# Regeneration ecology of the climber *Flagellaria guineensis* (Flagellariaceae) in the Transkei Coastal Forests, South Africa

**N. Tshaduli[a,b,*], C.J. Geldenhuys[a] & P.W. Chirwa[a]**

[a] Forest Postgraduate Programme, Department of Plant & Soil Sciences, University of Pretoria, South Africa

[b]PO Box 193, Tshilwavhusiku, Limpopo, 0983

*Corresponding author, e-mail: lynettendivhuwo@yahoo.com

## Highlights

- This 1-study covered an active vegetative phase (seedling/shoot growth) and a passive reproductive phase (flower/fruit)
- The seasonal variation in phenological states is important in sustainable harvesting of climbing stems for basket-making
- Culm development varied in cluster diameter and culm diameter/length but not culms per cluster across stand conditions

## Abstract

Earlier studies showed that local people benefit by harvesting culms of the "climbing bamboo" *Flagellaria guineensis* from Transkei Coastal Forests in South Africa. However, little is known about the regeneration ecology of this species that often forms tangles in forest stand conditions. This study assessed the regeneration ecology of *F. guineensis* in different forest stand conditions (forest gaps and edges, and closed canopy stands). Intensity ratings were applied to determine the monthly phenological states, i.e. presence and amount of phenological stages in Bulolo and Mtambalala Forests. Relatively few flowers and fruits were seen; in Mtambalala only during the rainy season and in Bulolo during the rainy and dry seasons. Regeneration (seedlings, shoots from rhizomes and at growing tips) was constant during the 12-month study period in both forests. This suggested that during the study period, this climbing bamboo was in an active vegetative growth stage but not in a reproductive stage. Culm development in forest stand conditions in Mnenga, Mtambalala and Manubi Forests showed significant differences ($P \leq 0.05$) in cluster diameter, culm diameter and culm length but not in the number of culms per cluster ($P > 0.05$). Mean cluster and culm diameters were highest in Manubi (185.5 and 1.0 cm) and lowest in Mnenga (64.1and 0.8 cm). The longest culms were recorded in Manubi (11.1 m). Culm diameter and length differed significantly ($P \leq 0.05$) between forest stand conditions, but not cluster diameter and culm numbers ($P > 0.05$). Culm numbers were not significantly related to cluster diameter; similarly culm length was not related to culm diameter. Flowering and fruiting of *F. guineensis* differed between seasons and sites, and culm development is influenced by forest stand conditions and differed between forests. Recommendations for more sustainable harvesting of culms for basket-making included focusing on tangles in tree crowns to be harvested during the dry season with minimal flowering or fruiting, further studies on growth of seedlings and shoots into the forest canopy, and productive cultivation of this climbing bamboo outside the forest.

**Keywords:** Climbing bamboo, culm, forest stand condition, phenology, regeneration

## 1. Introduction

Culms (stems) of the ‘climbing bamboo’ *Flagellaria guineensis* Schumach. (locally known as Ugonothi) in the South African coastal forests, are harvested for basket-making. The species regenerates both from seed (as product of flowering and fruiting) to maintain genetic variation, and vegetatively to ensure persistence in a site. The question is: How would an understanding of the phenological stages of flower, fruit, shoot and seedling formation, help towards sustainable harvesting of the species from the forests?

*Flagellaria* is a genus in the bamboo-like family Flagellariaceae (order Poales). It is not a bamboo (Poaceae family) but it is a climbing evergreen perennial plant and the stems resemble a slender bamboo, and hence-forth, in this paper, it will be called a climbing bamboo, as it is generally called in the literature. The genus consists of four or more species, including *F. guineensis* and the closely related *F. indica*. *Flagellaria guineensis* occurs in the tropical and subtropical forests of mainland Africa (Baldwin and Speese, 1957; https://www.prota4u.org/database/protav8.asp?g=pe&p=Flagellaria+guineensis+Schumach. 2018). Some bamboos and climbing bamboos occupy a dominant position in the understory of temperate and subtropical forests (Kleinhenz and Midmore, 2001; Giordano et al., 2009). The persistence of this climbing bamboo is sustained by the development of new shoots and culms. The shoot is the new growth from the dense root rhizome system (Muller and Rebelo, 2010) that develops into a culm, *i.e.* the individual bamboo-like stem (Kigomo, 2007). In the case of the climbing bamboos, the developing culms may climb by various means from ground level under the forest canopy to the top of the host trees. The changing light conditions may determine the successful flowering-fruiting behaviour of the species.

Many of the trees in tropical and subtropical forests are colonized by woody climbers or lianas (Campanello et al., 2012). Such climbers need a support structure, such as other plants and specifically trees, to reach the canopy, and where the canopy is low, more climbers enter the host-tree canopy vertically (Balfour and Bond, 1993). Climbing bamboos act in a similar way. Their culms are slender, solid and composed of well-demarcated nodes and internodes, a factor that makes them different from other climbers and from other bamboos because of their need for support from host trees. When high supports are lacking, the bamboo *Chusquea abietifolia*, for example, succeeds very well in climbing over low shrubs (Seifriz, 1920). Forest trees in the Transkei Coastal Forests, Eastern Cape, South Africa, are colonized by *F. guineensis*. This climbing bamboo requires support from host trees to grow vertically and to reach the canopy.

Many woody bamboos are typical examples of invasive or pioneer plants, having many attributes of successful pioneers (Lima et al., 2012). Lianas often increase in density when the forest canopy is disturbed (Lowe and Walker, 1977), which relates to better light conditions. They develop dense tangles on forest margins (Williams-Linera, 1990), forest gaps and disturbed sites (Campanello et al., 2007). In large open sites, the growth habit of the *Chusquea* bamboos is more arched and the culms of the different clumps are intermingled, forming an impenetrable thicket; passage is only possible by creeping below or climbing over the culm mat (Widmer, 1998). Young *F. indica* plants cannot survive under full sun exposure and requires shade in order to grow. However, adult plants are known to be strongly light-demanding (heliophytic) (Rabenantoandro et al., 2008).

The reproductive success of a plant depends on its flowering time being adapted to the environment in which it grows (Ramanayake, 2006). Patterns of bamboo regeneration through the production of new seedlings can be influenced by forest canopy conditions (Taylor et al., 2004). Forest canopy density has a strong influence on bamboo regeneration from seed. Some bamboos are monocarpic, which means that they flower once and then die, with masses of seedlings establishing, but it may take many years for the seedlings to develop into mature plants (Taylor and Qin, 1993). This behaviour has not been recorded for *F. guineensis*.

The culms of Ugonothi in the South African coastal forests are extensively used for basket-making (Cawe and Ntloko, 1997; Cawe 1999; Cawe and Geldenhuys, 2007). It plays a significant role in local income of rural people around Port St Johns (Cawe & Ntloko, 1997) and the plant has many uses in other parts of the continent (Bosch, 2010). In the Port St Johns area, it is sold in bundles, locally called head loads (Cawe & Geldenhuys, 2007). This raised concerns over the sustainability of such harvesting. The current study was motivated by the concerns that foresters have about the suppressing appearance of *F. guineensis* on the canopy of its host trees along forest edges, as a possible indication of unsustainable harvesting of this species. *Flagellaria guineensis* appeared to be shading the canopy of adult trees on the forest edge. However, the culms also produce the flowers and fruits that would ensure maintenance of the genetic pool of the species. This requires a good understanding of the critical life history stages of flower, fruit, shoot and seedling formation, to ensure sustainable harvesting of the species from the forests. In the case of the forest fern *Rumohra adiantiformis*, harvested for its leaves (fronds) for the florist industry, it was critical to synchronise frond harvesting with specific phenological stages in frond development (Geldenhuys and Van der Merwe, 1988). The study of plant phenology involves the observation, recording and interpretation of the timing of such life history events (Fenner, 1998). The switch to flowering is the most important event in the life cycle of a plant, signaling its commitment to set seed, ensuring survival of the species

(Ramanayake, 2006). In bamboos, the duration of the vegetative phase and switch to flowering varies according to the species (Ramanayake, 2006).

The main aim of this study was to assess the regeneration ecology of *F. guineensis* in the Transkei Coastal Forests in the Eastern Cape Province of South Africa. The specific objectives were: (1) To describe the phenological stages of flowering, fruiting and regeneration of the species; and (2) To compare the development patterns of the shoots and culms between different forest stand conditions such as forest edges (margins), forest gaps and mature forest stands. The following questions were addressed: (1) What are the phenological patterns of flowering, fruiting, shoot development and seedling production in the species over one year? (2) How and under what conditions do the seedlings establish and grow? (3) What is the nature of the rootstock from which the plant develops new shoots? (4) How does development of the plant vary between forest edges (margins), forest gaps and mature, closed-canopy forest? (5) How do the shoots climb into a tree if they continuously start at ground level?

## 2. Materials and Methods

### *2.1. Study forests and species*

The study was conducted in four forests along the Wild Coast of the Eastern Cape: Bulolo Forest (31°8'36.25"S, 29°30'58.55"E; 6–100 m above sea level or asl), Mnenga Forest (31°36'27.94" S, 29°34'33.96" E; 80–125 m asl), Mtambalala Forest (31°32'57.22" S, 29°36'19.99" E; 50–125 m asl) around of Port St Johns, and Manubi Forest (32°26'34.83" S, 28°35'42.02" E; 100–200 m asl) north of East London (Fig. 1). Rainfall is usually >700 mm per year and is more prevalent during summer. Total monthly rainfall during the study period was obtained from the Silaka

Nature Reserve near Port St Johns, close to the Bulolo forest (Fig. 2), showing two dry periods between May to August and January to February, and two rainy seasons between March to April and September to December. The area along the coast has a moderate climate with mean minimum temperature of 17°C and a mean maximum of 20°C (Von Maltitz et al., 2003). The geology is mainly sandstone outcrops, syenitic granites and rhyolites, and the soils are generally less acidic and medium to coarse-grained (King, 1940; Von Maltitz et al., 2003).


**Fig. 1.** Location of the four forests used in the two studies in the Transkei Coastal forests in the Eastern Cape, South Africa.

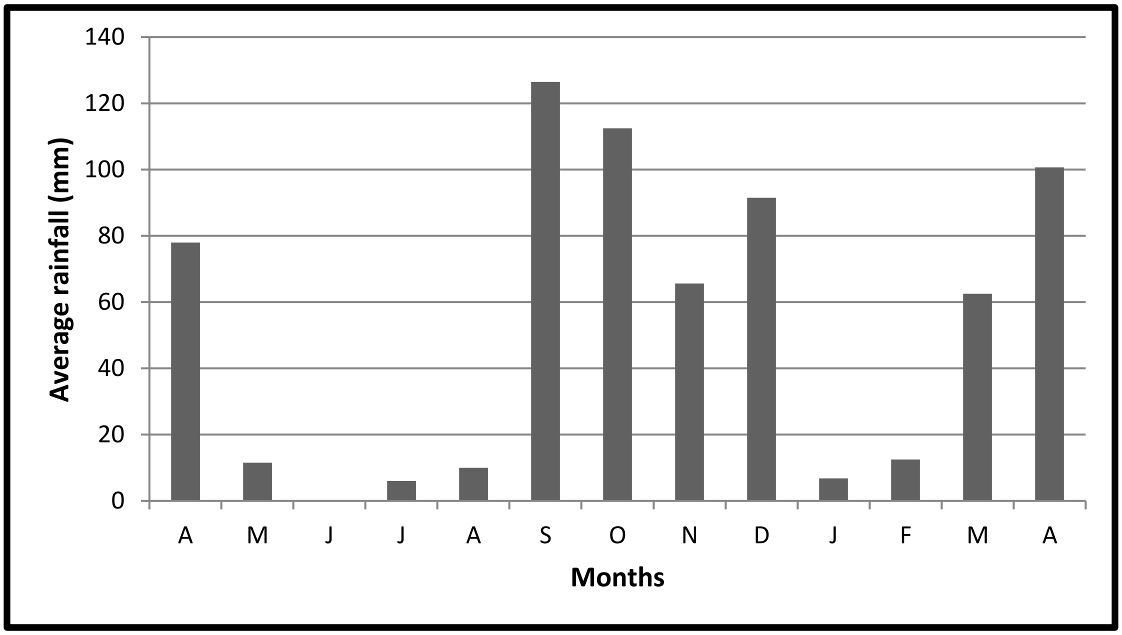


**Fig. 2.** Rainfall diagram for the study period from April 2014 to April 2015 (data from Silaka Nature Reserve).

The Transkei Coastal Forests (Von Maltitz et al., 2003; Mucina 2018) are characterized by low to high canopies (10-30 m) with a smooth to uneven surface, but relatively closed. Stand structure comprises three distinct strata, restricting light penetration onto the forest floor: a tree stratum of canopy trees, with a well-developed sub-canopy tree stratum with seedlings and saplings, and a poorly developed herb layer (King, 1940; Geldenhuys and Rathogwa, 1995; Cawe and Geldenhuys, 2007). The forests are found on sloping coastal platforms as well as steep scarps in deeply incised valleys. The tree and climber species vary in importance in different forests in this coastal zone. Common tree species include *Buxus macowanii*, *Buxus natalensis*, *Drypetes gerrardii*, *Englerophytum natalense*, *Harpephyllum caffrum*, *Heywoodia lucens*, *Millettia grandis* and *Ptaeroxylon obliquum.* Herbaceous climbers include *Flagellaria guineensis* and *Thunbergia alata*. Common shrubs and scramblers include *Scutia myrtina*, *Grewia occidentalis* and *Eugenia natalitia* (Von Maltitz et al., 2003; Mucina and Geldenhuys, 2006).

*Flagellaria guineensis* in these coastal forests is woody with sympodial rhizomes and is patchily distributed. Leaves are distichous, with the leaf apex extending into a simple, involutely coiled tendril that clings to all available host trees for support. The plant regenerates from both seed and rhizome shoots (Fig. 3).

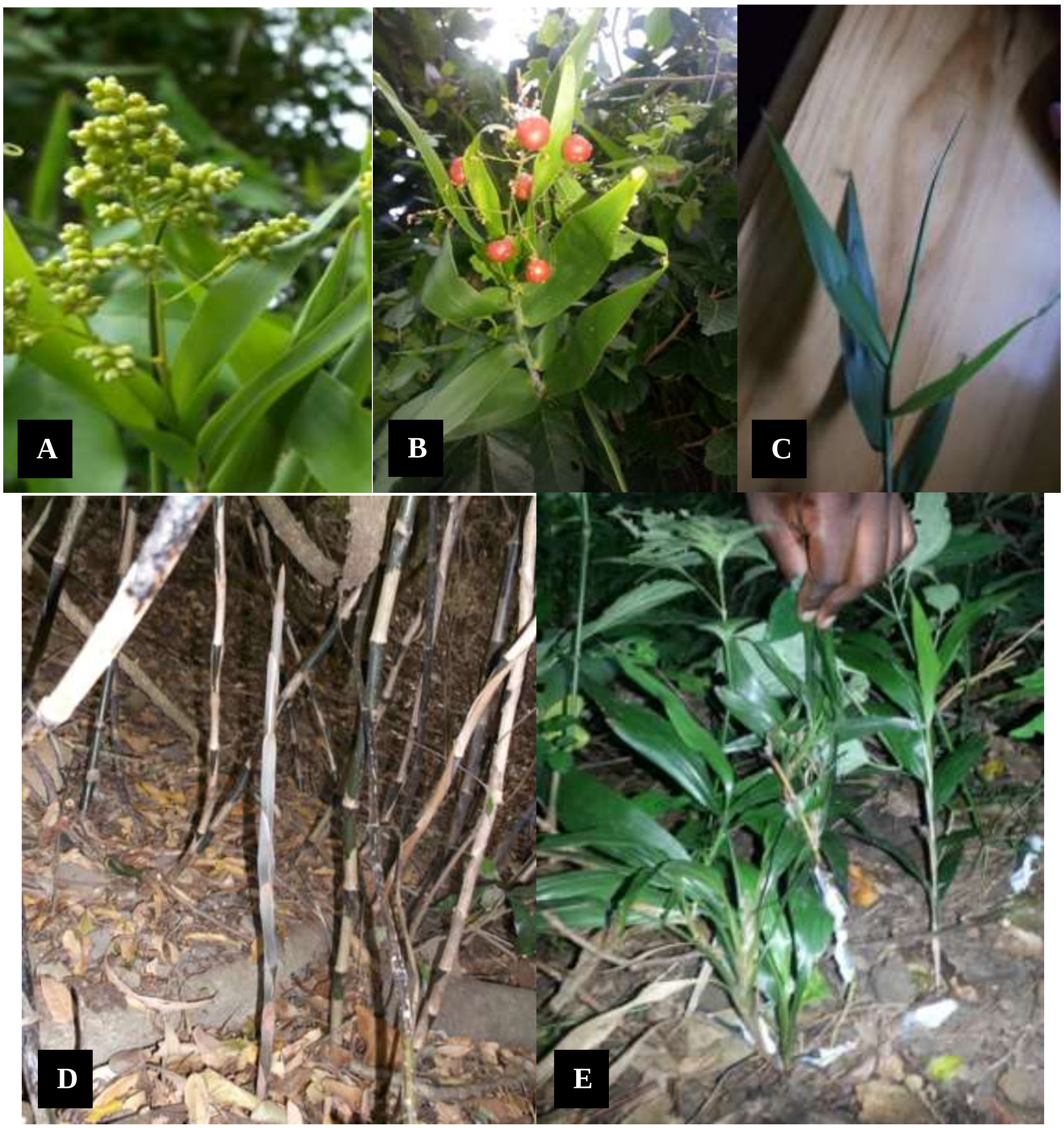


**Fig. 3**. Phenological states of Flagellaria guineensis: (A) Flower buds with some open flowers; (B) Ripe fruit; (C) Leaf shoots; (D) Rhizome shoots, developing from the underground rhizome; (E) Seedlings.

*2.2. Data collection*

*2.2.1. Flowering, fruiting and growth phenology*

Phenological observations were confined to the Bulolo and Mtambalala Forests due to logistical constraints during this short-term study. In each forest, 30 observation spots (one bamboo cluster) were selected, 10 m apart, with 10 spots in each of the three forest stand conditions: Forest edge E (exposed to the sun during the morning, i.e. east or south, with cooler conditions), Forest edge W (exposed to the sun after midday, i.e. west or north, with warmer conditions), and Forest interior I (inside the forest below the canopy). There were not many clusters at a spot, and therefore, any available cluster closest to a random point was selected. In total, 60 plants were observed in the two forests. In each forest the observation spots were marked with a number (1 to 30) on a tree stem, and the geographic coordinates were recorded with a GPS. At each spot, site information was recorded: forest stand condition (closed canopy, gap or edge), altitude and geographic coordinates. The presence and abundance of the following phenological stages were recorded for each observed plant (Fig. 3): flower buds, flowers, fruits, leaf shoots, rhizome shoots and seedlings. Abundance of each observed state was recorded as follows: 0 = none; 1 = few; 2 = intermediate; and 3 = abundant. Abundance ratings varied between phenological stages, and the assigned ratings were relative within a phenological stage. Some plants presented different states at the same time, such as flowering and fruiting. Observations were done once every month, during the last week of the month.

*2.2.2. Culm development in forest stand conditions*

Culm development was assessed in the Mnenga, Mtambalala and Manubi Forests. In each forest, six *F. guineensis* clusters were randomly chosen from each of the three stand conditions: forest edge, canopy gap and closed mature forest, giving a total of 18 clusters per forest, and a total of

54 clusters overall. A cluster is the group of culms developing from an underground rootstock of a seemingly single *F. guineensis* plant. For each cluster, the following parameters were recorded: forest stand condition (closed canopy, gap or edge), location coordinates next to each cluster using GPS, and species, height and stem diameter at breast height (dbh) of all host trees. Each *F. guineensis* cluster was measured and recorded as follows: diameter of the cluster at ground level (distance between shoots or culms on the edge of the cluster in two perpendicular directions, recorded as the mean of the two distances), height at which the culms start to climb the host trees, number of culms in each cluster, the diameter and length of each culm in a cluster (each culm was pulled down to ground level for measuring length and basal diameter).

*2.3. Data analysis*

Quantitative data on the phenological state of *F. guineensis* were obtained from a survey made from April 2014 to April 2015. Microsoft Excel and descriptive statistics in SPSS were used to analyze the data. The phenological observations of *F. guineensis* in the two forests and their forest stand conditions were compared, using two formulas for calculating the monthly mean intensity of occurrence of a specific phenological state (flower buds, open flowers, fruits, leaf shoots, rhizome shoots and seedlings) per forest and per stand condition:

(1) To compare the mean monthly phenological state for each forest:

Mean intensity per month = (No of clusters with few flowering * 1) + (No of clusters with intermediate flowering * 2) + (No of clusters with abundant flowering * 3) ÷ 30, where 30 is the number of clusters observed in a forest.

(2) To compare the mean monthly phenological state per stand condition for each for

Mean intensity per month = (No of clusters with few flowering * 1) + (No of clusters with intermediate flowering * 2) + (No of clusters with abundant flowering * 3) ÷ 10, where 10 is the number of clusters observed per stand condition.

For the culm development, data were analysed for variance in GenStat Ver 12.1. One-way ANOVA was used to test for the statistical significance of differences between mean values of cluster diameter, number of culms per cluster, culm diameter and culm length in different forest stand conditions and forests. If the ANOVA value was found to be significant, the parameter mean values were considered significant at $P<0.05$. Log transformation was used for the response variable ‘‘number of culms per cluster,’’ which was in the form of count data. Regression analysis was carried out to determine the relationship between cluster diameter and number of culms, and between culm length and culm diameter, that could help in the monitoring of the species.

## 3. Results

### *3.1. Flowering, fruiting and shoot phenology*

#### *3.1.1. Flower bud phenology*

The presence of flower buds (Fig. 3A) for the 60 plant clusters varied widely between the two forests and their forest stand conditions (Table 1). In Bulolo Forest, few clusters showed some presence of flower buds, with a few flower buds present during April 2014. The main period of presence was from September 2014 to March 2015, in both rainy and dry seasons (Fig. 2), and a peak during December 2014 to February 2015. More flower buds were present on both exposures of forest edges, with relatively low presence in the forest interior. In Mtambalala

Forest, flower bud production was generally low, with flower buds seen from April to October 2014, in some of the clusters and then again during February 2015 (both rainy and dry seasons).

**Table 1**: Flower bud intensity on 30 *Flagellaria guineensis* clusters in each of Bulolo and Mtambalala Forests during the study period April 2014 to April 2015.

| Month | **A14** | **M** | **J** | **J** | **A** | **S** | **O** | **N** | **D** | **J15** | **F** | **M** | **A** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bulolo Forest | | | | | | | | | | | | | |
| Mean intensity of flower bud presence in each category | | | | | | | | | | | | | |
| All | 0.03 | | | | | 0.13 | 0.13 | 0.10 | 0.67 | 0.67 | 0.70 | 0.27 | |
| Edge E | 0.10 | | | | | 0.30 | 0.30 | 0.20 | 0.90 | 0.90 | 1.40 | 0.20 | |
| Edge W | | | | | | 0.10 | 0.10 | | 1.00 | 1.00 | 0.60 | 0.30 | |
| Interior I | | | | | | | | 0.10 | 0.10 | 0.10 | 0.10 | 0.30 | |
| Mtambalala Forest | | | | | | | | | | | | | |
| Mean intensity of flower bud presence in each category | | | | | | | | | | | | | |
| All | 0.07 | 0.10 | 0.13 | 0.07 | 0.07 | 0.03 | 0.03 | | | | 0.03 | | |
| Edge E | | 0.30 | 0.10 | | | 0.10 | | | | | 0.10 | | |
| Edge W | 0.20 | | 0.20 | 0.10 | 0.10 | | | | | | | | |
| Interior I | | | 0.10 | 0.10 | 0.10 | | 0.10 | | | | | | |

### *3.1.2. Flowering phenology*

Presence of open white to light creamy flowers for the 60 plant clusters varied widely (Table 2). In Bulolo forest they appeared in the late dry season (August, September and November 2014), and then with a peak (53% of clusters showing flowers) during March 2015 (rainy season) with some during April 2015. Forest edges showed more flowers than the forest interior. In contrast, in Mtambalala Forest, flower production was generally low and only seen during March 2015 (rainy season).

**Table 2**: Open flower intensity on 30 *Flagellaria guineensis* clusters in each of Bulolo and Mtambalala Forests during the study period April 2014 to April 2015.

| Month | A14 | M | J | J | A | S | O | N | D | J15 | F | M | A |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bulolo Forest | | | | | | | | | | | | | |
| Mean intensity of flower presence in each category | | | | | | | | | | | | | |
| All | | | | | 0.03 | 0.10 | | 0.07 | | | | 0.80 | 0.07 |
| Edge E | | | | | 0.10 | 0.20 | | | | | | 1.30 | 0.20 |
| Edge W | | | | | | 0.10 | | | | | | 1.00 | |
| Interior I | | | | | | | | 0.20 | | | | 0.10 | |
| Mtambalala Forest | | | | | | | | | | | | | |
| Mean intensity of flower presence in each category | | | | | | | | | | | | | |
| All | | | | | | | | | | | | 0.10 | |
| Edge E | | | | | | | | | | | | 0.30 | |
| Edge W | | | | | | | | | | | | | |
| Interior I | | | | | | | | | | | | | |

### *3.1.3. Fruiting phenology*

The presence of fruit varied widely between the two forests and their forest stand conditions (Table 3). In Bulolo Forest, clusters were bearing fruit during April 2014 and February to April 2015 (rainy seasons), with occasional few fruits on a few clusters during May, July, October, November 2014 and January 2015. Fruiting peaked during March 2015, with 50% of the clusters bearing fruit, with more on both exposures of forest edges, and relatively low presence in the forest interior. In Mtambalala Forest, the fruit production was low; fruits were only seen during the rainy season (April 2014, and February to April 2015).

**Table 3**: Fruiting intensity on 30 *Flagellaria guineensis* clusters in each of Bulolo and Mtambalala Forests during the study period April 2014 to April 2015.

| Month | **A14** | **M** | **J** | **J** | **A** | **S** | **O** | **N** | **D** | **J15** | **F** | **M** | **A** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bulolo Forest | | | | | | | | | | | | | |
| Mean intensity of fruit presence in each category | | | | | | | | | | | | | |
| All | 0.47 | 0.03 | | 0.03 | | | 0.03 | 0.03 | | 0.03 | 0.67 | 0.73 | 0.60 |
| Edge E | 0.20 | | | 0.10 | | | 0.10 | 0.10 | | | 1.00 | 1.10 | 1.00 |
| Edge W | 1.00 | 0.10 | | | | | | | | | 0.90 | 0.90 | 0.70 |
| Interior I | 0.20 | | | | | | | | | 0.10 | 0.10 | 0.20 | 0.10 |
| Mtambalala Forest | | | | | | | | | | | | | |
| Mean intensity of fruit presence in each category | | | | | | | | | | | | | |
| All | 0.17 | | | | | | | | | | 0.47 | 0.43 | 0.10 |
| Edge E | 0.30 | | | | | | | | | | 0.90 | 0.70 | |
| Edge W | 0.20 | | | | | | | | | | 0.50 | 0.60 | 0.20 |
| Interior I | | | | | | | | | | | | | 0.10 |

### *3.1.4. Leaf shoot phenology*

Leaf shoots were abundant in almost all clusters throughout the study period in all stand conditions in both forests (Table 4), but the intensity was higher during April to August 2014 and then December 2014 to January 2015. Leaf shoot production was high in both forest edges and forest interior.

**Table 4**: Leaf shoot intensity on 30 *Flagellaria guineensis* clusters in each of Bulolo and Mtambalala Forests during the study period April 2014 to April 2015.

| Month | **A14** | **M** | **J** | **J** | **A** | **S** | **O** | **N** | **D** | **J15** | **F** | **M** | **A** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bulolo Forest | | | | | | | | | | | | | |
| Mean intensity of leaf shoot presence in each category | | | | | | | | | | | | | |
| All | 2.40 | 2.40 | 2.40 | 2.40 | 2.03 | 1.63 | 1.50 | 1.70 | 2.23 | 2.40 | 1.43 | 1.70 | 1.77 |
| Edge E | 2.70 | 2.80 | 2.80 | 2.80 | 2.40 | 2.00 | 1.90 | 2.30 | 2.10 | 2.30 | 1.70 | 2.10 | 2.30 |
| Edge W | 2.40 | 2.30 | 2.30 | 2.30 | 2.00 | 1.40 | 1.30 | 1.70 | 2.60 | 2.80 | 1.20 | 1.90 | 1.80 |
| Interior I | 2.10 | 2.10 | 2.10 | 2.10 | 1.70 | 1.50 | 1.30 | 1.10 | 2.00 | 2.10 | 1.40 | 1.10 | 1.20 |
| Mtambalala Forest | | | | | | | | | | | | | |
| Mean intensity of leaf shoot presence in each category | | | | | | | | | | | | | |
| All | 2.57 | 2.57 | 2.57 | 2.43 | 2.30 | 1.87 | 1.50 | 1.63 | 2.60 | 2.63 | 1.63 | 1.33 | 1.63 |
| Edge E | 2.70 | 2.60 | 2.60 | 2.50 | 2.30 | 1.80 | 1.60 | 1.90 | 2.60 | 2.60 | 2.10 | 1.20 | 1.90 |
| Edge W | 2.50 | 2.60 | 2.60 | 2.40 | 2.40 | 1.90 | 1.60 | 1.70 | 2.40 | 2.50 | 1.50 | 1.50 | 1.60 |
| Interior I | 2.50 | 2.50 | 2.50 | 2.40 | 2.20 | 1.90 | 1.30 | 1.30 | 2.80 | 2.80 | 1.30 | 1.30 | 1.40 |

### *3.1.5. Rhizome shoots phenology*

Recording of the rhizome shoot production (Fig. 3D) started in June 2014 and continued to April 2015 at both study sites (Table 5). The rhizome shoots were seen throughout the study period in all three forest stand conditions in both forests. Many clusters produced few shoots. Bulolo Forest produced more shoots in the forest interior, whereas in Mtambalala Forest, shoot production was very similar in the different forest stand conditions.

**Table 5**: Rhizome shoot intensity of 30 *Flagellaria guineensis* clusters in each of Bulolo and Mtambalala Forests during the study period June 2014 to April 2015.

| Month | J14 | J | A | S | O | N | D | J15 | F | M | A |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Bulolo Forest | | | | | | | | | | | |
| Mean intensity of Rhizome shoot presence in each category | | | | | | | | | | | |
| All | 0.77 | 1.03 | 1.03 | 0.80 | 1.00 | 0.87 | 0.97 | 0.90 | 0.87 | 1.07 | 1.20 |
| Edge E | 0.50 | 0.50 | 0.70 | 0.50 | 0.50 | 0.90 | 0.90 | 0.60 | 0.40 | 0.80 | 0.60 |
| Edge W | 0.50 | 0.60 | 0.90 | 0.80 | 1.00 | 0.60 | 0.70 | 0.70 | 1.10 | 1.00 | 1.10 |
| Interior I | 1.30 | 2.00 | 1.50 | 1.10 | 1.50 | 1.10 | 1.30 | 1.40 | 1.10 | 1.40 | 1.90 |
| Mtambalala Forest | | | | | | | | | | | |
| Mean intensity of Rhizome shoot presence in each category | | | | | | | | | | | |
| All | 0.70 | 0.80 | 1.03 | 0.93 | 1.07 | 0.83 | 1.23 | 1.23 | 1.07 | 1.30 | 0.93 |
| Edge E | 0.60 | 0.70 | 0.80 | 0.90 | 0.90 | 1.00 | 1.20 | 1.20 | 1.20 | 1.50 | 0.90 |
| Edge W | 0.80 | 0.70 | 1.20 | 1.10 | 1.20 | 0.80 | 1.00 | 1.00 | 0.90 | 1.20 | 0.80 |
| Interior I | 0.70 | 1.00 | 1.10 | 0.80 | 1.10 | 0.70 | 1.50 | 1.50 | 1.10 | 1.20 | 1.10 |

### *3.1.6. Seedling phenology*

Seedlings developed in the vicinity of the clusters and were seen throughout the study period in both study sites (Table 6). Many clusters had only few seedlings next to them at both study sites, but every month >50% of the clusters had seedlings of *F. guineensis* next to them. The forest interior in both forests showed a higher intensity of seedlings than the forest edges. In Bulolo Forest, Forest edge W had more seedlings than Forest edge E. In Mtambalala Forest, Forest edge W had more seedlings than Forest edge E during April to October 2014, but from November 2014 to April 2015, Forest edge E had more seedlings than Forest edge W.

**Table 6**: Seedling intensity at 30 *Flagellaria guineensis* clusters in each of Bulolo and Mtambalala Forests during the study period April 2014 to April 2015.

| Month | A14 | M | J | J | A | S | O | N | D | J15 | F | M | A |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bulolo Forest | | | | | | | | | | | | | |
| Mean intensity of seedling presence in each category | | | | | | | | | | | | | |
| All | 0.60 | 0.80 | 0.77 | 0.73 | 0.73 | 0.63 | 0.77 | 0.83 | 0.97 | 0.97 | 1.03 | 1.30 | 1.33 |
| Edge E | 0.50 | 0.50 | 0.40 | 0.20 | 0.40 | 0.40 | 0.80 | 0.30 | 0.30 | 0.30 | 0.20 | 0.80 | 0.80 |
| Edge W | 0.40 | 0.70 | 0.70 | 0.80 | 0.80 | 0.70 | 0.60 | 1.10 | 0.90 | 1.00 | 1.00 | 1.40 | 1.20 |
| Interior I | 0.90 | 1.20 | 1.20 | 1.20 | 1.00 | 0.80 | 0.90 | 1.10 | 1.70 | 1.60 | 1.90 | 1.70 | 2.00 |
| Mtambalala Forest | | | | | | | | | | | | | |
| Mean intensity of seedling presence in each category | | | | | | | | | | | | | |
| All | 1.07 | 1.17 | 0.90 | 0.93 | 0.97 | 0.93 | 0.77 | 1.23 | 1.33 | 1.33 | 0.93 | 1.60 | 1.70 |
| Edge E | 0.60 | 0.80 | 0.60 | 0.60 | 0.90 | 0.90 | 0.60 | 1.10 | 1.30 | 1.40 | 0.70 | 1.50 | 1.70 |
| Edge W | 0.70 | 1.00 | 1.10 | 1.20 | 1.10 | 1.00 | 0.80 | 0.80 | 0.90 | 1.00 | 0.70 | 1.40 | 1.30 |
| Interior I | 1.90 | 1.70 | 1.00 | 1.00 | 0.90 | 0.90 | 0.90 | 1.80 | 1.80 | 1.60 | 1.40 | 1.90 | 2.10 |

### *3.2. Culm development*

The mean values for cluster diameter, number of culms per cluster, culm diameter and culm length of *F. guineensis* varied between the three sampled forests and the forest stand conditions (Table 7). *Mean cluster diameter* was significantly larger ($p < 0.05$) in Manubi Forest (185.5 cm) than in Mtambalala (67.3 cm) and Mnenga (64.1 cm) Forests. In Manubi Forest, cluster diameter decreased from closed forest to forest edge. Mnenga and Mtambalala Forests showed the opposite trend, *i.e.* cluster diameter was largest in forest edge and smallest under the closed canopy. However, the differences were not significant. The *mean number of culms per cluster* varied between the different forests and stand conditions but was not significantly different. It was highest on the forest edge in Mnenga Forest and lowest in the forest gaps at Mtambalala. *Mean culm diameter* was marginally significantly different ($P<0.05$) between the forests, with the highest value in forest edges in Manubi Forest. The value was very similar in the other

**Table 7**: (A) Mean values for cluster/culm variables of *Flagellaria guineensis*, and (B) ANOVA results to assess the significance of differences between forests, stand conditions, and their interactions (*= significant (P < 0.05), ns= non-significant (P ≥ 0.05) )

| A. Mean values for variables | Forests | Forest edge | Forest gaps | Closed canopy |
|---|---|---|---|---|
| | Manubi | 163.9 | 185.4 | 207.2 |
| | Mnenga | 72.2 | 71.3 | 48.6 |
| Cluster diameter (cm) | Mtambalala | 85.8 | 51.0 | 65.0 |
| | Manubi | 11.8 | 11.0 | 16.2 |
| | Mnenga | 18.8 | 13.0 | 9.7 |
| Number of culms | Mtambalala | 13.5 | 7.8 | 12.3 |
| | Manubi | 1.2 | 0.8 | 1.0 |
| | Mnenga | 0.8 | 0.9 | 0.8 |
| Culm diameter (cm) | Mtambalala | 0.8 | 0.9 | 0.8 |
| | Manubi | 9.9 | 9.2 | 14.1 |
| | Mnenga | 9.2 | 9.6 | 8.6 |
| Culm length (m) | Mtambalala | 9.1 | 8.9 | 9.1 |

| B. ANOVA's | S.E | d.f | MS | P-value |
|---|---|---|---|---|
| | | Cluster diameter(cm) | | |
| Forests | 15.83 | 2 | 86199 | <0.001* |
| Stand Conditions | 15.83 | 2 | 125 | $0.946^{ns}$ |
| Forests × Stand C | 27.41 | 4 | 2801 | $0.307^{ns}$ |
| | | Number of culms | | |
| Forests | 2.003 | 2 | 0.2903 | $0.292^{ns}$ |
| Stand Conditions | 2.003 | 2 | 0.3256 | $0.252^{ns}$ |
| Forests × Stand C | 3.47 | 4 | 0.4396 | $0.124^{ns}$ |
| | | Culm diameter(cm) | | |
| Forests | 0.0668 | 2 | 0.17526 | 0.02* |
| Stand Conditions | 0.0668 | 2 | 0.0172 | 0.654* |
| Forests × Stand C | 0.1157 | 4 | 0.13784 | $0.016^{ns}$ |
| | | Culm length (m) | | |
| Forests | 0.787 | 2 | 24.101 | 0.019* |
| Stand Conditions | 0.787 | 2 | 9.887 | $0.182^{ns}$ |
| Forests × Stand C | 1.364 | 4 | 16.569 | 0.029* |

forests and their stand conditions, including forest gaps at Manubi. *Mean culm length* was significantly different (P<0.05) between the different forests, mainly because of the much higher culm length under closed canopy in Manubi Forest. Culm length was relatively similar in the other stand conditions and forests.

*3.3. Allometric relationship between cluster diameter and culm variables*

There appeared to be allometric relationships between cluster diameter and the number of culms, and between culm diameter and culm length. However, the statistical analyses showed no significant allometric relationships between cluster diameter and number of culms, and between culm diameter and culm length, except for some forests and in specific stand conditions (Fig. 4 and 5). In Mnenga Forest under closed canopy, the number of culms increased with increasing cluster diameter ($R^2$= 0.8342; Fig. 4), with 83% of the variation in cluster diameter being explained by the logarithmic relationship. In Mtambalala Forest, culm length was only weakly related to culm diameter, with only 24% of the variation in culm length explained by the logarithmic relationship with culm diameter (Fig. 5).

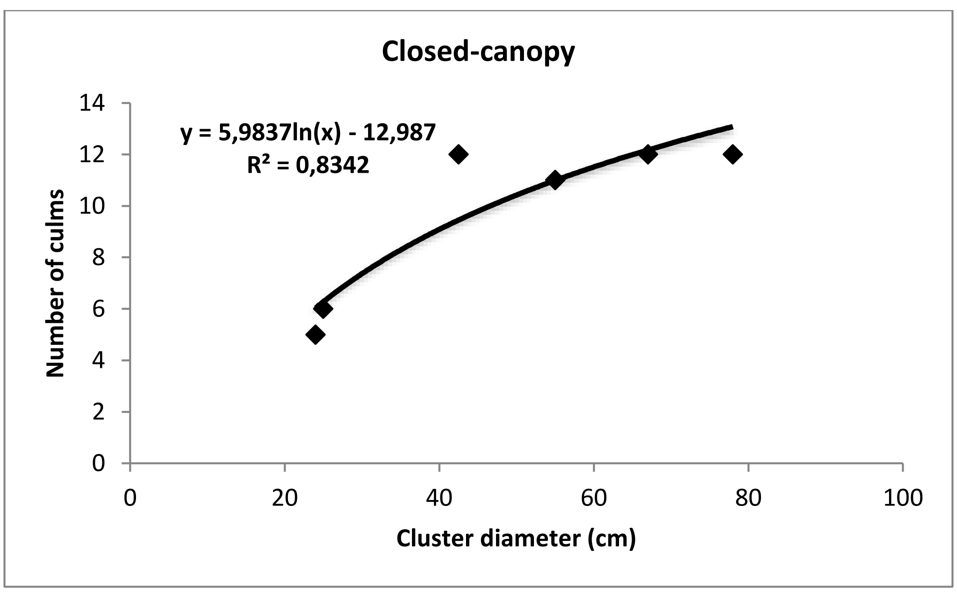


**Fig. 4.** Relationship between cluster diameter and number of culms of Flagellaria guineensis under closed canopy in Mnenga Forest.

Some moderate positive relationships were found between cluster diameter and number of culms under different specific forest stand conditions, but there were no significant general trends that would be useful to predict number of culms from cluster diameter, or culm length from culm diameter.

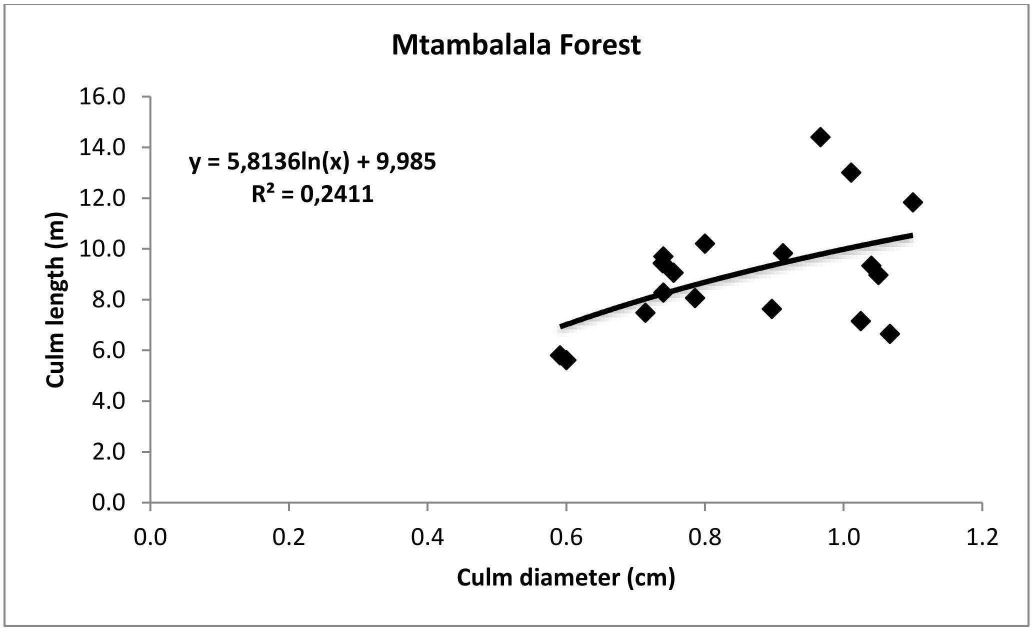


**Fig. 5.** Relationship between culm diameter and culm length of Flagellaria guineensis in Mtambalala Forest, Eastern Cape, South Africa.

### *3.4. Cluster development and host trees*

*Flagellaria guineensis* was observed climbing its host trees for vertical support in the forests. Trees of various species and of different size (height and stem diameter) have been observed to provide such support for climbing culms but there was no apparent preference for specific tree species. The *F. guineensis* culms cling onto tree trunks and grow towards the canopy of host trees. However, some culms in a cluster growing from the rhizome, appeared to reach for the canopy directly.

Culms of *F. guineensis* in a cluster along forest edges and gaps tend to form dense mats on the canopy of host trees. In a mature forest with closed canopy, the culms of a cluster tended to climb on different host trees (with some distance between host trees). Seedlings of both host trees and *F. guineensis* were seen on the forest floor. The *F. guineensis* seedlings developed into young culms that would climb small trees and then reach for canopy trees whereas shoots that grow from rhizomes can reach up to 4 m without climbing a tree (erect position without bending).

**4. Discussion**

This short-term study (one year) showed definite emerging patterns in terms of flowering and fruiting phenology, and culm development from seedlings and rhizomes in *F. guineensis*, even though the phenological stages were very variable between forests, stand conditions and clusters. Some plants showed no sign of flowering or fruiting. New buds and flowers did not always result in fruit production, and sometimes fruit production was recorded with no observation of previous flowering. During the study period, *F. guineensis* was in a stage of vegetative production of abundant leaf and rhizome shoots, but also seedlings, and a relatively low early reproductive stage with few flowers and fruits. In Bulolo Forest, relatively abundant open flowers occurred only during March 2015. In Mtambalala Forest, only a few clusters produced flowers, and only in March 2015. Ripe fruits were found in February until April (rainy season) in both Bulolo and Mtambalala Forests, but in Bulolo Forest fruits were also seen in the dry season.

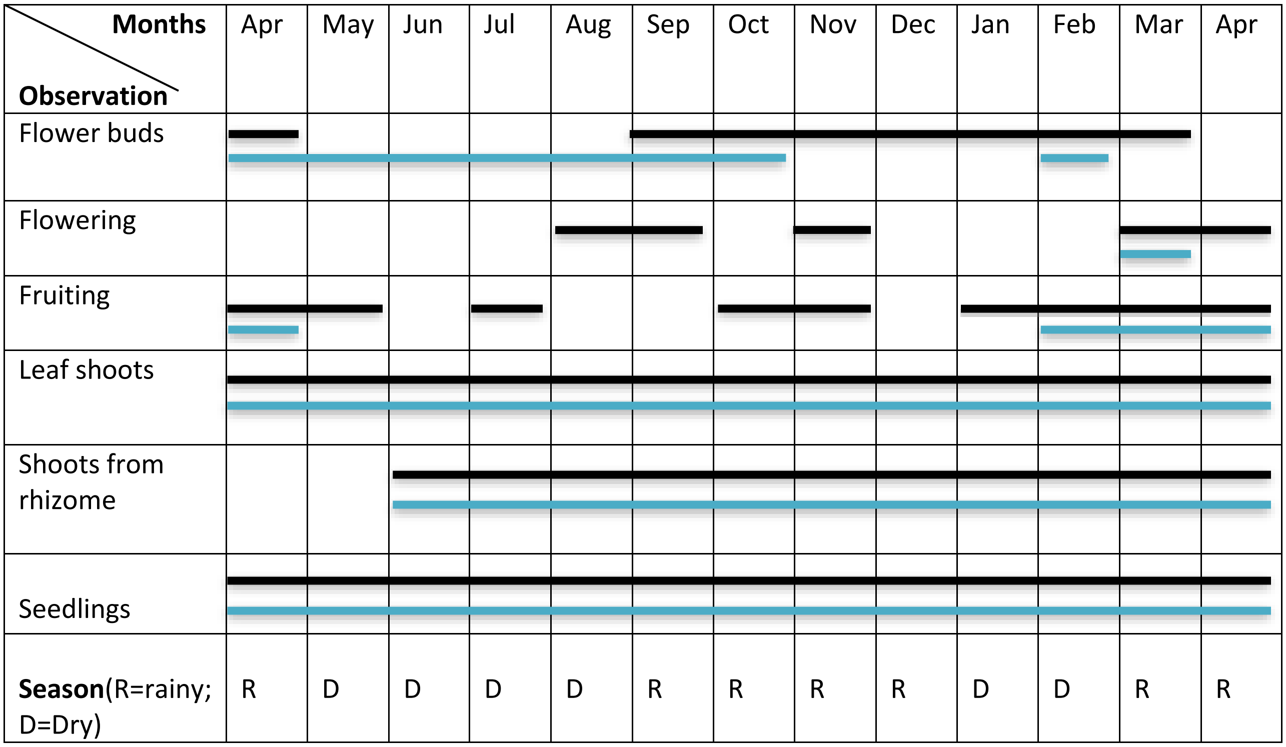


**Fig. 6.** Phenological sequence of reproductive (flowering, fruiting and seedlings) and vegetative (leaf and rhizome shoots) production of Flagellaria guineensis in Bulolo (black lines) and Mtambalala (blue lines) Forests from April 2014 to April 2015.

Figure 6 summarizes the phenological sequence of flowering, fruiting, leaf shoots, rhizome shoots and seedlings of *F. guineensis* in the two forests. This suggests that there is at least a two-year cycle between the reproductive stage of flowering and fruiting and the vegetative stage of developing new leaf and rhizome shoots. This is in contrast to the annual cycle in frond development stages in the fern *Rumohra adiantiformis* (Geldenhuys and Van der Merwe, 1988). The seedlings seen in the forests may have come from a previous season of flowering and fruiting. The assessed seedlings may not reflect the current flowering and fruiting patterns, but may become established over an extended period of more than one year after fruiting. The relatively low level of flower or fruit production makes it difficult to determine the reason why flower and fruit production was relative higher in Bulolo Forest than in Mtambalala Forest, which had a better developed edge and a more fully developed canopy. It would be useful to implement a phenological study with selected marked plants in different forest stand conditions over a longer time period.

During the study period, the culms of clusters did not flower at the same time; some culms in a cluster remained in a vegetative state while others were flowering. Some partial die-back of a few culms per cluster was seen in the forest, but there were no signs of monocarpic behaviour in *F. guineensis*, i.e. mass synchronous flowering and fruiting followed by mass die-back, as occurs in some bamboo species (Taylor and Qin (1993), particularly in *Chusquea* in South America (González et al., 2002; Giordano et al., 2009).

*Flagellaria guineensis* regenerates by producing seedlings from seeds and shoots from the rhizome. Seedlings develop smooth, long, narrow dark green leaves. Their new culms are protected by sheaths that are attached to each node (Fig. 3E). As they mature, the sheaths covering the culms dry out, leaving the nodes of the culms exposed; with the leaves only at the top of the culms. A seedling over time develops a root system composed of tangled rhizomes. Shoots develop from the rhizome and into the culms that grow up to the crowns of trees in the canopy or on edges of gaps and forest margins. Initially the culm growing tip produces new leaf shoots, but eventually clusters of creamy flower buds develop that open and eventually produce red fruits (drupes).

The position of the plants in relation to sunlight in the forest edge does influence the production of new shoots and seedlings. Numbers of shoots and seedlings were more in the forest edge with a western exposure to sunlight during the afternoon with warmer conditions, with fewer shoots and seedlings in forest edges with eastern exposure and cooler conditions, suggesting that warmer conditions were benefitting development of seedlings and shoots. However, shoots and seedlings grew in greater abundance in the forest interior compared to the forest edge conditions. This suggests that the climbing bamboo requires some shade to regenerate, i.e. shady conditions under the forest canopy increased the number of shoots and seedlings on the forest floor. This is in line with the behaviour of *Flagellaria indica*, in which young plants require shade to grow, but adult plants are strongly light-demanding (Rabenantoandro et al., 2008).

The appearance of *F. guineensis* on the canopy of its host trees is different in different forest stand conditions under the closed-canopy, in gaps or on the forest edge. The plant forms dense tangles on the canopy of its host tree on the forest edges, conforming to other studies that dense tangles of climbers are often found on forest margins (Williams-Linera, 1990; Widmer, 1998; Campanello et al., 2007). Harvesting of culms from such tangles may reduce the pressure, if any, of such tangles on the host trees.

This species can regenerate from seed, thereby maintaining genetic diversity from reproductive regeneration. But it has the ability to persist on site through vegetative regrowth through culm development, growing from a sympodial rhizome. The culms cling to the host trees with their leaves. If there are no nearby host trees to climb, the culms grow sideways to climb surrounding small trees and then reaching for taller trees. As the plants mature, the number of culms also increases, as new shoots grow from the rhizome, with more than 20 culms per rhizome, and reaching up to 20 m in length and 2.5 cm in diameter. Cluster diameter increased with rhizome expansion, and was greatest in Manubi Forest. Culm diameter was highest in open habitats (forest edge and gaps). Culm length was the longest in closed-canopy stands, such as in Manubi forest with high, closed canopy. The culms grow until they are on top of the host canopy, indicating their need for light but ability to continue growing under relatively shady conditions below the canopy. Generally, host trees in forest edges and gaps tend to be shorter than in the interior of closed-canopy mature stands.

The information on culm development under different stand conditions is important for the development of sustainable resource use practices. The relationship between cluster diameter and number of culms, and between culm length and culm diameter showed much variation between forest stand conditions. This aspect needs further study to know how to use such information to monitor the impact of the harvesting of culms of *F. guineensis* for basket-making. Such information forms an important part of the monitoring of sustainable harvesting of fronds (leaves) of *Rumohra adiantiformis* fern from the Southern Cape forests (Geldenhuys and Van der Merwe, 1988). It would also be useful to monitor the regrowth potential of new culm shoots from the rhizomes with different intensities of culm harvesting. Such information could guide the growth of *F. guineensis* within planted tree stands to develop an alternative resource away from the forest, for basket-making close to the households of people involved in basket-making, similar to what had been done with growing *R. adiantiformis* fern outside the forest under plantation tree stands (CJ Geldenhuys, personal observation).

## 5. Conclusions and recommendations

This study showed the seasonal flowering, fruiting and shoot growth patterns of *F. guineensis* in different forest stand conditions in Transkei Coastal Forests. In general, flowering and fruiting intensity was relatively low during the one-year study, with relatively higher, but still low, production of flowers and fruits in Bulolo Forest than in Mtambalala Forest, and along the forest edges than in the forest interior. By contrast, the species was in a vegetative production stage during the study period, and that there may be a sequential cyclic change between the vegetative and reproductive stages. The phenological information provides good indication of when (rainy season) and under what conditions (short host trees where *F. guineensis* forms a dense mat on the canopy of the host tree) to collect fruit for growing the plant.

This study showed that the perceived relationships between cluster diameter and number of culms, and between culm diameter and culm length, i.e. allometric relations in *F. guineensis* development, were not significantly different between different forest stand conditions (forest edge, forest gaps and in mature forest with closed canopy), and varied much between stand conditions. There were a few exceptions, such as the significantly longer culm length in the taller canopy in the Manubi Forest interior. Information on culm development under different stand conditions is important for the development of sustainable resource use practices. This aspect needs further study to know how to use such information to monitor the impact of the harvesting of culms of *F. guineensis* for basket-making.

Host tree observations showed that *F. guineensis* used small plants to provide vertical support to reach for canopy trees. It interacted with different host tree species of different diameters in the different forests for support. Though *F. guineensis* forms tangles on the canopy of its host in forest edges, the observations in the forests suggest that there is no direct damage caused to host trees.

Based on the results from this study, recommendations are made for better harvesting of *F. guineensis* and for further studies. Harvesting of *F. guineensis* from these forests should be pursued according to the following guidelines:

- Harvesting should be done during the dry season (May-August) when there are no or very few flowers and fruits on the *F. guineensis* clusters.
- Harvesting of culms from tangles in the crowns of host trees may reduce the pressure, if any, of such tangles on the host trees, but need to be dome with care to minimize damage to the host tree crowns.
- Cultivation of *F. guineensis* within planted tree stands to develop an alternative resource of culms for basket-making, away from the forest, and close to the households of people involved in basket-making.

Studies need to be pursued in terms of the following topics to guide sustainable resource harvesting practices of *F. guineensis* culms:

- It is possible to develop a better understanding of the reproductive phenological stages when the plants are in a reproductive state. It is therefore recommended that the phenological study should be conducted with selected marked plants in different forest stand conditions over a longer period, at least 3 years. Recording of intensity of reproductive phenological states should be done once every week when the flower buds start to show up. Such a study needs to include the collection of weather data (rainfall, temperature and wind speed) and temperature, humidity and light conditions in different stand conditions.

- Monitoring the development of seedlings and shoots from rhizomes, the rate of their growth into the canopy, and assessing the allometric relationships of the plants over time, using selected marked plants in different forest stand conditions. This would provide a basis for monitoring resource harvesting impacts.
- Monitoring the regrowth potential of new culm shoots from the rhizomes with different intensities of culm harvesting. Such information could guide the growth of *F. guineensis* within planted tree stands outside the forest as an alternative resource of culms.


**Acknowledgement**

The authors would like to thank foresters in Port St Johns, Manubi and Lusikisiki, and people around those forests, for sharing their knowledge of this climbing bamboo. We acknowledge the useful comments from two reviewers towards improving the manuscript. This work was financially supported by South African Forestry Company Limited.


**References**


Baldwin, J.T., Speese, B.M., 1957. *Flagellaria guineensis* Schumach. Bulletin of the Torrey botanical Club 84, 90–93.

Balfour, D.A., Bond, W.J., 1993. Factors limiting climber distribution and abundance in a Southern African forest. Journal of Ecology 81, 93–100.

Bosch, C.H., 2010. Flagellaria guineensis Schumach. Records from protabase. In PROTA (Plant Resources of Tropical Africa/Resources Vegetales de l' Afrique Tropicale). Edited by M.

Brink, E.G. Achigan-Dako. Wageningen, Netherlands. http://database.Prota.org/search.htm [Accessed 2 November 2012].

Campanello, P.I., Villagra, M., Garibaldi, J.F., Luis, J., Ritter, L.J., Araujo, J.J., Goldstein, G., 2012. Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest. Forest Ecology and Management 284, 213–221.

Cawe, S.G., Ntloko, S.S.T., 1997. Distribution, uses and exploitation patterns of Flagellaria guineensis Schumach, with particular reference to Port St Johns, South Africa. South African Journal of Botany 63, 233–238.

Cawe, S.G., 1999. Spatial and temporal utilization patterns of *Flagellaria guineensis* Schumach. In demarcated forests of the Lusikisiki district of Transkei, South Africa. South African Journal of Botany 65, 69–74.

Cawe, S.G., Geldenhuys, C.J., 2007. Resource status and population dynamics of target species in natural forests of the Port St Johns Forest Estate: A basis for sustainable resource use. Report for Project 2006-397. Directorate: Forestry Technical Services, Department of Water Affairs and Forestry, South Africa, Pretoria, 102 pp.

Fenner, M., 1998. The phenology of growth and reproduction in plants. Perspectives in Plant Ecology, Evolution and Systematics 1, 78–91.

Geldenhuys, C.J., Van der Merwe, C.J., 1988. Population structure and growth of the fern *Rumohra adiantiformis* in relation to frond harvesting in the southern Cape forests. South African Journal of Botany 54, 351–362

Geldenhuys, C.J., Rathogwa, N.R., 1995. Growth and mortality patterns over stands and species in the Manubi forest growth study site: report on 1995 measurements. Report FOR-DEA 943, Division of Forest Science and Technology, CSIR, Pretoria. 24 pp.

Giordano, C.V., Sánchez, R.A., Austin, A.T., 2009. Gregarious bamboo flowering opens a window of opportunity for regeneration in a temperate forest of Patagonia. New Phytologist 181, 880–889.

González, M.E., Veblen, T.T., Donoso, C., Valeria, L., 2002. Tree regeneration responses in a Lowland Nothofagus - Dominated Forest after Bamboo Dieback in South-Central Chile. Plant Ecology 161, 59–73.

Kigomo, B.N., 2007. Guidelines for Growing Bamboo. KEFRI Guideline Series: No. 4. Kenya Forestry Research Institute, Nairobi, Kenya, 45 pp.

King, N.L., 1940. The Manubi forest. Journal of the South African Forestry Association 4, 24–29.

Kleinhenz, V., Midmore, D.J., 2001. Aspects of bamboo agronomy. Advances in Agronomy 74, 99–153.

Lima, R.A.F., Roher, D.C., Muler, A.E., Lepsch, I.F., Rodrigues, R.R., 2012. Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot. Biological Conservation 147, 32–39.

Lowe, R.G., Walker, P., 1977. Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. Journal of Applied Ecology 14, 897–903.

Mucina, L., 2018. Vegetation survey and classification of subtropical forests of southern Africa. Cham, Switzerland: Springer ISBN: 9783319678306.

Mucina, L., Geldenhuys, C.J., 2006. Afrotemperate, subtropical and azonal forests. In: Mucina L, Rutherford MC, The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, 584–614.

Muller, I., Rebelo, C., 2010. Bamboo Worldwide: the current market and future potential. EcoPlanet Bamboo Report. 30 pp.

Rabenantoandro, J., Randrihasipara, L., Randriatafika, F., Vincelette, M. and Rakoto, J., 2007. Testing the propagation and growth of the liana Flagellaria indica, used to make lobster traps, and Bambusa multiplex as an alternative source. Biodiversity, Ecology and Conservation of Littoral Forest Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin). JU Ganzhorn, SM Goodman and M. Vincelette (eds.), p.363.

Ramanayake, S.M., 2006. Flowering in bamboo: an enigma. Ceylon Journal of Science (Biological Sciences) 35, 95–105.

Seifriz, W., 1920. The length of the life cycle of a climbing bamboo. A striking case of sexual periodicity in *Chusquea abietifolia* Griseb. American Journal of Botany 7, 83–94.

Taylor, A.H., Qin, Z., 1993. Bamboo regeneration after flowering in the Wolong giant panda reserve, China. *Biological Conservation* 63, 231–234.

Taylor, A.H., Huang, J., Zhou, S., 2004. Canopy tree development and undergrowth bamboo dynamics in old-growth Abies-Betula forests in southwestern China: a 12-year study. Forest Ecology and Management 200, 347–360.

Von Maltitz, G., Mucina, L., Geldenhuys, C.J., Lawes, M.J., Eeley, H., Aidie, H., Vink, D., Fleming, G., Bailey, C., 2003. Classification system for South African Indigenous Forests. An objective classification for the Department of Water Affairs and Forestry. Unpublished report, No. ENV-P-C-2003-017, Environmentek, CSIR, Pretoria, pp 189–204.

Widmer, Y., 1998. Pattern and Performance of understory bamboos (*Chusquea spp*.) under different canopy closures in old-growth oak forests in Costa Rica. Biotropica 30, 400–415.

Williams-Linera, G., 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology 78, 356–373.