Flower production and sexuality in *Bequaertiodendron magalismontanum*

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Flowering propensity, flower distribution and the duration of anthesis in a natural population of *Bequaertiodendron magalismontanum*, located in a part of the Magalisberg mountain range, were assessed during two successive flowering seasons. Relative sex ratios and secondary sex characters of morphologically hermaphrodite and female plants are given. Selective pressures underlying the evolution of morphological gynodioecy in *B. magalismontanum* are discussed.

Die blomgeneigheid, verspreiding van blomme en duur van antese in 'n *Bequaertiodendron magalismontanum*-populasie, beleë in 'n deel van die Magaliesbergreeks, is gedurende twee opeenvolgende bloemseisoene bepaal. Relatiewe verhoudings en sekondêre geslagskenmerke van morfologies tweeslagtige en vroulike plante in die populasie word gegee. Selektiewe druk verantwoordelik vir die ontwikkeling van morfologiese gynodioeisie in *B. magalismontanum* word bespreek.

Keywords: Anthesis, flowering propensity, gynodioecy, male-sterility, secondary sex characters

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Introduction

The Sapotaceae is an almost circumtropical family (Meeuse 1963) comprising about 50 ill-defined genera with 800 species (Wagenitz 1964), or 500-600 species (Kupicha 1983). Only a few representatives of the family extend into subtropical or semi-arid regions. *Bequaertiodendron magalismontanum* (Sond.) Heine & J.H. Hemsley is one such species. It is widely distributed in tropical Africa, but also occurs southwards through Angola to Botswana, the Transvaal, Natal and Swaziland (Meeuse 1963). In southern Africa this species is seemingly associated with quartzite or granite rock (Hemsley 1966; Palmer & Pitman 1972). It is therefore a well-known floristic element of the Magalisberg mountain range and is frequently found on exposed hillside as a low-growing evergreen shrub (Hemsley 1966). In more favourable localities the plants develop into trees of up to 15 m tall (Kupicha 1983).

*B. magalismontanum* flowers profusely in spring. The small, short-pedicelled, greenish-white and strongly-scented bisexual flowers are borne in few-flowered fascicles in the axes of leaves, which are crowded towards the apices of young branches. More prominently, however, fascicled flowers usually develop in great numbers on the lower, leafless parts of these young branches as well as on the old wood where the fascicles often occur on large, raised warts. The single-seeded, plum-shaped berries are therefore more often found massed around the older branches and main trunks, hence the vernacular name 'stem-fruit' (Codd 1951).

The stem-fruit is widely distributed and well adapted in the Transvaal and because of its edible fruits (Watt & Breyer-Brandwijk 1962) has locally been known and utilized for a long time. Because it has great economic potential (Codd 1951; Palmer & Pitman 1972; Verdoorn 1939; Watt & Breyer-Brandwijk 1962) it is a likely candidate for selective breeding, however, except for fragmentary data on flower sexuality, the reproductive biology of the stem-fruit has not been studied. The occasional appearance of unisexual, male-sterile or female flowers has been reported (Heine & Hemsley 1960; Kupicha 1983; Meeuse 1960, 1963), but data on the spatial distribution of these flowers is insufficient. A branch with female flowers illustrated by Engler (1904) and plants with ‘imperfect’ flowers (Gerstner 1948) were regarded as abnormalities caused by frost and/or prolonged drought (Gerstner 1948; Meeuse 1960, p. 337). In the present study on the production of flowers in a *B. magalismontanum* population the possible occurrence and spatial distribution of female flowers were reinvestigated.

Materials and Methods

One hundred and twenty-eight plants were randomly selected and tagged along an east–west orientated nature trail through a natural population of *B. magalismontanum*, located on a ridge in the Pretoria Botanical Gardens, Brummeria, Nelspruit, South Africa. The tagged plants were visited weekly during the flowering seasons of 1986 and 1987 and the following factors relating to flower production were assessed: the number of times an individual came into flower during the flowering season, the number of plants that flowered in the population (flowering propensity), the distribution of flowers on the circumference of the plants and on new wood or old wood, as well as the number of flowers on the branches (flower density). The latter was estimated on a 1–5 point scale (1 = low, 5 = high). Life form and flower sexuality were recorded for each plant. The sexual characters of the flowers on hermaphrodite and female plants were tested for inconstancy by randomly chosing 15 branches on 3 hermaphrodite and 1 female plant (60 branches). A distal, central and proximal fascicle with associated buds and flowers were collected from each branch and 3 flowers/mature buds from each fascicle were examined under a dissecting microscope (540 flowers). Seven hermaphrodite and 7 female plants were chosen and fully open flowers were measured in the veld. The duration of anthesis for individual flowers was assessed during the first week of October 1987 by tagging opening flowers on 3 individuals of each sexual type and recording daily changes until the flowers had closed.

Observations and Discussion

Life form and habitat

The *B. magalismontanum* population comprises both shrubs (60%) and trees with multiple trunks. Virtually no true trees with single trunks were found. Polycormic trees, defined and regarded by Guédès (1982) as giant shrubs, comprise the older members of the population. The plants were nearly always found on rocky outcrops, the separate stems/trunks often emerging from different openings.
among the rocks. The association of these plants with such situations may be due to the favourable microsites for seed germination that the rock crevices provide.

Flower production

Flowering propensity

In 1986, 52% of the population did not initiate flowers whereas this value decreased to 30% in 1987 (Table 1). These non-flowering individuals were mainly found on the steep northern and western summit of the ridge. The flower-bearers of 1986 showed varying degrees of flower initiation and bud development. In 20% of the population, flower initiation did not proceed beyond the initial bud stages, i.e. small, brown spots appeared on the new wood in early July, but did not develop any further. In 8% of the population, well-developed buds did occur, but were arrested before anthesis. Abortive buds did not fall off, but could still be seen on the plants months later. Mature flowers were therefore found on only 20% of the population, comprising polycomic trees (31%) and shrubs (69%), the latter often not more than 1 m high. In 1987, 70% of the population initiated and matured flowers and no abortion of advanced bud stages occurred (Table 1).

| Table 1 Flowering propensity of | 1986 | 1987 |
|--------------------------------|------|------|
| Bequaertiodendron magalismontanum |      |      |
| (128 plants sampled)           |      |      |
| Response                       |      |      |
| No response                    | All buds aborted | Open flowers produced |
| % of population                | 52   | 28   |
| Number of plants               | 66   | 36   |

| Table 2 Density, distribution and sexuality of flowers on flower-bearers of Bequaertiodendron magalismontanum |
|-----------------------------------------------------------------------------------------------------------|
| Response                                                                                                   |
| Number of plants | % flower-bearers | Number of plants | % flower-bearers |
|------------------|------------------|------------------|------------------|
| Flower density   |                  |                  |                  |
| low (1-3)        | 20"              | 77"              | 34               | 38               |
| high (4-5)       | 6"               | 23"              | 56               | 62               |
| Flower distribution |                  |                  |                  |
| on south-facing branches | 14           | 52               | 28               | 31               |
| all around tree   | 12               | 48               | 62               | 69               |
| Flower sexuality  |                  |                  |                  |
| female           | 6"               | 23"              | 22               | 24               |
| Hermaphrodite    | 20"              | 77"              | 68               | 76               |

Similarity in figures: "m" coincidental

Flower density

Flowers were grouped together in clusters (fascicles) in leaf axils (Figure 1) or on warty outgrowths on bare branches (Figure 2). The structure and homology of these warts have not been investigated and they are provisionally referred to as brachyoblasts. At the beginning of the flowering season these brachyoblasts are covered with small spots (buds), some of which might develop into flowers during the current season. Due to a lack of further information at this stage, we have referred to the visual appearance of these buds as ‘flower initiation’. On most plants the flower-bearing brachyoblasts were far apart, each bearing only a few flowers, as many flowers aborted at an early, and approximately the same developmental stage (Figures 1 & 2). In 1986, only 23% of the flower-bearers had branches densely covered with flowers (density = 4-5, Table 2) whereas this value increased to 62% in 1987.

Flower distribution

Of the 1986 flower-bearers, 52% bore flowers on the south-facing branches only (Table 2). In these less prolific plants, no flowers developed on the old wood. The remaining 48% of the flower-bearers (Table 2) were considered prolific as flowers occurred all over the tree/shrub, on new as well as old wood, from the axils of current leaves near ground level on the main trunks/stems. These prolific flower-bearers occurred in the more favourable habitats of the area, along natural streams, or on the lower southern and northern slopes of the ridge, facing the cultivated parts of the Botanical Gardens. In 1987, 69% of the flower-bearers were considered prolific (Table 2).

Flowering phenology

In both flowering seasons, any individual plant flowered only once. Flowering took place in two flushes in 1986 (Figure 3), but only 3 plants produced flowers later in the season (in October) and then only the youngest branches came into bloom. Open flowers were found on most plants from the third week in August to the first week in September. In 1987 the flowering season started later and flowering took place in a single flush (Figure 3). On most of the prolific flower-bearers, opening of flowers continued for more than 3 weeks, but in plants with flowers on south-facing branches or new wood only, the flowering season was shorter (Figure 4). Most plants were in full bloom (i.e. open flowers occurred on all the brachyoblasts) during the second week of October (Figures 3 & 4).

Plants that did not come into bloom in 1987 had also been without flowers in 1986 and again occurred mainly on the northern and western summit of the hill. All flower-bearers of 1986 again produced flowers in 1987. However, the heaviest bearers of 1986 did not repeat their flowering performance in 1987, while some plants that had carried only a few flowers on some of the branches in 1986, were among the most prolific flower-bearers of 1987.

The low (20%) flowering propensity of the population in 1986 should be seen against the background of the drought prevailing at that time. Although temperatures were not recorded, absence of flowers in both flowering seasons on north-facing branches and the north-facing summit, which represents the warmer and drier part of a mountainous area (van der Schijff 1985) indicates that high temperatures may have a limiting effect on flower production. According to unpublished climatological data obtained from the Weather Bureau in Pretoria, the precipitation in the Pretoria area had been below average for at least 8 years, up to 1986. During the months preceding flower initiation, the precipitation was exceptionally low (only 177.2 mm of rain fell from January to May 1986, compared with a normal mean of 343 mm for this period). In addition, the spring rains came later than usual. Under
these circumstances, only plants growing in the most favourable localities would still have adequate resources available for flowering. A flowering propensity of 20% in 1986 could be regarded as a possible minimum for *B. magalismontanum*. In 1987 precipitation was higher (293 mm) than in 1986 during the first half of the year and the
spring rains that came earlier (7 September 1987 versus 17 October 1986), were followed by good summer rains. The higher precipitation and shorter dry season were reflected in many aspects of flower production, e.g. an increase in flowering propensity, no abortion of advanced bud stages, higher values for prolific flower-bearers and flower density (Tables 1 & 2) and no interruption (i.e. a single flush) in the flowering season (Figures 3 & 4).

Anthesis and the morphological sexual system
A study of the duration and morphological details of anthesis revealed the sexually dimorphic nature and morphologically gynodioecious breeding system of the population. The latter thus comprises morphologically hermaphrodite and male-sterile (hereafter called female) individuals, with a marked preponderance of hermaphrodites (Table 2). The ratio of female to hermaphrodite flower-

Figures 5-8 Male-sterility in *B. magalismontanum*: 5. Corolla tube of hermaphrodite flower with epipetalous stamen indicated by arrow (scale bar = 1 mm). 6. Corolla tube of female flower with petalloid staminodes indicated by arrows (scale bar = 1 mm). 7. Flowering branch of hermaphrodite plant with fully opened flowers (scale bar = 5 mm). 8. Flowering branch of female plant with fully opened flowers (scale bar = 2 mm).
bears, however, remained very nearly the same in both flowering seasons. This study should be continued over several further consecutive seasons before further concrete conclusions can be drawn. Such data would contribute towards a better understanding of the factors responsible for the numerical superiority of hermaphrodites in the population.

The hermaphrodite flower has 5 epipetalous stamens (Figure 5), but in the female flower the androecium has been reduced to 5 sterile, petaloid staminodes (Figure 6). The ovaries of both morphs contain 5 well-developed ovules. Among the hermaphrodites, there are transitional forms with partially sterile anthers, some of which do not dehisce. These flowers were larger and more widely opened than female flowers. All the flowers on an individual, whether female, hermaphrodite or transitional, had the same sexual characters and no transitional stages occurred within the same plant.

Hermaphrodite and female plants could be distinguished during the flowering season only. They were primarily determined by secondary sex characters (Lloyd & Webb 1977), and not necessarily according to the presence/absence of fertile anthers.

(1) Hermaphrodite flowers exceeded female flowers in length (6.79 mm ± 0.37 mm versus 4.85 mm ± 0.48 mm) and diameter (4.99 mm ± 0.46 mm versus 3.29 mm ± 0.40 mm), a tendency that is by no means rare (Baker 1948). (2) Female flowers (Figure 8) opened only slightly, so that they were campanulate and resembled buds, while hermaphrodite flowers (Figure 7) opened wider and became cup shaped. Hermaphrodite flowers stayed open for 3 days, while female flowers remained open for at least 6 days. (3) Although nectar is secreted by hidden nectaries at the base of the pistil in both morphs, the nectar remained at the base of the corolla tube in the hermaphrodite flower, but was often forced out of the female flower as a glistening droplet. Honey bees as well as ants were seen collecting the nectar during the day, but nightly visitors were not investigated. Females showed no obvious niche preferences and occurred in the southern as well as the northern parts of the area, usually within a few metres of hermaphrodites. The females were all shrubs, many of which were dwarfed, while hermaphrodites occurred as shrubs and polycormic trees.

**Concluding remarks**

The only reports we could find on the breeding system of the Sapotaceae are those of Yampolsky & Yampolsky (1922), Bawa (1974) and Sutherland & Delph (1984). However, none of these publications mention the occurrence of gynodioecy in the Sapotaceae. In *Bequaertiodendron* morphological gynodioecy has not previously been recognized as such. Gerstner (1948) observed plants 'with imperfect female flowers... before the first rains arrived and after a severe drought of several months'. Later in the season, after sufficient rain had fallen, these same plants developed complete flowers (Gerstner 1948). No evidence of sex changes were found during either the 1986, or the 1987 flowering season among tagged individuals at our study site. However, inconstancy is a normal feature of many gender dimorphisms in plants (Lloyd & Bawa 1981) and there is overwhelming evidence that femaleness can be induced by environmental stresses (Freeman, Harper & Charnov 1980). Nevertheless, according to the latter authors, few researchers have examined the same individual plant year after year. This procedure will have to be followed in the stem-fruit to determine whether sexual expression varies in an individual over a prolonged period.

*B. magalismontanum* exhibits all the characters of the dioecious syndrome as pointed out by Bawa (1980) and Wilson (1983), viz. the plants are woody perennials with tropical affinities, producing small, greenish-white, insect-pollinated flowers, which give rise to fleshy, few-seeded, animal-dispersed fruits. Why then is the stem-fruit morphologically gynodioecious and not morphologically dioecious? A plausible explanation may lie in the view of Bawa & Beach (1981) that the evolution of a particular sexual system is influenced by the dynamics of the pollination system and selection for the sterilization or abortion of stamens in hermaphrodite flowers occurs when the pollen in the flowers interferes with the deposition of incoming pollen. In *B. magalismontanum* the stigma lies only slightly below the anthers (Figure 6), which dehisce as soon as the flower starts opening. At the slightest touch, a cloud of pollen descends upon the stigma. Pollinators trying to reach the nectar cause clogging of the stigma by self-pollen. It therefore seems likely that selective pressure against clogging of the stigmas by the plants' own pollen could have been responsible for the evolution of female plants in *B. magalismontanum*. The pollination system of *B. magalismontanum* may, however, be imposing a constraint upon the evolution of morphological males. The main attractant for pollinators is nectar, which is secreted by nectaries occupying the large, basal part of the ovary. There would therefore be strong selection against the loss of pistils and the establishment of easily detectable male plants. A gradual loss of female fertility in the hermaphrodites by sterilization of the five proximally placed ovules, might be possible. These male plants will go undetected in the veld during the flowering season, but may be revealed by a detailed embryological investigation and/or an account of post-fertilization events, e.g. fruit and seed development and fruit set. No data is as yet available on these aspects in *Bequaertiodendron*.

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