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Studies on *Thonningia sanguinea* Vahl.: Reproductive Phenology, Sex Ratio and Insect Visitors in Okomu National Park, Nigeria

*[1]Imarhiagbe, O. and [2]Aigbokhan, E. I.
[1]Department of Biological Science, Edo University Iyamho, Edo State, Nigeria
[2]Department of Plant Biology and Biotechnology, University of Benin, Benin City, Nigeria
*imarhiagbe.odoligie@edouniversity.edu.ng +2348031984621

ABSTRACT

The present study investigated the phenology, sex-ratio, and potential pollinators of *Thonningia sanguinea* in Okomu National Park, southern Nigeria. Data were collected through regular visits to sites habouring the plant. Results show that *T. sanguinea* flowers all-year-round, with varying frequencies across different months of the year. A significant correlation (r=0.917; p=0.000) was observed between the frequency of flowering and rainfall. Overall, the incidence of female plants surpassed male plants by approximately a 2:1 ratio. Also, 71 % of the sites had only a single-sex type, i.e either male or female inflorescence, while 29 % of the sites had both male and female inflorescences. The ant *Technomyrmex* species were the most common floral visitors, accounting for a 55.54 % frequency of occurrence. Consequently, the lengthy reproductive phenology period and persistent interactions with a diverse faunal species indicate *T. sanguinea* as a keystone species in forested habitats and it is recommended that such habitats should be treated as an area of importance for biodiversity conservation

Keywords: cryptic, parasitic plant, phenology, pollination, sex ratio, *Thonningia sanguinea.*

INTRODUCTION

Phenology is the study of cyclic and seasonal events of an organism, in relation to other environmental and climatic factors (Durant et al. 2005). One of such events, particularly in plants is flowering. The reproductive success of a plant's population is largely dependent on the schedule of flowering and pollinator availability (Fenner, 1998; Stucky et al. 2018). According to Cascaes, Citadini-Zanette, & Harter-Marques. (2013), flowering and fruiting periods are of critical importance in the survival of the plant species and faunal visitors who rely on it for food and subsequent pollination activity. In some plant species, like members of Balanophoraceae, growth habit is totally subterranean and only visible during the flowering period.

Thonningia sanguinea is one of the few representative members of Balanophoraceae in Nigeria. Members of this family are parasitic and are notable for their bizarre inflorescence development, obscure host affinity, and are mostly noticed by their inflorescence that grows above ground. Despite these interesting attributes, the reproductive biology of these unusual species is yet to be fully understood. Although there exist reports on the potential pollinators of some members, for instance, *Lophophytum mirabile* (Borchsenius & Olesen, 1990, *Dactylanthus* (Ecroyd, 1996), *Balanophora tobiracola* (Kawakita & Kato 2002), *T. sanguinea* Goto,Yamakoshi, & Matsuzawa, (2012). *B. fungosa* (Suetsugu & Aoyama, 2014), and *Langsdorffia hypogaea* (Freitas *et al.*, 2017), more research is required to fully understand their biology. For *T. sanguinea*, the likelihood of pollen transfer from a male to a female inflorescence was not established due to the limited availability of female inflorescence (Goto, Yamakoshi, & Matsuzawa, 2002).

T. sanguinea is a cryptic, obligate holoparasitic plant endemic to forested areas of tropical Africa. Beyond the visual parasitism of *T. sanguinea* on the roots of forest trees, not much is known about its reproductive biology and mechanism of pollination. The dearth of information on *T. sanguinea* is probably due to its prevalence in only tropical Africa, where limited resources are committed to research. Its status as either dioecious, monoecious, or both is still contentious among different researchers. More so, inconsistent records about the sex ratio and the fact that seeds are unknown indicate that pollination and seed production are extremely rare. However, a preliminary investigation report suggests a slightly balanced sex ratio between male and female individuals, which further attests to the limited research attention *T. sanguinea* has received so far. For a proper understanding of the reproductive biology of *T. sanguinea*, it is imperative to ensure ample availability of both sexes, which was a major limitation in earlier studies, particularly that of Goto, Yamakoshi, & Matsuzawa, (2002). Hence, the present study was conducted to investigate the reproductive phenology, sex ratio, and identify insect visitors of *T. sanguinea* in Okomu National Park, Southern Nigeria.

MATERIALS AND METHODS

Study Area

The mapped area of the Okomu National Park (ONP) is presented in Figure 1. It is situated in Ovia South-West, Edo State, Nigeria; with a coordinate of longitude 5^{o}16’0” E and latitude 6 ^{o}20’0” N. The park, comprising of a forest area of about 200 km^2, is now regarded as refugia of the former Nigerian lowland forests that was once a continuous forest belt that stretches across the Niger River, west of the Dahomey Gap in Benin republic (Williams, 2008). The climatic condition of the park is tropical; with a mean annual rainfall of 2100 mm, which peaks around March through October. The relative humidity and mean monthly temperature are mostly around an average of 65 percent and 30.2^{c}C respectively. The soils are made up of sandy loams derived from deep loose deltaic and coastal sediments that date back from the Eocene period and it is markedly acidic with an average pH of 5.0 (Greengrass, 2009). The much diverse ecosystem of ONP comprising areas of swamp-forest, high forest, secondary forest, and open scrub, undoubtedly qualifies it as one of the best examples of a mature secondary forest in Southern Nigeria (WWF, 2017). *Thonningia sanguinea* populations were located in the following compartments (Comp.) of the Park: Comp. 33 (N 06^{o}24.113” E 005^{o} 19.44”), Comp .53 (N 06 ^{o}24.113” E 005^{o} 19.44, Comp. 55 (N 06^{o} 21, 656” E 005^{o} 21.587”), and Comp. 61 (N 0 ^{o} 20.764” E 005 ^{o} 20.697”).

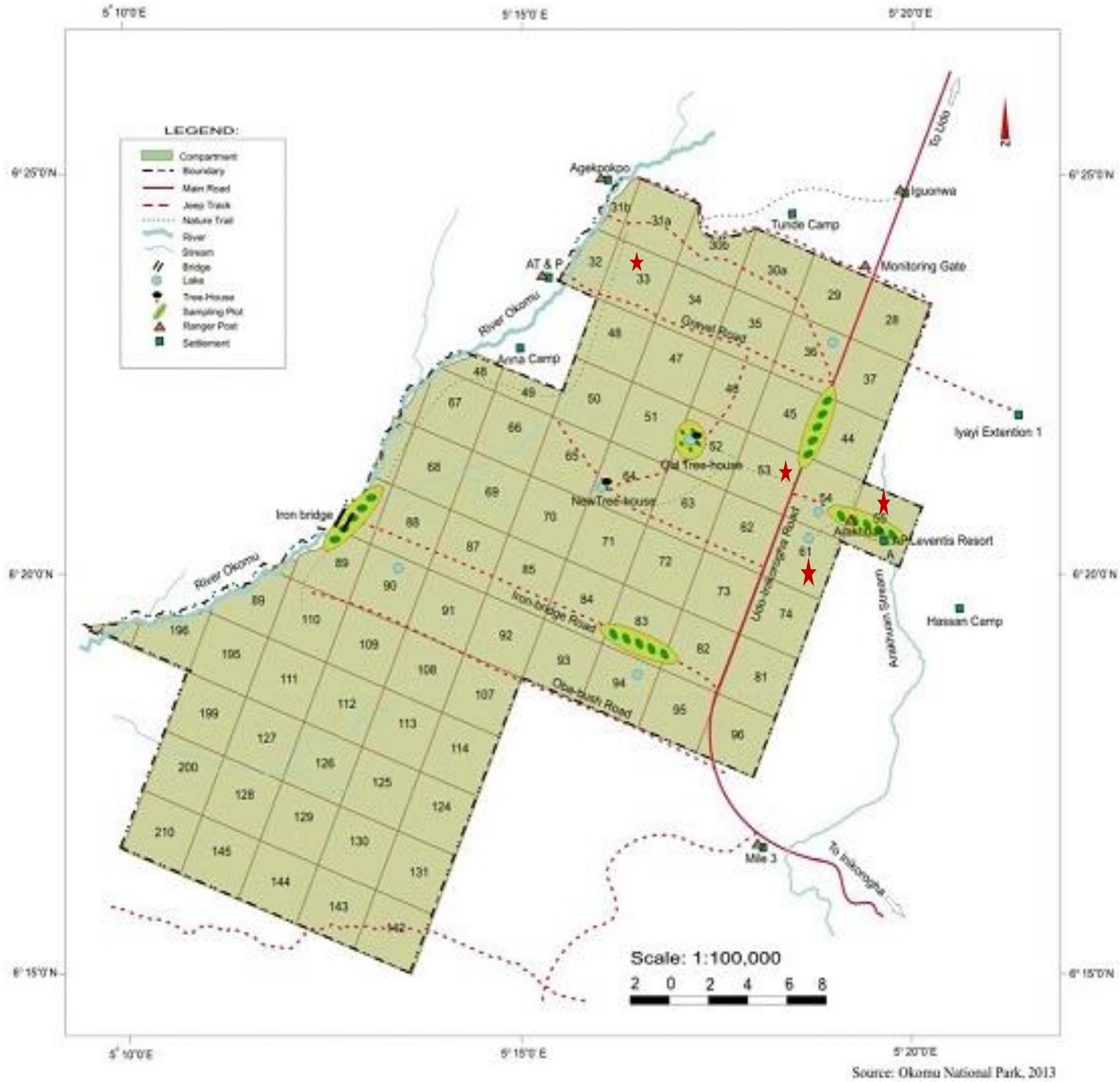

Figure 1. Map of study area showing quadrat sites (33, 53, 55 and 61) in Okomu National Park

Population Sampling

Thonningia sanguinea population were accessed using meander searches and personal communications. Stratified sampling method was used to evaluate *T. sanguinea* populations in line with the objectives of the study. Where *T. sanguinea* population was spotted, a (10 x 10) m quadrat size was mapped to accommodate the number of host trees present.

Reproductive phenology

Bi-monthly visits to sites harbouring *Thonningia sanguinea* in Okomu National Park was carried out from January-December, 2016, to observe and record the flowering period and frequency of flowering. Data were collected on the frequency of male and female inflorescence and fruiting heads. Following the method of Cascaes, Citadini-Zanette, & Harter-Marques. (2013), the period of occurrence of different stages of the reproductive phenophases (under-ground bud development, above ground bud development, anthesis, fruit development, and dry out) were assessed from direct observations. Ten (10) *T. sanguinea* plants were tagged at each site and observed on a daily basis to record developing flowering shoots. Upon bud initiation, data were taken through the period of inflorescence development to fruiting stage. To assume synchronicity in constructing the phenogram, the period of a phenophase was based on the period (days) taken for 50 % of tagged buds to change from one reproductive phenophase to another. To determine whether there was a correlation between phenology (flowering and fruiting) and rainfall, Spearman correlation analysis (α=0.005) was employed. Rainfall data of the Park were accessed from the Nigerian Meteorological Agency (NIMET), Benin City.

Sex Ratio

Data on the distribution of inflorescence, grouped by single or co-occurrence of sex-type, was collected and analyzed in percentage. In order to arrive at a more comprehensive sex ratio for *T. sangunea*, the numbers of male and female capitulum were recorded at different sites and subjected to the Chi test (Goodness of fit).

Fauna Visitors (potential pollinators)

A total of 54 visits were made to monitor insect visitors of *T. sanguinea* during day-time periods (from 7.00 am to 2.00 pm). Insects found on *T. sanguinea* inflorescence bud were collected, identified, and recorded. Photographic shoots, video photography, and complemented visual observations were used to monitor inflorescence-insect interactions. The following data were collected during the survey: foraging time (time spent on flowers (male and female) from arrival to departure), foraging sequences (the number of inter and intra plant movement), insect species number, percentage visit by insect species using the formula below

$$\% \ of \ visits = \frac{Number \ of \ visits \ per \ species \times 100}{The \ grand \ total \ of \ all \ insect \ visits}$$

Following the method outlined by Southwood & Henderson (2000), the Berger -Parker index was used to identify the most dominant species of insect visitors. Insect specimens encountered during the survey were identified using standard insect identification keys.

Statistical Analysis

Using Microsoft Office Excel package, 2010, a combined chart was used to show the pattern of relationship between phenology and rainfall. Chi-square Test (goodness of fit) was used to assess the sex ratio pattern in *T. sanguinea*

RESULTS

The reproductive phenology (flowering and fruiting) of *Thonningia sanguinea* at different compartments of the Okomu National Park is presented in Figure 2 (a-d). Flowers were recorded all-year-around, however, the frequency of inflorescence varied across different months of the year. The rainfall pattern was uniform for all compartments. The frequency of rainfall rose steadily from January, and experienced a fairly constant rate around May to August, before reaching its peak around September and October. For compartment 33 (Figure 2a), the frequency of male inflorescences was observed to increase steadily from January to June. Beyond this period, there was a temporary drop in June and August, before reaching a peak in September. The highest and lowest frequencies of male inflorescence were recorded in September and January respectively. The number of female inflorescences increased steadily from January, and slightly dropped around March and increase steadily to reach its peak in August. The highest and lowest frequency of female inflorescence value were recorded in

August and March respectively. For the number of fruiting heads, the highest and lowest frequencies were recorded in December and June respectively. For compartment 53 (Figure 2b), the frequency of male inflorescences was observed to increase in from January to March and July to September. However, no record of male inflorescence was observed in May and June. However, for female inflorescence, the highest and lowest frequency of female inflorescence values were recorded in August and November respectively. The highest frequency of fruiting heads was recorded in January and none was observed for June.

For compartment 55 (Figure 2c), the frequency of male inflorescences was observed to increase steadily from March to June. The highest frequency of male inflorescence was recorded in June while none was observed for December, January, and February. The numbers of female inflorescence increased steadily from March to June and dropped gradually through November to total absence around December, January, and February. For the number of fruiting heads, the highest and lowest frequencies were recorded in December and June respectively. For compartment 61 (Figure 2d), the frequency of male inflorescences was observed to increase steadily from April to June and temporarily dropped in august and again increased in September before reaching its peak value in October. No record of the male inflorescence was observed in December and January. The numbers of female inflorescence increased steadily from February through July and temporarily dropped in August and again increased in September before reaching its lowest value in December. No record of the male inflorescence was observed in January. For the number of fruiting heads, the highest and lowest frequencies were recorded in December and June respectively.

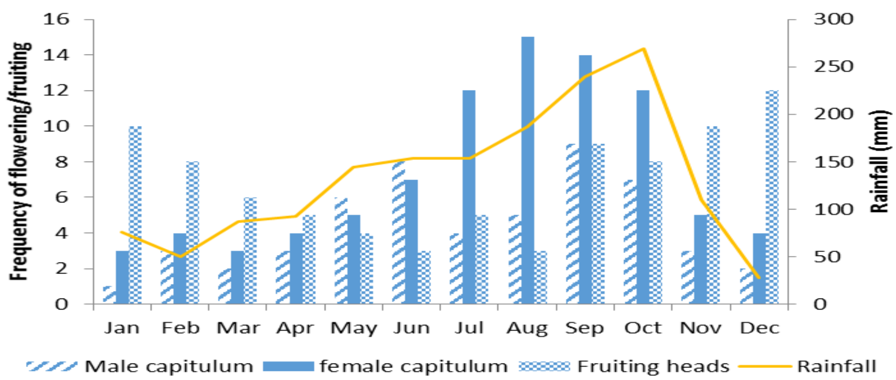

Figure 2a: Reproductive phenology of *Thonningia sanguinea* at compartment 33 of the Okomu National Park

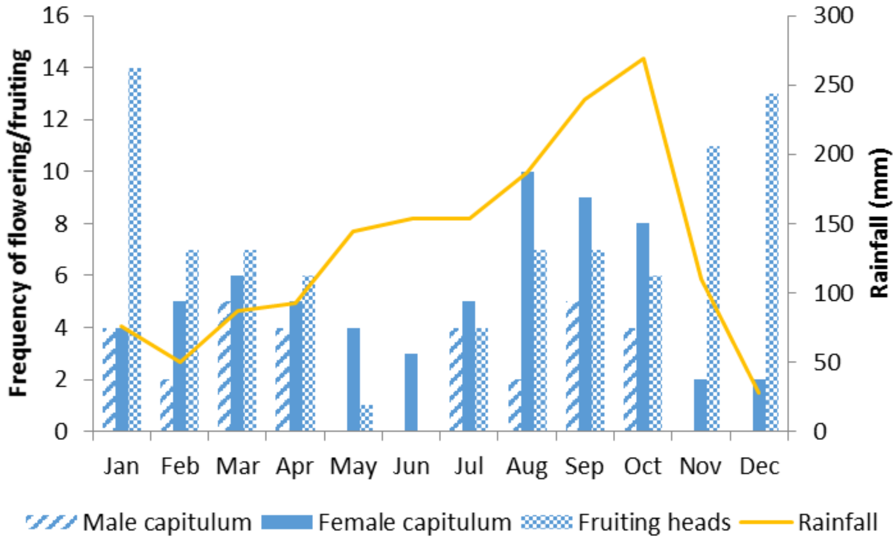

Figure 2b: Reproductive phenology of *Thonningia sanguinea* at compartment 53 of the Okomu National Park

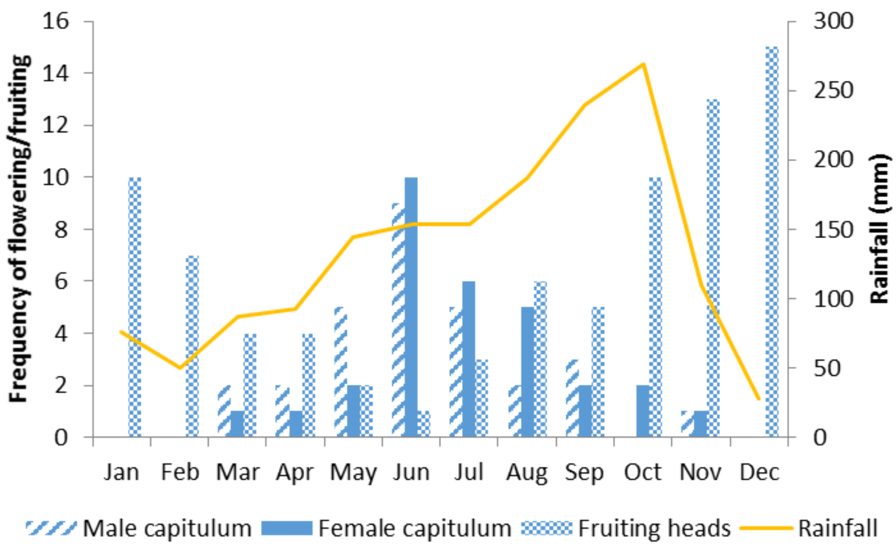

Figure 2c: Reproductive phenology of *Thonningia sanguinea* at compartment 55 of the Okomu National Park

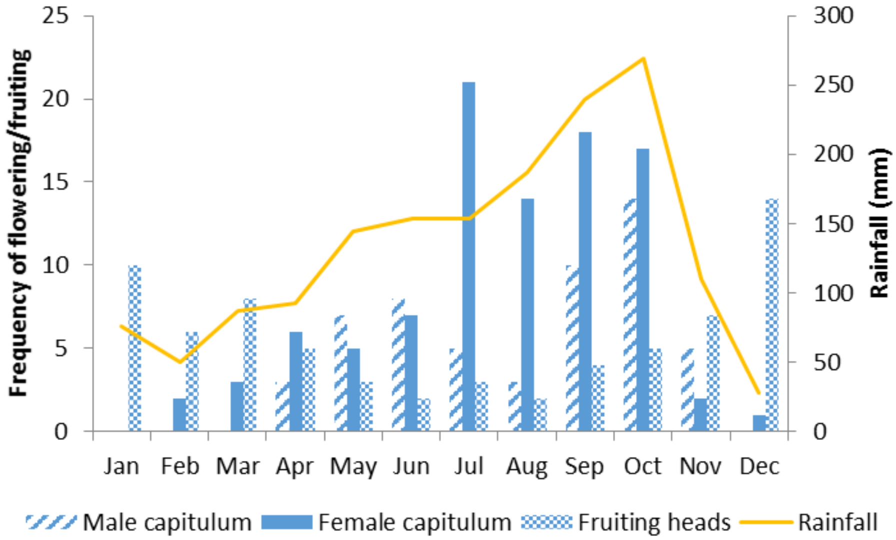

Figure 2d: Reproductive phenology of *Thonningia sanguinea* at compartment 61 of the Okomu National Park

The reproductive phenophases for both male and female *Thonningia sanguinea* inflorescence is presented in figure 3. The flowering cycle (from bud establishment to flower maturity) for male and female plants, take an average of 31 and 40 days respectively. Underground bud development to its visibility above-ground takes an average of 14-day period; however, this is subject to the depth level of the underground rhizome. Anthesis takes an average of 6 days for both male and female inflorescence, while flower development in female plant takes 15 days.

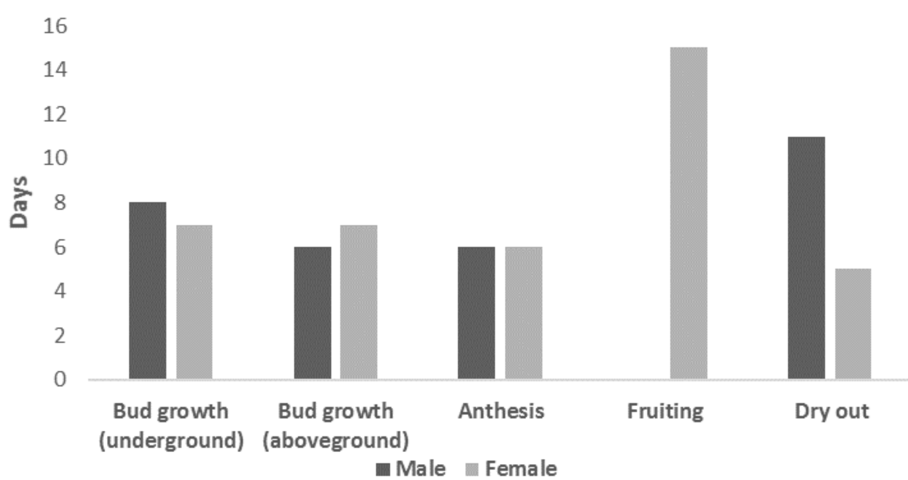

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Figure 3: Phenological chart for male and female *Thonningia sanguinea* inflorescence

The relationships between the frequency of flowering and fruiting of *Thonningia sanguinea* and the rainfall pattern in Okomu National Park is presented in Figure 4a and b respectively. A statistically significant correlation was observed between the frequency of flowering and rainfall patterns at 0.005 level of significance (R=0.917; P=0.000). The correlation between the frequency of fruiting and rainfall was not statistically significant. However, a negative correlation coefficient was recorded (R= -0.28; P=0.370).

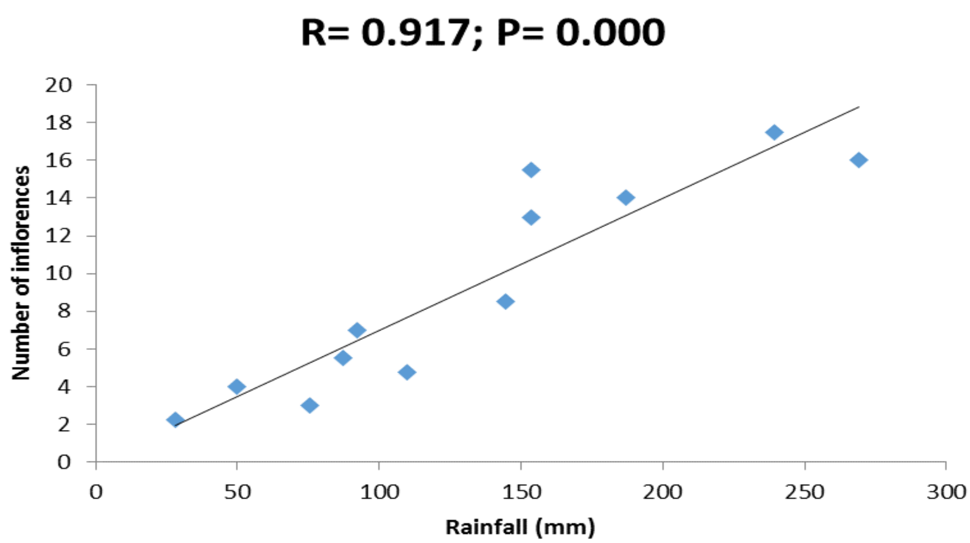

Figure 4a: The relationship between the frequencies of flowering vs. Rainfall pattern of *Thonningia sanguinea* in Okomu National Park.

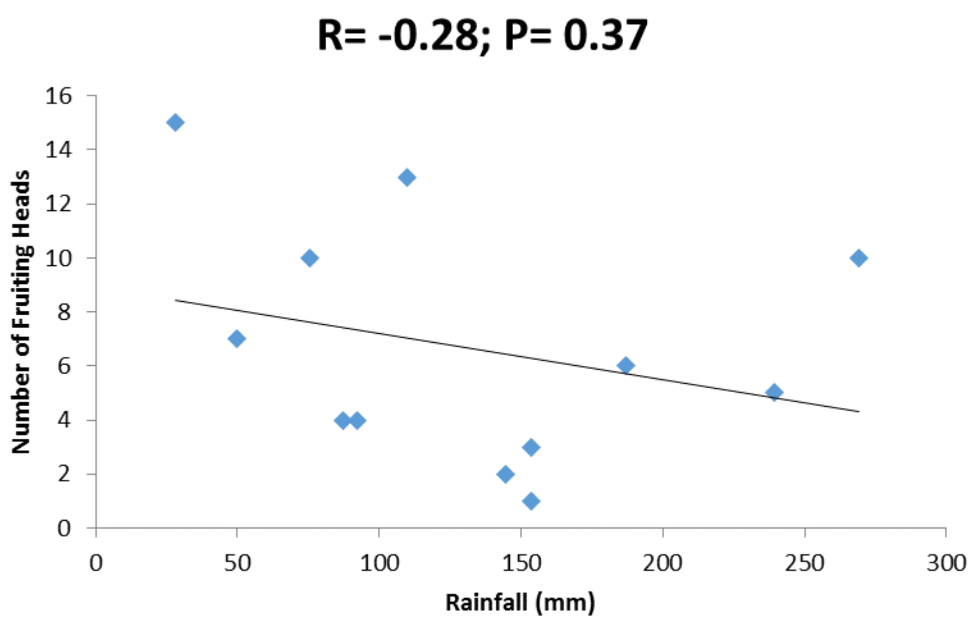

Figure 4b: The relationship between the frequencies of fruiting vs. Rainfall pattern of *Thonningia sanguinea* in Okomu National Park.

The percentage distribution of *Thonningia sanguinea* based on single or co-occurrence of sex-type among the different sites is presented in Figure 5. The result revealed that 71 % of the sites were found to harbour a single-sex type, i.e male and female inflorescences while, 29 % of the sites were found to harbour both. A close co-occurrence of both sex was recorded in one of the sites (compartment 54), with a spatial distance of approximately 6 cm, regrettably, due to the breakable nature of the rhizome, it was impossible to link both flower heads as a single plant in order to ascertain if it was monoecious.

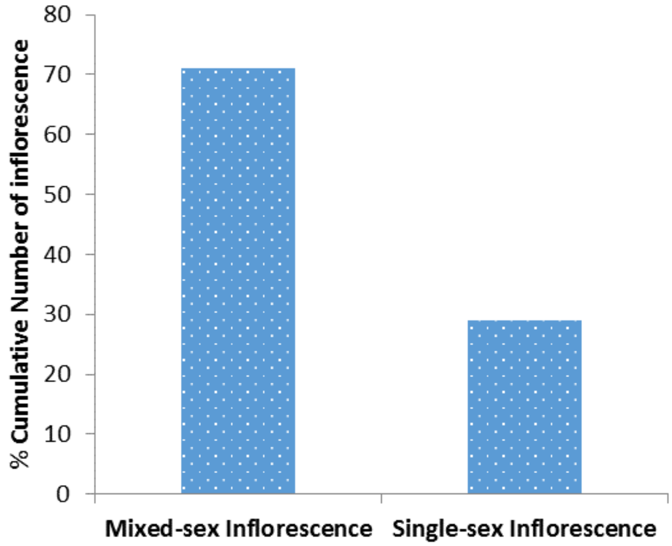

Figure 5: Percentage distribution of inflorescence grouped by single or co-occurrence of sex-type

Table 1 shows the chi-square result of *Thonningia sanguinea* inflorescence sex ratio. The total number of inflorescence head recorded was 371. The number of male inflorescence head was 153 while the female inflorescence head was 218. The sex ratio was statistically significant with a P-value of 0.001. This demonstrates that the sex ratio in *T. sanguinea* is skewed towards the male plant with an approximate sex ratio of 2:1.

Table 1: Goodness of fit test of *Thonningia sanguinea* Sex Ratio

Factors	**N_{total}**	**Male**	**Female**	**Sex ratio (M/F)**	**P-value**
Value	371	153	218	0.70	0.001

N_{total}- total number of inflorescence recorded; χ^2- Chi square

Table 2 shows the relative frequency of insect visitors of *Thonningia sanguinea* in Okomu National Park**.** The following insect species were observed: *Technomyrmex* sp., *Monomorium* sp. *Tetramorium* sp. (all in the order Hymenopteran), *Chrysomya* sp. *Morellia* sp, (Diptera), and some unidentified species such as species 1 (Lepodotera), species 2 (Orthoptera) and species 3 (Orthoptera). The relative frequencies of insect interaction with *T. sanguinea* inflorescences show that *Technomyrmex* sp (Hymenopteran) had the highest percentage frequency of floral visits with a percentage value of 33.3 %, followed by the *Chrysomya* sp. (Diptera) with 18.51 %, species 3 (Orthoptera) however, had the lowest percentage frequency of insect floral visit with 3.7 %. *Technomyrmex* sp (Hymenopteran) had the highest number of insect species per capitulum at a particular time with an average value of 13.4, followed by *Monomorium* sp (Hymenopteran) with 3.67, species 3 (Orthoptera) however, had the lowest insect species number per capitulum head with just one at a time. *Technomyrmex* sp also had the highest Berger -Parker index with a value of 0.52, followed by the *Chrysomya* sp. (Calliphoridae) with 0.14 and species 3 (Orthoptera) had the lowest Berger -Parker Index value of 0.04. In terms of the behavioral characteristics expressed by the visiting insects, *Technomyrmex* sp (Hymenopteran) and *Chrysomya* sp. (Diptera), were observed to forage both in the male and the female inflorescence head, while *Morellia* sp, (Diptera), species 2 (grasshopper) and Orthoptera (cricket) were found foraging only on the female inflorescence head. Breeding sites of *Technomyrmex*, *Chrysomya* sp. (Diptera), and an unidentified species of Lepidotera order was observed on the male as well as female *T. sanguinea* inflorescence. In addition to insect species visitation, shreds of evidence from footprints on sites harbouring emasculated *T. sanguinea* inflorescence heads indicate herbivory by some suspected forest ruminant (*Galarella sanguinea* and *Cephalophus* sp.) in Okomu National Park

Table 2: Relative frequency of insect visitation on flowers of *Thonningia sanguinea* estimated from a data collected on a 54 visit account

Insect visiting species	**Order**	**Frequency of visits**	**Percentage frequency of visits (%)**	**Average number of Insect**	**Berger - Parker Index**
Technomyrmex sp.	Hymenopterans	18	33.00	13.4	0.52
Monomorium sp	Hymenopterans	7	12.96	3.67	0.14
Tetramorium sp.	Hymenopterans	5	9.25	2	0.07
Chrysomya sp.	Diptera	10	18.51	1.67	0.06
Morellia sp.	Diptera	5	9.25	2	0.07
Morellia sp.	Lepodotera	2	3.70	1	0.04
Species 1 (butterfly)	Orthoptera	5	9.25	1	0.04
Species 2 (grasshopper)	Orthoptera	2	3.70	1	0.04
Total		**54**	**100**	**25.74**	**1.00**

Figure 7. Insect visitors of *Thonningia sanguinea* in Okomu National Park, Nigeria (A, B, D & K- *Technomyrmex* sp), (E & F-Ant sp.), (H- *Monomorium*), (G- *Morellia*), (I- *Chrysomya*), (J- Orthoptera), (L- Lepidotera- Caterpillar)

DISCUSSION

Reproductive Phenology

The study presents the first report on the phenology of *Thonningia sanguinea* in a rainforest habitat in Nigeria. *T. sanguinea* was observed to have an all-year-round flowering period but with varying frequencies across different months of the year. Flowers were recorded for up to 11 months. A similar flowering pattern had previously been reported by Ecroyd (1996) for *Dactylanthus taylori*, another member of Balanophoraceae in New Zealand, where it was observed to have a long flowering period with the peak of flowering usually in March or April. In terms of the relationship between climatic factors and flowering patterns in *T. sanguinea*, a statistically significant correlation was observed between the frequency of flowering and rainfall patterns. Similarly, according to Ecroyd (1996), *Dactylanthus* seems to flower slightly at lowland sites with a warm-weather condition than at higher altitude sites with a cold-weather condition. Based on the flowering patterns of both species, it is reasonable to assume that weather condition appears to play a key factor in the pattern of flowering in both species. It is not yet clear how *T. sanguinea* utilizes the correlated pattern of flowering and rainfall to its ecological advantage, but one observable explanation is that the period of rainfall creates a moist-soil condition that allows the easy proliferation of the inflorescence, allowing visibility of the inflorescence head above ground. Another unique feature of the flowering pattern in *T. sanguinea* is the occurrence of flower synchrony in male and female plants. The frequency of flowering in male and female plants was relatively synchronized with both having peak values from June through November and low values from December to March. Such synchronized events can be advantageous especially in species that undergo sexual reproduction. Also, as stressed by Bawa (1980), the synchronization of flowering events in dioecious plants (i.e. with separate sexes) is an obligatory requirement to achieve sexual reproduction success. The fruiting periods were markedly noticed around October to March, which corresponds with the dry period. With such a long reproductive phenology period, the perennial nature of *T. sanguinea* is significant for ants, caterpillars, and mammals that prey and browse on the fruiting heads of *T. sanguinea*, allowing for an all-year-round supply of food resources even in a season of scarcity.

Sex ratio

The sex ratio for *T. sanguinea* was significantly female-biased, with a skewed figure of approximately 2:1. The sex ratio of most dioecious plant species commonly deviates from the equilibrium expectation of 1:1, presenting an excess either male or female plant (Field, Pickup, & Barrett, 2013). According to Godfray and Werren (1996), the allocation of resources to male and female progeny is a major component of the reproductive strategies of all sexually reproducing dioecious plants. Ecroyd (1996), recorded a sex ratio of 5:1 male to female inflorescences in *Dactylanthus taylorii* (Balanophoraceae) in New Zealand. Therefore, with a fairly skewed ratio in *T. sanguinea*, there will be likely exclusion of reduced reproductive fitness, low seed production, and pollen limitation. Furthermore, there has been a controversy in the literature as to whether *T. sanguinea* is dioecious or monoecious. Bullock (1948) reported observing some dioecious specimens. Heide-Jørgensen (2008) reported that *T. sanguinea* is dioecious but monoecious specimens have been found. In the present study, based on the percentage distribution of inflorescence grouped by single or co-occurrence of sex-type/quadrat, 71 % of the total quadrat had *T. sanguinea* populations of a single sex-type (male or female) while the remaining 29 % were mixed sex-type (both sexes). The closest spatial proximity between both sexes was observed in compartment 54 of the Okomu National Park; with a measured distance of 7 cm. however, the breakable nature of the rhizome made it difficult to link both inflorescences as a single plant. Our data, therefore, suggest that *T. sanguinea* is usually, but not strictly dioecious. However, molecular techniques may be useful in authenticating the sex of the plant to ensure accurate inference of the ratio of male to female plants.

Insect visitors

A number of insect visitors that includes *Technomyrmex* sp (Hymenopterans), *Monomorium* sp (Hymenopterans), *Tetramorium* sp. (Hymenopterans), *Chrysomya* sp. (Diptera), *Morellia* sp (Diptera), an unidentified species of grasshopper (Orthoptera), and an unidentified species of cricket (Orthoptera) were observed to interact with the inflorescence of *Thonningia sanguinea*. According to Herrera (1989), a species can increase seed set by having a high individual efficiency as a pollen vector and a high frequency of flower visitation. Ants were the most abundant pollinators, accounting for 55.54 % of insect floral visits, The Hymenoptera order; particularly *Technomyrmex* sp. (ant) was the most frequent in both male and female inflorescence, hence had a Berger-parker index value of 0.52. However, after visiting, subsequent movement of the ant species was in a zigzag pattern and consequently, no foraging sequences involving male to female inflorescence head or verse versa was observed.

Apart from ant species, *Chrysomya* sp (Diptera) was observed to forage between a male and female inflorescence head; indicating a possible agent of pollen transfer. However, the visitation made by flying insects were low compared to ant species. De Vega, Arista, Ortiz, Herrera, & Talavera, (2009) reported that the presence of high ant visitation of a species could discourage flying pollinators from visiting its flowers. In addition, *T. sanguinea* may have had a high frequency of ant visitation because of its position on the ground, in combination with floral scents, nectar, and a large amount of pollen produced by the inflorescence. Based on our observation, we suggest a high chance of myrmecophily pollination in *T. sanguinea*, but the possibility of a myophily occurrence is possible. Hymenoptera, Diptera, and Lepidotera were observed to utilize *T. sanguinea* inflorescence (male and female inflorescences) as a food resource and an oviposition site. This study further confirms the earlier report on the brood -site pollination mutualism between *Morellia* sp. and *T. sanguinea* by Goto, Yamakoshi, & Matsuzawa, (2012). But in addition, the presence of the larvae of *Chrysomya* sp (Diptera) and a member of the Lepodotera was observed on the female inflorescence.

CONCLUSION

The study has established the phenological pattern of *T. sanguinea* to be on an all-year-round basis. However, the frequency of flowering varies across different months of the year, and it is most prevalent during the rainy periods. The lengthy reproductive phenology qualifies *T. sanguinea* as a keystone species in the forest community and consequently, ants, caterpillars, and forest ruminants have an all-year-round food resource supply, even in a season of scarcity. Therefore it is recommended that *T. sanguinea* habitats should be treated as an area of importance for biodiversity conservation.

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