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## SEXUAL SYSTEM, SEXUAL POLYMORPHISM AND RESOURCE PARTITIONING IN A *GARCINIA KOLA* (HECKEL) POPULATION AT ONNE, RIVER STATE NIGERIA

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**ABSTRACT:** There is a controversy in literature over the sexual system of *Garcinia kola*. This suggests the possibility of within species diversity of sexual system in the species occasioned by variations in environmental conditions. The present study investigates the sexual system, sexual polymorphism and resource allocation in a population of *G. kola* in the humid tropical rainforest south of Nigeria. Nine (9) trees that have been observed to flower regularly were randomly selected for the study. A total of 100 inflorescence was 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. Four (4) flowering twigs were randomly collected from the crown of three (3) each of the sexes (male, female, and cosexual trees). Twigs were subsequently separated into floral parts (flowers, and inflorescences) and vegetative parts (leaves and stem) and air-dried at ambient temperature until constant weigh was achieved. Results showed that the *G. kola* population studied was subdioecious (trioecious) presenting male, female and bisexual flowers i.e., male trees bore unisexual staminate flowers, female trees unisexual pistillate flowers, while cosexuals either bore staminate and bisexual flowers (hermaphrodite or perfect flowers) or staminate and pistillate flowers on individual trees. Frequency of sex expression in the population was male trees 25%, female trees 55%, and cosexual trees 20%; reproductive allocation was male tree 7.89%, female tree 26.39%, and cosexual tree 21.98%; vegetative dry weight was male tree 18.05g, female tree 4.55g, and cosexual tree 21.62%; while, floral dry weight was male tree 0.98g, female tree 1.10g, and cosexual tree 4.76g. Analysis of variance showed that there were significant differences in vegetative dry weight, floral dry weight, and reproductive allocation among the tree sexes.

**Keywords:** Subdioecious, flowers, cosexual, trioecious, bisexual

### 1. INTRODUCTION

The *Garcinia* genus is reportedly well distributed in pantropical and neotropical areas with around 250 species (Joseph and Murthy (2014). High sexual system

diversity has been associated with the geographic spread of the genus. Examples of sexual systems that have been reported in the genus thus far are dioecious (Sweeny 2008), gynodioecious (Pangsuban *et al.* 2007), androdioecious (Berg 1979, George *et al.* 1992),

monoecious and andromonoecious (Leal *et al.* 2013) species. Purely apomictic reproductive behaviour where male flowers were completely absent in the species has been reported in some species in the genus such as Asian *Garcinia mangostana* L Richards (1990a, b, 1997). Within species diversity of sexual system has also been reported in the genus *Garcinia*. For example, the sexual system of *G. indica* is said to be controversial (Joseph and Murthy, 2014); whereas Rawat and Bhatnagar (2005) consider the species to be gynodioecious, Rajasekharan and Ganeshan (2002) reported it as polygamodioecious.

Hermaphroditism as a sexual system is the evolutionary origin of all the spectrum of plant sexual systems observable today. Dioecy, for example evolved from hermaphroditism by way of five possible pathways (Ross 1980, 1982; Webb 1999), i.e. (1) via monoecy, (2) directly from hermaphroditism, (3) via gynodioecy, (4) via distyly and (5) via androdioecy. Two main pathways, the gynodioecious and the monoecious, are considered prevalent in the evolution of dioecy (Webb 1999). The gynodioecious pathway (Lloyd 1975; Ross 1982) suggests that dioecy evolved from hermaphroditic or cosexual ancestors in a two-step process. In the first step, a male sterile mutation first spreads through the population, rendering some individual females, while others remain hermaphrodite (i.e., gynodioecy; Darwin 1877; Charlesworth and Charlesworth 1978a). In the second step, the selection acting on the pollen-producing hermaphrodites favors specialization in the male function, and hermaphrodites gradually lose their female reproductive function. The monoecious pathway suggests that dioecy evolved from hermaphroditic individuals through an intermediate stage of monoecy, i.e., separate male and female flowers on the same individual (Ross 1982), which gradually specialized toward the male or female functions.

Empirical evidence indicates that production of only bisexual flowers is the ancestral conditions in angiosperms (Richards 1997; Doyle 1998; Endress 2001). Hence, all the diversity in the arrangement of bisexual and unisexual flowers has repeatedly evolved from a cosexual ancestor. Earlier studies suggested that dioecy evolved through the gynodioecious pathway (Darwin 1877; Lewis 1942; Westergaard 1958) although monoecy appeared to be ancestral to dioecy in a few instances (Cronquist 1988). Modern empirical assessment based on comparative data suggests that hermaphroditism gave rise to dioecy mainly through the monoecious pathway (Weiblen *et al.* 2000; Torices *et al.* 2011).

The gynodioecious pathway usually involves two mutations, one determining the male sterility and other determining the female sterility (Charlesworth and

Charlesworth 1978b) whereas the monoecious pathway involves multiple mutations in combination with environmental regulation of sex expression (Lloyd 1975, 1980; Freeman *et al.* 1997; Renner and Won 2001). Along these pathways, intermediate stages can exist in which individuals may produce rudimentary, intermediate and complete sexual structures of the other sex leading to sexual systems such as trimonoecy, subdioecy or trioecy (Charlesworth and Charlesworth 1978b; Willson 1979; Bawa and Beach 1981; Bertin 1982). Such subdioecious or trioecious species (Sakai and Weller 1999) are widespread (Darwin 1877; Ehlers and Bataillon 2007). It has been suggested that patterns of sexual inconstancy or biased expression in trioecious species can shed light on the evolutionary pathways to dioecy (Ross 1982). Generally, dioecious taxa that evolve through the gynodioecious pathway tend to have female plants that are invariant in sexual expression, and male plants which occasionally set seed (Lloyd 1975; Ross 1982). In the monoecious pathway, flowers of the other sex might occur both in male and female plants (Charlesworth and Charlesworth 1978b; Ross 1982). Thus, the study of species with intermediate stages close to dioecy provides insights into the most likely pathway of evolution of dioecy.

There is a controversy in literature over the sexual system of *G. kola*: whereas Keay *et al.* (1964) reported the species is monoecious, Manourova *et al.* (2019) consider the species to be predominately dioecious and bearing sometimes bisexual flowers. This suggests the possibility of the presence of within species diversity of sexual system in the species occasioned by variations in environmental conditions. The present study investigates the sexual system, sexual polymorphism and resource allocation in a trioecious population of *G. kola* in the humid tropical rainforest south of Nigeria.

## 2. MATERIALS AND METHODS

### 2.1 Study Area

The study was conducted at the Swamp Forest Research station, of the Forestry Research Institute of Nigeria at Onne Rivers state. The area is located on Latitude 4°42' - 10°32'N and Long. 7°10' - 32°46'E, with 2400 mm mean annual rainfall, relative humidity 78% in February (dry season) and 89% in July (rainy season), mean annual temperature 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.

## 2.2 Study Population and Floral Sex Studies

The study population is a mixture of 30-year-olds and 10-year-olds consisting of around 100 *G. kola* trees. Nine (9) trees that have been observed to flower regularly for three years were randomly selected for the study. A total of 100 inflorescence was 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.

## 2.3 Resource Partitioning Studies

Five (5) flowering twigs were randomly collected from the crown of three (3) trees each of the sexes (male, female, and cosexual trees) to make a total of nine (9) trees. Twigs were subsequently separated into floral parts (flowers, and inflorescences) and vegetative parts (leaves and stem) and air-dried at ambient temperature until constant weigh was achieved. Reproductive allocation (RA) was calculated viz;

$$RA = \frac{\text{Dry weight of Flower or inflorescence}}{\text{Vegetative dry weight of the plant}} \times 100 \dots (1)$$

## 2.4 Data Analysis

The experiment was completely randomized design in its layout where tree sex were the treatments; hence data analysis of carried out using one-way analysis of variance (ANOVA) and pairwise t-test used to compare treatments as two independent variables at 5% probability level.

## 3. RESULTS AND DISCUSSION

### 3.1. Sexual System and Sexual Polymorphism in Trioecious *G. kola* Population

*Garcinia kola* population studied at Onne was subdioecious (trioecious) comprising of male, female and bisexual flowers i.e. male trees bore unisexual staminate flowers, female trees unisexual pistillate flowers, while cosexuals either bore staminate and bisexual flowers (hermaphrodite or perfect flowers) or staminate and pistillate flowers on individual trees. Frequency of sex expression in the population was male trees 25%, female trees 55%, and cosexual trees 20%. Of the 20% cosexuals, 10% bore predominantly staminate flowers and around 0.00001 % pistillate flowers (a phenomenon known as *male sex inconstancy* (Barret, 2013)); while 10% bore staminate and bisexual flowers (Figure 1). The pattern of floral sex variation portrayed by the *G. kola* population studied bears semblance with the case of *Sagittaria latifolia* reported by Dorken *et al.* (2022): about 5% of male trees in some populations of the species bear some pistillate flowers (though the species is primarily dioecious); some populations of the species have also been found showing subdioecious sexual system (female, males, and hermaphrodites),

androdioecious (males and hermaphrodites), and gynodioecious (females and hermaphrodites). Subdioecious sexual system is associated with reversions from dioecy. Lloyd (1975) reported a case of complete reversion from dioecy to monoecy in some species of *Cotula* and *Momordica* (Schaefer and Renner, 2010). Sexual systems evolution is driven by the forces of natural selection and they only become perennial when they are adaptive while non adaptive sexual systems only appear temporarily in populations.

Sexual-system-specific molecular-markers based studies have shown that subdioecious populations arise from two separate evolutionary mechanisms: (1) from dioecious populations by way of multiplication of sex inconstant males, or (2) through hybridization between monoecious and dioecious populations (Barrett *et al.* 2010). The *G. kola* population investigated in the present study is an isolated plantation that is surrounded by mangrove forests, settlements, and massive coastal developments. It is therefore unlikely that the route of emergence of the present subdioecious sexual system in the population is through hybridization between monoecious and dioecious populations. The sexual system most likely evolved through increase in the frequency of sex inconstant males in a dioecious sexual system. Moreover, the study population is a plantation grown from seeds collected from drier provenances when compared to the plantation growth environment. Therefore, we conclude that the adaptive sexual system of the population is dioecism and that the subdioecious sexual system is a transition phase in the adjustment of the population to the new environmental realities. Furthermore, the presence of sex invariant females and inconstant males (a characteristic feature of dioecious populations or taxa that evolved from gynodioecy (Lloyd 1975; Ross 1982)

corroborates the conclusion that the *G. kola* population studied is a dioecious population in a temporary phase of trioecy.

Subdioecism (trioecy) as a sexual system has been reported in other species in the genus *Garcinia*. For example, Joseph and Murthy (2014) reported trioecy in seven populations of the species *G. indica* in India. Other sexual systems that have been reported in the *Garcinia* genus are: dioecious (Sweeny 2008), gynodioecious (Pangsuban *et al.* 2007), androdioecious (Berg 1979,

George *et al.* 1992), monoecious and andromonoecious (Leal *et al.* 2013) species. Moreover, Richards (1990a, b, 1997) reported apomixis in some pantropical species of *Garcinia* in Asia such as *Garcinia mangostana* particularly in which male trees were never found (Richards 1990b). The genus *Garcinia* is therefore characterized by a diversity of sexual system and provides opportunity for studies on sexual system transitions as well as the environmental cues that trigger the switch.

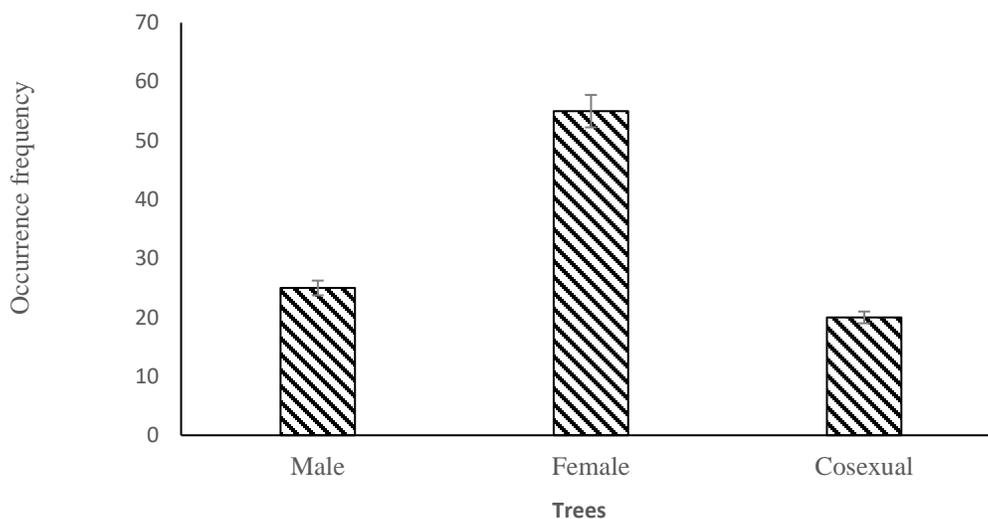


Figure 1. Sexual polymorphism in trioecious *G. kola* population

### 3.2 Intersexual Variation in Resource Partitioning in Subdioecious (Trioecious) Sexual System

Reproductive allocation in the population was male 7.89%, female 26.39%, and cosexual 21.98%; vegetative dry weight was male 18.05g, female 4.55g, and cosexual 21.62%; while, floral dry weight was male 0.98g, female 1.10g, and cosexual 4.76g (Figure 2). Analysis of variance showed that there were significant differences in vegetative dry weight, floral dry weight, and reproductive allocation among the sexes (Table 1). This shows that male and cosexual trees allocated more resources to vegetative growth than female trees; while female trees allocated more resources to reproduction than male and cosexual trees. Pairwise t-test comparison (Table 2) showed that resource allocation to vegetative growth in female trees was significantly different from male and cosexual trees; resource allocation to vegetative growth in male trees, however, was not significantly different from the cosexuals. Table 2 further showed that

though resource allocation to floral growth was not significantly different between male and female trees, they were, however, significantly different from cosexual trees. Finally, Table 2 showed that, resource allocation to reproduction in female and cosexual trees was not significantly different, they were however, significantly different from the male trees. This showed that female function in the trioecious population involved a trade-off between vegetative growth and reproduction. This is consistent with the argument (Bazzaz, 1997; Ehlers and Bataillon, 2007; Cepeda-Cornejo and Dirzo 2010; Shivannah and Tandon, 2014) that female trees in dioecious populations allocate more resources to reproduction than male. Even cosexuals by mere fact of having female flowers allocated lesser resources to vegetative growth than male trees. The finding has significant consequences for nursery growth and sexual differentiation of *G. kola* in the nursery. Variations in growth performance can therefore be used to separate the sexes even at the nursery level. Similar observations were made by Cepeda-Cornejo and Dirzo (2010) on the

species *Chamaedorea alternans*, *C. pinnatifrons*, and *C. ernesti-augusti*. These species showed variations in reproductive and vegetative allocation between the male

and female plants: intersexual variation within the species extended even up to physical toughness of tissue (leaf), and chemical defense against herbivory.

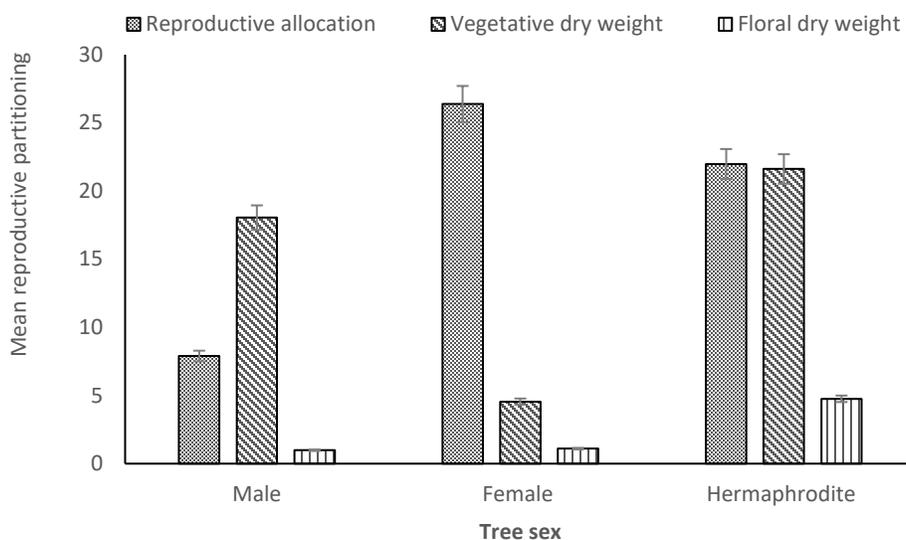


Figure 2. Resource allocation in a subdioecious (trioecious) *G. kola* population.

Table 1. ANOVA reproductive partitioning among the tree sexes

Sources	SS	df	MS	F	p-value
Reproductive allocation	1865.9	2	932.95	28.25	<b>0.000**</b>
Floral dry weight	92.08	2	46.04	198.601	<b>0.000**</b>
Vegetative dry weight	1620.73	2	810.36	11.28	<b>0.000**</b>

\*\*=significant i.e.,  $p < 0.05$ .

Table 2. Pairwise T-test comparison of resource partitioning among tree sexes in trioecious *G. kola* population.

Comparison of reproductive partitioning	p-value	Mean
Female vegetative dry weight vs male vegetative dry weight	<b>0.015**</b>	13.496
Female vegetative dry weight vs hermaphrodite vegetative dry weight	<b>0.000**</b>	17.068
Male vegetative dry weight vs hermaphrodite vegetative dry weight	0.456*	3.572
Female floral dry weight vs male floral dry weight	0.449*	0.122
Female floral dry weight vs hermaphrodite floral dry weight	<b>0.000**</b>	3.654
Male floral dry weight vs hermaphrodite floral dry weight	<b>0.000**</b>	3.776
Female reproductive allocation vs male reproductive allocation	<b>0.000**</b>	18.493
Female reproductive allocation vs hermaphrodite reproductive allocation	<b>0.000**</b>	14.03
Male reproductive allocation vs hermaphrodite reproductive allocation	0.129*	4.41

\*\*=significant i.e.  $p < 0.05$ ; \*=not significant  $p > 0.05$

#### 4. CONCLUSION

1. The sexual system of *Garcinia kola* population studied was subdioecious (trioecious) with its characteristic sexual polymorphism of flowers viz: staminate (unisexual male flowers), pistillate (unisexual female flowers), and hermaphrodite or perfect (bisexual) flowers.

2. Trees were either unisexual male, unisexual female, or cosexual (bearing either male and very few female flowers or male and bisexual flowers).
3. There were significant variations in resource partitioning among the sexes. The study provides some insight into the sexual system and polymorphism of *G. kola*. Moreover, knowledge of the pattern of resource partitioning among the sexes

provides a tool for differentiating the sexes in the nursery at seedling level.

4. The findings of the study corroborate the conclusions of similar studies on different other species of the genus *Garcinia* that the genus is sexually diverse.

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