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RESEARCH ARTICLE

# Bioecology of *Imbrasia epimethea* (Drury, 1773) caterpillars consumed in Kwilu province, Democratic Republic of the Congo

*F. Madamo Malasi*[1,2]*, *F. Francis*[1] *and R. Caparros Megido*[1]

[1]Laboratory of Functional and Evolutionary Entomology, Gembloux, University of Liege/Gembloux Agro-Bio Tech, Passage des déportés 2, 5030, Belgium; [2]Institut Supérieur Pédagogique de Bandundu, B.P. 363, RD Congo; *madamofranc@gmail.com; entomologie.gembloux@uliege.be

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### Abstract

*Imbrasia epimethea* is one of the most esteemed and popular caterpillar species for its remarkable organoleptic and nutritional values. Its consumption extends throughout the Kwilu province and nearly the entire Democratic Republic of the Congo, but its supply is very limited. The high anthropogenic pressure and the poor harvesting techniques employed by the population of Kwilu pose a major threat to the conservation of the species. This study aims to investigate the bioecology of *I. epimethea* in order to develop semi-captive breeding techniques for these caterpillars, making them accessible to the population. In order to determine the host plants of *I. epimethea*, a survey was conducted among 424 caterpillar collectors from two populated and forested territories in the Kwilu province. To study the influence of changes in the caterpillars' diet on their growth and determine their developmental cycle, a breeding experiment was conducted. This study revealed that the caterpillars of *I. epimethea* do not accept transfers from *Petersianthus macrocarpus* to *Funtumia africana*. It also confirms the polyphagy of these caterpillars while indicating that, overall, *P. macrocarpus* proved to be the most suitable host in the Kwilu province. *I. epimethea* is a social species with a development cycle, from hatching to emergence, lasting approximately 115.33 ± 3.06 days. The larval stage lasts about a month but with a prolonged period of nymphal diapause. Further analysis of the leaves of *P. macrocarpus* and *F. africana*, as well as the analysis of the caterpillars themselves, along with several breeding trials, will provide further clarification on this matter.



### Keywords

semi-captive breeding – reforestation – generalist – host tree – life cycle


## 1 Introduction

In the Democratic Republic of the Congo (DRC), similar to the African continent (Kelemu *et al.*, 2015; Van Huis, 2020), Lepidoptera caterpillars, with a total of 88 recorded species, is the insect order with the highest number of edible species (Bomolo *et al.*, 2017; Latham *et al.*, 2021; Nsevolo *et al.*, 2023). These species account for approximately 60% of the documented edible insects and belong to 13 families, with Saturniidae being the predominant family, comprising 53 species. This dominance of Saturniidae is confirmed in studies conducted across several provinces of the country (Bocquet *et al.*, 2020; Latham, 2008; Leleup and Daems, 1969; Looli *et al.*, 2021; Madamo Malasi *et al.*, 2023; Malaisse, 1997), as well as on the African continent (Balinga *et al.*, 2004;

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Jongema, 2017; Van Huis, 2003). The favorable climate and the abundance of food plants that support their development are factors that could explain the abundance of caterpillars (Twine *et al.*, 2003; Van Huis *et al.*, 2014).

Among the emblematic caterpillars of Saturniidae, *Cirina forda* (Westwood, 1849) and *Imbrasia epimethea* (Drury, 1773), sometimes confused with *Imbrasia ertli* (Rebel, 1904) (Lunga, 2017; Mapunzu, 2004), are the caterpillars with the highest organoleptic values and are highly appreciated and widely traded in the region (Mapunzu, 2004; Nsevolo *et al.*, 2023). However, unlike *C. forda*, which is continuously sold on the market until the new season, *I. epimethea* is only available in small quantities and during the abundant harvesting season, which varies according to geographical regions. For example, in the Kwilu province, the harvest is relatively abundant during the rainy season (from November to December) in the Masi-Manimba territory, while it is more abundant during the dry season (from May to August) in the Idiofa territory (Madamo *et al.*, 2023). Highly popular, its widespread distribution covers almost all provinces of the country, such as Equateur, Bas-Uélé, Haut-Katanga, Haut-Uélé, Ituri, Kongo Central, Kwango, Kwilu, Mai-Ndombe, Mongala, Nord and Sud-Ubangi, Tshopo, and Tshuapa (Mapunzu, 2004; Mutwale Kapepula *et al.*, 2022; Latham, 2016; Lisingo *et al.*, 2010; Looli *et al.*, 2021; Madamo Malasi *et al.*, 2023; Malaisse, 1997; Ngbolua *et al.*, 2022; Payne *et al.*, 2016; Yabuda *et al.*, 2019). It is also widely consumed across Africa, including countries such as South Africa, Angola, Cameroon, Côte d'Ivoire, Gabon, Ghana, Guinea, Guinea-Bissau, Equatorial Guinea, Kenya, Mozambique, Nigeria, Uganda, Central African Republic, Republic of the Congo, Sierra Leone, Tanzania, Togo, Zambia, and Zimbabwe (Balinga *et al.*, 2004; De Prins *et al.*, 2022; Kelemu *et al.*, 2015; Latham, 2003; Lautenschläger *et al.*, 2017; Silow, 1976). The species has several synonyms, and the list has been recently updated to include: *Phalaena attacus epimethea*, *Imbrasia nadari*, *Imbrasia epimedea*, *Imbrasia crameri*, *Imbrasia paradoxa*, *Imbrasia diomede*, *Bunaea dorcas*, and *Bombyx nicitans* (De Prins *et al.*, 2022).

Despite the discrepancies in results due to the different laboratory analysis methods used by various authors, all indicate the nutritional significance of *I. epimethea* caterpillars, constituting a significant source of protein (58.3-73.1 g/100 g dry weight (DW)) with a balanced supply of essential amino acids, totaling 513.3 mg/g of proteins, which exceeds the upper levels (269 mg/g of proteins) recommended by the Food and Agriculture Organisation (FAO). Lipids (5.9-22.8 g/100 g DW) with considerable amounts of α-linolenic acid, carbohydrates (5.2-11.1 g/100 g DW), and minerals (e.g. iron: 13.01-80 mg/100 g DW) are also well represented in *I. epimethea* (Adriaens, 1953; Fogang *et al.*, 2019; Kodonki *et al.*, 1987; Lautenschläger *et al.*, 2017; Mabossy-Mobouna *et al.*, 2021; Malaisse and Parent, 1980). Thus, the valorisation as a food source for humans could be a solution to address the prevailing protein deficiency issue in the country, particularly in provinces like Kwilu (Mapunzu, 2004; Mbemba, 2013). Currently, the caterpillars of *I. epimethea* are still traditionally harvested using destructive methods that can harm the species or its habitat. For instance, there is a total harvest of the caterpillars before their final stage of development, no conservation of individuals for reproduction purposes, and even the cutting down of trees. Additionally, no large-scale production programs have been initiated, posing a significant risk for conservation of the species.

The main objective of this study is to investigate the biology and ecology of *I. epimethea* in the Kwilu province in order to establish a breeding program for these caterpillars, ensuring an adequate supply for the local population. For that purpose, data were collected on the specieshost plants found in the province and investigated the influence of these different host plants on the development of the caterpillars.

## 2 Materials and methods

***Study locations***

The Kwilu province (5°02′01″ South, 18°50′01″ East) is a densely populated agricultural province with an estimated population of over 8 million people and a total area of 79,071 km² (Bruneau, 2009; CAID, 2016; Gouvernorat du Kwilu, 2017). The Kwilu province falls within the tropical wet climate zone of type AW (i.e. savanna climate with a dry winter or dry season), according to the Köppen climate classification. This climate is characterized by the presence of two distinct rainy seasons and relatively cool nights (Fehr, 1990). The province is composed of five territories: Bagata, Bulungu, Gungu, Idiofa, and Masi-Manimba. It is home to nearly 25 ethnolinguistic groups, with the Mbala, Mbun, Pende, and Yansi being the predominant ones (Anonymous, 2005; Bruneau, 2009; CAID, 2016).

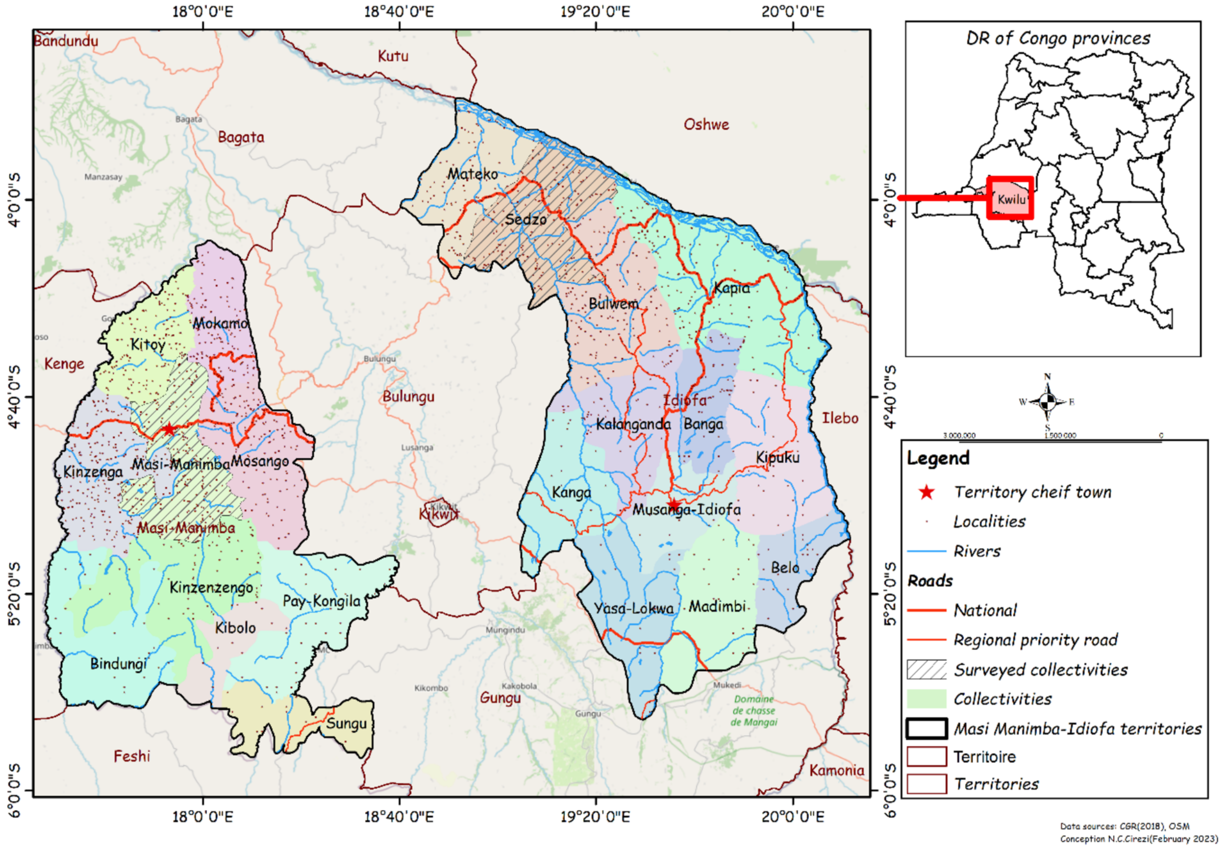


FIGURE 1 Administrative map of Kwilu province (western Democratic Republic of the Congo) illustrating the study site. The study was conducted in the Masi manimba and Idiofa territories and more specifically in the Masi manimmba and Sedzo communities, where the surveys were carried out. Experimental site has also been set up in the Sedzo sector.

### *Ethno-entomological surveys*

Ethno-entomological surveys and the collection of caterpillar samples and host plants were conducted in the two most populated territories in the central province (Figure 1), Idiofa and Masi-Manimba, during the period from 29th July to 1st November 2022, throughout the rainy season (which spans from 15th August to 15th May).

In each of these two areas, the most densely populated sector has been selected., with Masi-Manimba representing the Masi-Manimba territory and Sedzo representing Idiofa. A questionnaire (Annex S) on the host plants of the caterpillar was administered to 212 caterpillar collectors in each territory and sector (Masi-Manimba and Sedzo), primarily adults randomly selected, resulting in a total of 424 respondents.

### *Collection and identification of host food plants*

Based on the information obtained from the respondents regarding the host plants of *I. epimethea*, the forests recognised by the authorities in the two targeted sectors (Masi-Manimba and Sedzo) as highly important "reservoirs" for *I. epimethea* caterpillars were selected. Contacts with various village chiefs helped in finding experienced local guides (operators) with whom six field surveys were conducted, three per sector, during the period from 29th July to 1st November 2022. The purpose of these surveys was to collect branches of the host plants and create an herbarium for identification purposes.

The identification of the collected branches of plants was carried out using the national herbarium of the DRC, specifically at the Laboratory of Systematics, Biodiversity, and Nature Conservation of the Department of Environment at the University of Kinshasa. The botanical families and scientific names were determined for each host plant.

### *Growth of* **I. epimethea** *caterpillars on selected host trees*

The experiment was carried out in Sedzo, from 29th July to 27th November 2022, on four trees (n = 3) of each of the four species *Funtumia africana*, *Holarrhena floribunda*, *Petersianthus macrocarpus*, and *Uapaca guineensis*. The twelve trees had similar characteristics, including a height of about 7 m and a number of branches


FIGURE 2 Experimental set-up for semi-rearing *I. epimethea* caterpillars in the Sedzo area. Each basket attached to the trunk of *F. africana* (a) and *P. macrocarpus* (b) trees contains 100 L1-stage larvae from the same colony. They are used to facilitate the ascent of the caterpillars to the leaves and avoid their manipulation.

ranging from 13 to 15. They were spaced approximately ten meters apart. Around each tree, the vegetation was pruned up to 3 meters on either side of the tree to facilitate observations. To protect caterpillars from predators such as birds, lizards, or insects, mosquito netting was used to cover the branches caterpillars.

The larvae (first instar phase, L1) were collected from three different *P. macrocarpus* host trees (400 larvae from the same colony per tree). One hundred larvae were distributed in rattan baskets which was tied to the trunk of one of the four target host trees (Figure 2a,b). Last instar larvae (L5) were placed in baskets filled with humus and raised on a wooden structure for pupation (Figure 2c).

Measurements of caterpillar length, width and head capsule width were taken every two days after each molt using a graduated ruler and millimeter paper on 10 randomly selected caterpillars per tree and replicate. Mortality was also recorded at the end of the experiment based on the number of larvae entering the pupal stage.

Dates were recorded from larval emergence to butterfly emergence to determine the total duration of the developmental cycle and the duration of each larval stage. The dates of molts and nymphosis were also recorded during the larval period.

***Statistical analysis***

All the statistical analyses were performed using the R software (version 4.2.2) with RStudio. Prior to conducting the analysis of variance (ANOVA), the Shapiro and Leven tests were performed on the data to assess their normality. As the conditions for application were met, a one-way ANOVA was used to compare the means of the pupae size measurements. A two-way ANOVA was used to compare the growth progression of the caterpillars by stages and by host plant species, as well to evaluate their survival. The relationships among the different growth parameters, body length, body width, and head capsule width were examined using linear regression analysis only for L5 as the most consumed larval stage. All tests were performed at a 5% significance level

## 3 Results

***Survival of caterpillars during the cycle***

Depending on the host plant species and larval stage, the survival of *I. epimethea* larvae varied (Figure 3). Significant mortality rates were recorded throughout the cycle and at each caterpillar development stage, but the highest peaks occurred during the first and second larval stages, as well as during molting and pupating.

The percentage of larvae surviving to the last instar varied significantly according to host plants ($P < 0.001$; F = 2,694.27) and larval stage ($P < 0.001$; F = 100.02). It was highest for larvae consuming *P. macrocarpus* leaves (75.0 ± 2.65), followed by those consuming *H. floribunda* (61.0 ± 5.29), *U. guineensis* (58.0 ± 2.52) and no survival on *F. africana*. During the experiment, it was observed that almost all *I. epimethea* larvae, in contrast to the others, immediately fled (or turned back) upon contact with *F. africana* leaves. Only about 5% of the larvae cut the leaves. The percentages of larvae reaching the second instar were 81.0 ± 2.0, 70.0 ± 3.0 and 62.0 ± 1.73, respectively (except *F. africana* were no larvae were available). For the third instar larval percentage on the three respective hosts are 75.0 ± 2.65, 64.0 ± 4.58 and 58 ± 2.65. With the exception of *H. floribunda*, where very low mortality was recorded in the fourth instar, the percentages remained stable.

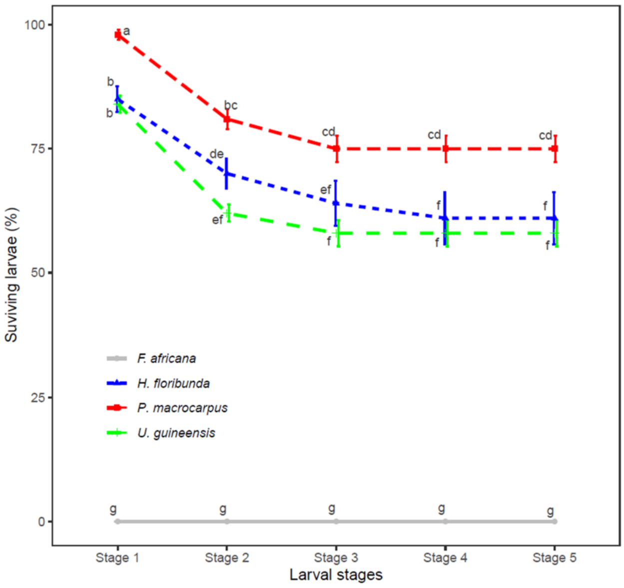


FIGURE 3 Mean percentages of surviving *I. epimethea* larvae fed on *P. macrocarpus* (blue), *H. floribunda* (red), *U. guineensis* (green) and *F. africana* (yellow) per stage. The vertical bar represents the standard error on the mean for the same points. All curves, with the exception of *F. africana*, are descending. Different letters represent statistically different averages.

**I. epimethea *caterpillar growth***

The growth parameters were compared in pairs to verify the existence of a potential relationship (Figure 4). Increases in body length were positively correlated with increases in body width ($r^2 = 0.71$, $P < 0.001$) and head capsule width ($r^2 = 0.58$, $P < 0.001$). An increase in body length was correlated with an increase in body width and head capsule size. The regression line is higher for the *P. macrocarpus* plant, especially regarding the length of the caterpillar body and the width of the head capsule.

There was a significant effect of the host plant on the three measured growth parameters in final stage caterpillars (Figure 5), except for *F. africana*, which did not support caterpillar development. The length of the last instar caterpillars is significantly influenced by the different host plant species ($P < 0.001$; F = 19922), especially *P. macrocarpus* and by the different larval stages ($P < 0.001$; F = 18368). In addition, there is an interaction between host plants and larval stages ($P < 0.001$; F = 2718). The average length of last instar caterpillars reared on *P. macrocarpus* was significantly higher (83.18 ± 2.42 mm) than those reared on *H. floribunda* (75.12 ± 2.34 mm) and *U. guineensis* (73.90 ± 2.72 mm).

Late instar caterpillars fed on *P. macrocarpus* leaves had significantly ($P < 0.001$; F = 1983.3) greater body widths than those fed (15.02 ± 1.14 mm) on *H. floribunda* (12.49 ± 1.68 mm) and *U. guineensis* (11.50 ± 1.46 mm). The average width of the head capsules of caterpillars fed on *P. macrocarpus* was also significantly ($P < 0.001$; F = 1952.7) larger (11.1 ± 1.17 mm), than on the other two host plants (*H. floribunda*, 9.45 ± 1.66 mm and *U. guineensis*, 7.90 ± 1.05 mm). For all the growth parameters studied, size evolves with stage.

***Life cycle of* I. epimethea**

Larval development

The larval development of *I. epimethea* on all the host trees used in this experiment consists of five larval stages (Figure 6) and it lasted an average of 31.11 ± 1.80 days under semi-captive conditions. Therefore, each stage lasts approximately 7.00 ± 0.82 days, except for stage 5, which lasts 6.22 ± 0.51 days.

The mean total larval development time (Figure 6) of caterpillars on the *P. macrocarpus* diet was 28.67 ± 0.48 days and was significantly faster ($P < 0.001$; F = 8152.46) than on the *H. floribunda* and *U. guineensis* diets, where the mean times for both were 32.33 ± 0.48 days and 37.01 ± 0.43 days. Caterpillars reared on *P. macrocarpus* had significantly shorter development times than those subjected to regime change (*H. floribunda* and *U. guineensis*). For example, caterpillars on *P. macrocarpus* took fewer days than others, 21.33 ± 0.48 days, to reach the average length of 60.0 ± 1.25 mm for the L4 stage and 28.67 ± 0.48 mm to reach the average size of 83.18 ± 2.42 mm for the L5 stage. Caterpillars on *H. floribunda* took 24.67 ± 0.48 days and 32.33 ± 0.48 days to reach 50.95 ± 2.40 mm at L4 and 75.12 ± 2.34 mm at L5, respectively. Caterpillars on *U. guineensis* grew even more slowly than the others, reaching the smallest size, 49.54 ± 3.21 mm after 24.67 ± 0.48 days for stage 4 and 73.90 ± 2.72 mm after 32.33 ± 0.48 days for L5.

The caterpillars feed in small groups and gradually move from branch to branch as they consume all the leaves. The larvae in the early stages feed minimally, but they become highly voracious in the later stages (3th-5th), where they produce large quantities of excrement and experience rapid growth.

At the end of the fifth stage, when the caterpillars reach full maturity, they stop feeding, and there is an absence of digestive content, making them more palatable. They typically fall between 4 am and 5 am and tend to move away from their host, resulting in losses during harvesting.

The transition from one stage to another is marked by molting. The first and fourth molts occur on the leafy stems, while the second and third molts (Figure 7) take place along the trunk, near the ground (approximately

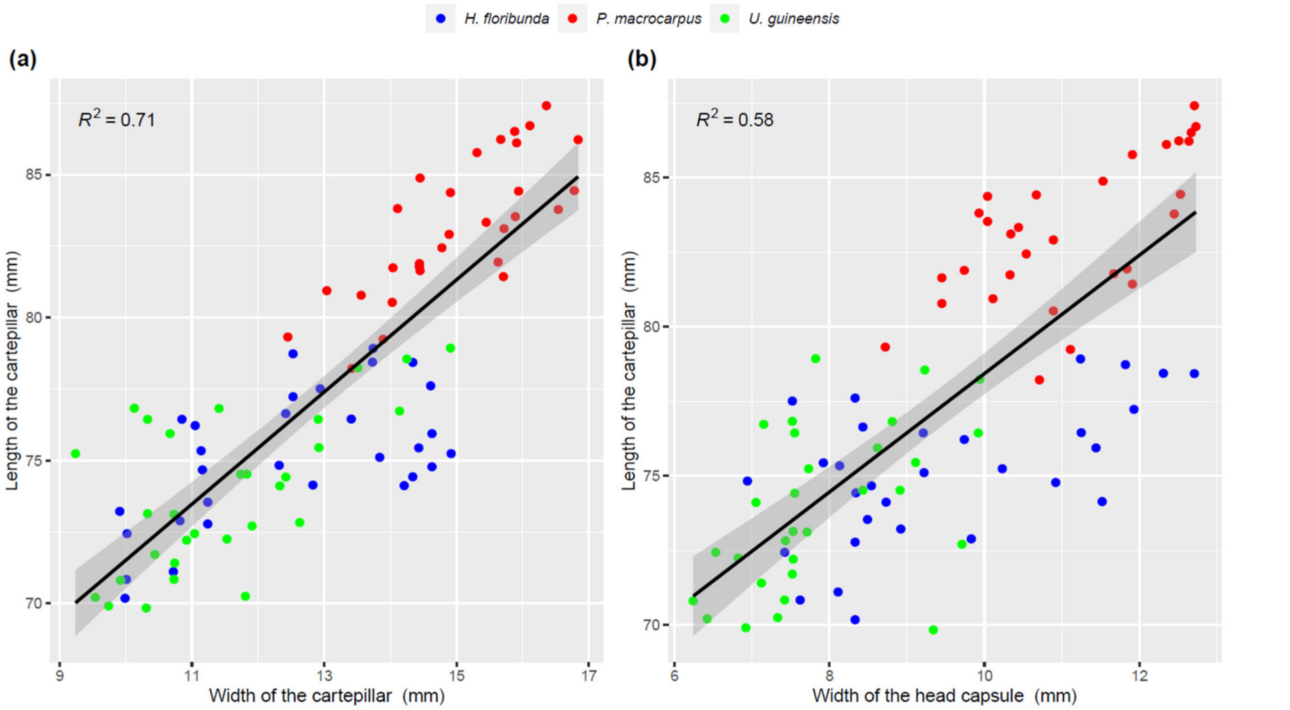


FIGURE 4 Simple linear regression of I. epimethea growth parameters as a function of host plant: *P. macrocarpus* (blue dots), *H. floribunda* (red dots), *U. guineensis* (green dots) and *F. africana* (yellow dots). The grey line represent confidence interval at 95%. (a) Positive relationship between body length and width and (b) Positive relationship between body length and head capsule.

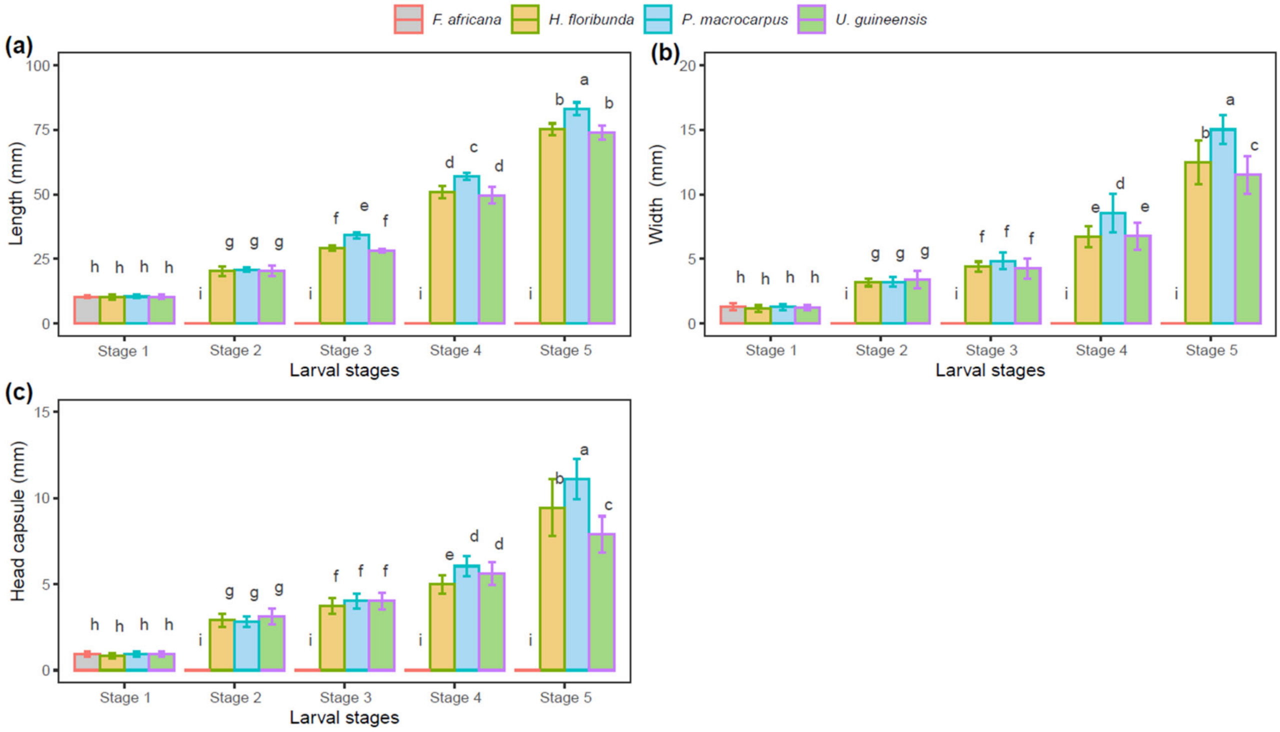


FIGURE 5 Growth parameters of *I. epimethea* measured (mm) during the larval development of I. epimethea. (a) Average length; (b) Average width of larval body; (c) Average width of head capsule by host plants: *P. macrocarpus* (blue), *H. floribunda* (yellow), *U. guineensis* (green) and *F. africana* (grey). Data are means ± SE. Different letters show significant differences between different host plants and larval stages.

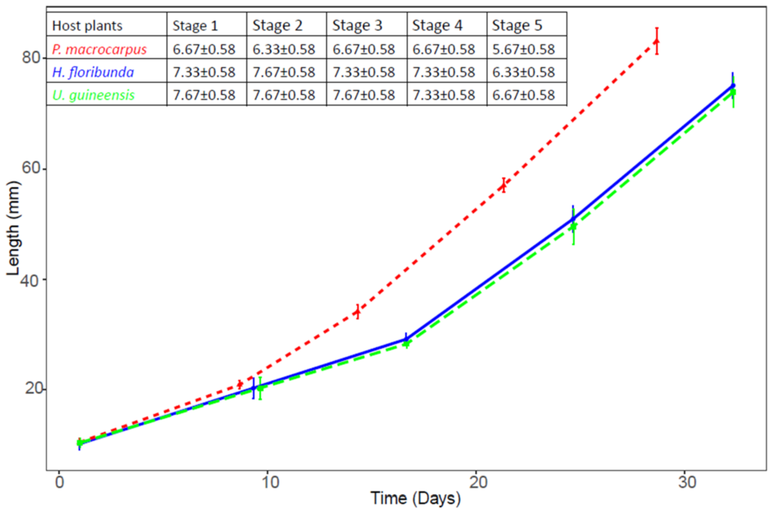


FIGURE 6 Evolution of *I. epimethea* length growth as a function of time and host plant. The mean total larval development time of caterpillars on the *P. macrocarpus* (red dotted line), *H. floribunda* (blue line), *U. guineensis* (green dotted line). The bars represent standard deviations. The average duration of each stage per host plant species is shown in the table attached to the figure.

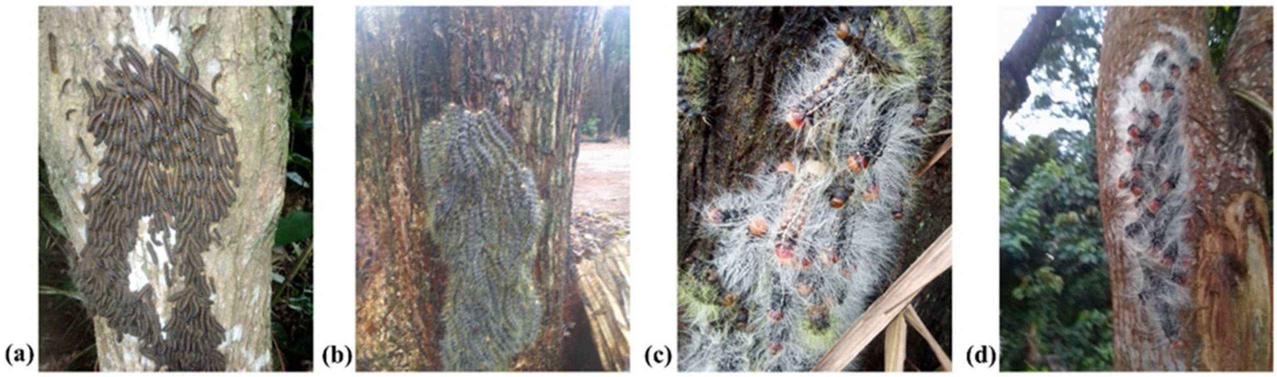


FIGURE 7 (a) Preparing for the 2nd moult, (b) Preparing for the 3rd moult, (c) Beginning of 3rd moult, (d) End of 3rd moult along the trunk, close to the ground (about one meter above the ground). The white hairs on the caterpillars indicate that they are moulting.

one meter above the ground). Unlike the final molt, which corresponds to the shedding of hairs, each of the other three molts leaves intact clusters of larval exuviae with their cephalic capsules, and it is marked by the whitish color of the caterpillar's hairs (Figure 7c,d). During the molting preparation phase (Figure 7a,b), which lasts between 48-72 hours, the caterpillars stop feeding. After molting, the caterpillars remain in their cluster for about five hours before ascending back to the foliage to feed for three to five days before descending again for the next molt.

The nymphal stage

The onset of the nymphal stage is characterised by the cessation of feeding, the search for suitable locations for pupation, immobilisation, and the shrinking or reduction in length of the mature caterpillar. The first and last pupae were obtained 5.50 ± 0.58 days and 10.50 ± 0.58 days after the fifth larval stage on *P. macrocarpus*, then 6.75 ± 0.58 days and 11.25 ± 0.96 days after the L5 stage on H. floribunda and *U. guineensis*.

The color change of the pupa was observed, ranging from reddish at the beginning of pupation to a dark color (Figure 8) for the older ones. The size of the pupae is significantly affected by the caterpillars' diet (Figure 9). Length was significantly ($P < 0.001$; $F = 73.62$) greater for larvae fed on *P. macrocrapus* (44.43 ± 3.55 mm), followed by those fed on *H. floribunda* (39.61 ± 3.06 mm) and *U. guineensis* (35.70 ± 1.20 mm). Comparisons of body width ($P < 0.001$; $F = 94.33$) and head capsule width ($P < 0.001$; $F = 61.08$) showed that the widest caterpillars were fed on


FIGURE 8 Color change of chrysalids during pupation from early red (a) to black (b). The red color marks the beginning of pupation, while the black color characterizes the older ones. Failure to pupate, with the larva's skin sticking to the chrysalis, is a frequent occurrence.

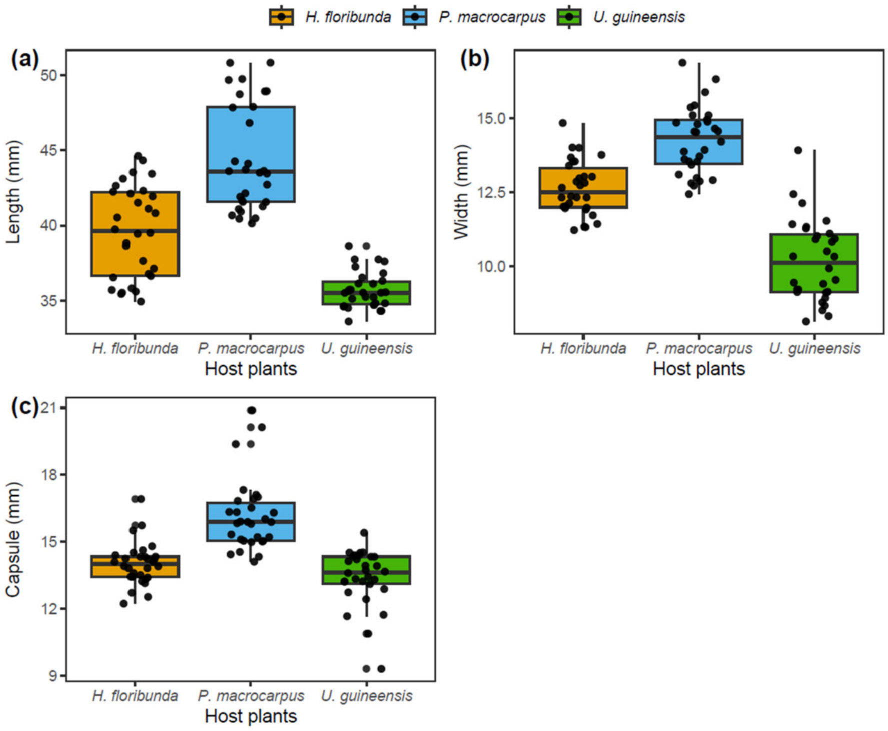


FIGURE 9 Comparison of average pupal size according to host plants. (a) Average length. (b) Average width of larval body. (c) Average width of head capsule by host plants: *P. macrocarpus* (blue), *H. floribunda* (orange-yellow), *U. guineensis* (green) and *F. africana* (grey). Data are means ± SE.

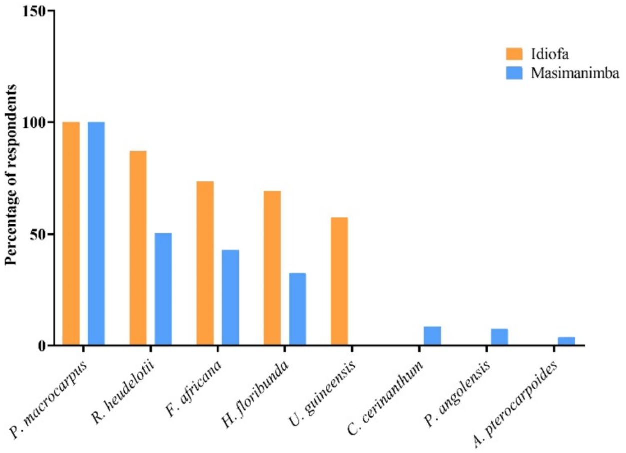


FIGURE 10 Proportions of I. epimethea host plant citations by territory, Idiofa and Masi-Manimba. Eight plants have been identified in the region as hosts for *I. epimethea*, including *F. africana*, *H. floribunda*, *H. floribunda*, *P. macrocarpus* and *R. heudelotii* in both territories. *P. macrocarpus* is identified by the entire population and, generally speaking, the frequency of citations of common species is very high in Idiofa.

*P. macrocrapus* (14. 26 ± 1.13 mm and 16.16 ± 1.61 mm), followed by those fed on *H. floribunda* (12.65 ± 0.91 mm and 14.02 ± 0.95 mm) and *U. guineensis* (10.19 ± 1.38 mm and 13.42 ± 1.25 mm).

The nymphal diapause period lasted approximately 71.67 ± 1.53 days and the peaks of larval mortality were recorded during the pupation stage.

***Range of host plants***

The respondents in the territories of Idiofa and Masi-Manimba identified eight species of host plants (Figure 10) two belonging to family Apocynaceae (*F. africana* and *H. floribunda*), while the others were represented by only one species each (Euphorbiaceae (*Ricinodendron heudelotii* (Baill.) Pierre ex Hecke), Fabaceae (*Amphimas pterocarpoides* Harms), Lecythidaceae (*P. macrocarpus*), Myristicaceae (*Pycnanthus angolensis* (Welw.) Warb), Phyllanthaceae (*U. guineensis*) et Rubiaceae (*Craterispermum cerinenthum* Hiern).

The literature reveals a range of 42 species of host plants (Supplementary Table S1) belonging to 15 families for Africa, with a dominance of Fabaceae (51.35%), followed by Apocynaceae (9.52%) and Burseraceae (7.14represented by two species (4.76%), all the others comprise a single species (Annonaceae, Cannabaceae, Irvingiaceae, Myristicaceae, Phyllanthaceae, Rhamnaceae, Rhizophoraceae, Sterculiaceae et Ulmaceae). All the families identified in the Kwilu Province, except for Rubiaceae, are also consumed by *I. epimethea* in other phytogeographic zones. However, several families recorded elsewhere (Annonaceae, Burseraceae, Cannabaceae, Combretaceae, Irvingiaceae, Rhamnaceae, Rhizophoraceae, Sterculiaceae, and Ulmaceae) are not part of the range of food plants for these caterpillars in the Kwilu Province.

Food trees mentioned by respondents in both areas include *F. africana*, *H. floribunda*, *P. macrocarpus* and *R. heudelotii* (Figure 10). Of these species, apart from *P. macrocarpus*, which was cited by all respondents (100%), all others were cited more frequently (over 69%) in Sedzo (Idiofa) than in Masi-Manimba (Masi-Manimba). *R. heudelotii* was mentioned by 87.26% of the population in Idiofa and 50.47% in Masi-Manimba, followed by *F. africana*, mentioned by 73.58% of the population in Idiofa compared to 42.92% in Masi-Manimba, and *H. floribunda*, cited by 69.34% in Idiofa compared to 32.55% in Masi-Manimba. However, *U. guineensis* is only cited in Idiofa, while *P. angolensis*, *A. pterocarpoides* and *C. cerinanthum* are only cited (at low frequencies) in Masi-Manimba.

## 4 Discussion

***Survival of caterpillars during the cycle***

Our results on larval survival, characterized by high mortality during the cycle, are consistent with those of Priddle (1966) for larvae of *Hyalophora cecropia* (L., 1758), another Saturniidae species. The high mortality of the first larval stages is confirmed by Zalucki *et al.* (2002), who found a mortality of 57% in the first stages of polyphagous lepidopterans (exposed feeders with high mortality). In addition, they point out that species that lay high level of eggs, as in the case of *I. epimethea*, tend to have a high mortality rate in the first instar (60%). This indicates that I. epimethea is one of those insects with an “r” development strategy, with high fecundity and low chances of survival to sexual maturity (Bonneil, 2005). The variability in survival rates between host species, as well as the high mortality of early instar larvae, can be explained by a complex interaction of numerous and variable factors, such as the inability of larvae to establish on plants and factors related to the host, weather conditions and predators (Courtney and Duggan, 1983; Zalucki *et al.*, 2002). Contrary to some authors, such as Feeny *et al.* (1985), pointing to predation as the main source of larval mortality, plant quality has a greater direct effect on survival and larvae at early stages may be more sensitive to secondary metabolites than later stages (Lille and Marquis, 2001; Zalucki *et al.*, 2002).

Mortality in the early stages may have been exacerbated on new host plants due to a temporary fasting period caused by the change in diet (Scriber, 1979). This corresponds to the observations of Konda Ku Mbuta and Ambühl (2022) who indicate that *I. epimethea* is one of the species that is faithful to its host tree. Its host selection behavior is shaped by the adult feeding experience following the Hopkins' Host Selection Principle (HHSP) (i.e. adult females prefer to lay eggs on the same plant species on which they themselves developed as larvae) (Bernays and Minkenberg, 1997; Jeffrey *et al.*, 2016). In addition, manipulation of larvae during the first two weeks after hatching (L1 and L2 larvae) may have undesirable effects on their survival and they frequently die after being moved to a new feeding (Priddle, 1966). Our results are also in agreement with those of Garraway *et al.* (1993), who suggest that failure to moult may also explain the low survival (or high mortality) of larvae.

The inability of *I. epimethea* to develop on *F. africana* has been confirmed by local breeders who have observed that the caterpillars accustomed to the leaves of *P. macrocarpus* cannot adapt to the bitter leaves of *F. africana*. It seems that adaptation can only occur in the opposite direction (Madamo, unpubl. data). The same effect, where survival was negatively affected by an inappropriate diet, was also observed in *C. forda* larvae (where 100% after 72 hours were reared exclusively on a diet based on old leaves...) (Odebiyi *et al.*, 2009). This phenomenon can be explained by the high levels of secondary metabolites in the latter, especially considering that Apocynaceae is a family known for its abundance of alkaloids from various structural classes, particularly steroidal alkaloids and polyphenolic compounds (Karim *et al.*, 2022; Nnadi *et al.*, 2017; Oyaseiye *et al.*, 2022).

Furthermore, the development of the caterpillars on *H. floribunda*, which is also an Apocynaceae, unlike *F. africana*, can again be justified by the differences, however small (belonging to the same subfamily Apocynoideae and the same tribe Malouetieae), in the quality of the leaves, as clearly shown by Zalucki *et al.* (2002). Some authors point out that latex has mechanical, repellent and toxic effects on lepidopterans, which would justify the fact that the larvae leave the leaves on first contact (which is a behavioral response for the caterpillars) (Zalucki *et al.*, 2002). *F. africana* is therefore the least adapted plant for caterpillars accustomed to *P. macrocarpus*, but it does influence the survival of *I. epimethea* when it is chosen by the female as an oviposition site.

### **I. epimethea** ***caterpillar growth***

In general, the results regarding the length of mature *I. epimethea* caterpillars, regardless of the tree species, are similar to those reported by Konda Ku Mbuta and Ambühl (2022), who stated that they measure over 70 mm in length and fall within the length range of 65 to 90 mm as reported by Akanbi (1973). These results confirm the generalist feeding behavior of *I. epimethea* (Bernays and Minkenberg, 1997; Konda Ku Mbuta and Ambühl, 2022).

The longest and widest *I. epimethea* caterpillars were found on *P. macrocarpus* (82.95 ± 2.20 mm long and 14.96 ± 1.04 mm wide), confirming Bernays' observation (1986) that larger larvae also have larger heads. This size is in the range reported for African Saturniidae. It is almost as long as *Gonimbrasia belina* (Westwood, 1993), *I. ertli* (Rebel, 1904), *I. obscura* (Butler, 1878) (approx. 83, 80, 80 mm, respectively); smaller than *Bunaea alcinoe* (Stoll, 1780) (approx. 90 mm) but larger than *C. forda* (Westwood, 1881) (approx. 60 mm) (Latham *et al.*, 2021).

However, the fact that *P. macrocarpus* is the original host species on which the collection was made may still have influenced the success of the caterpillars reared on it. The caterpillars developing on *P. macrocarpus* had the advantage of continuing their growth on their original host plant species, while the other caterpillars had to adapt to a new food source, as described by Konda Ku Mbuta and Ambühl (2022), who referred to these caterpillars as "faithful" to their host tree (Bernays and Minkenberg, 1997; Karowe, 1989).

Indeed, these results align well with the local knowledge of the communities, which classify *P. macrocarpus* as the primary host plant for *I. epimethea* caterpillars, both in Kwilu and in the Democratic Republic of the Congo (Bocquet *et al.*, 2020; Latham, 2003; Lisingo *et al.*, 2010; Looli *et al.*, 2021; Koni and Bostoen, 2008; Muyay, 1981; Ngbolua *et al.*, 2022; Okangola e*t al.*, 2016; Payne *et al.*, 2016).

### ***Life cycle of*** **I. epimethea**

Larval development

The results concerning the duration of larval stages are in line with those by Akanbi (1973) and Konda Ku Mbuta and Ambühl (2022) which also indicate five larval stages for the same species. These data, in addition to corresponding to those of previous authors, align with the information gathered from the farmers in Idiofa and Masi-Manimba. According to them, *I. epimethea* undergoes a cycle of activity and latency of 3-4 days (i.e. the caterpillars spend three to four days of intense feeding activity followed by three to four days of fasting and molting preparation), resulting in a duration of six to eight days for each of the first four stages and five days for the final stage.

The data on the number and duration of larval stages are similar to those reported for other Saturniidae such as *B. alcinoe*, *C. forda*, *G. hecate* (Rougeot, 1955) and *I. obscura* (Latham *et al.*, 2021; Sagara *et al.*, 2019). The results on the growth evolution of *I. epimethea* larvae are in line with those obtained by Sagara *et al.* (2019), who reported the average size of *G. hecate* larvae for all larval stages (10.03 ± 1.27 mm; 14.90 ± 2.74; 29.33 ± 6.38 mm; 57.82 ± 5.92 mm and 77.14 ± 9.74 mm, respectively). The same evolutionary trend can be observed in *Caio richardsoni* (Druce, 1890), a saturniid from Mexico (Wolfe and Pescador, 1994).

The nymphal stage

These results are similar to those of Akanbi's (1973) experiment, which indicated a pupation period of 10 to 13 days from L5. The color change of the pupa refers to the one indicated by Akanbi (1973) for the same species and Sagara *et al.*, 2019 for *I. hecate*. The mean pupal size of *I. epimethea* is similar to that of *I. obscura*, but larger than that of *C. forda* and *G. hecate* (Latham *et al.*, 2021; Sagara *et al.*, 2019). The largest and widest specimens were obtained from larvae fed on *P. macrocarpus*, while the smallest ones were from *U. guineensis*. The results once again confirm the relationship between the size of the mature caterpillar and the pupa (Suwarno *et al.*, 2007). The nymphal diapause period obtained in this experiment falls within the range reported by Akambi (1973) where the average duration was 50 days and 80 days for the first and second generation, respectively. Peaks of larval mortality recorded during pupation stage can be explained by excess humidity, as previously observed by Akanbi (1973), since the pupation setup was placed under wood to simulate natural conditions.

***Range of host plants***

Based on the frequency of citation of host plants of *I. epimethea* by the respondents and the available data in the literature, it is appropriate to classify the species as polyphagous with a diet that varies according to the phytogeographic zones, depending on the dominance of host plants in the environment. However, in the province of Kwilu, the order of importance of its host plants remains *P. macrocarpus*, *R. heudelotii*, and *F. africana*, which is similar to the trend observed in the Republic of Congo (Mabossy-Mobouna *et al.*, 2021).

The importance of Fabaceae in the diet of *I. epimethea* in Africa, as shown in the literature, is consistent with the findings of Stone (1991), for whom these plants, which belong to the Fabales, one of the oldest orders, would probably have been well established and available as food sources before the evolution of the Saturniidae (the family of the caterpillar mentioned above). Furthermore, the prevalence of Fabaceae as host plants of *I. epimethea* may be due to the presence of phenolic compounds on their leaves (Aligwekwe and Idaguko, 2021; Amos-Tautua *et al.*, 2017; Hassan *et al.*, 2007; Nwandu *et al.*, 2019; Uzoekwe and Hamilton-Amachree, 2016; Yakubu *et al.*, 2018). These findings are consistent with those of Janzen (1985) and Wink (2013), who indicated that the diet of Saturniidae is rich in phenolic compounds (tannins and resins).

These results indicate that the caterpillar is highly generalist in the Kwilu Province as it feeds on seven plant families in the Masi-Manimba territory and four in Idiofa. These differences by territory can be attributed to the typical ecology of each environment. Idiofa (Sedzo sector) has forests of near equatorial rainforest (lush forest, generally composed of tall, broad-leaved trees, usually found in humid tropical uplands and lowlands around the equator), while Masi-Manimba has gallery forests or riparian forests (vegetation along rivers and streams) (Anonymous, 2005; Bruneau, 2009; CAID, 2016). So, this diversity of *I. epimethea* host plants, different from one region to another, is proof that the caterpillars' diet varies with their ecology (Lisingo, 2010, Latham, 2008). All respondents mentioned *P. macrocarpus*, considering it as the main plant from which the various vernacular names for the caterpillar derive (e.g. "Misa" in Mbala, Yansi, Ngongo languages, referring to caterpillars from the *P. macrocarpus* tree, whose vernacular name is "Musa" (Koni and Bostoen, 2008; Muyay, 1981). The same plant is also reported in several provinces of the Democratic Republic of the Congo, such as Kongo Central (Latham, 2003), Equateur (Bocquet *et al.*, 2020), Mai-Ndombe (Payne *et al.*, 2016), Nord-Ubangi (Ngbolua *et al.*, 2022), Tshopo (Lisingo *et al.*, 2010; Looli *et al.*, 2021; Okangola *et al.*, 2016), as well as in other African countries such as Cameroon, Central African Republic, and Republic of Congo, all of which are part of the Congo Basin (Mabossy-Mobouna *et al.*, 2022; N'Gasse, 2003; Ngute *et al.*, 2020). Moreover, the respondents from Kwilu and several authors from the Democratic Republic of the Congo have mentioned that *P. macrocarpus* serves as a host for other species of caterpillars, such as *Achaea catocaloides* (Guinée, 1852), *Bunaea alcinoe* (Stoll, 1780), *Gonimbrasia hecate* (Rougeot, 1955), *Gonimbrasia petiveri* (Guérin-Méneville, 1845), *Imbrasia truncata* (Aurivillius, 1909), and an unidentified species referred to as "Mishidi," "Mitshil," "Misil," "Michil" in Mbala, Ngongo, Yansi, and Lorri languages, respectively. (Bocquet *et al.*, 2020; Lisingo *et al.*, 2010; Looli *et al.*, 2021; Ngbolua *et al.*, 2022; Okangola, 2007; Okangola *et al.*, 2016; Yabuda *et al.*, 2019).

Another important plant as a host tree for *I. epimethea* in Kwilu is *R. heudelotii*. The abundant presence of this pioneer plant in the secondary equatorial forests in Idiofa can be explained by the proximity to the Sedzo forests of the vast equatorial forest of the Democratic Republic of the Congo (Tailfer, 1989). It is also mentioned for the same use in other provinces such as Equateur (Bocquet *et al.*, 2020), Kongo Central (Latham, 2003), and Nord-Ubangi (Ngbolua *et al.*, 2022; Yabuda *et al.*, 2019), as well as in Tshopo (Lisingo *et al.*, 2010; Looli *et al.*, 2021). In addition to being consumed by caterpillars of *B. alcinoe* and *I. truncata* (Konda Ku Mbuta and Ambühl, 2022; Looli *et al.*, 2021; Ngbolua *et al.*, 2022; Okangola, 2007; Okangola *et al.*, 2016; Yabuda *et al.*, 2019).

*F. africana*, the third most frequently cited host of *I. epimethea*, is also found in certain provinces of the Democratic Republic of the Congo, such as Kongo Central, Equateur, Nord-Ubangi, and Tshopo (Bocquet *et al.*, 2020; Latham, 2003; Lisingo *et al.*, 2010; Ngbolua *et al.*, 2022; Okangola *et al.*, 2016). It appears to be exclusive to the Democratic Republic of the Congo as a host tree for *I. epimethea*, but it is also a host tree for *G. hecate* (Lisingo *et al.*, 2010; Ngbolua *et al.*, 2022; Okangola *et al.*, 2016).

Among the hosts of *I. epimethea* mentioned in both sites, *H. floribunda*, recorded in both the Democratic Republic of the Congo (Kongo Central and Tshopo) and Ghana and Nigeria (Akanbi, 1973; Bocquet *et al.*, 2020; De Prins *et al.*, 2022; Latham, 2003; Wagner *et al.*, 2008), appears to have limited use as a caterpillar host.

*U. guineensis* is mentioned as a host of *I. epimethea* only by the respondents from Sedzo (Idiofa), which is part of the Kasaï phytogeographic district (Lubini and Mandango, 1981). Looli *et al.* (2021) also indicate that it serves as a host for caterpillars such as *Bunaeopsis aurantiaca* (Rothschild, 1895), *I. obscura* (Butler, 1878), and *I. truncata*. *P. angolensis* and *A. pterocarpoides* appear to be consumed to a lesser extent by the caterpillars of *I. epimethea* in Kwilu, while their usage seems to be significant in other provinces of the Democratic Republic of the Congo (Equateur and Tshopo) and in other African countries (Cameroon and Republic of Congo) (Bocquet *et al.*, 2020; Lisingo *et al.*, 2010; Ngute *et al.*, 2020; Mabossy-Mobouna *et al.*, 2022).

## 5 Conclusion

The results demonstrate that *I. epimethea* is a highly popular and consumed species among several ethnolinguistic groups in the Democratic Republic of the Congo. The local population possesses a good ecological knowledge of the species and considers its most important host trees to be, in descending order, *P. macrocarpus*, *R. heudelotii*, and *F. africana*.

The change in the diet of the caterpillars collected from their natural host plant significantly affected their growth. While *F. africana* proved to be an unsuitable host for the caterpillars collected from *P. macrocarpus*, *H. floribunda* and *U. guineensis* can be considered as alternative hosts for the species. Despite several constraints that prevented the successful development of a new generation, the preliminary results obtained confirm the polyphagy of *I. epimethea* on three different plant families, namely Apocynaceae, Lecythidaceae, and Phyllanthaceae (not to mention those indicated by the local population and the literature). To maximise production, it is ideal to avoid transferring the larvae to various potential host trees. Further research is necessary to identify the compounds that reduce or inhibit the development of caterpillars on certain host plants and to characterize the ability of the caterpillars to develop on these plants over multiple generations.

Finally, semi-captive rearing appears to be the suitable system for *I. epimethea*, where the larvae are transferred to their pre-planted host trees to make them available for the population of the Kwilu province and the Democratic Republic of the Congo.

## Supplementary material

Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.24968691

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## Author's contributions

Françoise Madamo Malasi: conceptualization, methodology, validation, formal analysis, investigation, data curation, visualization, writing – original draft. Frédéric Francis: conceptualization, project administration, supervision, validation, writing – review and editing, funding acquisition. Rudy Caparros Megido: conceptualization, methodology, formal analysis, supervision, validation, visualization, writing – review and editing, visualization, funding acquisition.

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