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ASPECTS OF THE FLORAL AND FRUIT BIOLOGY OF *ALLANBLACKIA STUHLMANNII* (CLUSIACEAE), AN ENDEMIC TANZANIAN TREE

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ABSTRACT

Various economically important tropical tree species are not well known biologically. We studied the floral and fruit biology of *Allanblackia stuhlmannii* (Clusiaceae), a dioecious tree species endemic to the Eastern Arc Mountains of Tanzania and Kenya that has become the subject of recent interest by the food industry because of the edible oil that can be extracted from the seeds. We characterised qualitative and quantitative similarities and differences between male and female flowers, the flowering and fruiting phenology, and examined the relationship between fruit crop production and tree size, seeds per fruit, and seed number as a function of fruit mass. There was no significant difference in sugar concentration of nectar between male and female flowers, but male flowers contained significantly more nectar than female flowers. Male trees had larger flowering displays with a tendency for the population to mast profusely between January and March, which coincided with the peak fruiting period. The fruiting period was pronounced from January to March, which appeared to be preceded by a smaller peak in October. Fruit crop was strongly related to tree size, with mean seed number per fruit being 38. Seed quantity per fruit showed a

trend to increase with fruit mass, but this relationship was not significant. General physical resemblance of female flowers to male flowers, the latter of which offer multiple floral cues to attract pollinators, suggests a pollination-by-deceit strategy. Our results provide important insights on the natural history of this tree species and carry implications for its future use.

Keywords: dioecious, economic species, flower, fruit, masting, pollination

INTRODUCTION

Knowledge about the various components of plant reproduction, such as flowering and fruiting, is essential in order to understand a plant's breeding characteristics. Such basic information is, however, scant for many African trees that are of high economic potential (Rodger *et al.*, 2004). Specific information such as flowering and fruiting patterns, nectar volumes, sugar concentration of nectar, and pollen quantity in flowers is often absent. Information on reproductive outputs such as fruit crop sizes and number of seeds per fruit is also poorly documented, but is needed to understand how to promote forest regeneration, restoration and domestication in tropical ecosystems threatened by agricultural expansion and other developments.

In sub-Saharan Africa, a number of native forest tree species of economic importance are dioecious and this poses particular challenges for management, which requires investigation of reproductive strategies and regeneration potential. Dioecious trees are more common in the tropics than in temperate regions (Bawa, 1974; Bawa & Opler, 1975; Bawa, 1980a) and require pollination between individual trees of opposite sexes through wind or animal dispersal (Bawa & Opler, 1975; Bawa, 1980a; Renner & Ricklefs, 1995; Osunkoya, 1999). Whereas staminate (male) flowers provide pollen and nectar to pollinators, pistillate (female) flowers often have only nectar as a reward (Bawa, 1983; Lloyd & Bawa, 1984). Dissimilar rewards offered by flowers of different sexes may affect pollinator visitation and thus influence patterns of reproduction (Bawa, 1980b; Farwig *et al.*, 2004). Such knowledge on African species is poor but badly needed, especially for species of economic and conservation importance. Here, we describe aspects on the flower and fruit biology of *Allanblackia stuhlmannii* (Engl.) Engl. (Clusiaceae), a dioecious tree species endemic to the Eastern Arc Mountains of Tanzania, and part of a genus consisting of about ten species occurring in the humid forests of Africa, from Tanzania to the DR Congo and into Ghana, Gabon, Nigeria and Cameroon (Hutchinson *et al.*, 1954; Bamps, 1969; Cable & Cheek, 1998). Currently, the species is listed as "Vulnerable" on the IUCN Red List (IUCN, 2007) because of its restricted distribution and human threats to the forest in which it is found.

The seed of *A. stuhlmannii* yields an oil used for centuries by local inhabitants for food and soap production and that was adopted during World War I as an alternative edible fat to butter by German soldiers in the region (Williamson, 1975; Bamps *et al.*, 1978; Saka, 1995; Monela *et al.*, 2001; Osemeobo, 2005). Recently, there has been increased interest in turning *A. stuhlmannii* into a significant commercial species for edible oil production in global food markets (Amanor *et al.*, 2003). However, little is known about the biology of the species that can help guide its conservation management in forest and when cultivated in farmland. In the present study, we therefore investigated flower and fruit biology to (i) identify qualitative and quantitative similarities or differences between flowers of both sexes; and (ii) quantify the

reproductive output expressed as fruit and seed crops. As part of examining flower biology, we examined the phenomenon of masting, which is when a majority of individuals from a population flower or fruit at the same time.

MATERIALS AND METHODS

Study site

Amani Nature Reserve (ANR) comprises 8380 ha of lowland to submontane forest in the southern part of the East Usambara Mountains (4°48'-5°13'S, 38°32-48'E) of north-eastern Tanzania. These mountains are considered to be one of the most important forests for biodiversity in Africa, with at least 3450 species of vascular plants recorded, one quarter of which are endemic or near-endemic, and many of which are threatened by human activity (Iversen, 1991; Burgess *et al.*, 2007; Gereau e*t al.*, 2008). There are several dominant tree species in the submontane forest canopy, including *A. stuhlmannii*. The climate and vegetation of the region is generally influenced by the close proximity to the Indian Ocean. Mean annual rainfall is 1918 mm at Amani (and up to 2262 mm at nearby Kwamkoro), and is generally sustained throughout the year by constant flow of moist currents from the nearby Indian Ocean (Hamilton & Bensted-Smith, 1989). Humidity is high and mean annual temperature at Amani is 20.6 °C (Hamilton, 1989).

Background on flowers and fruits of the study species

Dioecious *Allanblackia stuhlmannii* reaches 45-50 m in height, often with a clear bole to 9 m (Brenan & Greenway, 1949), and a mean ($\pm$ SD) crown radius of 5.9 $\pm$ 1.7 m for forest-dwelling trees (n = 24 trees, Cordeiro & Ndangalasi, unpublished data). The bark is dark grey-brown and yields a clear exudate when slashed (Schulman *et al.*, 1998). Female and male flowers are large and succulent, grow singly in the axils and have 6-8 cm long pedicels (plate 1); male flowers may be crowded at ends of shoots with short internodes and appear terminally racemose if leaves have fallen (Bamps *et al.*, 1978) (plate 1). Male flowers have ~3-4 cm long and 2-3 cm wide petals that are rounded or spathulate and creamish in colour, flash scarlet at the base or all scarlet, with anthers covered with yellow pollen grains; sepals are rounded, ovate, and pale yellowish-pink. Staminal bundles are ~2 cm long and wide, 1 cm thick, and generally unequal in length and size, thick and fleshy, and crimson; staminate disc lobes are green. Female flowers have petals up to 2.5 cm long and wide, stamens reduced to a few free with filaments more or less 0.5 cm long, and an ellipsoid or conical ovary that is ~1.5 cm tall. The stigma is peltate, sessile, ~1 cm wide and 0.5 cm high. Fruits are brown or reddish brown and vary considerably in shape and size, but generally they are oblong, tapering cylindric-oblong or subglobose, 16-34 cm long and 15-17 cm in diameter (Bamps *et al.*, 1978; Lovett *et al.*, 2007) (plate 1). According to Bamps *et al.* (1978), fruits weigh 2.5-6.8 kg with 7-28 seeds in each of the 5 locules. The seeds have four obtuse angles, and are ~4 cm long, ~3 cm wide, with one angle consisting of fleshy pulp and a crustaceous testa (plate 1).

Flower development observations

To monitor flower development, five male and five female flowers were tagged on three trees of each sex. Daily records were kept on flower development from mature buds to full opening (for both sexes), on fertilization (in females, when the stigma changes colour after pollen has been intercepted), and on sepal, petal or whole flower falling (again, for both



Plate 1. *Flowers, fruits and seeds of* Allanblackia stuhlmannii *(Clusiaceae) from the East Usambara Mountains, Tanzania. Rotating clockwise starting in the top left hand corner:* ***female tree*** *with fruits at the forest edge (photo: M.R. Munjuga), inset of* ***seeds*** *(photo: N.J. Cordeiro);* ***fruit*** *on ground penetrated by rodent (photo: N.J. Cordeiro);* ***male flowers*** *with yellow pollen loads (photo: H.J. Ndangalasi);* ***female flower, red morph****, fertilised as indicated by blackened stigma with adjacent flower with petals and sepals dropped, and close to early fruit development (photo: N.J. Cordeiro);* ***female flower, white morph****, freshly opened with faint pinkish stigma (photo: N.J. Cordeiro);* ***female flower, red morph****, freshly opened with white stigma, and distinctive scarlet red from base to middle of petals, and clearly visible nectaries at base of corolla (photo: N.J. Cordeiro); and* ***male flowers*** *in buds and just freshly opened (photo: H.J. Ndangalasi).*

sexes). Determination of anthesis, the process of pollen release and viability, was not studied due to logistical difficulties. Because the budding stage (flower development) was intercepted late in the flowering season of January 2007, the length of time that a flower remained in bud is unknown. During these observations we also noted differences in female flowers that suggested the presence of two morphs that we describe.

Determining nectar quantity and sugar concentration

A sample of five male and five female flowers was selected from each of the three different male and female trees subject to observations described above. At dawn (between 6:00 and 7:30 h), all the nectar was drawn from each nectary area of the flower (see plate 1) using graduated micro-syringes (10-50 *cc*) and the volume measured. From the same flowers, the sugar concentration (percentage sucrose) of nectar was measured using a hand-held refractometer (Portable Brix Refractometer, model RHB-32ATC, range concentration 0-32° Brix units); Brix units were converted to g/L (Kearns & Inouye, 1993). The refractometer was cleaned and dried between measurements. Separate nested ANOVA analyses, with flower nested by tree, and tree sex as a factor, were used to test if nectar volume and sugar concentration differed in flowers of the two sexes (SYSTAT version 8.0, SAS Institute, Inc.).

Measuring pollen quantity

Pollen was counted for three flowers each collected from five different trees. Each flower was collected just upon opening and stored in 70% ethanol. Digital images were taken from different aspects, and pollen grains were observed on entire anthers based on composite images using the counter programme in ImageJ (Rasband, 2008). Each aspect of an anther was carefully delineated on a composite image to reduce errors of double counting; such errors were likely minimal given the size and distinctiveness of the pollen grains. Average pollen grain numbers per flower per tree were compared using 95% confidence intervals.

Flower and fruit phenology

Flowering and fruiting phenology of 29 marked female trees of reproductive size was tracked on a monthly basis from January to December 2006. For each tree, we recorded whether flower buds and/or flowers and immature and/or ripe fruits were evident, and distinguished trees in the analyses as those that showed signs of only flowering, only fruiting, and synchronously fruiting and flowering on a monthly basis. Data from March 2006 was not recorded and analyzed.

To gauge masting in the population, where many individuals within a population flower (male/female) or fruit (female) in the same period, we used data collected from a separate study undertaken from January to March 2006 (Cordeiro & Ndangalasi, unpublished data). In this study, 45 randomly located vegetation plots of 200 x 50 m were used to sample *A. stuhlmannii* trees in the extensive and continuous forest of Amani Nature Reserve, forest fragments surrounded by tea plantations, and cultivated or semi-abandoned land surrounding the forest. Trees were identified based on flowering (males/females) or fruiting (females), and where sex could not be determined in this particular flowering/fruiting season, trees were categorised as "sex unknown". We also used our collective qualitative observations on masting over the last nine years.

To identify the minimum tree size for flowering or fruiting to be observed, data were collected systematically and opportunistically on tree size by measuring the diameter at breast

height (DBH) of reproductive individuals. Data are summarized here and will be reported elsewhere as part of a broader ecological study (Cordeiro *et al.*, in prep.).

Characterising fruit and seed production

We weighed 48 ripe fruit (whole mass) from 26 different trees from seven widely distributed sites in and around ANR in March 2006. All seeds that appeared viable based on relative weight and feel were then removed from each fruit, counted, cleaned and weighed. Data collected from fruit of 20 trees during February 2000 were additionally used. Overall fruit production was estimated by counting all fruit on 15 trees from each of five widely distributed sites in ANR (total sample size = 79, one site with 19 trees). Total fruit counts were made in December 2005 just before fruit fall between late December and early April 2006. Fruit crop size was regressed with tree size, where size referred to DBH^2.

RESULTS

Flower development

Male and female flowers open gradually, mostly at night, starting with slight opening on the first day and then full opening by the second to third day. The life span of individual male flowers is two weeks from bud maturation to abscission. After fully opening, the male flowers remain so for three to eight days before dropping (median = 5.5 days), wilting one to two days before dropping. Male trees flower for about three months, from late December to well into March. After the budding stage, female flowers remain open for seven to 14 days before dropping. Sepals drop first and then petals: flower abscission can extend for an additional seven days.

Two female flower colour morphs occur, a red-coloured and a white-coloured morph (plate 1), growing on separate trees. The red-coloured morph has flash scarlet at the base extending toward the middle of petals; the white morph is sometimes faintly tinged with pink at the base of the petals, but often lacks this colouration (plate 1). The red-flowered morph has a pink ovary, which turns brown on shedding the petals and sepals; the white-flowered morph has a yellowish-green ovary that initially turns green on shedding the sepals and petals, but later turns brown.

Nectar quantity and sugar concentration

Male flowers had significantly more nectar than female flowers ($F_{1,8} = 26.38$, $p < 0.001$; mean $\pm$ SE: male flowers 1.15 $\pm$ 0.09 ml; female flowers: 0.4 $\pm$ 0.05 ml; figure 1A). Sugar concentration did not differ significantly between the two sexes ($F_{1,8} = 3.39$, $p = 0.09$; mean $\pm$ SE: male flowers 92.22 $\pm$ 7.46 g/L; female flowers: 67.07 $\pm$ 6.28 g/L, figure 1B). In analyses for both nectar volume and sugar concentration, the effect of tree was not significant (nectar volume: $F_{8,20} = 1.64$, $p = 0.18$; sugar concentration: $F_{8,20} = 2.00$, $p = 0.10$).

Pollen quantity

The overall mean ($\pm$ SD) number of pollen grains per flower was 1686 $\pm$ 479 (range 805-2380) in the 15 trees studied. Visual inspection of 95% confidence intervals showed an overlap that indicated that the mean number of pollen grains per flower did not differ significantly between trees (figure 2).

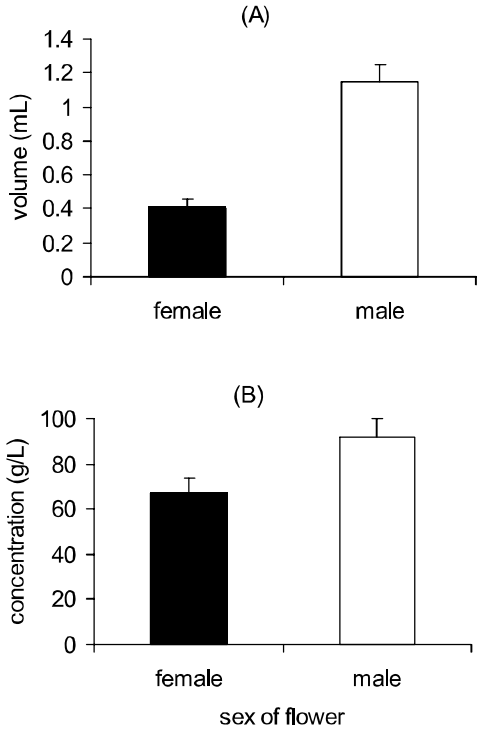


Figure 1. Volume of nectar (A) and sugar concentration (B) in male and female flowers of Allanblackia stuhlmannii *(Clusiaceae) in Amani Nature Reserve.*

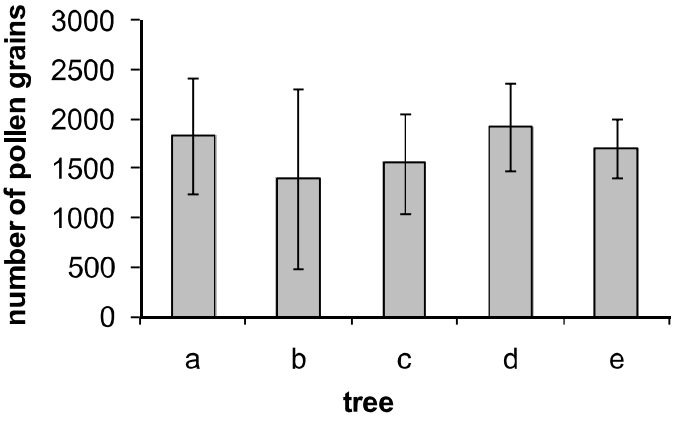


Figure 2. Number of pollen grains in male flowers at five trees of *Allanblackia stuhlmannii* (Clusiaceae) in Amani Nature Reserve. Each tree is coded by a different letter.

Flower and fruit phenology

Of the 29 female trees observed in 2006, flowering and fruiting patterns were generally comparable (figure 3). The presence of flower buds and flowers peaked in the hot season (January to February), and declined until July with a small peak in August and September. During November and December, fewer trees had mature flowers but the proportion of trees with flower buds increased (figure 3). Fruiting and flowering trends were generally similar from January to August, but the proportion of trees with immature fruits declined as ripe fruits steadily increased from September to December (figure 3).

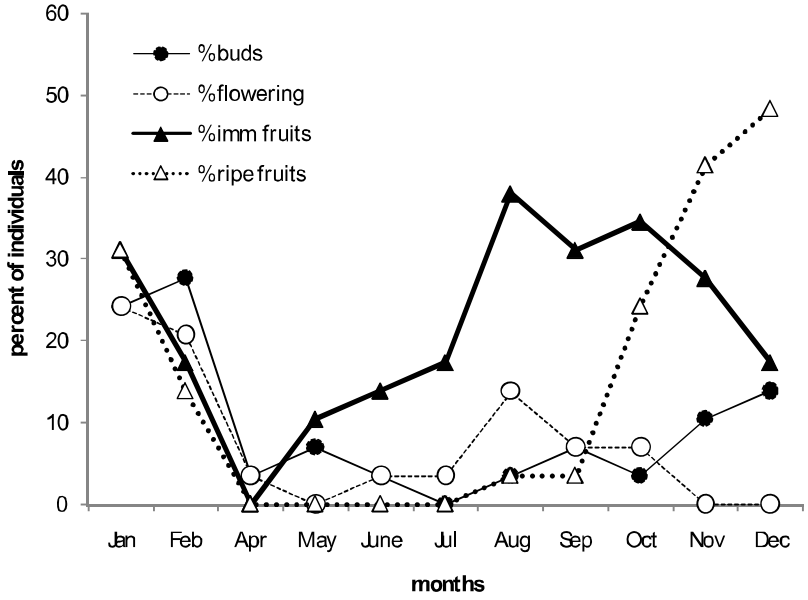


Figure 3. Phenology of flowering and fruiting of female Allanblackia stuhlmannii *(Clusiaceae) trees in Amani Nature Reserve. Data are from 29 marked trees followed monthly between January and December 2006.*

Slightly more than half of the 29 female trees were not reproductively active in the first few months of the year. Many of these trees also had no evidence of flowering or fruiting until August or September, and by November and December, 21 trees were reproductively active (figure 4). Some trees showed evidence of reproduction over at least two successive seasons whereas others did not: of the 14 that fruited in the previous season (January 2006 counts as the 2005/2006 season), only seven re-fruited in the 2006/2007 season, together with a further 14 new trees. These patterns are evident in the evaluation of reproductive effort, where proportionately more trees fruited and flowered synchronously in January and February 2006 than in the following season (November to December 2006). Few trees were observed as only flowering and not fruiting throughout the year, whereas many more trees fruited and did not show signs of synchronous flowering later in the year (figure 4).

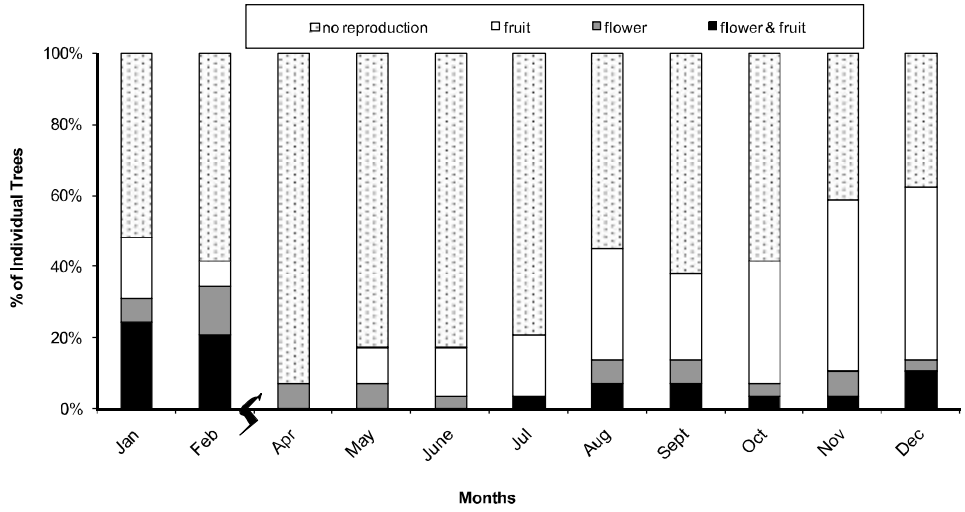


Figure 4. Percentage of female trees of Allanblackia stuhlmannii *(Clusiaceae) observed as flowering only, fruiting only or synchronously flowering and fruiting in Amani Nature Reserve. Data is from 29 marked trees followed monthly between January and December 2006.*

The period of December 2005 into March 2006 was a period of ripe fruit fall and flowering for male and female trees. Of 399 mature trees (*i.e.* $\geq$ 30 cm DBH) sampled in 45 vegetation plots in farmland, forest and forest fragments during this period, about a two-thirds of these were male flowering (n = 148) or female flowering/fruiting (n = 118) trees, and the remaining third were trees of reproductive size categorised as "sex unknown" (n = 133) as they showed no evidence of fruiting or flowering. Qualitative observations made between 2000 and 2009 reveal that male trees mast extensively in some years with hundreds to a few thousand flowers per tree, whereas female trees have at most 100 to 500 flowers per tree (pers. obs.).

Most trees demonstrate reproductive maturity at or above 30 cm DBH; however, based on our observations a few trees with smaller girths have been observed to produce flowers or fruits in cultivation on farms (as little as 26.9 cm DBH), and in forest fragments (as low as 24.9 cm DBH). Others have reported that trees as small as 7 m tall with a DBH of 21.4 cm and even down to 15 cm DBH can bear flowers and fruit (pers. obs.; H. Hendrickx, pers. comm.).

Fruit and seed production

In general, fruit production of forest dwelling trees showed a strong positive relationship with tree size (*i.e.* DBH^2) (figure 5). The total number of seeds per fruit varied from 14 to 90, with a similar mean (38) and median (37, n = 48) (2006 observations). Preliminary data obtained from 20 trees during the February 2000 fruiting season gave similar results, with a mean ($\pm$ SE) of 36 $\pm$ 2.0 and median of 35. A regression of the number of seeds (wet weight, g) per fruit with fruit weight (wet weight, kg) demonstrated a strong positive trend (figure 6). The range of wet seed weight of 1839 freshly collected seeds was 3.2 to 25.1 g, with a comparable median (11.2 g) and mean (11.24 $\pm$ 0.08 g).

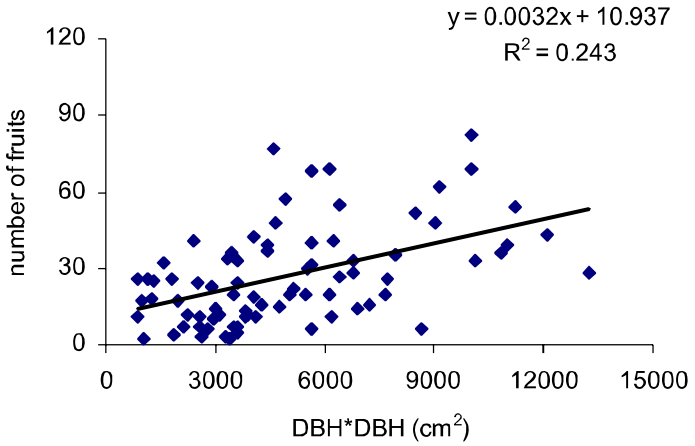


*Figure 5. Positive relationship between tree size (DBH*DBH) and number of fruits for trees in the forest at Amani Nature Reserve.*

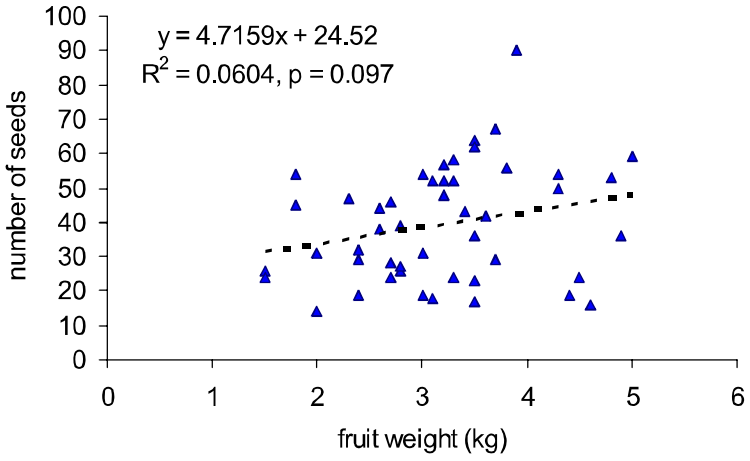


Figure 6. Relationship between fruit weight and number of seeds per fruit. A marginal relationship between fruit weight and number of seeds per fruit is evident.

DISCUSSION

Male and female flowers of *A. stuhlmannii* exhibit some similarities, such as in flower colouration and size, but there are several qualitative and quantitive differences between them that are consistent with current theory and supporting empirical evidence about breeding strategies of dioecious species (Bawa, 1983; Mayer & Charlesworth, 1991). For example,

one would expect female flowers with few ovules per flower, compared to the high number of pollen grains per flower, to invest more in attracting pollinators in this dioecious system. This is not the case with *A. stuhlmannii* where even though sugar concentration was similar between male and female flowers, male flowers have significantly more nectar. In a review on the pollination systems of dioecious tropical tree species, Renner & Feil (1993) found that almost a third of 40 well-studied species had no nectar rewards in female flowers; in species that have nectar in both sexes of flowers, males tend to have significantly more than females (*e.g.* Bawa & Opler, 1975). Renner & Feil (1993) further found that species which lacked rewards in female flowers exhibited "mistake" pollination (*sensu* Baker, 1976) or pollination by deceit, where the female flower resembles the male flower but offers only a small nectar reward or none at all. Without further study we can only speculate that the pollination strategy for *A. stuhlmannii* may be by deceit. Male and female flowers do not appear to differ significantly in colouration, brightness and size to the human eye (plate 1). In order for the pollinators to be deceived and female flowers to be fertilised, floral cues would need to be sufficiently attractive to guarantee that even brief pollinator visits deliver pollen to stigmas. Coupled with production of many male compared to fewer female flowers per tree, typical of many dioecious species (Delph *et al.*, 1996), resemblance of female to male flowers that exhibit high or predictable rewards might deceive pollinators into visiting them.

Male *A. stuhlmannii* trees probably increase their attractiveness to pollinators by using multiple rewards. In dioecious species, a number of studies have revealed greater visitation rates by pollinators to male than female flowers (Bawa, 1980b; Ågren *et al.*, 1986; Charlesworth, 1993; Vamosi & Otto, 2002; Farwig *et al.*, 2004). A combination of masting in male trees that have relatively high numbers of flowers advertising both pollen grains and a provision of high amounts of nectar per flower, may be a strategy to enhance pollination by attracting either a high diversity of pollinator species or large numbers of a specific pollinator species or guild. Masting in *A. stuhlmannii*, where a large proportion of the population displays numerous, bright red flowers, is predictable yearly between January and March (pers. obs.). Massive flowering events over a relatively short period attract numerous animals, such as Sykes' Monkey *Cercopithecus mitis* (Sykes), small-eared greater galago *Otolemur garnetti* Ogilby, birds (particularly sunbirds), moths, bees, wasps, flies, beetles and other insects, fruit bats and lizards. Without a detailed study of flower visitors and the pollination biology of *A. stuhlmannii*, it is difficult to determine which animal taxa are actual pollinators. The large and ornamental flower structure, and the positioning of the nectaries (plate 1), suggest that large insects, birds and bats are most likely involved; smaller insects are probably nectar robbers rather than effective pollinators. Nonetheless, because *A. stuhlmannii* trees of different sex are on average spaced between 10 and 20 m apart in natural forest (pers. obs.), during peak flowering in male trees, a high frequency of foraging pollinators moving between male trees may therefore guarantee sufficient 'accidental' visits to female flowers.

In addition to the apparent deceptive pollination strategy, the flower and fruit phenology of *A. stuhlmannii* is also unusual because of synchronous fruiting and flowering among individuals. Preliminary results show that flowering and fruiting was high in January and February, and then low until September, when both were high again as the next reproductive season approached. Synchronous flowering and fruiting was observed in a larger proportion of individuals in the January-February 2006 period as compared to the subsequent fruiting period (November-December 2006), but this is likely an artefact of observations not continuing past December 2006, when many fruits would have fallen and flowers start forming and opening on different branches of the same tree. Mugasha (1980) first reported

synchronous flowering and fruiting in *A. stuhlmannii* and suggested that the period from fertilisation to mature fruit fall was about one year. In our study, the number of mature fruits appeared high from June to September, probably because we recorded fruits as mature based on size, and did not account for when they actually fell as ripened fruits. This is more clearly depicted from October to December, when immature fruits decline and mature fruits increase, reflecting the maturation of the immature fruits. However, the peak in August may indeed be real for a small proportion of fruiting trees, particular those whose mature fruits ripened in November-December and then produced flowers which were subsequently fertilised. This observation may be key to the possibility of bimodal fruit seasons, with peak fruiting of a larger proportion of the population occurring between late December into March of the following year, and a subsequent smaller proportion of individuals fruiting in October as described by local villagers (pers. comm.). Certainly, tropical forest trees exhibit a wide range of fruiting patterns, including unimodal or bimodal flower and fruiting peaks (Zhang & Wang, 1995; Kinnaird, 1992; Hamann, 2004), but we do not yet have sufficient quantitative data to show how and if the bimodal fruiting peaks is valid, and if so, if this is consistent among years.

In summary, the results from this study provide a basic understanding of the flower and fruit biology of a tree species endemic to the Eastern Arc Mountains for which very little information is available. Our results and observations point to some similarities in flower resemblance and sugar concentration of nectar between flowers sexes, and moreover, clear differences in nectar amount and flower abundance between male and female trees. The resemblance of male and female flowers and the higher rewards in male than female flowers suggest a deceptive pollination strategy. Further observations and experiments on the pollination biology will be necessary to test the deceptive pollination hypothesis and to improve upon our current understanding of flower differences. For example, while sugar concentration showed a trend for being higher in male than in female flowers, bagging flowers to exclude animal visitors would control for increased nectar removal which may alter sugar concentration (Ordano & Ornelas, 2004). Our current data suggest that the fruiting season is an extended one, with some fruits falling in October and November, but the peak period of ripening being in January and February. Our results also indicate synchronous flowering and fruiting for a proportion of the population between November and March in a given year. Finally, for trees from the forest interior, we found a positive relationship between tree size and fruit crop size as is the case with most tropical forest trees (*e.g.* Chapman *et al.*, 1992). These initial findings will hopefully help to direct further research to promote the conservation of this endemic and globally threatened species, as well as to aid in its production in farming systems.

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