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Authors: Nzekwu, A. N., and Akingbohungbe, A. E.

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The effects of various host plants on nymphal development and egg production in *Oedaleus nigeriensis* Uvarov (Orthoptera: Acrididae)

A. N. Nzekwu and A. E. Akingbohungbe

(ANN) Natural History Museum, Obafemi Awolowo University, Ile-ife, Nigeria. E-mail: anzekwu@yahoo.com
(AEA) Department Of Plant Science Obafemi Awolowo University Ile-ife, Nigeria.

Abstract

O. nigeriensis Uvarov is widely distributed in the moist grassland habitats of Nigeria. Although this area is used for intensive agricultural activities, providing more than 90% of the grains needed in the country, the insect has been reported to cause only minor damage to agricultural crops while the closely related *O. senegalensis* is a serious pest of crops. The reason for the minor pest status of *O. nigeriensis* is unknown and only adequate study of the insect/host-plant relationship will provide some clues.

Nymphs and adults of *O. nigeriensis* were reared on selected food plants (grasses) in the laboratory; this included *Axonopus compressus*, *Cynodon dactylon*, *Eleusine indica*, *Seteria gracilipes*, used singly and as a mixture of all four. Development of the nymphs was shortest when rearing was on a mixed diet: 60 d compared to 105 to 127 d for single host plants. Rearing the adults on *S. gracilipes* promoted faster oocyte development than the other treatments. The present pest status of the insect is discussed based on the data obtained.

Key words

Development, host plant, grasshopper feeding, diet, life history

Introduction

The acridid grasshopper genus *Oedaleus* Fieber is represented in Nigeria by two species: *O. senegalensis* (Krauss) and *O. nigeriensis* Uvarov. *O. senegalensis* is restricted to the drier northern part of the country where it is a serious pest of crops, especially millet, a principal subsistence crop in subsaharan Africa (Batten 1969, Popov 1988). *O. nigeriensis* on the other hand is widely distributed in moist grassland habitats across Nigeria, especially in the core agricultural areas that are well known for the cultivation of grains. While *O. senegalensis* has been reported as a serious pest of crops, surprisingly *O. nigeriensis* is known to cause only minor damage — *Pennisetum* (Golding 1946, Harris 1949), maize (Descamps 1954), tobacco and yam (Libby 1968). Thus its present assessment in terms of economic importance is that of an occasional minor pest (COPR 1982). Given present efforts in the expansion of agricultural activities and the subsequent creation of new biotopes in the distribution area of *O. nigeriensis*, it is possible that the pest status of the insect may change in future. The reason for the minor pest status of *O. nigeriensis* is presently unknown and only adequate study of the insect/host plant relationship may produce some clues.

Since grasshoppers are largely phytophagous insects, there have been very extensive studies on food selection in grasshoppers: these have been adequately reviewed by Uvarov (1977) and Chapman (1990). It has been shown that plant availability in a habitat is very important in establishing the diet breadth of a grasshopper species. However, diet breadth is determined not only by the relative abundance of individual plant species, but also by individual plant species' phenological, nutritional and pathological condition (Chapman 1990). Understandably, many experimental studies have shown striking differences in the development and fecundity of the same grasshopper species fed on various host plants (Afolabi 1973, McFarlane & Thorsteinson 1980, Fanny *et al.* 1999). Nzekwu and Akingbohungbe (1999) studied the host plant associations of *O. nigeriensis* along a transect through the different vegetation zones of Nigeria and reported that the insect is principally graminivorous and polyphagous. The present study is an attempt to record the effects of some host plants associated with *O. nigeriensis* in the field, as reported in our earlier study on the development of the nymphs and adults in the laboratory. The data obtained may throw some light on the present minor pest status of the insect and should be of benefit in avoiding or preventing any possible future outbreak.

Materials and Methods

Stock Culture.— Studies were designed to investigate the effects on the development of the grasshopper of feeding on various host plants. Four host plants, all grasses, with which the insect was associated during the field surveys, were used for the experiments: *Axonopus compressu*, *Cynodon dactylon*, *Eluseine indica* and *Seteria gracilipes*. They were grown in the greenhouse and 3 to 4 week-old plants were used for all experiments. The stock culture consisted of adult females from the field and was only established to provide a regular source of nymphs and adults for the actual experiment, which was carried out on only one generation.

Gravid females of *O. nigeriensis* were collected from the field in and around Ogbomoso, Nigeria (lat 8˚ 10′ N, long 4˚ 12′ E). The insects were mass-reared separately in five cages measuring 90 X 90 X 60 cm on the selected host plants and combinations of them. The cages were kept in the laboratory where the temperature fluctuated between 26˚ and 30˚ C with relative humidity from 60 to 80%. These temperature and relative humidity regimes are similar to field conditions. Egg trays filled with moist sand were placed in all the cages for oviposition. Nymphs and adults from the egg-pods laid were used for the subsequent experiments.

Nymphal development.— Ten newly emerged first instar nymphs were obtained from the stock culture and transferred singly into 1.25-l plastic jars. Thus, there were 10 replicates for each of 5 treatments. Each treatment was a different host plant, with one being a mixture of all. Insects were reared to adult, feeding the designated host plant *ad lib*. The host plants were cuttings, immersed in water and changed daily. Developmental periods were recorded for every instar through to the adult.

Life History Statistics of the Adult.—Newly emerged adults from the stock culture were paired (one male and one female) in 1.25-l plastic jars filled with moist soil to one-fifth of the soil's capacity to serve as oviposition medium. Five replicates were set for each food plant and their mixture. The insects were maintained till all died. The following parameters were scored: pre-oviposition period, longevity, pods per female and number of eggs per pod.

Data obtained from the two experiments were subjected to a one-way analysis of variance with repeated measures and significant means were determined using Duncan's New Multiple Range Test (DNMRT).

Results

Nymphal Development.—The effects of various host plants on the nymphal development of *O. nigeriensis* are shown in Tables 1 and 2. The different host plants affected the developmental periods of the nymphs significantly, and the effect varied in particular nymphal instars. In the first instar, feeding on *S. gracilipes* led to the fastest development and was comparable to the stadia of nymphs fed on *E. indica*, but significantly different from those reared on *A. compressus* and *C. dactylon*. In the second instar, feeding on *A. compressus* led to completion of development in about half the time taken by nymphs reared on any of the other single host plants. The mixed diet led to a developmental period which was 3 d faster than *A. compressus*, although not significantly different. In the third instar, feeding on *S. gracilipes* led to a significantly shorter stadium than on *E. indica* (1 w shorter), as well as for the other single host plants (2 w shorter). The mixed diet, however, led to the shortest period. In the fourth instar, feeding on *C. dactylon* resulted in the fastest development which occurred in 11.3 d. This was comparable to the stadia of nymphs fed on *A. compressus* and *E. indica*, but significantly different from those reared on *S. gracilipes* (8 d faster). The mixed diet also led to a developmental period that was comparable to the single host plants except *S. gracilipes*. In the fifth instar, the developmental period did not differ significantly among nymphs fed on either *A. compressus*, *E. indica* or *S. gracilipes*; but it was significantly longer in nymphs fed on *C. dactylon* by about 3 d.

Summing up these findings to give the mean total developmental periods: no significant differences were observed among the nymphs that were fed on any of the 4 single host plants. However, the mixed diet led to a significantly shorter total developmental period, which was generally about half of the period on any of the single host plants.

Life History Statistics.— Our findings on the effects of the various host plants on the life history statistics of the adults of *O. nigeriensis* are shown in Tables 3 and 4. The various host plants significantly affected the pre-oviposition period, longevity, number of pods and number of eggs per pod. Adult females lived longest when fed on any of *C. dactylon*, *E. indica*, and *S. gracillipes* and longevity was significantly reduced when they were fed on *A. compressus*. The shortest pre-oviposition period was observed in adults fed on *S. gracilipes*: they started laying eggs about 2 w after their final molt. Feeding adults on *C. dactylon* and *E. indica* led to prolonged pre-oviposition periods of about 4 w or greater, while the mixed diet also gave a prolonged period of about 3 w.

Adults fed on *E. indica*, *S. gracilipes* and the mixed diet laid the highest number of egg-pods (3.6 or more), followed by adults fed on *A. compressus*. The least number of egg-pods were laid by adults fed on *C. dactylon*. However, the mean number of eggs per pod was highest in adults fed on mixed diet. This was followed by adults fed on *E. indica* in which the number of eggs was less by about six. The least number was laid by adults fed on *C. dactylon*, *A. compressus* and *S. gracilipes*; and each had about 8 to 9 eggs less per pod. Similarly, the total number of eggs laid per female was considerably greater in the adults fed on mixed diet (96 eggs), followed by adults fed on *E. indica* (73 to 79 eggs) and *S. gracilipes* (65 eggs), while those fed on *C. dactylon* gave the least number of total eggs per female (25 eggs).

Table 1. ANOVA table for the effects of host plants on nymphal developmental periods of *O. nigeriensis.*

Source	*df*	MS					
		Nymphal Development Periods					Total Nymphal Period
		I	II	III	IV	V	
Treatment (5)	(t-1)=4	56.2	1610.9	1542.3	113.8	57.9	6025.3
Replication (10)	(r-1)=9	5.1	31.8	10.0	4.3	6.7	47.4
Error	(t-1)(r-1)=36	1.9	21.0	15.6	3.4	4.9	52.3
$F_{5.50}$		29.6*	79.7*	98.7*	33.5*	11.8*	115.2*

* Significant p< 0.05

Treatments: *A. compressus*, *C. datylon*, *E. indica*, *S. gracilipes*, Mixed

Table 2. Effects of various host plants on nymphal development of *O. nigeriensis*.

Plants	Mean developmental period (days $\pm s_{\bar{x}}$)					Total period ($\pm s_{\bar{x}}$)
	Instars					
	I	II	III	IV	V	
Axonopus compressus	15.20 ±0.69[a]	15.30 ±0.66[b]	48.50 ±1.34[a]	12.40 ±0.78[b]	13.60 ±1.01[b]	105.80 ±1.14[a]
Cynodon dactylon	14.50 ±0.63[a]	35.60 ±4.90[a]	49.10 ±1.59[a]	11.33 ±0.60[b]	16.70 ±0.75[a]	127.40 ±4.34[a]
Eleusine indica	10.30 ±0.35[c]	38.00 ±0.56[a]	41.80 ±0.57[b]	11.50 ±0.47[b]	13.40 ±0.63[b]	115.20 ±0.44[a]
Setaria gracilipes	9.70 ±0.22[c]	36.30 ±0.94[a]	34.50 ±0.47[c]	19.40 ±0.49[a]	12.70 ±0.58[b]	112.50 ±1.63[a]
Mixed	11.50 ±0.45[b]	12.30 ±0.44[b]	15.50 ±0.47[d]	11.00 ±0.54[b]	9.60 ±0.49[c]	60.10 ±1.49[b]
$F_{5, 50}$	29.6*	76.7*	98.8*	33.5*	11.8*	115.2*

Means in the same column followed by the same letters are not significantly different from one another at 5% level of probability (DNMRT).
* p< 0.05

Table 3. ANOVA table for the effects of host plants on the life history statistics in adult *O. nigeriensis.*

Source	*df*	MS				
		Pre-oviposition period	Oviposition Period	Longevity	Pods per female	Eggs per pod
Treatment (5)	(t-1) = 4	156.5	81.9	443.2	4.5	201.2
Replication (5)	(r-1) = 4	7.5	45.9	28.9	0.3	3.3
Error	(t-1)(r-1) = 16	7.7	33.6	59.5	0.4	8.5
$F_{0.05}$		20.3*	2.4 ns	7.4*	11.3*	23.6*

* = p< 0.05
ns = not significant p= 0.05

Treatments:(*A. compressus, C. datylon, E. indica, S. gracilipes*, Mixed)

Table 4. Effect of various host plants on the life history statistics of adult *O. nigeriensis*.

Host plants	Pre-oviposition period $\pm s_{\bar{x}}$	Oviposition period (days $\pm s_{\bar{x}}$)	Longevity (days $\pm s_{\bar{x}}$)	Mean pods per female	Mean eggs per pod
A. compressus	19.70 ±1.34[c]	25.33 ±5.78	41.20 ±5.52[b]	2.20 ±0.41[b]	17.70 ±0.18[c]
C. datylon	30.00 ±0.82[a]	23.50 ±1.22	63.20 ±1.68[a]	1.40 ±0.22[b]	17.60 ±0.43[c]
E. indica	27.20 ±0.72[ab]	33.25 ±3.90	66.4 ±1.76[a]	3.60 ±0.22[a]	20.22 ±0.31[b]
S. gracilipes	15.20 ±0.54[d]	28.50 ±1.22	54.70 ±2.53[a]	3.70 ±0.22[a]	17.60 ±0.43[c]
Mixed	24.00 ±1.87[bc]	23.75 ±1.37	64.20 ±2.19[a]	3.70 ±0.22[a]	26.00 ±0.59[a]
$F_{5, 50}$	20.3*	2.4 ns	7.4*	11.3*	23.6*

Means in the same column followed by the same letters are not significantly different from one another at 5% level of probability (DNMRT).
* = p< 0.05
ns = not significant p= 0.05

Discussion

The experiments involving rearing of *O. nigeriensis* on various host plants, presented singly or as mixed diet, clearly show that the type of food plant can be a significant factor in the development of the insect. For single host plants, feeding on *S. gracilipes* gave the shortest nymphal development for the 1st, 3rd and 5th nymphal instars, while feeding on *A. compressus* similarly gave the shortest nymphal developmental period for the 2nd instar. Thus, variable developmental periods could occur in nature, depending on the preponderance of particular food plants in various localities.

However, in localities where there are mixed populations of food plants, these can serve as complements to one another. McFarlane & Thorsteinson (1980) reported that mixed plant diets are superior for *Melanoplus bivittatus* (Say), by promoting higher survival, larger adults and higher growth indices than any single plant diet. Adams and Bernays (1978) had earlier shown that a range of chemicals having antifeedant properties for nymphs of *Locusta migratoria* (L.) is additive in its effects. However, Bernays and Bright (1991) provide evidence that individual polyphagous grasshoppers do switch more between dietary items and mix intake more on two different complementary foods, than when the two foods are nutritionally adequate and identical. Fanny *et al.* (1999) found that in *Oxya nitidula* (Walker), the shortest nymphal periods were obtained when rearing was on *Panicum maximum*. Adequate diet is expected to reduce nymphal developmental period, which is very important for the fitness and survival of the insect (Price *et al.* 1980).

In the adult, feeding on single host plants such as *A. compressus* and *S. gracilipes* led to a shorter pre-oviposition period than when feeding was on *C. dactylon* and *E. indica*. This suggests that the former plants have qualities that enable them to promote faster maturation and oocyte development. The mean number of pods per female was highest and similar when the adult females were fed on *E. indica*, or *S. gracilipes* or mixed diet. Lee and Wong (1978) demonstrated that food plants have significant effects on oocyte development in *Oxya japonica* Willemse, related to the nutritional requirements of the insect as well as the chemical composition and amount of food ingested. In the closely related *O. senegalensis*, Boys (1978) showed that feeding on millet was opportunistic, while mature females were observed to feed preferentially on milky grains of millet in the field and in the laboratory. For the present study, particular host plants may possess unique factors that better promote egg-pod production in *O. nigeriensis*, and such factors may not be subject to dilution, even in the mixed diet. The total number of eggs per female was greatest when the grasshoppers were fed a mixed diet, indicating improved fertility on mixed diet. This shows that the overall nutritional value of the mixed diet, in terms of adult fertility, is superior to that of the single host plants.

It may be concluded that in *O. nigeriensis*, while mixed diet is highly favored for optimum nymphal development and higher fertility, certain single host plants could adequately promote adult maturation and egg-pod production. However in nature, selection pressure may favor habitats with mixed host plants, since these will ensure adequate nutritional requirements for the development and survival of the nymph, a stage that is regarded as the most important with respect to population regulation among grasshoppers (Joern & Gaines 1990, Lockwood 1993). This may not be a bad strategy for the insect considering the fact that *O. nigeriensis* is included among the group of acridid species that do not readily move from their natural grassland habitats into crops to become pests (Popov 1988).

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