

Pattern of Sexual Dimorphism in *Garcinia kola* (Heckel) Plantation

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Abstract

A study was designed to investigate the pattern of sexual dimorphism in a plantation of *Garcinia kola*. Twenty trees were randomly selected for the study and have been observed to flower regularly. A total of 100 inflorescence were randomly collected from the crown of each tree and 500 flowers randomly assessed within the period of four (4) flowering seasons. Floral sex assessment was done visually and with a hand magnifying lens; floral morphometric measurements (i.e. pedicel and perianth length and breadth), inflorescence length, and breadth) was taken using a veneer caliper; number of flowers per inflorescence and inflorescence per twig was counted; while, data analysis was conducted on excel using analysis of variance and pairwise t-test comparison. Four floral sexes were identified in the *G. kola* plantation studied which were unisexual male flowers, unisexual female flowers, cosexual unisexual male flowers, and cosexual hermaphrodite flowers. Three tree sexes were identified viz: inconstant male, invariant female, and cosexual trees. The plantation was significantly sexually dimorphic in floral sex and phenotypic traits (i.e. pedicel and perianth size), and as well as sexually dimorphic in tree sex and reproductive phenotypic traits (i.e. inflorescence size, number of inflorescences per twig, and number of flower bud per inflorescence). The sexual system of the plantation was therefore trioecious with features suggestive of evolving dioecy through the gynodioecious pathway.

Key Words: pistillode, invariant-female, gynodioecy, inconstant-male, staminode

Introduction

Sexual dimorphism is a phenomenon associated with differences in morphological, physiological and life history traits between individuals within populations of a species arising from sexual variation (Barrett and Hought 2013). Sexual dimorphism is a usual characteristic of sexual systems with sexual polymorphism such as monoecious, dioecious and subdioecious populations; although in monoecious populations sexual dimorphism is limited to floral dimorphism (i.e. presence or absence of male or female reproductive organ between two flowers on the same tree)

(Yakimowski et al. 2011). Sexual dimorphism is the result of differential selection intensities between the sexes in a population; pollinator behaviour and resources availability are some factors that can influence the selection or persistence of patterns of sexual dimorphism in a population (Ashman 2000; Delph and Ashman 2006). For example, when the pattern of sexual dimorphism is pollinator driven flower size and display size often is large (Yakimowski et al. 2011). This is often the case in populations where male floral displays are reportedly more than females; floral display size and flower size dimorphism arise due to competition for pollinator visitation in outcrossed populations where

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pollination success may be limited by access to mates (Ashman 2000). Female flower dimorphism on the other hand is controlled more by resources availability than mating competition because of the higher reproductive cost of the female function which is exacerbated by the need for fruit and seed maturation (Delph et al. 1996). Generally therefore sexual dimorphism in unisexual flowers often occur as variations in flower and inflorescence size between male and female flowers such that larger and more conspicuous floral displays are associated with male than female flowers (Delph et al. 1996; Eckhart 1999; Costich and Meagher 2001): although studies in tropical ecosystems have sometimes reported contrary findings (Delph et al. 1996; Humeau et al. 2003).

In dioecious populations the pattern of sexual dimorphism is often traced to the trade-off between male and female functions (Humeau et al. 2003). This trade-off often viewed as reproductive costs is the reason female trees expend and require more resources compared to males; yet the female trees of some species are smaller in size despite higher resources needs due mainly to investment in seed and fruit production as well as defence to ensure reproductive fitness; while male trees are able to invest more on vegetative growth and hence larger in size because their reproductive budget is only for flower and pollen production (Delph 1996; Obeso 2002; Cepeda-Cornejo and Dirzo 2010). In monoecious or cosexual populations such trade-offs may sometimes be absent and floral dimorphism non-existent (Costich and Meagher 2001). This can be linked to self-fertilization or inbreeding in these sexual systems that reduce the intensity of sexual selection and hence a reduction in the potential for evolution of floral dimorphism (Worley and Barrett 2000; Sargent et al. 2007). Self-fertilization is virtually non-existent in dioecious populations since they are obligately outcrossing (Charlesworth 1991, 2002; Nicolas et al. 2005). Drivers of patterns of sexual dimorphism in any population are therefore traceable to genetics and ecology. Since populations are unique in their genetics and ecological vagaries it follows that the pattern of sexual dimorphism would vary from one population to the other as a result of differential sex-specific selection pressure (Fenster and Carr 1997; Sugiyama and Bazzaz 1998). Studies related to sexual dimorphism in any population may provide insights into how selection drives patterns of di-

morphism in sexual systems (Ashman and Diefenderfer 2001; Delph and Ashman 2006).

The genus *Garcinia* (Clusiaceae or Guttiferae) according to Joseph and Murthy (2015) thrives in pantropical and neotropical regions and consists of about 250 species. *Garcinia* is reported to show high diversity of sexual systems including dioecious (Sweeny 2008), gynodioecious (Pangsuban et al. 2007), androdioecious (George et al. 1992), monoecious and andromonoecious (Leal et al. 2013) species. While, Richards (1990a, 1990b) and Richards (1997) has suggested the occurrence of apomixis in pantropical species of *Garcinia* especially in Asian *Garcinia mangostana* L. in which males were not found. In particular, the sexual system of *G. kola* is controversial: Keay et al. (1964) for example considered the species as androdioecious with male and bisexual flowers, whereas Manourova et al. (2019) reported the species is predominantly dioecious but sometimes found with bisexual flowers. Empirical studies of the sexual system and pattern of sexual dimorphism in *G. kola* is therefore largely rare despite the growing literature on the uses and conservation of the species. The study was therefore designed to investigate the pattern of sexual dimorphism in *G. kola*.

Materials and Methods

Plantation description

The study was conducted in an artificial mono-plantation of *Garcinia kola* propagated from seed at the Swamp Forest Research station, of the Forestry Research Institute of Nigeria (FRIN), Onne Rivers state Nigeria. The plantation consists of about 13 stands of 30-year-old trees and more than 80 stands of 11-year-old trees. Flowering and fruiting began in the 11-year-old trees at the age of 8-10 years while the 30-year-olds have flowered and fruited for approximately 20-years already. Flowering and fruiting events occur in the plantation about 3-4 times in a year and overlap i.e. flowers and fruits are present in the plantation almost all year round. Flowering and fruiting intensity per event however is variable but peaks in August-October. The plantation is located on Latitude 4°42'-10°32'N and Longitude 7°10'32°46'E, with 2,400 mm mean annual rainfall, relative humidity 78% in February (dry season) and 89% in July (rainy season), mean annual temperatures

of 27°C in February and 25°C in July. Soils are ultisols derived of coastal sediments, highly acidic (pH 4.4), with low fertility, and classified as siliceous, isohyperthermic, typic paleudult, usually deep, chemically poor, well drained with good physical properties. The vegetation is a humid rainforest in a mangrove transition forest zone (Okonkwo et al. 2020).

Species description

Garcinia kola commonly known as bitter kola is an ever-green tropical rainforest species found in West and Central Africa within which Nigeria and Cameroon are considered the areas of highest endemism (Isawumi 1993; Manourova et al. 2019). *G. kola* is mostly found in moist or coastal forests, lowland rainforests, and derived savannah in West Africa, a distribution pattern largely influenced by rainfall and temperature (Agwu et al. 2020). In the wild *G. kola* trees can grow up to 12 m high and trees as high as 27 m has been reported (Keay et al. 1964). The bole is mostly straight

with brownish smooth bark that produces sticky-yellow water proof latex when wounded which is a trademark of the Clusiaceae family and crown is usually dense, especially in female trees, with slightly drooping branches (Keay et al. 1964; Manourova et al. 2019). Mature *G. kola* leaves are dark green in colour while younger leaves are light greenish and can be up to 6.35-13.97 cm long and 2.5-6.35 cm wide, elongated elliptic to broadly elliptic, acute or shortly acuminate, and cuneate. The leaves are also leathery with very distinct resinous canals; the inflorescence is a terminal umbel with greenish-white flowers on short stalks about 7.62 mm long. Flowers are about 19.05 mm wide with stamens in four broad bundles that alternate with the four fleshy lobes of the disc; ovary is finely hairy, stigmas are 4-lobed and flattened; Male flowers usually are smaller but with more prominent stamens *G. kola* flowers between December and January and fruits between July and October; fruits are reddish yellow and about 63.5 mm wide with 2-4 brownish seeds; the wood is close grained, hard, yellow in colour but darkens to brown at the centre (Keay et al. 1964; Manourova et al. 2019).

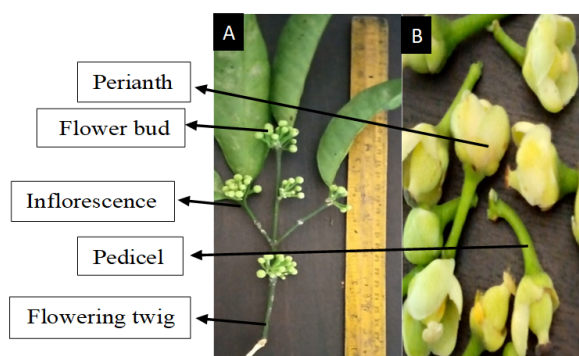


Fig. 1. Description of floral dimorphic traits measured. (A) Flowering twig, (B) Flower.

Floral sex study and morphometric measurements

Twenty trees were randomly selected for the study and have been observed to flower regularly. A total of 100 inflorescence were randomly collected from the crown of each tree and 500 flowers randomly assessed within the period of four flowering seasons.

Floral sex assessment was done visually and with a hand magnifying lens, while floral morphometric measurements (length and breadth of pedicel, length and breadth of perianth) (Fig. 1B), inflorescence length, and breadth was tak-

Table 1. Floral sex description

Flower sex	Description
Male flowers	Unisexual staminate flowers occurring on individual trees alone. Although once in a while (during some flowering season) about 0.00001% unisexual pistillate flowers occur on male trees. In which case a lone fruit could sometimes be found hanging on a predominantly male tree (a phenomenon known as male inconstancy).
Female flowers	Invariant unisexual pistillate flowers found occurring on individual trees alone.
Cosexual male flowers	Unisexual staminate flowers occurring together with hermaphrodite flowers on individual trees in varying proportions.
Cosexual hermaphrodite flowers	Bisexual flowers (perfect flowers, i.e. having male and female reproductive organs all in one single flower) occurring together with male flowers on individual trees.

en using a veneer caliper, while number of flowers per inflorescence and inflorescence per twig was counted (Fig. 1A). Data analysis was done using analysis of variance (ANOVA), pairwise comparison done using t-test, while test of normality was conducted using Shapiro-Wilk.

Results and Discussion

Flower and tree sex

Four flower types occurred in the *G. kola* plantation namely: male flowers (staminate), female flowers (pistillate), cosexual hermaphrodite flowers (staminate and pistillate), and cosexual male flowers (staminate); sterile rudimentary pistil (pistillode) was present in both the male and cosexual male flowers; while in the female flower the staminode is partially rudimentary which suggests it could carry viable pollen (Table 1, Fig. 2). Pollination or pollen viability studies will be required to ascertain the viability of the female flower pollen; there is also a possibility that female flowers produce viable pollen at certain flowering season when male flowers are in short supply, which often is the season before mass flowering; this later hypothesis stems from a preliminary apomixis study in the plantation where a couple of female flowers bagged before anthesis fruited (Okonkwo, *personal communication*).

Hence, three tree sexes were found in the population viz: Invariant females, inconstant males, and cosexual trees; a trioecious sexual system pattern of tree sex mix character-

istic of gynodioecious pathway of dioecy evolution (Sakai and Weller 1999; Okonkwo and Omokhua 2022). Evolution of dioecy through the gynodioecious pathway proceeds from cosexual or hermaphrodite ancestors as a result of two forms of mutation. The male sterile mutation obliterates the male function of hermaphrodite flowers that give rise to female trees and hermaphrodite trees (gynodioecy); in the second type of mutation female function of hermaphrodite flowers is suppressed to give rise to purely male trees (Charlesworth and Charlesworth 1978a; Joseph and Murthy 2015). Dioecy evolution through the monoecious pathway is assumed to proceed from hermaphrodite ancestors when male sterile and female sterile mutations occur simultaneously on individual trees to give rise to monoecy that gradually give rise to dioecy through the specialization of individuals in male or female functions (Charlesworth and Charlesworth 1978b; Ross 1982). The completely rudimentary status of the pistillode in the male flowers suggests that the female sterile mutation is at its advanced stage; while the partially rudimentary nature of the female flower staminode suggests that the male sterile mutation is at its intermediate stage. The female sterile mutation therefore preceded the male sterile mutation in the plantation; this conclusion is corroborated by the fact that the cosexual trees bear bisexual flowers and male flowers with completely suppressed pistillode; an indication of female sterile mutation completion and a starting of loss of bisexual flowers (this can be further confirmed through a study that estimates the ratio of male to bisexual flowers per inflorescence in the cosexual trees). This agrees with the proposition of Bawa and Beach (1981) and Bertin (1982) that rudimentary, intermediate, and complete sexual structures of the opposite sex can exist in the evolution of dioecy from hermaphrodite ancestors. These findings confirm the hypothesis proposed by Joseph and Murthy (2015) that trioecious populations provide opportunity for understanding the dynamics of the evolution of sexual systems.

Pedicle dimorphism among floral sexes

The female flowers recorded the longest pedicel with average pedicel length of 3.3 ± 0.49 mm and 0.43 ± 0.15 mm breadth, male flowers were the second longest with an average pedicel length of 1.27 ± 0.59 mm and 0.2 ± 0.1 mm breadth, this is followed by the cosexual male flower,

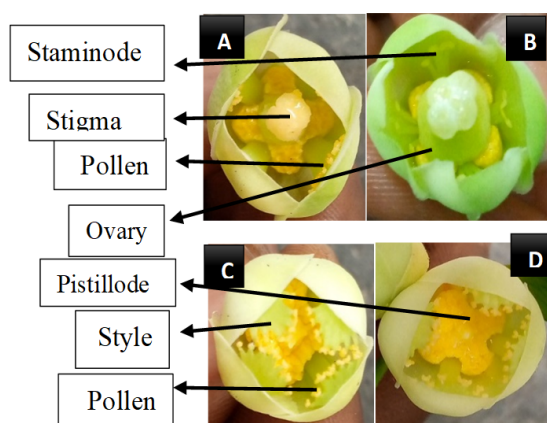


Fig. 2. Flower types (morphs) in the *G. kola* plantation. (A) Cosexual hermaphrodite flower, (B) Female flower, (C) Male flower, (D) Cosexual male flower.

0.8±0.26 mm pedicel length and 0.4±0.35 mm breadth, and the smallest flowers were the cosexual hermaphrodites that recorded 0.7±0.52 mm pedicel length and 0.1±0.01 mm breadth (Table 2). There were significant differences in pedicel length among the flowers (Table 3) and pairwise T-test comparison (Table 4) showed that only female flowers were significantly different in pedicel length from all other sexes i.e. there were no significant differences in pedicel length between male, cosexual male and cosexual hermaphrodite flowers. There were no significant differences in pedicel breadth among the flower sexes (Table 3), however, pairwise T-test comparison (Table 4) showed that female flower pedicel breadth was significantly different from the males and cosexual hermaphrodites. There were no significant differences in pedicel breadth between male, cosexual male, and cosexual hermaphrodite trees.

Female flowers may have evolved larger sized pedicel

due to the need to support the weight of growing fruits which weigh between 100 g to 200 g (Okonkwo, *personal communication*) at maturity. In *Garcinia indica* however, which equally has fairly large fruits, male flowers have longer pedicel than females (Joseph and Murthy 2015). Whereas, in *Jacaratia mexicana*, which also bear fairly large fruits, female flowers have longer pedicel than males (Aguirre et al. 2009). Hence, the hypothesis proposed above that large female flower pedicel size in *G. kola* may have evolved due to the potential to carry large and heavy mature fruits may need to be investigated further. Dimorphism in male and female flower pedicel size needs to be investigated between large fruit bearing and small fruit bearing species to clearly determine the role of fruit size in the evolution of flower pedicel size.

Table 2. Mean values of phenotypic traits of flower and tree sex morphs

	Flower sex			
	Male	Female	Cosexual hermaphrodite	Cosexual male
Pedicel length	1.27±0.59	3.3±0.49	0.7±0.52	0.8±0.26
Pedicel breadth	0.2±0.1	0.43±0.15	0.1±0.01	0.4±0.35
Perianth length	0.5±0.08	0.8±0.26	0.23±0.12	0.4±0.01
Perianth breadth	0.6±0.07	0.78±0.13	0.23±0.12	0.4±0.01
	Tree sex			
	Male	Female	Cosexual	
Inflorescence length	21.5±3.1	30.3±3.06	3.1±0.46	
Inflorescence breadth	0.1±0.01	0.35±0.14	0.1±0.01	
Inflorescence per twig	3.3±0.48	2.3±0.48	3.1±0.11	
Flower bud per inflorescence	15.9±4.93	5.2±0.79	11±3.61	

Table 3. ANOVA of phenotypic traits of flower and tree sex morphs

Source of variance	SS	df	MS	F	p
Pedicel length	13.27	3	4.423333	26.33242	0.000603**
Pedicel breadth	0.23	3	0.076667	1.508197	0.284947 ^{ns}
Perianth length	1.72688	3	0.575627	26.33242	3.42E-09**
Perianth breadth	1.72368	3	0.57456	60.31071	4.09E-14**
Inflorescence length	1,163.14	2	581.5712	38.93413	3.41E-11**
Number of flower bud	1,867.633	2	933.8167	81.75019	1.81E-17**
Inflorescence per twig	75.41667	2	37.70833	18.78979	7.71E-06**

p≤0.05=significant, while p>0.05=not significant.

Table 4. Pairwise T-test comparison of phenotypic characters of flower and tree sex morphs in trioecious *G. kola* population

Group 1	Group 2	p-value	Mean
Stalk length			
Male flower	Female flower	0.011417**	2.033333
Male flower	Cosexual hermaphrodite	0.279273 ^{ns}	0.566667
Male flower	Cosexual male	0.303832 ^{ns}	0.466667
Female flower	Cosexual hermaphrodite	0.00372**	2.6
Female flower	Cosexual male	0.005631**	2.5
Cosexual hermaphrodite flower	Cosexual male	0.785984 ^{ns}	0.1
Stalk breadth			
Male flower	Female	0.035653**	0.233333
Male flower	Cosexual hermaphrodite	0.225403 ^{ns}	0.1
Male flower	Cosexual male flower	0.51285 ^{ns}	0.2
Female	Cosexual hermaphrodite	0.009852**	0.333333
Female	Cosexual male	0.907188 ^{ns}	0.033333
Cosexual hermaphrodite	Cosexual male	0.355497 ^{ns}	0.3
Flower length			
Male flower	Female flower	0.00509**	0.3
Male flower	Cosexual hermaphrodite	1.99E-05**	0.272
Male flower	Cosexual male flower	0.003772**	0.1
Female flower	Cosexual hermaphrodite	2.82E-05**	0.572
Female flower	Cosexual male flower	0.000849**	0.4
Cosexual hermaphrodite	Cosexual male flower	0.001329**	0.172
Flower breadth			
Male flower	Female flower	0.002248**	0.18
Male flower	Cosexual hermaphrodite	4.36E-07**	0.372
Male flower	Cosexual male	2.86E-05**	0.2
Female flower	Cosexual hermaphrodite	1.25E-08**	0.552
Female flower	Cosexual male	7.61E-06**	0.36
Cosexual hermaphrodite	Cosexual male	0.001329**	0.172
Inflorescence length			
Cosexual hermaphrodite + male	Male	0.572579 ^{ns}	0.705263
Cosexual hermaphrodite + male	Female	1.72E-09**	9.915789
Male tree	Female	1.95E-08**	9.210526
Inflorescence breadth			
Cosexual hermaphrodite + male	Male	1 ^{ns}	0.1
Cosexual hermaphrodite + male	Female	3.26E-07**	0.2
Male	Female	3.26E-07**	0.2
Number of flower bud per inflorescence			
Cosexual hermaphrodite + male	Male	2.87E-06**	7.4
Cosexual hermaphrodite + male	Female	8.28E-09**	6.25
Male	Female	1.25E-10**	13.65
Number of inflorescences per twig			
Cosexual hermaphrodite + male	Male	0.00492**	2.75
Cosexual hermaphrodite + male	Female	0.00064**	3.75
Male	Female	0.00021**	1

$p \leq 0.05$ = significant, while $p > 0.05$ = not significant.

Perianth size dimorphism

Mean largest perianth size was recorded in the female flowers at 0.8 ± 0.26 mm length and 0.78 ± 0.13 mm breadth; male flowers were the second largest at 0.5 ± 0.08 mm length and 0.6 ± 0.07 mm breadth, this is followed by the cosexual male flowers at 0.4 ± 0.01 mm length and 0.4 ± 0.01 mm breadth, while the smallest flowers were the cosexual hermaphrodite flowers at 0.23 ± 0.12 mm length and 0.23 ± 0.12 mm breadth (Table 2). Analysis of variance showed there were significant differences in perianth size (length and breadth) among the four flower sexes (Table 3). Pairwise T-test comparison showed there were significant differences in perianth length and breadth between each pair of the four floral sexes (Table 4).

Garcinia indica shows exactly the exact opposite of perianth dimorphism observed above in *G. kola*: i.e. bisexual flowers of *G. indica* were largest, followed by males while female flowers were the smallest (Joseph and Murthy 2015). Furthermore, bisexual and cosexual male flowers perianth size in the *G. kola* population studied were intermediate between the male and female flower perianth size; a situation associated with developmental instability in most subdioecious populations (Joseph and Murthy 2015). Diversity of perianth and sexual structure forms, ranging from rudimentary, intermediate, to complete structures is characteristic of gynodioecious and monoecious pathways of dioecism evolution; this accounts for the sexual polymorphism associated with trimonoecy and trioecy or subdioecy (Charlesworth and Charlesworth 1978b; Wilson 1979; Bawa and Beach 1981; Bertin 1982). Sexual inconstancy and biased expression of sexes in trioecious populations provide opportunities for understanding the evolutionary pathway of dioecy. Often, when dioecy evolves through the gynodioecious pathway, they feature invariant females and inconstant males that sometimes bear fruit or set seed (Lloyd 1975; Ross 1982). While the monoecious pathway features opposite sex flowers emergence on unisexual trees (Charlesworth and Charlesworth 1978b; Ross 1982). This therefore suggests the *G. kola* population studied shows features synonymous with the process of evolution of dioecism through the gynodioecious pathway as evidenced by the presence of intermediate sexual structures, invariant females, and inconstant males (Table 1).

Perianth size dimorphism can be mediated by pollinator, pollination method, heritability of floral traits, and size of the reproductive organ they protect (Delph 1996; Delph et al. 1996; Eckhart 1999). Contrary to the general idea that in most animal pollinated unisexual flowers male flowers are usually larger than female (Delph et al. 1996; Eckhart 1999); our findings show a *G. kola* plantation where unisexual female flowers that are animal pollinated (Okonkwo, personal communication) are larger than male flowers. Male flowers may have traded size for number of flowers per inflorescence since according to Worley and Barrett (2000) and Sargent et al. (2007) such trade-offs do happen and can be a consequence of resource constrain; while the female flower size could be due to the large ovary size (i.e. 1.01 ± 0.2 mm (Okonkwo, personal communication)) and not pollinator mediated.

Inflorescence dimorphism

Female trees recorded the longest inflorescence length 30.3 ± 3.06 mm and breadth 0.35 ± 0.14 mm: male trees recorded the second longest inflorescence length 21.5 ± 3.1 mm and 0.1 ± 0.01 mm breadth; cosexual trees recorded the shortest inflorescence length 3.1 ± 0.46 mm and 0.1 ± 0.01 mm. Number of inflorescence per twig was highest in male trees 3.3 ± 0.48 ; followed by the cosexuals 3.1 ± 0.11 ; female trees recorded the lowest number of inflorescence per twig 2.3 ± 0.48 . Number of flower buds per inflorescence was highest in male trees 15.9 ± 4.93 , followed by cosexual trees 11 ± 3.61 ; female trees recorded the lowest number of flower buds per inflorescence 5.2 ± 0.79 (Table 2). Inflorescence size (length and breadth), number of inflorescences per twig, and number of flower bud per inflorescence was significantly different among the tree sexes (Table 3). Pairwise T-test comparison (Table 4) showed that female tree inflorescence size was significantly different from male and cosexual trees: while there were no significant differences in inflorescence size between male and cosexual trees (Table 3). Number of inflorescences per twig and flower bud per inflorescence was significantly different between each pair of the three tree sexes (Male, female, and cosexual) (Table 4).

There was no correlation between inflorescence length and flower production in this study. In *Thymus vulgaris* there were no significant differences in inflorescences mor-

phology or flower production between male and female trees (Assouad et al. 1978). However, in consonance with the findings of this study Yakimowski et al. (2011) and Joseph and Murthy (2015) found there were significant differences in inflorescence morphology and number of flowers per inflorescence between male and female plants of *Sagittaria latifolia* and *G. indica*. Selection for higher male flower production is associated with unisexual flowers (Yakimowski et al. 2011) as is the case in this study. This is so because of the lesser cost of the male function per flower when compared to the female function; which makes selection for increased mating opportunities to favour higher male floral display (Delph 1996; Eckhart 1999; Costich and Meagher 2001).

Conclusion

The pattern of sexual dimorphism in the artificial *Garcinia kola* plantation is akin to an evolving dioecy from an ancestral hermaphrodite via the gynodioecious pathway. A graphical illustration of the stage of the evolutionary process is portrayed by the presence of male flowers with rudimentary sterile pistillode, functional bisexual flowers, female flowers with partially rudimentary staminodes, invariant female trees and inconstant male trees; all of which showed that: first, the female sterile mutation that turns hermaphrodite flowers to males is completed; second, the male sterile mutation that produces female flowers is at its intermediate stage; third, invariant female and inconstant male trees are evidence of the gynodioecious intermediate of an evolving dioecy. Hence the sexual dimorphic character of the plantation evidenced by significant differences in pedicel, perianth, and inflorescence size, number of inflorescences per twig, and number of flowers per inflorescence between the sexes are only pointers to the dynamic nature of the sexual system of the plantation. The plantation therefore affords the opportunity for the study of the evolution of sexual systems particularly for the genus *Garcinia*.

References

- Aguirre A, Vallejo-Marín M, Piedra-Malagón EM, Cruz-Ortega R, Dirzo R. 2009. Morphological variation in the flowers of *Jacaratia mexicana* A. DC. (Caricaceae), a subdioecious tree. *Plant Biol (Stuttg)* 11: 417-424.
- Agwu OP, Bakayoko A, Bolanle-Ojo OT, Jimoh SO, Stefan P. 2018. Influence of Climate, Seed Sizes and Land Use Types on the Germination and Early Growth of *Garcinia kola* and *Cola nitida* in Nigeria. *Agri Res Tech* 19: 556083.
- Ashman TL. 2000. Pollinator selectivity and its implications for the evolution of dioecy and sexual dimorphism. *Ecology* 81: 2577-2591.
- Ashman TL, Diefenderfer C. 2001. Sex ratio represents a unique context for selection on attractive traits: consequences for the evolution of sexual dimorphism. *Am Nat* 157: 334-347.
- Assouad MW, Dommée B, Lumaret R, Valdeyron G. 1978. Reproductive capacities in the sexual forms of the gynodioecious species *Thymus vulgaris* L. *Bot J Linn Soc* 77: 29-39.
- Barrett SC, Hough J. 2013. Sexual dimorphism in flowering plants. *J Exp Bot* 64: 67-82.
- Bawa KS, Beach JH. 1981. Evolution of Sexual Systems in Flowering Plants. *Ann Mo Bot Gard* 68: 254-274.
- Bertin RI. 1982. The evolution and maintenance of andromonoecy. *Evol Theory* 6: 25-32.
- Cepeda-Cornejo V, Dirzo R. 2010. Sex-related differences in reproductive allocation, growth, defense and herbivory in three dioecious neotropical palms. *PLoS One* 5: e9824.
- Charlesworth B. 1991. The evolution of sex chromosomes. *Science* 251: 1030-1033.
- Charlesworth B, Charlesworth D. 1978a. A Model for the Evolution of Dioecy and Gynodioecy. *Am Nat* 112: 975-997.
- Charlesworth D. 2002. Plant sex determination and sex chromosomes. *Heredity* 88: 94-101.
- Charlesworth D, Charlesworth B. 1978b. Population genetics of partial male-sterility and the evolution of monoecy and dioecy. *Heredity* 41: 137-153.
- Costich DE, Meagher TR. 2001. Impacts of floral gender and whole-plant gender on floral evolution in *Ecballium elaterium* (Cucurbitaceae). *Biol J Linn Soc* 74: 475-487.
- Delph LF. 1996. Flower size dimorphism in plants with unisexual flowers. In: *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants* (Lloyd DG, Barrett SCH, eds). Chapman and Hall, New York, pp 217-237.
- Delph LF, Ashman TL. 2006. Trait selection in flowering plants: how does sexual selection contribute? *Integr Comp Biol* 46: 465-472.
- Delph LF, Galloway LF, Stanton ML. 1996. Sexual Dimorphism in Flower Size. *Am Nat* 148: 299-320.
- Eckhart VM. 1999. Sexual dimorphism in flowers and inflorescences. In: *Gender and Sexual Dimorphism in Flowering Plants* (Geber MA, Dawson TE, Delph LF, eds). Springer, New York, pp 123-148.
- Fenster CB, Carr DE. 1997. Genetics of sex allocation in *Mimulus* (Scrophulariaceae). *J Evol Biol* 10: 641-661.
- George ST, Latha AKB, Mathew KL, Geetha CK. 1992. Pattern

- of flowering and flower development in kodapuli (*Garcinia cambogia* Desr.). *Indian Cocoa Arecanut Spices J* 16: 68-70.
- Harder LD, Barrett SCH. 1996. Pollen dispersal and mating patterns in animal-pollinated plants. In: *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants* (Lloyd DG, Barrett SCH, eds). Chapman and Hall, New York, pp 140-190.
- Humeau L, Pailler T, Thompson J. 2003. Flower size dimorphism in diclinous plants native to La Réunion Island. *Plant Syst Evol* 240: 163-173.
- Isawumi AM. 1993. The common edible fruits of Nigeria, Part II. *Niger Field* 58: 1-2.
- Joseph KS, Murthy HN. 2015. Sexual system of *Garcinia indica* Choisy: geographic variation in trioecy and sexual dimorphism in floral traits. *Plant Syst Evol* 301: 1065-1071.
- Keay RWJ, Onochie CFA, Stanfield DP. 1964. *Nigerian Trees*. Department of Forest Research, Ibadan.
- Leal DO, Benevides CR, Silva RCP, Santiago-Fernandes LDR, Sá-Haiad B, Lima HA. 2013. *Garcinia brasiliensis*: insights into reproductive phenology and sexual system in a Neotropical environment. *Plant Syst Evol* 299: 1577-1585.
- Lloyd DG. 1975. Breeding Systems in *Cotula*. III. Dioecious Populations. *New Phytol* 74: 109-123.
- Maňourová A, Leuner O, Tchoundjeu Z, Van Damme P, Verner V, Přebyl O, Lojka B. 2019. Medicinal Potential, Utilization and Domestication Status of Bitter Kola (*Garcinia kola* Heckel) in West and Central Africa. *Forests* 10: 124.
- Morgan M. 1993. Fruit to flower ratios and trade-offs in size and number. *Evol Ecol* 7: 219-232.
- Nicolas M, Marais G, Hykelova V, Janousek B, Laporte V, Vyskot B, Mouchiroud D, Negruțiu I, Charlesworth D, Monéger F. 2005. A gradual process of recombination restriction in the evolutionary history of the sex chromosomes in dioecious plants. *PLoS Biol* 3: e4.
- Obeso JR. 2002. The costs of reproduction in plants. *New Phytol* 155: 321-348.
- Okonkwo HO, Eric EE, Ejizu AN. 2020. Tree-to-Tree Variation of Seed Germination Characteristics in a *Garcinia kola* (Heckel) Plantation in the Humid Tropical Rainforest. *J Agric Food Environ* 7: 1-6.
- Okonkwo HO, Omokhua GE. 2022. Sexual system, sexual polymorphism and resource partitioning in a *Garcinia kola* (Heckel) population at Onne, River state Nigeria. *J For Sci Environ* 7: 49-55.
- Pangsuban S, Bamroongrugsa N, Kanchanapoom K, Nualsri C. 2007. An evaluation of the sexual system of *Garcinia atroviridis* L. (Clusiaceae), based on reproductive features. *Songklanakarin J Sci Technol* 29: 1457-1468.
- Richards AJ. 1990a. Studies in *Garcinia*, dioecious tropical forest trees: the agamospermy. *Bot J Linn Soc* 103: 233-250.
- Richards AJ. 1990b. Studies in *Garcinia*, dioecious tropical forest trees: the phenology, pollination biology and fertilization of *G. hombroniana* Pierre. *Bot J Linn Soc* 103: 251-261.
- Richards AJ. 1997. *Plant Breeding Systems*. 2nd ed. Chapman and Hall, London.
- Ross MD. 1982. Five Evolutionary Pathways to Subdioecy. *Am Nat* 119: 297-318.
- Sakai AK, Weller SG. 1999. Gender and sexual dimorphism in flowering plants: a review of terminology, biogeographic patterns, ecological correlates, and phylogenetic approaches. In: *Gender and Sexual Dimorphism in Flowering Plants* (Geber MA, Dawson TE, Delph LF, eds). Springer, New York, pp 1-31.
- Sakai S. 1993. Allocation to attractive structures in animal-pollinated flowers. *Evolution* 47: 1711-1720.
- Sargent RD, Goodwillie C, Kalisz S, Ree RH. 2007. Phylogenetic evidence for a flower size and number trade-off. *Am J Bot* 94: 2059-2062.
- Sugiyama S, Bazzaz FA. 1998. Size dependence of reproductive allocation: the influence of resource availability, competition and genetic identity. *Funct Ecol* 12: 280-288.
- Sweeney PW. 2008. Phylogeny and Floral Diversity in the Genus *Garcinia* (Clusiaceae) and Relatives. *Int J Plant Sci* 169: 1228-1303.
- Willson MF. 1979. Sexual Selection in Plants. *Am Nat* 113: 777-790.
- Worley AC, Barrett SCH. 2000. Evolution of floral display in *Eichhornia paniculata* (Pontederiaceae): direct and correlated responses to selection on flower size and number. *Evolution* 54: 1533-1545.
- Yakimowski SB, Glaetli M, Barrett SCH. 2011. Floral dimorphism in plant populations with combined versus separate sexes. *Ann Bot* 108: 765-776.