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Gender expression and inflorescence structure of *Pappea capensis* Eckl. and Zeyh. (Sapindaceae)

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Abstract

Gender and the structure of the inflorescence and flowers of *Pappea capensis* (Sapindaceae) are investigated in a locality around Pretoria (22–27°S and 25–32°E). The trees flower over a long period (December to April) and are basically monoecious, starting with male flowers followed by female flowers towards the end of the flowering period, although some trees may be predominantly male and some predominantly female. The inflorescence is a reduced thyrse with small flowers. Male flowers have five ephemeral petals, eight stamens and a rudimental pistil. Female flowers comprise a 3-lobed ovary, a single style and stigma and eight staminodes.

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1. Introduction

Pappea capensis (Sapindaceae) is a small tree or shrub, indigenous to Africa with a wide distribution from the southern Cape in South Africa to Ethiopia in the north. The seed of *Pappea capensis* contains about 74% edible oil (Coates Palgrave, 1977; Landsell, 1920; Venter and Venter, 2007) that can be used for various purposes and might also be a source for bio-diesel. No information about seed production is available and there is still disagreement about the sexuality of the trees as well as the structure and type of the inflorescence. Most authors of books on indigenous trees of Southern Africa concur that the trees are dioecious (Coates Palgrave, 1977; Landsell, 1920; Palmer et al., 1972; Van Rooyen, 1984; Van Wyk and Van Wyk, 1997; Van Wyk, 1984; Venter and Venter, 2007; White, 1962). However, Fivaz and Robbertse (1993) and Davies and Verdcourt (1998) supplied evidence showing that the trees are monoecious, first producing male flowers and later producing female flowers, either on the same inflorescence or on separate inflorescences. Fivaz and Robbertse (1993) also

referred to other monoecious members of Sapindaceae with male and female flowers on the same inflorescence.

Some authors describe the inflorescence as a catkin-like raceme (Coates Palgrave, 1977) without distinguishing between male and female inflorescences. Landsell (1920) and Palmer et al. (1972) describe the inflorescence as a panicle up to 15 cm, while Van Wyk and Van Wyk (1997) describe it as “drooping spikes.” Davies and Verdcourt (1998) described the male inflorescence as a “lax or a dense thyrse” while most authors regard the female inflorescence as a raceme (Coates Palgrave, 1977; Landsell, 1920; Palmer et al., 1972). According to Van Wyk (1984) “Male and bisexual flowers are borne on separate trees; petals of bisexual ones (3) white and the hairy ovaries buff-green, in spikes up to 6 cm long.”

According to Richards (1990), monoecious plants tend have an unstable sex expression as seen in Cucurbitaceae (melons and squashes), where high temperatures and long days stimulate the production of mostly male flowers, whereas under opposite conditions (low temperatures and short days) the plants tend to produce more female flowers. Male flowers are also produced over a longer period in a relatively proximal position on the plant, whereas female flowers tend to be produced later in the season over a shorter period in a more distal position on the plant. Furthermore, younger monoecious trees are inclined to be

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mostly or wholly male while older trees have more resources and tend to be mostly or wholly female (Richards, 1990).

From the above brief overview, it is clear that the descriptions of the sexuality, inflorescences and flowers of *P. capensis* found in books on Southern African trees are either incomplete or even erroneous. With the exception of Fivaz and Robbertse (1993), no proper study has ever been done on gender expression or inflorescence structure in *P. capensis*. We accordingly studied these aspects in plants locality around Pretoria (22–27°S and 25–32°E).

2. Materials and methods

Observations over a period of 3 years were made on two trees in a tree collection on the experimental farm of the University of Pretoria (UP) (25°45' S, 28°16' E). Twenty more trees growing in the wild in a locality 30 km north of Pretoria were marked during December 2009 and visited at monthly intervals. Material was also collected during field trips to other parts of the wider study area (22–27°S and 25–32°E). Herbarium specimens from the National Herbarium of Pretoria, the Schweickerdt Herbarium at the University of Pretoria, and the Compton Herbarium in Cape Town were also consulted. Specimens collected during field trips and from the marked trees have been deposited in the Schweickerdt Herbarium at the University of Pretoria.

No special technique was applied to score sex expression of trees. Trees that were observed in the male phase were each bearing hundreds to thousands inflorescences, each bearing male flowers only, while inflorescences on trees in the female phase, borne only female flowers or female flowers with remains of some dead male flowers amongst the female flowers.

Most herbarium specimens found in the different herbaria were collected with male flowers and very few with female flowers. The descriptions in this paper are therefore mainly based on material collected and observations made during field excursions and visits to the marked trees.

3. Results and discussion

3.1. Inflorescence

Trees in and around Pretoria usually start flowering in December/January and may continue to flower until April. Inflorescences are produced singly in the axils of the first-formed leaves of the new flush of both short and long shoots, and consist of an erect main axis up to 12 cm long, containing reduced dichasia in the axils of the bracts along the main axes (Fig. 1). According to White (1962), the inflorescences can be up to 21 cm, but no such inflorescences were found in this study. Based on the sex expression of the flowers, three inflorescence types are found (Fig. 2), namely, male, female and mixed inflorescences, but the basic structure conforms to a reduced, indeterminate thyse (Sensu Weberling, 1992). Especially in young inflorescences, the hypopodia of the dichasia are extremely reduced or lacking and the dichasia are then sessile (Fig. 1). The development of a dichasium starts with the terminal, first order flower with two

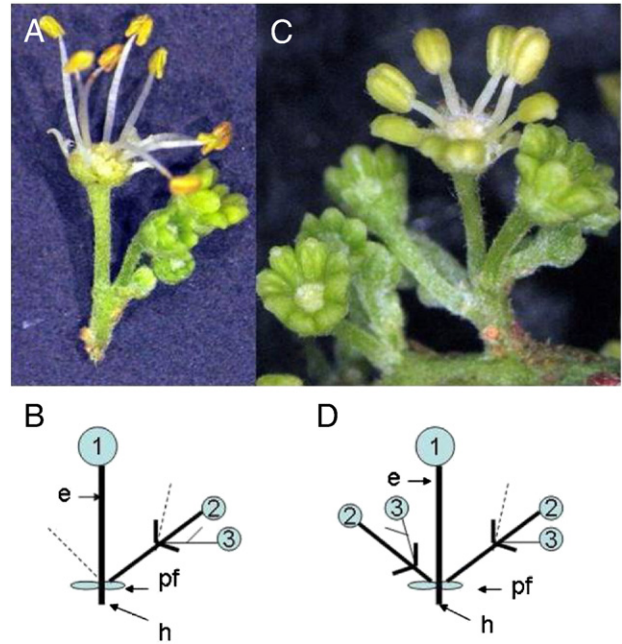


Fig. 1. Dichasia and young inflorescence of *Pappia capensis*. Real (A) and diagram (B) of reduced dichasium showing reduced hypopodium (h), epipodium or pedicel (e) of first order flower (1), prophylls (pf) and second and third order flowers (2 and 3). Real (C) and diagram (D) of young dichasium (right) and reduced dichasium (left).

bracts (prophylls) at the base of the pedicel (epipodium), close to the bract on the main axis (Figs. 1A and 4A). A second order bud, also with two prophylls at its base, then develops in the axil of one, or both first order flower prophylls. The process is repeated

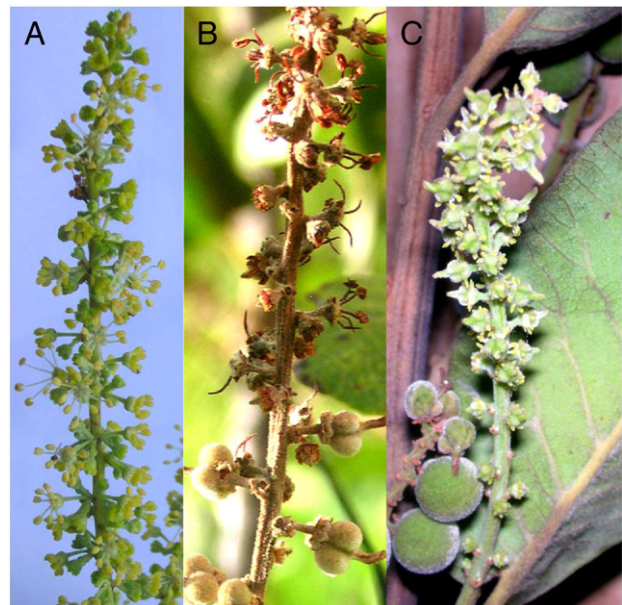


Fig. 2. Three inflorescence types found on *P. capensis* trees at different times of the flowering period. A, inflorescence producing male flowers. B, inflorescence with male flowers followed by female flowers. C, inflorescence with female flowers. Young fruit on separate inflorescence bottom, left.

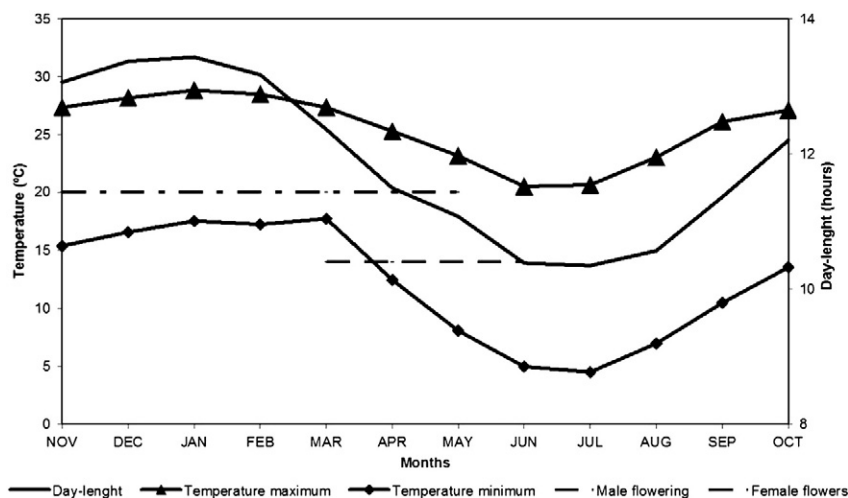


Fig. 3. Diagram showing long term maximum and minimum temperatures and day length in Pretoria, South Africa, in relation to production of male and female flowers of *P. capensis* (information from the South African Weather Services, 2009).

several times with higher order flower buds developing in the axils of either one or both prophylls of successive flower orders (Figs. 1B and 4B). The result is high numbers of flower orders crowded on reduced axes, rendering it very difficult to interpret. Limited space on the dichasia can result in various missing flower orders (Figs. 1B and 4B), transforming some dichasia into monochasium-like units. The inflorescence of *Pappea capensis* is morphologically a reduced thyrse and not a true raceme or spike as interpreted by some authors.

3.2. Flowers

Male flowers (Fig. 4) are small and yellowish green, with five minute sepals, five, white, triangular ephemeral petals, usually eight stamens, and an aborted pistil, reduced to a hairy protrusion. Petals are only observed in freshly opened flowers. The stamens have relatively long (up to 4 mm) filaments with long hairs at the base and the prominent anthers are bi-lobed and triangular. Cells at the apex of the connective are enlarged and more transparent than surrounding cells. Anthers dehisce by means of longitudinal slits and the pollen is tricolporate.

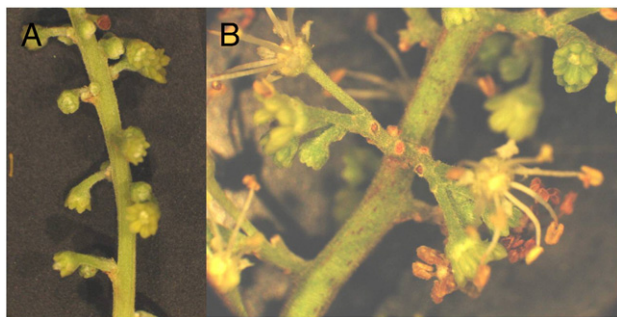


Fig. 4. Young (A) and old (B) male inflorescences showing progressive flower production on reduced lateral branches (dichasia).

The sepals and petals of the female flowers are similar to those of the male flowers, but the petals are often lacking. Stamens are reduced to staminodes (Fig. 2C). The tri-lobed, hairy pistil consists of three carpels fused at the base and a basal style (sometimes twisted), inserted deeply in the centre of the ovary. Each carpel contains a single, anatropous ovule. After fertilization each ovary may give rise to one to three semi-separate fruits, joined at the base (Fig. 5).

Transitional flowers with shorter filaments and partially developed pistils have been observed on inflorescences switching from male to female. Van Wyk (1984) described bisexual flowers with white petals and a hairy (pubescent), green ovary but we found no bisexual flowers during this study. The pistils of the transitional flowers are under-developed and each locule contains a small, underdeveloped ovule. The stamens are slightly shorter than those of the male flowers.

3.3. Gender

The two trees on the experimental farm of UP behaved as shown in Table 1. During 2008/2009, tree No 1 flowered profusely while tree No 2 flowered only on the southern side where it produced female flowers only. During 2009/2010, tree



Fig. 5. Male and female flowers of *P. capensis*. A, male flower with eight stamens, five ephemeral petals and three-lobed, aborted pistil. B, female flower with three-lobed ovary, single style and eight staminodes.

Table 1
Gender expression of two trees on the experimental farm, University of Pretoria, over a 3-year period.

Year/month	Tree no.	Dec	Jan	Feb	March	April
2007/2008	1	M	M	M	—	—
	2	M	M	M/F	F	Fruit
2008/2009	1	M	M	M	—	—
	2	M	M	M/F	F	Fruit
2009/2010	1	—	M	M	M	—
	2	—	M	M	M/F, F	Fruit

M=inflorescences with male flowers.

M/F=higher order flower buds on dichasia of previously male Inflorescences produce female flowers and newly formed inflorescences produce female flowers.

F=old and young inflorescence with female flowers.

No 1 had very few inflorescences while tree No 2 flowered profusely.

During 2009, 4/20 of the marked trees in the location 30 km north of Pretoria switched from male to female, 3/20 produced only female flowers, 6/20 produced only male flowers and the rest remained sterile. During 2010, most of the trees remained sterile while 3/20 switched from male to female, 4/20 produced male flowers and 2/20 only female flowers. Some sterile trees were damaged by fire and therefore did not flower. The collection dates of the specimens and the gender of the trees observed during field trips to different parts of the wider study area (22–27°S and 25–32°E) and of visits to the marked trees in and around Pretoria emphasise the extended availability of male flowers and the switch from the male to female phase in some trees later in the flowering period (Fig. 6).

From the 111 herbarium specimens, containing flowers or fruit, collected over many years from the study area and deposited in the three mentioned herbaria, 60% had only male flowers, 31% had fruit, 6% had both male and female flowers and 3% had only female flowers.

After observing the marked trees and studying herbarium specimens, the following general description will apply: On some trees, especially young trees or trees starting to flower around December/January, all flower orders on a dichasium are usually male (Fig. 1) and are eventually sloughed off (Fig. 4B).

Such trees bear only male inflorescences (Fig. 2A) and are therefore functionally male. Other trees, possibly older trees with more resources, start flowering during December/January and also produce male inflorescences but towards the end of February/ beginning March, the male flowers are sloughed off and higher order flower buds on the same dichasia produce female flowers. Inflorescence in these trees is therefore sexually mixed (Fig. 2B). On the same trees, new inflorescences formed during March/April in the axils of young leaves do not produce male flowers but only female flowers (Fig. 2C). Older, healthy trees flowering later in the season tend to produce only female inflorescences and are therefore functionally female. In most female inflorescences, only the first and sometimes the second order flowers of the dichasia develop, due to the pollination of and subsequent fruit development on the first or second order flowers. This might explain why some authors interpret such inflorescences as racemes or spikes (Coates Palgrave, 1977; Van Wyk and Van Wyk, 1997).

Temperature and/or day length correlate closely with and may play an important role in the sex expression of the trees. Male flowers are produced as long as night temperatures during November to March remain above 15 °C and/or day length above 13 h (December to March), while female flowers are produced when day length drops below 12 h and/or temperature below 16 °C (February to April) (Fig. 3). However, from the herbarium specimens collected from the study area since 1926, it is clear that there are many deviations from this “general rule,” although the collecting dates of the majority of the specimens support this statement. Evidence to support this statement will be supplied in a follow-up paper on the phenology of *P. capensis*.

Phenologically *P. capensis* seems to show both dioecious and monoecious characteristics. Since inflorescences are formed in the leaf axils at the base of the new growth flush, and since this new flush is dependent on climatic conditions, the onset of flowering may vary from season to season. Sex expression of the flowers, on the other hand, is probably determined by temperature and day length (Fig. 3), although more research is required to determine whether one or both factors are involved (Fig. 3). This relationship was also claimed by Richards (1990), who observed that in monoecious plants, high temperatures and long days may stimulate the formation of

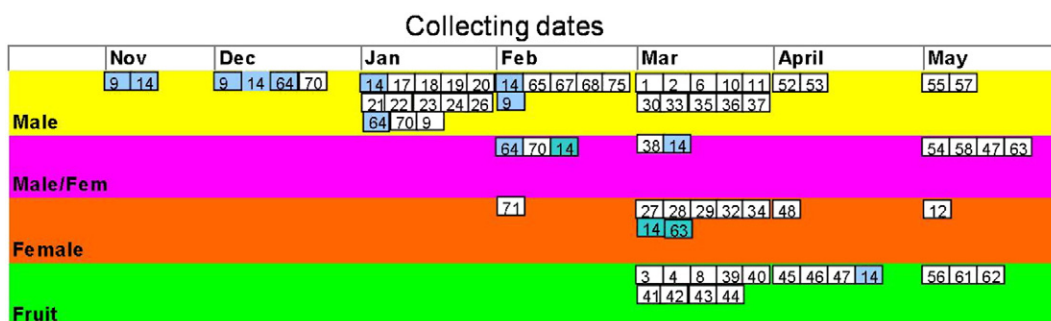


Fig. 6. Diagram showing flower gender, fruit set and collection date of *P. capensis* herbarium specimens collected during field trips and from marked trees during this study. Numbers in shaded blocks refer to specimens collected from the same trees at different dates.

male flowers while lower temperatures and short days may stimulate the formation of female flowers. Indications that the age and virility of *P. capensis* trees also play a role in the sex expression also seem characteristic of other monoecious plants (Richards, 1990).

Richards (1990) states that “sex expression can be controlled by environment, irrespective of size and age” and that “... less salubrious niches tended to induce maleness, and more optimal sites tended to induce femaleness.” The fact that 60% of the herbarium specimens of *Pappea capensis* were collected in the male phase and that more male plants than female plants were encountered during field excursions, can be ascribed to the longer male phase of the trees, quite apart from any possible environmental factors. Korpelainen (1998), working on a large variety of plant taxa, stated that stress caused by less than optimal levels of light, nutrition, weather or water, often favour maleness. Kang (2007), working with pine trees, found that over a 5-year period, 37% of the trees changed their sexual system at least once, ranging from monoecy to male.

From our investigations, we conclude that *P. capensis* trees are genetically monoecious but exhibit temporal dioecism. Due to the continued production of new flowers from higher flower bud orders on the dichasia, male flowers are produced over a long period while female flowers are produced only towards the end of the flowering period, either on the previously male inflorescences or on newly produced female inflorescences. Sex expression in *Pappea capensis* is therefore not stable and appears to be affected by environmental conditions, especially day length and temperature, and possibly also by tree age. The combination of these various influences will render some trees more male and others more female, depending on tree age, virility and time of flowering.

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