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First records of flower biology and pollination in African Annonaceae: *Isolona*, *Piptostigma*, *Uvariodendron*, *Monodora* and *Uvariopsis*

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ABSTRACT

Seven species from five genera of Annonaceae were studied with regard to their flower biology and pollination in the Southwest Province of Cameroon, West Africa. They have protogynous hermaphroditic flowers, with exception of Uvariopsis species, which are monoecious. Fused petals of Isolona campanulata remain apically spreading and open during anthesis but form a deep basal urceolate tube around the reproductive organs. At anthesis the yellow pendent flowers emit a fruit-like scent and attracted small beetles, the likely pollinators. Piptostigma sp. flowers also emit a fruit-like scent but provide a closed pollination chamber formed by the three inner petals. Small staphylinid beetles attracted during the female stage of anthesis are released from the flowers at the end of the male stage 2-3 days later. Both species have diurnal anthesis, attracting and releasing the flower visitors during daytime. In contrast, Uvariodendron connivens and U. calophyllum have nocturnal anthesis with floral thermogenesis, produce spicy, aromatic and fruity scents and attract large Scarabaeidae beetles, the pollinators, along with many curculionid beetles, which were principally predators of the thick petals. The very large flowers of Monodora tenuifolia have yellowish petals which are spotted with dark red markings. Together with the sweetish, slightly disagreeable scent the flowers attract flies, principally dung flies. The two investigated Uvariopsis species are monoecious with pistillate and staminate flowers being functional at the same time. The violet red flowers of *U. bakeriana* visually seem to mimic the fruiting body of certain stinkhorn fungi (Phallaceae) although without producing their strong unpleasant carcass stench. Flower-visiting dung flies were rare. Conversely, U. congolana has a strong fungus-like scent, its flowers are presented at litter height and dung flies living in the litter were the flower visitors, albeit sporadic. The 4–5 days lasting anthesis of both *Uvar*iopsis species appears to be an evolutionary consequence of their diffuse pollinator spectra. The studied African Annonaceae therefore have either cantharophilous or myiophilous/sapromyiophilous flowers with, in part, respectively, remarkably long anthesis, thermogenesis, and widely open, large flowers – all attributes unknown or rare in the hitherto better studied Neotropical Annonaceae.

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Introduction

Annonaceae, with about 135 genera and 2500 species, are the largest family in the early divergent order Magnoliales (Chatrou et al., 2004). Representatives of this group, trees, shrubs or lianas, are distributed in all tropical regions worldwide and play a key ecological role especially in tropical lowland rainforests (Gentry, 1993). Due to their pantropical distribution and great morphological and functional diversity, systematic and ecological studies of Annonaceae provide important insights into the evolution of tropical floras (e.g., Couvreur, 2008; Erkens et al., 2007; Maas et al., 2003; Pirie et al., 2006).

The African Annonaceae are still relatively poorly known compared to the Neotropical and Southeast Asian representatives (Couvreur, 2008). Data on pollination of African species in their natural habitats are practically non-existent (Couvreur, 2008). As far as we are aware there are only observations on the floral biology of one African Annonaceae, the savanna species *Annona senegalensis*, investigated in Ivory Coast (Deroin, 1989).

For a long time the Annonaceae were thought to be pollinated predominantly or nearly exclusively by beetles. Studies during the last decades on New and Old World representatives of this group revealed, however, that they are unexpectedly more diversified with regard to pollination. Besides pollination by beetles (cantharophily), which is indeed the predominant mode of the majority of species worldwide, there is also pollination by thrips (Thysanoptera), flies (myiophily and sapromyiophily), cockroaches and even bees (melittophily) – for reviews see Gottsberger (1989,

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1999), Webber and Gottsberger (1995), Silberbauer-Gottsberger et al. (2003), Teichert et al. (2009), Saunders (2010). Thus, a more differentiated picture of pollination modes in the Annonaceae has become apparent, revealing distinct adaptations of flowers to their particular flower-visiting insect group.

The Annonaceae have a quite constant basic flower construction (bauplan) with a trimerous (occasionally dimerous or tetramerous) perianth, which differentiates in one whorl of sepals and two whorls of petals. The numerous stamens and carpels are helically arranged, and the fruits are usually apocarpous with monocarps, or rarely syncarpous or pseudosyncarpous. Besides this basic morphological construction, there are several functional characteristics of the flowers that appear to be adaptations or pre-adaptations to certain flower-visiting insect groups. Many Annonaceae close their petals over the flower center during anthesis, thus enclosing the reproductive organs and forming a scent-emitting "pollination chamber", which entices principally beetles to enter it. The flowers are protogynous, which is a form of dichogamy that functions best with long-staying insects, like beetles, which deposit pollen onto the receptive stigmas upon entering the floral chamber and receive fresh pollen upon leaving the male stage flower after several hours. The flat, sclerified connective shields of the majority of species and genera as well as the sweet (sugar-containing), sticky stigmatic exudates appear to be mainly antipredator structures against the rough eating and gnawing habits of beetles (see Gottsberger, 1988, 1999). In contrast to cantharophilous Annonaceae, melittophilous species maintain their petals more or less widely spread and open, thus enabling direct access to the flower interior by bees. Thus, particular floral features, as well as color, scent or thermogenesis (warming during anthesis) of floral organs and the duration of anthesis are expressions of pollination events and a particular flower biology. Co-evolution with different insect groups has influenced and shaped the Annonaceae flower and accompanied the diversification of species and genera of this old angiosperm lineage (Gottsberger, 1999; Silberbauer-Gottsberger et al., 2003).

Initial observations in 2005 of one of the authors (SP) in Cameroon had shown that SW Cameroon is rich in Annonaceae taxa and that beetles visited flowers of, e.g., *Uvariodendron calophyllum*. Aim of the present study is to give a first insight into the flower biology and pollination of African Annonaceae, based on observations in March 2007 of seven more or less concomitantly flowering species belonging to five genera at one site in Cameroon. Rhythm and functioning of the flowers and their visitors were observed and compared with the relevant knowledge about species from the Neotropics, Southeast Asia and Australia.

Material and methods

Species studied

A short description of the characteristics of the genera and the respective species follows informing about their habit and known geographical distribution. The study focuses on seven species in the genera *Isolona*, *Piptostigma*, *Uvariodendron*, *Monodora* and *Uvariopsis*.

Isolona

Isolona species are trees or shrubs with bisexual (hermaphroditic) flowers. The six petals are basally and conspicuously fused forming a more or less deep tube which contains the reproductive organs. The genus consists of 20 species with a distribution throughout tropical West and Central Africa, in Tanzania, Kenya and Madagascar. The species studied, Isolona campanulata Engl. & Diels, has a disjunct distribution from Sierra

Leone to Ghana and in southeastern Nigeria, western Cameroon and Gabon (Couvreur, 2008). We observed one abundantly flowering tree with a height of about 15–18 m, which we detected principally by its dropped flowers and petals on the ground. No further individuals were found in the surroundings during our study.

Piptostigma

According to the last revision and compilation by Fries (1959), the genus *Piptostigma* has c. 15 species (c. 12 according to Kessler, 1993), which are trees of different sizes, occurring in West Africa, from Ivory Coast to the Congo region with Cameroon being the center of distribution, from where seven species are known. We discovered and studied two small subpopulations of a yet undetermined species (*Piptostigma* sp.) with one to three individuals in each. These plants consisted of slender treelets of 3–7 m height. The flowers are hermaphroditic, with six free petals, of which the outer are small and triangular and the inner are much larger and elongated.

Uvariodendron

12 species of *Uvariodendron* are known to occur in tropical West Africa. Again, Cameroon is a center of distribution with 7 species occurring alone in this country. The genus comprises trees and shrubs with hermaphroditic, often cauliflorous flowers (Fries, 1959). Two species were studied, *U. calophyllum* R.E. Fr., which occurs from Ghana to Cameroon (Hawthorne et al., 2006) and *U. connivens* (Benth.) R.E. Fr., distributed in Cameroon and on the island Bioko, Equatorial Guinea (Fries, 1959).

Monodora

The genus *Monodora* has a total of 14 species, which are distributed in West, Central, East and Southeast tropical Africa and form shrubs and trees up to 40 m tall. The investigated species, *Monodora tenuifolia* Benth., forms 20–30 m tall trees and has a distribution from East to Central tropical Africa, from Guinea to the east of the Democratic Republic of Congo (Couvreur, 2008). One flowering tree, about 15 m tall, could be closer investigated.

Uvariopsis

With only c. 11 or 12 species, the genus *Uvariopsis* is also relatively small; it occurs only in tropical West Africa. It consists of monoecious or dioecious trees and shrubs with unisexual flowers. They appear to be dimerous, having two sepals and the two whorls of petals often connate into a 4-petaled corolla (Fries, 1959; Kessler, 1993). The two species studied, both monoecious treelets, were *Uvariopsis bakeriana* (Hutch. & Dalziel) Robyns & Ghesq. and *U. congolana* (De Wild.) R.E. Fr. The former occurs in southern Nigeria and Cameroon and the latter from Cameroon to the Democratic Republic of Congo (Fries, 1959).

Study site, location, climate, vegetation

Studies were conducted in the Southwest Province of Cameroon, West Africa, near the Banyang Mbo Wildlife Sanctuary (BMWS; 5°8′ to 5°34′N and 9°30′ to 9°47′E). The area is situated between the coastal lowlands and the mountainous regions of western Cameroon. The study site was located near the western border of the BMWS, 40 km east of the Korup National Park, close to the village of Nguti. It consists of flat terrain that slopes slightly towards the rivers that cross the sanctuary. Our study took place in the regions below 500 m which are covered by hygrophilous coastal

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