



SEXUAL SYSTEM POLYMORPHISM IN FOREST TREES: A LATENT TOOL FOR SUSTAINABLE FOREST MANAGEMENT IN NIGERIA

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Abstract

Production of progeny in the tropical rainforest starts with flower development, and different tree species have different sexual types and sexual systems. Pollination can occur either within a flower or between flowers of the same tree (cross-pollination) or flowers of different trees (cross-pollination). Mating among relatives results in the loss of heterozygosity that is reflected in phenotypic traits of adaptive or economic significance. However, some tree species have self-incompatibility systems. Out-crossing, which is the movement of pollen from a tree to another tree, often results in increased genetic diversity. Thus, such species' capability for adaptation and survival under hazardous environmental conditions are improved. One major factor influencing intra and inter-population variation in forest trees is the sexual system. Unfortunately, this factor is usually neglected by researchers in Nigeria, yet information on the sexual system of forest trees is needed for sustainable management. Therefore, this review provides information on the sexual types and sexual systems found in forest trees. It also emphasizes the need for adequate knowledge of the sexual characteristics of individual trees in Nigeria's forest reserves to guarantee sustainable forest management

Keywords: incompatibility system, forest trees, genetic diversity, sustainable forest management

Introduction

One major factor influencing intra and inter-population variation in forest trees is the sexual system. Unfortunately, this factor is usually neglected by researchers in Nigeria, yet information on the sexual system of forest trees is needed for sustainable management (Duminil *et al.* 2016). Progeny production in forest trees usually begins with bud formation and flower development. Flowers are reproductive structures in forest trees that facilitate reproduction through the union of pollen with ovules.

Moon *et al.* (2013) revealed the sequential stages of flower development to include the early stage that permits the gametes' development through cell differentiation in inconspicuous bud. Flower formation was controlled by selector homeotic genes (Coen and Meyerowitz, 1991).

Different tree species have different sexual types and sexual systems. According to Onokpise and Akinyele (2011), the type of gametes a tree produces is its sexual type of and fertilization can only occur when the stamen and pistil are mature. Since trees are immobile, mechanisms naturally put in place will depend on the flower morphology and structure. However, a tree could be zoochorous or anemochorous (Onokpise and Akinyele, 2011). Pollination can occur either within a flower or between flowers of the same tree (cross-pollination) or flowers of different trees (cross-pollination). Fertilization will occur when mature pollen is transferred to the stigma that is ready to receive it. However, when the pollen does not fall on the ready stigma, no seed will develop (Armbruster *et al.*, 2014).

Pollen exchange within the same tree or among related trees is referred to as selfing (Finkeldey and Hattemer, 2007). Selfing or inbreeding often leads to the loss of heterozygosity, which negatively impacts adaptive and economic traits. Survival, growth rate and stem straightness are some traits in forest trees that are negatively impacted by inbreeding; this negative impact is regarded as inbreeding depression (Finkeldey and Hattemer, 2007).

The ability of tree species to survive in response to environmental changes is related to the genetic variability in that species (Lawal *et al.*, 2019). The mating system has since been reported to have an important influence on the amount and distribution of gene difference within and among populations of tree species (Hamrick and Godt, 1989). To ensure intra-specific diversity of forest trees, forest managers must rely on information about the reproductive systems and mechanisms of trees (Doligez and Joly, 1997). Therefore, this review provides information on the sexual types and sexual systems found in forest trees. It also emphasizes the need for adequate knowledge of the sexual systems of individual trees in Nigeria's forest reserves to guarantee sustainable forest management.

Sexual types in forest trees

Finkeldey and Hattemer (2007) discovered that male and female gametes have to come together to produce the zygote. This zygote will then develop through mitosis into an embryo, seed, seedling, and finally, a mature tree that can produce a gamete. A tree sexual type could either be cosexual (female and male gametes are produced) or unisexual (female or male) or sterile (tree not capable of producing any functioning gametes) (Finkeldey and Hattemer, 2007).

Sexual systems in forest trees

As shown in Figure 1, sexual systems comprise gender expression and its occurrence at many levels, such as intra-floral, individual, population, or species levels (Cardoso, *et al.*, 2018). A sexual system, according to Leonard (2019), is the pattern of distribution of male and female functions among individuals within a population or species. The reproductive feature of trees is a flower. It can either be unisexual, with just functional male (staminate flower) or female (pistillate flower) components, or bisexual, with both pistils (female organs) and stamens (male organs) (Finkeldey and Hattemer, 2007).

A sexual system known as cosexuality is one in which members of a population only display bisexual blooms with functioning stamens and pistils in the same flower (Barrett and Hough, 2013). A population only displays unisexual (diclinous) blooms in a monoecious sexual system, in which the same individual produces both staminate and pistillate flowers (Kafer *et al.*, 2017).

Individuals of a population with an andromonoecious sexual system display bisexual and staminate flowers, while those with a gynomonoecious sexual system have both bisexual and pistillate flowers (Jong *et al.*, 2008). In a population, trimonoecy (polygamomonoecy) is characterized by the coexistence of bisexual, staminate, and pistillate flowers in the same individual (Torices *et al.*, 2011). Individuals in the dioecy sexual system are completely unisexual, meaning that staminate and pistillate flowers are organized in various plants within a population (Barrett and Hough, 2013; Kafer *et al.*, 2017). Androdioecy, which is connected to mutations that cause female sterility, is the coexistence of individuals with bisexual flowers and those who only have staminate flowers (Barrett and Hough, 2013; Kafer *et al.*, 2017). Gynodioecy is the coexistence of individuals with pistillate flowers and those with bisexual flowers (Kafer *et al.*, 2017).

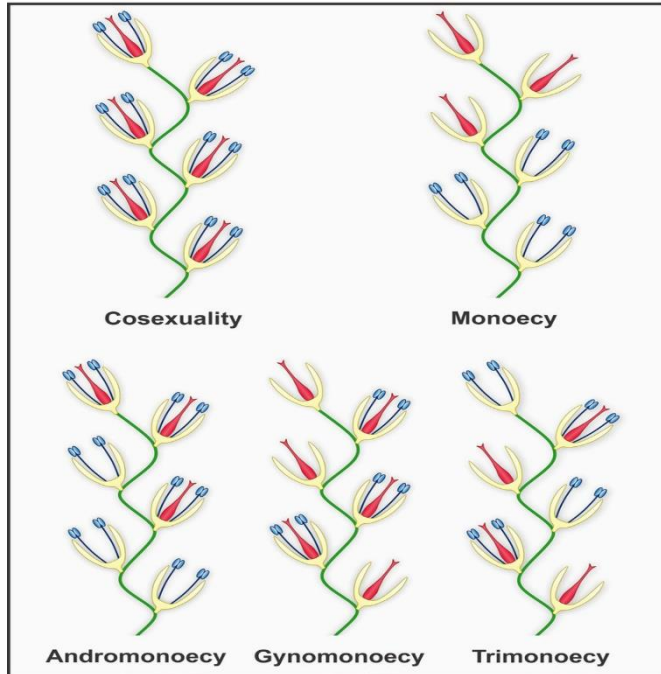


Figure 1: sexual systems that can be found in forest trees.

Stamens and pistils are expressed respectively in blue and red shades (adapted from Cardoso *et al.*, 2018).

Table 1: Sexual system and sexual types of some trees in Nigeria

S/N	Sexual system	Sexual types	Examples
1	Cosexuality (monoecy or hermaphroditic)	f/m	<i>Albizia feruginea</i> , <i>Barteria fistulosa</i> , <i>Brachystegia enricoma</i> , <i>Chrysophyllum albidum</i> , <i>Mansonia altissima</i> etc
2	Dioecy	f, m	<i>Diospyros barteri</i> , <i>Entandrophragma angolense</i> , <i>Khaya grandifolia</i>
3	Trioccy	f, m, f/m	<i>Zanthoxylum zanthoxyloides</i>
4	Gynodioecy	f, f/m	<i>Rhizophora mangle</i> , <i>Ficus</i> species
5	Androdioecy	m, f/m	<i>Bauhinia unguate</i> , <i>Terminalia superb</i>

Sources: Finkeldey, 2005; Ugbogu *et al.*, 2016; Guendehou *et al.*, 2018)

Cosexual and dioecious taxa

Finkeldey and Hattemer (2007) made a distinction between two types of cosexuality: (i) hermaphroditic trees have complete blooms that produce both types of gametes in one flower; and (ii) monoecious trees produce both types of gametes but in different flowers. For hermaphroditic trees, Finkeldey and Hattemer (2007) made distinctions between several pollination types. They define autogamy as the fertilization of an ovule using pollen from the same flower, while geitonogamy refers to the fertilization of an ovule using pollen from a different flower. Allogamy includes both antogamy and geitonogamy, but xenogamy entails pollinating a separate tree and causes out-crossing.

Mitchell and Diggle (2005) considered monoecy as a derived condition in angiosperm trees. According to Cardoso *et al.* (2018), the andromonoecy route hypothesis proposes that andromonoecy serves as a transitional stage between cosexuality and monoecy. This hypothesis, according to Jong *et al.* (2008), is supported by the idea that the existence of staminate blooms would make it easier for those bisexual plants to produce strictly pistillate flowers. The other pathway, which uses gynomonoecy as a transition stage, is seen as implausible because it calls for an enormous fruit to be produced by both bisexual and pistillate flowers (Cardoso *et al.*, 2018). According to Weiblen *et al.* (2000), there are still a few instances where monoecy reverts to cosexuality.

A tree that produces only one type of gamete is termed dioecious. They can either be male or female. According to Renner (2014), dioecious individuals make about 43% of angiosperm families. Ohya *et al.* (2017) highlighted some problems associated with the population growth of cosexual and dioecious taxa. According to them, the populations of coexisting

cosexual taxa may expand more quickly than those of dioecious plant species. Due to their inability to self-pollinate and need for a partner to reproduce, dioecious plants are more likely to experience problems with pollination (Xia *et al.*, 2013, Schlessman *et al.*, 2014). Although self-incompatible plants also need a partner to reproduce, all interplant pollinator movement may help produce seeds (Ohya *et al.*, 2017). They mentioned that pollinator travel from male to female is necessary for seed formation, hence pollinator movement direction is crucial for dioecious plants. According to studies by Vamosi *et al.* (2006), De Jong *et al.* (2005), and Otero-Arnaiz and Oyama (2001), female dioecious trees produced more fruit when surrounded with males trees.

Using mathematical models, Wilson and Harder (2003) investigated how dioecious and cosexual organisms competed for space. They demonstrated that sex differences increased plant variability in seed output and fertilization probabilities, and that reproductive uncertainty decreased the mean recruitment of dioecious species.

Special adaptations for out-crossing in forest trees

There have been several mechanisms identified that could prevent self-fertilization and promote outcrossing in flowering plants. Mechanisms separating the male and female functions, either in time (dichogamy) or in space (herkogamy), are among the most common (Armbruster *et al.*, 2014 and Cardoso *et al.*, 2018).

Self-incompatibility (SI) or self-sterility (SS) in forest trees

In self-incompatibility (SI) or self-sterility (SS), the pollen grain is unable to germinate on its stigma but will germinate on another flower of the same species. That is, when pollen grain produced in a tree with SI or SS reaches a stigma of the same tree, the process of pollen germination, pollen-tube growth, and embryo development will be inhibited, and consequently, no seeds will be produced (Cardoso *et al.*, 2018). In this case, self-pollination becomes impossible. According to Wang *et al.* (2018), the self-incompatibility mechanism is based on protein-protein interactions and is managed by a single locus known as S, which contains a variety of alleles in the population of the species. The S-locus, according to Wang *et al.* (2018), has two fundamental protein-coding regions, one of which is expressed in the pistil (female determinant) and the other in the anther and/or pollen (male determinant). Due to their close proximity, S-haplotypes are genetically connected and passed down together (Wang *et al.* (2018). Two proteins that are the translation products of the two regions of the S-locus interact with one another to stop pollen germination and/or pollen tube elongation, which triggers a SI response and prevents fertilization (Gibbs, 2014). Nevertheless, there will be no self-incompatibility and fertilization will take place when a female determinant interacts with a male determinant of a different haplotype.

Pollination is undoubtedly an important part of generative propagation, and the spread of plants is strongly related to pollinators and biodiversity (Yang *et al.*, 2017). Finkeldey and Hattemer (2007) state that pre-fertilization mechanisms are considered incompatibility systems, and that cosexual species lacking incompatibility reactions frequently develop self-sterility systems that cause early termination of the embryo after fertilization. Mixed mating systems are common in seed plants (Goodwillie *et al.*, 2005) because the ability to set seed after selfing is advantageous when mating partners or pollinators are scarce (Kalisz *et al.*, 2004). According to estimates, 33% of plant species are intermediate between selfing and outcrossing, while 20% of plant species exhibit significant levels of selfing (Vogler and Kalisz, 2001). However, compared to outcrossed individuals, selfed individuals frequently have worse vegetative and reproductive fitness (i.e. inbreeding depression; Husband and Schemske, 1996). To prevent or limit self-fertilization in blooming plants, many mechanisms have been developed.

Sexual system and forest management

A forest is typically defined as "a land covering more than 0.5 hectares composed of trees with the ability to grow to a minimum height of 2 to 5 meters at maturity in situ and a canopy cover of more than 10%" (Ananta, 2020). Forests in Nigeria have been severely degraded and fragmented (Lawal and Adekunle, 2013). Intra- and inter-specific variation in forest trees could be linked to the ability of the forest manager to maintain the populations of trees with their sexual types and systems in a forest ecosystem.

Selective logging of trees with superior characteristics, which is a common practice in Nigeria, has a negative influence as tree species with inferior characteristics would be left for reproduction (Lawal *et al.* (2019). Eckert *et al.* (2010) revealed that selective logging implies a reduction of "mate" (seed tree) densities, which in theory can affect plant reproductive success. Furthermore, a better knowledge of the sexual systems of forest trees will go a long way to sustain the population of dioecious species. For instance, where a forest reserve is dominated by dioecious species with a few of them producing female gametes, harvesting those female gamete-producing trees will negatively impact the successional status of such species, and a reduction in genetic diversity will result. De Jong *et al.* (2005) and Otero *et al.* (2001) found that female dioecious trees produced more fruit when adjacent males were present. According to Heilbuth *et al.* (2000), only 50% of the individuals in a population of dioecious species contribute to seed production, which limits their capacity to colonize deserted places. In dioecious tree species, seed dispersal was restricted to the area around female plants, resulting in a densely clumped distribution of seedlings, as discovered by Montesinos *et al.* (2007) and Nanami *et al.* (1999). These drawbacks, according to Baker (1995), would negatively impact the capacity of dioecious trees to colonize new areas.

The majority of tropical tree species are hermaphroditic (Finkeldey and Hattemer, 2007). Due to the hermaphroditic nature of the majority of tropical forest trees, selfing—the strongest form of inbreeding depression caused by autogamy and geitonogamy—is a possibility. Mechanisms that prevent selfing therefore provide a significant evolutionary advantage. According to Finkeldey and Hattemer (2007), the most crucial mechanisms before fertilization are incompatibility systems. Cosexual species without incompatibility reactions frequently evolve self-sterility systems, which leads to early termination of the embryo following fertilization. Many studies have been conducted in developed countries to estimate selfing rates in forest tree populations (Feres *et al.*, 2012; Hamrick, 2011). But in Nigeria, studies on the incompatibility and self-sterility of hermaphroditic species are scarce.

Conclusion and recommendation

There are various sexual systems in forest trees. The production of progenies through pollination depends on the availability of gametes. Hermaphrodite, monoecious, dioecious, trioecious, gynodioecious, or androdioecious trees can be found in the forest ecosystem. Some trees with both gametes may become self-sterile or develop incompatibility systems. Depending on the availability of mating partners and the pollination direction, forest trees will either outcross or self. Often, out-crossing, or the transfer of pollen from one tree to another, leads to an increase in genetic diversity. As a result, such species' adaptability potential and survival under perilous environmental conditions are enhanced. Many tree species in Nigeria are currently being threatened by extinction owing to unsustainable tree harvesting and conversion of forest estates to other land uses. A better knowledge of the sexual systems of individual trees in our forest reserves will help in sustainable forest management and increase the genetic diversity of tree species. Therefore, research to reveal the sexual system of the remnant trees in our forest reserves is recommended.

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