Response of larvae of *Cirina forda* Westwood (Lepidoptera: Saturniidae) to spatio-temporal variation in the nutritional content of foliage of *Vitellaria paradoxa* Gaertn. f. (Sapotaceae)

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ABSTRACT

Cirina forda, an economically important edible folivore of *Vitellaria paradoxa* in the moist and dry woodland savanna ecosystems of Nigeria, has become ecologically restricted to the upper dry woodland savanna ecozone. The larvae of this insect are good source of protein for human and livestock consumption and income. However, little information is available on the bioecology of the insect to facilitate mass production. The study investigated, therefore, the emergence pattern and the physiological responses of the larval stages of the pest to spatial and temporal variations in the nutritional quality of foliage of the host tree, and their role in ecological adaptation of this pest. Field studies showed that the emergence pattern of *C. forda* is entrained to coincide with the period of abundant leaves of *V. paradoxa* at the beginning of the rainy season in the dry woodland savanna. Occurrence of *C. forda* in Nigeria has become restricted to the northernly dry woodland savanna ecosystem principally due to variation in the nutritional quality of leaf diet, and this is directly related to foliage age and geographical location of the host, *V. paradoxa*. Older leaves contained significantly higher (P < 0.05) micronutrients than immature leaves of the same plant, and larvae developed faster with access to foliage of different ages significantly (P < 0.05) than those fed on exclusive diets. Variation in micronutrient content and, probably, phytosterols in the leaves of different ages were suspected to be major reasons for non-survival to adult on exclusive diets. The knowledge would aid laboratory culture and management of this pest.

RÉSUMÉ

Odebiyi, J. A., Omoloye, A. A., Bada, S. O., Awodoyin, R. O. & Oni, P. I. : *La reaction de larves de* Cirina forda *Westwood (Lepidoptera : Saturniidae) à la variation spatio-temporelle dans la teneur nutritive de foliation de* Vitellaria paradoxa *Gaertn. f. (Sapotaceae). Cirina forda*, folivore comestible de *Vitellaria paradoxa* qui est économiquement important, dans l'écosystème de la savane boisée, humide, et sèche du Nigéria est devenu écologiquement restreint à la haute écozone de la savane boisée sèche. Les larves d'insecte sont une bonne source de protéine pour la consommation humaine et bestiale ainsi que pour le revenu maïs peu d'information est disponible sur la bio-écologie d'insecte pour faciliter la production en série. Donc cette étude enquêtait l'ordre d'émergence et les réactions physiologiques de stades larvaires de cet insecte ravageur aux variations spatiales temporelles dans la qualité nutritionnelle de la foliation de l'arbre d'hôte et leur rôles dans l'adaptation écologique de cet insecte ravageur. Les études sur le terrain montraient que l'ordre d'émergence de *C. forda* est emmené pour coïncider avec la periode de feuilles abondantes de *V. paradoxa* au commencement de la saison des pluies dans la savane sèche boisée. L'occurence de *C. forda* au Nigéria est restreinte à l'écosystème de la savane boisée sèche du nord en raison de la variation dans la qualité nutritionnelle du regime feuillu et ceci est directement lié à l' âge de foliation et au site géographique de la hôte *V. paradoxa*. Les feuilles plus vieilles contiennent de micronutriments considérablement plus élevés (P < 0.05) que les feuilles jeunes de la même plante et les larves s'évoluaient plus rapidement avec accès à la foliation de différents âges considérablement

(P < 0.05) que ceux qui sont nourri avec les regimes exclusifs. La variation dans la teneur micronutriment et peut-être le sphytostérols dans les feuilles ayant de différents âges étaient soupçonnés d'être les raisons majeures pour la non survie d' adultes de regimes exclusifs. Cette connaissance aidera la culture de laboratoire et la lutte contre ces ravageurs.

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Introduction

The shea tree, *Vitellaria paradoxa* Gaertn. f. (Sapotaceae), is an economically important tree grown for its fruit from which the seed, used for production of the shea oil, is obtained. The wood is also important for timber and charcoal production. The geographical distribution of this tree in West Africa extends from east of Senegal across southern Mali and Burkina Faso through northern Guinea Bissau, Guinea, Sierra Leone and La Cote d'lvoire, Ghana and central Benin Republic to Nigeria, north-east Cameroon and southern Chad (Irvine, 1961; Hall *et al.*, 1996). In Nigeria, the plant occurs mostly in the wild, in the derived savanna (moist and dry woodland) and Guinea savanna; an expanse that constitutes about 45 per cent of the Nigeria's total land area (Keay, 1949; Hall *et al.*, 1996).

The plant is also sparingly found towards the southern boundary of the Sudan savanna, in southern Kano, as well as south-eastern part of Sokoto State. In these areas, the plant is encountered as part of various agro-forestry practices including silvo-pastoral, agro-silvo-pastoral, Taungya and Social forestry systems (Egunjobi, 1991; Popoola & Tee, 2001). This tree is attacked by the pallid emperor moth, *Cirina forda* Westwood (Lepidoptera: Saturniidae), an indigenous folivore which attacks the tree annually during the raining season (Boorman, 1970, 1978). The larvae feed voraciously on the leaves causing severe defoliation of this economic tree (Ande & Fasoranti, 1996, 1997).

Although a pest, *C. forda* is particularly important in Nigeria for its larvae that are gathered and consumed as a source of edible protein, as well as source of income by the local people. Some workers in Nigeria have attempted a mass culture of this pest for purpose of local consumption, as well as for local and foreign markets (Fasoranti & Ajiboye, 1983; Ande & Fasoranti, 1996; Oyegoke & Fasoranti, 1999) with very little success probably due to paucity of information on the bioecology of the insect. In particular, the authors were not aware of any information about the nutritional characteristics of leaves of different ages and their importance to the survival of the larvae and this could have been a major factor against successful laboratory culture of the insect in the past.

It is known that most insect folivores require young nutritious plant tissues to achieve maximum development and fitness (Abbiw, 1990). However, availability of young leaves is often variable both in time and space. In most trees, such variability in the distribution of young and new leaves could hinder herbivore populations and their impacts by the reduced access to all the new foliage at any one time (Neumann *et al.*, 1998). The degree of within-tree heterogeneity, either in the production of leaves or in their spatial arrangement, can affect or alter the species composition, distribution or abundance of insect folivores (Franklin & Ruberte, 1975; Basset, 1999; Omoloye *et al.*, 2002) and has been closely linked with tree crown architecture.

The study was conducted to determine whether consumption of new or old foliage of *V. paradoxa* reflects an adaptation to the limited distribution and ephemeral nature of new foliage. Laboratory experiments were, therefore, conducted to assess the effects of feeding on new and old foliage of *V. paradoxa* on some developmental and survival parameters of the larvae of *C. forda,* as well as the mechanisms and period of adult emergence after the extended period of pupal diapause.

Materials and methods

The day-old larvae used in the study were raised from eggs collected from the field at Matachibo village, Kontagora, Nigeria in June. Natural occurrence of *Cirina forda* is endemic in this site, located in the dry woodland savanna ecosystem within latitude l0.24^0 N; longitude 5.29^0 E and an altitude of 200–400 m above sea level. Annual rainfall at the site averaged 1350 mm and solar radiation I5 mj/m^2/day. The eggs collected were incubated in plastic cages (l2 cm × 7 cm × 7 cm) and laid with filter paper at ambient temperature, 70 per cent relative humidity and 12:12-h photoperiod at the Entomology Research Laboratory, Department of Crop Protection and Environmental Biology, University of Ibadan, Nigeria, following the method of Omoloye *et al.* (2001). The agro-ecological characteristics of Ibadan are different, being located in the moist woodland savanna with mean solar radiation of 18 mj/m^2/day. The annual rainfall averaged 2000 mm with a bimodal pattern. It lies between latitude 7.30^0 N and longitude 3.54^0 E at an altitude of about 200 m above sea level.

Mechanisms and period of adult emergence

Pupae of *C. forda* were dug out and collected from soil surrounding the host tree in the field at Matachibo village, Kontagora, Nigeria in August. All collected pupae (60) were carefully buried in the soil at 9 cm depth and transported to the screen house in large plastic (45 cm diameter) tubes at the Department of Crop Protection and Environmental Biology, University of Ibadan. The set up was left at ambient temperature and observed until emergence of the F_1 adults. Another set of 20 pupae was exhumed in like manner but placed inside glass kilner jars that had been laid with filter paper pretreated with M-Tegosept, a fungistatic solution to prevent attack by pathogens (Omoloye *et al.*, 2000). The mechanism of pupal eclosion was visually observed further at close range for behavioural characteristics associated with pupal eclosion and adult emergence. Data on the period of development to adult and process of emergence at pupal eclosion were observed and recorded.

Foliage collection and site

The leaves of *V paradoxa* used for the feeding experiments were collected from fruit bearing mature (>75 cm Girth at Breast Height, GBH) and immature non-fruit bearing stands (30 cm GBH). These two categories of foliage were collected from two sites: 1. The fallow site containing stands of mature *V. paradoxa* populations (37 stands/ ha) at Matachibo village, Kontagora, Nigeria, a region where natural populations of *C. forda* were high, 2. Fallow site located within the campus of the University of Ibadan. Two types of leaves were collected from both mature and immature stands from the two sites as follows: 1. Very young leaves made up of the first three leaves from the apical bud of each branch, 2. Older leaves taken from 8–11 leaves from the apical bud of each branch. Thereafter, the collected samples were kept protected in plastic coolers with ice and stored at 4 °C in the laboratory.

Effect of feeding on new and old leaves on survival and development of C. forda

Larvae of *C. forda* were reared exclusively on either new or old leaves from the two sites or on a combination of both old and new from both sites. All foliage was excised and two whole leaves were placed per plastic cage. Ten day-old larvae were carefully placed on the leaves using camel hairbrush per plastic cage in five replicates. The leaves were changed and the rearing cage cleaned of egested waste daily. Rearing continued until all larvae either died or pupated. Mortality records and other observation data were taken until pupation.

Nutritional characteristics of leaves of V. paradoxa

Three hundred grams (300 g) each of new and old leaves described above were obtained from the two sites. These were finely ground and oven-dried before wet digestion following the method described by Pitan *et al*. (2002). The digested materials were made into four solutions in different I00-ml graduated flasks, and some primary nutritional (total N, crude fibre, fats,) and mineral components (nitrogen, phosphorus, potassium, calcium, magnesium, sodium, iron, copper and sulphur) of leaves were determined using standard methods (Horwitz, 1985).

Statistical analyses

Data were analyzed using ANOVA. The means were, thereafter, separated using the Tukey Honestly significant difference tests at $P < 0.05$ (Gomez & Gomez, 1984).

Results and discussion

Mechanisms and period of emergence of C. forda

The last stage larval instars descended down the host tree to pupate within the surrounding soil 0-90 cm around the host tree in the last quarter of August (Odebiyi *et al*., 2003). This period coincides usually with period of abundant rainfall at the Kontagora site. The pupa remains quiescent in the soil until 9-10 months later in May and June when the adult emerges (Odebiyi *et al*., 2003). It was found that pupal eclosion occurred mainly at night. Before eclosion, the pupa wriggles from a depth of about 6-15 cm towards the soil surface to a depth of 3 cm where the wriggling activities created free areas of about 2 cm around the mature pupa. Thereafter, rapid muscular contractions were observed and this could have been triggered off by the various physiological activities going on within the pupa.

The newly emerged adult was wet and inactive at first but began to crawl almost immediately on the soil surface. These movements around the soil surface increased as the newly emerged adult adapted quickly to the surrounding for 3-7 min. Thereafter, it stretched the wings and attempted the maiden flight. The adult female is bigger than the male and has distended abdomen loaded with eggs. The process of egg deposition did not follow any rhythmic cycle, as the newly emerged female laid the eggs carelessly in batches of 60-80 eggs within the surroundings. The female deposited its eggs indiscriminately either in the soil or on the wall of the container if enclosed in a cage in the laboratory.

Studies on the detailed biology of the insect are on going but preliminary observation showed a rare phenomenon of hatching of unfertilized eggs probably indicating occurrence of F_1 progenies from fertilized and unfertilized eggs in the field. However, none of the larvae that hatched out of the unfertilized eggs developed to adult stage (Table 1). Further study to confirm this preliminary observation is still on-going. Oviposition by adult *C. forda* in May and June appeared to be endogenously timed to synchronize with favorable environmental condition that guaranteed optimum survival of the larvae. Emergence started within the first week of May and each adult female laid an average of 365 eggs. Of these, 65 per cent hatched to first instar although development did not proceed beyond this stage (Table 1) probably due to dietary limitations in the laboratory.

Ecological adaptation and occurrence of C. forda *in Nigeria*

The agro-ecological characteristics of the sites where *C. forda* is commonly found in Nigeria varied as presented in Table 2. In this study, occurrence of populations of *C. forda* was found to have become restricted to the more northernly drier parts of the Guinea savanna ecosystem and is reported here for the first time. Natural occurrence of *C. forda* was known to be originally endemic in the whole of the southern Guinea savanna ecosystem bordering latitude 9.24^0 N; longitude 4.29^0 E and an altitude of 200-400 m, commonly found in Shaki and its environs, and upwards to the upper boundary of the southern

TABLE 1

Adult Emergence of Field Collected Pupae of Cirina forda *at the Ninth Month of Diapause and Oviposition and Percentage Survival Emergents of Unfertilized Eggs Incubated in the Laboratory*

Period after diapause	*No. of adults emerged*	*Sex ratio (F:M)*	*No. eggs laid/female*	*Percent hatched*	*Percent survival to next developmental stage*			
					1st instar	*2nd instar*	*3rd instar*	*4th instar*
Week 1	2	1:0	375	65	100	0	0	0
Week 2	3	1:0	266	48	100	10	0	0
Week 3	5	3:1	341	74	100	21	5	0
Week 4	19	2:1	332	88	100	33	8	0
Week 5	6	1:1	378	85	100	25	4	0
Week 6	2	0:1	0	0	0	0	0	0

TABLE 2

Effect of Feeding on Leaves of Different Ages of Vitellaria paradoxa *from Different Geographical Locations on the Survival of Immature Stages of* C. forda *in the Laboratory*

Source of foliage	*Percent larval survival to the next developmental stage (n = 120)*					
	1st instar	*2nd instar*	*3rd instar*	*4th instar*	*5th instar*	*6th instar*
Young Leaf from IBADAN	46.7 (56)	5.8 (7)	0	0	0	0
Mature Leaf from IBADAN	0	0	0	0	0	0
Young Leaf from KONTAGORA	56.7 (68)	9.1 (11)	0	0	0	0
Mature Leaf from KONTAGORA	0	0	0	0	0	0
Young + Mature leaf from IBADAN *	63.3 (76)	28.3 (34)	18.3 (22)	11.7 (14)	7.5 (9)	2.5 (3)
Young + Mature leaf from KONTAGORA*	72.5 (87)	44.2 (53)	35.0 (42)	32.5 (39)	29.2 (35)	24.2 (29)

* = leaves systematically administered such that immature leaves (1st -3rd leaf from branch apex) were given to 1st & 2nd instar, moderately matured leaves (4th -6th leaf from branch apex) to 3rd and 4th instars while matured leaves (7th -10th leaf from branch apex) were given to 5th and 6th instars. (Number surviving to next stage in parenthesis).

Guinea savanna (Ande & Fasoranti, 1995). However, occurrence of infesting populations of the insect has disappeared in the southern fringes of the ecosystem and now restricted in distribution to the upper bounds of the Guinea savanna ecosystem in Bida (Ande & Fasoranti, 1996), Mokwa & Kontagora in Niger State, Nigeria. This is one major reason why most field studies on *C. forda* are conducted in these areas.

The sites of common occurrence of the insect are located within latitude l0.24^0 N; longitude 5.29^0 E at an altitude of 200-400 m above sea level. Annual rainfall in the sites averaged 1350 mm and solar radiation I5 mj/m^2/day. The disappearance of the insects from the southern fringes of the Guinea savanna ecosystem could be due to the rainfall pattern which is bimodal in the southernly part of the ecosystem compared to the unimodal pattern in the upper part of the ecosystem in Bida and Kontagora. It could also be a direct result of undue exploitation of the host trees in the wild for diverse purposes such as charcoal production and timber (Ande & Fasoranti, 1995). Still, the disappearance could be a direct consequence of the annual bush burning which exposes the larvae to natural enemies. Bush burning also affects the nutritional composition of the foliage of the host trees.

It is known that insect herbivory is affected by the nutritional quality of foliage. It is also known that the type and degree of occurrence of specific phytochemical compounds such as sterols in host plants (Marschner, 1995; Behmer & Grebenok, 1998; Yang *et al.*, 2001; Behmer & Elias, 1999, 2000; Omoloye & Vidal, 2007) could determine choice of the same host species for food. Intra-specific variations in the composition of such compounds in host plants are common and some have been found to influence a folivore's preference of a host plant for feeding, shelter or oviposition purposes (Svoboda, 1984; Marschner, 1995; Behmer & Grebenok, 1998; Yang *et al.*, 2001; Behmer & Elias, 2000; Moeser & Vidal, 2004). The consequences of these environmental factors, as well as the negative anthropogenic actions within the ecosystem impact either directly or indirectly on the survival of the insect and explains why *C. forda* is now restricted to the upper section of the Guinea savanna across the River Niger.

Temporal and spatial variation in the nutritional characteristics of foliage of V. paradoxa

The study has shown that the nutritional content of leaves of *V. paradoxa* obtained from the two ecologies covered in the study varied significantly (Tables 3 and 4). The macronutrients and their relative content did not differ significantly ($P > 0.05$) between locations apart from the percentage composition of nitrogen and magnesium which varied significantly ($P < 0.05$) between foliage of the same age from the two locations. This suggests that location did not affect the amount of the macro-nutrient in the leaves of *V. paradoxa*. It also suggests that the amount of macronutrients might not influence the choice of leaves of *V. paradoxa* for food by *C. forda*. However, there was a significant difference ($P < 0.05$) between the macronutrient content of mature and immature leaves of *V. paradoxa* from the same plant in the same location, being significantly higher in the mature leaves (Table 3). The difference in the macronutrient content of the leaves from the same plant could be the reason for the observed differential response of larvae to leaves of different ages in relation to survival of larvae to adult (Table 2). However, there was a significant difference ($P < 0.05$) between the amount of micronutrient of mature and immature leaves and between the two locations (Table 4).

The micronutrients assessed in the study were iron, manganese, copper and zinc. In terms of occurrence and abundance in leaves, however, copper was the least abundant both in the mature (11.66–14.77 µg/g) and the immature (9.94–11.62 µg/g) leaves. Apart from manganese, which was comparatively higher in the leaves from Kontagora, the micronutrients were significantly more abundant in leaves of *V. paradoxa* from Ibadan than leaves from Kontagora. Similarly, apart from iron that was comparatively (ca. 14%) less than that found in leaves from Kontagora, immature leaves from Kontagora contained significantly higher ($P < 0.05$) amount of all the micronutrients than the immature leaves from Ibadan. These suggest that the immature leaves from Kontagora which contained significantly higher amounts of the micronutrients in the immature leaves provided superior and suitable starter diet that encouraged and facilitated the survival of the insects. This result, however, does not preclude the direct or indirect influence of environmental factors of weather and the role of natural enemies, although the relative contributions of these factors could not be ascertained in the study.

The study also showed that the age of foliage within branches of *V. paradoxa* significantly ($P < 0.05$) affected the survival of *C. forda*. Larvae of this insect did not survive beyond the 2nd instar when fed exclusively on the new-leaf diet (first three leaves from a branch apex) from both Kontagora and Ibadan sites (Table 2). Similarly, there was 100 per cent mortality by 72 h of larvae of *C. forda* when reared exclusively on old-leaf diet (leaf number six and beyond from the branch

TABLE 3

Variations in the Macronutrient Constituents of Foliage of V. paradoxa *from Two Agro-ecological Sites*

Source of foliage	*Macro-nutrient (%)*							
	Total N	*Crude fibre*	*Fat*	*Phosphorus*	*Potassium*	*Calcium*	*Magnesium*	*Sodium*
Young Leaf IBD	1.40b	20.24b	3.23c	0.09a	4.087b	0.139a	0.038b	220.970d
Matured Leaf IBD	1.72a	25.74a	4.75a	0.08a	4.455a	0.116a	0.064a	454.545a
Young Leaf KONT.	1.08c	21.15b	4.01b	0.09a	4.534a	0.151a	0.035b	339.415c
Matured Leaf KONT.	1.59b	26.83a	4.68a	0.08a	4.455a	0.130a	0.045b	418.605b

Means followed by the same letter in the same column are significantly different at $P = 0.05$ (Tukey HSD).
Young leaf IBD = Young leaf from Ibadan, Nigeria; Matured leaf IBD = matured leaf from Ibadan, Nigeria;
Young leaf KONT. = Young leaf from Kontagora, Nigeria; Matured leaf KONT. = Mature leaf from Kontagora, Nigeria

TABLE 4

Variations in the Micronutrient Constituents of Foliage of V. paradoxa *from Two Agro-ecological Sites*

Source of foliage	*Micro-nutrients (µg/g)*			
	Iron	*Manganese*	*Copper*	*Zinc*
Young Leaf IBD	28.717b	23.194a	9.940c	32.030a
Matured Leaf IBD	35.227a	15.909b	14.772a	20.455c
Young Leaf KONT.	24.419b	24.419a	11.627b	25.456b
Matured Leaf KONT.	25.581b	18.031b	11.667b	18.605c

Means followed by the same letter in the same column are significantly different at $P = 0.05$ (Tukey HSD).
Young leaf IBD = Young leaf from Ibadan, Nigeria; Matured leaf IBD = matured leaf from Ibadan, Nigeria;
Young leaf KONT. = Young leaf from Kontagora, Nigeria; Matured leaf KONT. = Mature leaf from Kontagora, Nigeria

apex) after commencement of feeding. There was no visible sign of consumption of the old leaves by the newly emerged first instars (i.e. no area of the leaves consumed and there were no frass pellets left in the plastic cage). Thus, most of the larvae died apparently because they could not initiate feeding.

There was also no indication of cannibalism in any of the treatments. However, when larvae were provided with new foliage as a starter diet at the first two instars and, thereafter, in combination with moderately older leaves till the fourth instar before they were fed with very old leaves at the fifth instar, 72 per cent of the larvae survived to pupation. Since survival to adult was nil on the larvae fed on exclusive diets of old or very young leaves throughout, statistical analyses were restricted to comparison of feeding on combined diets. Therefore, the survival of larvae with access to foliage of different ages as development advanced with the instars was significantly higher ($P < 0.05$) than those fed exclusively on young diet. This suggests that for a successful culture at ambient temperature within the range of 25 ^{0}C and 29 ^{0}C and 75 ± 10 per cent at 12:12 h photo period, a starter diet of fresh young leaves from the top three leaves from the apex is required for the first two instars, then feeding with medium-aged leaves from the fourth to the sixth leaf is required for the third and fourth instar while the rest of the instars could be fed successfully with older leaves.

Conclusion

The study has shown that emergence of *C. forda* is endogenously entrained to coincide with the period of abundant leaves of *V. paradoxa* at the beginning of the rainy season for the survival of the larvae but egg eclosion and oviposition are not endogenously entrained. It also indicates that the newly emerged female *C. forda* did not display any inherent maternal characteristics but was rather careless at oviposition. The study also showed that *C. forda* in Nigeria became restricted to the northernly part of the Guinea savanna ecosystem due to environmental and human-related factors of which depletion of the quality of leaf diet, especially the micronutrients of leaves of *V. paradoxa,* could have been major.

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