit maturation period for *A. dolichocarpa*. However, the highly variable interval between flowering and the beginning of carpel swelling among different flowers was surprising. This variation apparently did not lead to synchronized fruit maturation. Possibly, these time differences between flowering and fruiting are rooted in different physiological conditions of trees, some of which may have been able to start fruit growth earlier than others.

5. Acknowledgments

6. References

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