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Oviposition Site Preference and Its Effects on Subsequent Development of Variegated Grasshopper (*Zonocerus variegatus* L.) under Laboratory Conditions

Saffea Joseph Torto[1], Abu James Sundufu[1], Alusaine Edward Samura[1], Sahr Ngoba Fomba[1], Dennis Peter Musa[2], Skeku Alfred Kanu[3], Prince Emmanuel Norman[4*]

[1]Department of Crop Protection, School of Agriculture and Food Sciences, Njala, Sierra Leone
[2]Department of Horticulture, School of Natural Resources Management, Njala University, Njala, Sierra Leone
[3]Department of Crop Science, School of Agriculture and Food Sciences, Njala University, Njala, Sierra Leone
[4]Germplasm Enhancement and Seeds Systems, Sierra Leone Agricultural Research Institute, Freetown, Sierra Leone
Email: sjtorto7@gmail.com, sjtorto@njala.edu.sl, alusaine.sam@njala.edu.sl, abuj.sundufu@njala.edu.sl, pdmusa@njal.edu.sl, kanusa@njala.edu.sl, snfomba@njala.edu.sl, *pnorman@wacci.ug.edu.gh, norman.prince64@gmail.com

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Abstract

Female grasshoppers can affect the fitness of their offspring through their selection of oviposition site. Knowledge of soil type on oviposition, and its effects on subsequent development can provide guidelines for habitat manipulations that reduce the harmful effects of these pests on farmers' fields. The influence of soil types on the oviposition site preference of variegated grasshopper (*Zonocerus variegatus* L.) reared some cassava (*Manihot esculenta* Crantz) varieties, was investigated in a cage trial carried out at the Bio factory laboratory, School of Agriculture and Food Sciences, Njala University, Sierra Leone during 2022/2023. The treatments comprised three soil types (Sandy, Loamy and Clay), each with three replications laid out in a randomized complete block design (RCBD) in wooden cages. Data were collected on the following development parameters including, Net reproductive growth ratio (R_0), Generation time (Tc), Intrinsic rate of increase (r_m), Finite rate of increase (λ), Doubling time (Dt), and overall survivorship. Findings revealed that, *Z. variegatus* L. preferred sandy soil in which, on average, most eggs were deposited (338, 6.62 ± 4.40), followed by loamy soil, 286 (5.53 ± 3.96), and then, clayey soil, 200 (3.91 ± 3.85); though, the differences were not significant. This study established that *Z. variegatus* deposited more eggs in sandy soil > loamy soil > clayey soil, respectively; and subsequent survivorship of the immature unto mature adult insect, revealed a similar order. This indicates that the sandy soil is the most preferred substrate for oviposition and subsequent development into adult insects.

Keywords

Development, Oviposition, Oviposition Site Preference, Soil Types, Variegated Grasshopper

1. Introduction

African variegated grasshopper (*Zonocerus variegatus* L.) is known as one of the key pests of many crops in West and Central Africa including Sierra Leone, which occupies extensive forest and savanna areas [1]. The impact of grasshopper infestation on crops increases with time, particularly under increased temperature [1]. *Zonocerus variegatus* has been well reported as a causal agent for the transmission of okra mosaic viruses in Ivory Coast and cowpea mosaic viruses in Nigeria [1] thereby causing huge yield losses in these crops. The pest is also reported to cause 25% - 80% yield loss in garden eggs [1] and 50% fresh root yield loss in cassava [2]. This pest not only accelerates grassland degradation and desertification, but also causes a large loss of foliage posing a serious threat to the production and livelihood of indigenous farmers and herdsmen [3]. Due to the significant damages caused by the outbreaks of these pests, the ability to predict and prevent the occurrence and spread of locusts and grasshoppers has become an urgent requirement to permit farmers to protect farmland ecologies and maintain the sustainable development of agriculture and animal farmland.

Understanding the reproductive behaviors of grasshoppers plays a significant role in predicting and controlling their populations. Oviposition in particular is an important concept in the process of insect ontogenesis that plays a vital role in the reproduction of offspring [4]. Selection of suitable oviposition sites is essential to the life history of phytophagous insects, as well as greatly affects the chance of survival of their offspring [4]. The oviposition site should provide both protection and potential food resources for the larvae to aid their growth and development during their most vulnerable stages [4] [5]. For instance, insects that lay their eggs in the soil such as *Oedaleusdecorus asiaticus* greatly reduce the exposure of their eggs to certain harmful factors including desiccation, predators, and parasitoids [6]. This behavioral survival mechanism ensures that their offspring have a relatively stable environment for growth and development [6].

A number of abiotic and biotic factors affect the oviposition behavioral pattern of locusts and grasshoppers. Vegetation type is one of the factors that exhibit a significant impact on female oviposition. *Locusta migratoria manilensis* (Meyen 1835) (Orthoptera: Acrididae) females were found to preferentially oviposit in habitats with *Phragmites australis* (Cav.) Trin. ex Steud (Poales: Poaceae), *Imperata cylindrica* (L.) Raeusch (Poales: Poaceae) and *Aeluropus sinensis* (Debeaux) Tzvelev (Poales: Poaceae), but not *Artemisia halodendron* Turcz. ex Besser (Asterales: Compositae) [4]. The solitary *Schistocerca gregaria* (Forskål, 1775) (Orthoptera: Catantopidae) females preferred ovipositing in the sites with *Heliotropium* spp. (~66%) and millet (~32%) seedlings. Moreover, vegetation type influences the number of eggs laid by locust and grasshopper females. For instance, it was reported that *L. m. manilensis* laid the most eggs when fed on *Zea mays* L. (Poales: Poaceae) in comparison to feeding them with *Triticum aestivum* L. (Poales: Poaceae) and *Setaria italica* (L.) P. Beauv. (Poales: Poaceae) [7]. The solitary nymphs of these pests were also shown to prefer to feed on those plants [7].

According to Li *et al.* [4], a limited number of researches have been done on habitat suitability in relation to oviposition behavior and hatching success of grasshoppers. One such study was conducted by Zang *et al.* [8], who investigated the effects of different soil types and soil moisture content on egg hatching of *O. d. asiaticus*. In Sierra Leone, there is a dearth of knowledge on the effects of soil types on the oviposition, hatching success, survivorship and related population parameters of variegated grasshopper (*Z. variegatus* L.) on cassava (*M. esculenta* Crantz). Thus, the objective of the present study was to assess the influence of soil types on oviposition, and related developmental parameters of grasshoppers.

2. Materials and Methods

2.1. Description of Study Area

The study was conducted at the Bio factory laboratory, School of Agriculture and Food Sciences, Njala University, Njala Campus, Sierra Leone. The University is located at latitude 8˚06' and longitude 12˚06' at an altitude of 51 m above sea level. The substrates were collected from the upland soils of Njala, which are generally highly weathered, well-drained, and acidic [9]. The climate is marked by a distinct rainy season (May-October), and a pronounced dry season (November-April). The mean annual rainfall during the experimental period from 2022 to 2023 was 2604.4 mm.

2.2. Experimental Material, Design and Treatments

The grasshoppers were field collected as large nymphs and maintained in the laboratory during the experimental period. The insects and choice tests were held in cages in an insect growth room at 30˚C - 32˚C with a photoperiod of 14:10 (L:D) and a relative humidity of 50% ± 10%. The 10 paired experimental materials were introduced in each of the cages on the same day. The nymphs were fed with fresh cassava leaves that were replaced when 80% had been consumed. The nymphs grew into adult insects and mated among themselves for 72 h. The adults oviposited their eggs on the various substrates at will for 16 days.

The trial was a one-factor experiment laid out in a completely randomized design (CRD) with three replications. The single factor investigated comprised three levels of soil types (sandy, loamy and clayey soils). Each soil type has different morphological characteristics that influence grasshopper oviposition. A total of three cages (replicates) were utilized for each of the three soil types. Each soil type was placed in the same laboratory conditions described above.

2.3. Experimental Variables Collected

With the developmental parameters obtained, the parameters for the construction of fertility life tables were estimated, according to Price [10], and included:

1) Net reproductive rate (R_0), the mean number of female offspring produced per female per generation, was determined as:

$$R_0 = \sum_{x=1}^{n} l_x m_x \quad (1)$$

where,

l is the age of first reproduction, and n is the age of the last reproduction (observed values);

x = age of parental females, age is considered starting in the egg phase;

l_x = specific survival rate to age x, expressed as a fraction per female and male (total adults);

m_x = specific fertility or number of offspring produced per female at age x;

$l_x \cdot m_x$ = age-specific maternity.

2) Generation time (Tc), is the mean longevity of a generation (average time between two successive generations) and was calculated as:

$$Tc = \frac{\sum_{x=1}^{n} x l_x m_x}{R_0} \quad (2)$$

3) Intrinsic rate of increase (r_m), is the number of eggs hatched per female per soil type in each of the cages, calculated as:

$$r_m = \sum_{x=1}^{n} l_x m_x e^{-rx} = 1 \quad (3)$$

4) Finite rate of increase (λ), is the number of times the population increases per time unit, was calculated as:

$$\lambda = e^{r} \quad (4)$$

5) Duplication time (Dt), the number of units of time required for the population to double in number, was calculated as:

$$Dt = \frac{\ln(2)}{r_m} \quad (5)$$

6) Age-specific survival (l_x) curves were plotted against each developmental stage, considering both males and females of each soil/cage trial until the couples were dead.

2.4. Data Analysis

Data on oviposition preference site, in the multiple-choice test, were analyzed using PROC ANOVA and means were compared using the Student-Newman-

Keuls test (P < 0.05). Data for the development parameters including, Net reproductive growth ratio (R_0), Generation time (Tc), Intrinsic rate of increase (r_m), Finite rate of increase (λ), Doubling time (Dt) were submitted to ANOVA and compared using the Student-Newman-Keuls test. All statistical analyses were conducted using the software package SAS.

3. Results and Discussion

3.1. Oviposition Preference Site

Grasshoppers (*Z. variegatus* L.) in the laboratory cages produced 338, 286, and 200 pods in sandy, loamy and clay soils, respectively. The relative number of egg pods produced by each population was not significantly (P = 0.1619) differ among the three soil substrates (**Table 1**), though on average, numerically, *Z. variegatus* L. deposited producing more eggs on the sandy soil, 338 (6.62 ± 4.40), followed by loamy soil, 286 (5.53 ± 3.96), and then, clayey soil, 200 (3.91 ± 3.85). Insects often select oviposition sites that enhance fitness of immature stages. Oviposition site selection and oviposition by females differ significantly with insect orders [11]. While phytophagous insects may prefer different plant surfaces or insides of plants [12], in predatory insects, oviposition is influenced by visual and olfactory cues [13], color of prey [14], volatiles released by prey infested plants [15], honeydew of prey [16], intensity of smell of prey [17], alarm pheromones of prey [18], quantity and quality of prey [19], and age of prey colony [20]. In oviparous species, oviposition-site choice is done by females based on assessment of potential nest sites and selection of a particular site. A female's decision about where to lay her eggs can have serious consequences for her own reproductive fitness, as oviposition site significantly affects embryo survival, juvenile performance, offspring phenotype, and potential survival of ovipositing female. Thus, the choice of oviposition site is a life-history trait of critical importance [21].

Sandy soil is normally loose and easy to penetrate for oviposition, while clay soil is hard to penetrate and easily dry out. Bhatti *et al.* [22] and Wohltmann *et al.* [23] reported that the females preferred soil with more than 70% sand for laying eggs some 6 inches deep in the soil. The present results are supported by Ingrisch [24], who investigated hatching of eggs, development of larval instars and abundance of grass hoppers and found that egg laying by grass hoppers was preferably associated with the soil texture. The above results are further supported by the finding of Ni *et al.* [25], who were of experience that egg survival and hatching of grass hopper were also affected by the soil condition including soil temperature soil water content salt content and soil texture. These findings agree with Krebs [26] and Carey *et al.* [27], who opined that soil types are crucial determinants in grasshopper oviposition site preference. The effect of different substrates in the oviposition site preference of grasshopper agrees with the effect of different food sources on population parameters as observed in *Helicoverpa armigera* [28], *Plutella xylostella* [29], *Spodopera litura* [30]. The fact that oviposition is curtailed by a lack of suitable substrate suggests that habitat manipulations are a potentially effective tactic to limit this pest's populations.

Table 1. Number of egg pods of grasshopper (mean ± SE) deposited on sandy, loamy and clayey soils.

Substrate/Soil type	Total number of eggs deposited	Mean ± SE
Sandy	338	6.62 ± 4.40a
Loamy	286	5.53 ± 3.96a
Clay	200	3.91 ± 3.85a
		$F = 1.89$; $P = 0.1619$

Means with the same letters are not significantly different from each other at P = 0.05 (SNK).

The total number of days taken to complete oviposition was 16 days in Sandy soil, 15 days in loamy soil and 13 days in clayey soil; and 58%, 44%, and 21% of the nymphs that developed on sandy, loamy and clay soils, respectively, reached the adult stage (**Figure 1**).

The effect of different substrates in the oviposition site preference of grasshopper agrees with the effect of different food sources on population parameters as observed in *Helicoverpa armigera* [28], *Plutella xylostella* [29], *Spodopera litura* [30]. The use of oviposition site preference surveillance is a crucial integrated pest management (IPM) technique in modern agriculture under the current climate change as an eco-friendly and suitable climate smart agriculture (CSA) for sustainable production of crops [31] [32] [33].

3.2. Developmental Parameters

Following the emergence of the nymphs, further development and survival to adult stage of our experimental insect in this study, is given in **Table 2**.

The results showed the influence of oviposition site selection on *Z. variegatus* population growth. The net rate of population growth (R_0) was greater than one, while the intrinsic rate of increase (r_m) and the finite rate of increase (λ) were positive, indicating population growth. The net reproductive rate (R_0) ranged from 1.33 to 3.30 offspring produced per female; with a significantly ($P < 0.05$) highest number of nymphs on sandy soil (3.30 ± 0.00), followed by loamy soil (2.54 ± 0.00), then clay soil (1.33 ± 0.00). The mean generation period (Tc) is the average time taken from when the eggs are laid until the female imago produces half of its offspring [34]. The species of a population with a lower Tc value will experience faster growth compared to population species with a high Tc value [35]. In line with this, the mean generation of *Z. variegatus* that deposited eggs on sandy soil was significantly ($P < 0.05$) the lowest (52.90 ± 0.62) days, compared to the others. The shortest time required for *Z. variegatus* to multiply (Dt) was also found in sandy soil (30.14 ± 9.01) days. The smaller Tc and Dt values indicated that the insects will reproduce and multiply faster. Furthermore, the intrinsic rate of increase (r_m) and finite rate of increase (λ) are influenced by several factors like development time, survivorship, and the overall physiological status of an insect in relation to its capacity to increase [36]. In the present study,

r_m and λ, were significantly (P < 0.05) highest in nymphs that emerged from sandy soil (r_m = 0.023 ± 0.01, λ = 0.063 ± 0.00) as compared to the other substrates. Thus, the variation in the life table and oviposition parameters was due to the soil morphology and characterization. With respect to further survival, the overall survivorship rate was highest in nymphs that emerged from sandy soil as compared to the other two substrates (loamy and clay soils) (**Figure 2**).

Basic information on the biology of an insect pest is necessary before deciding on any strategy to combat the pest [37]. In ecological research, life table study and oviposition site preference are central themes and widely useful techniques in insect pest management, where developmental stages are discrete and mortality rates vary widely from one life stage to another [38] [39] [40].

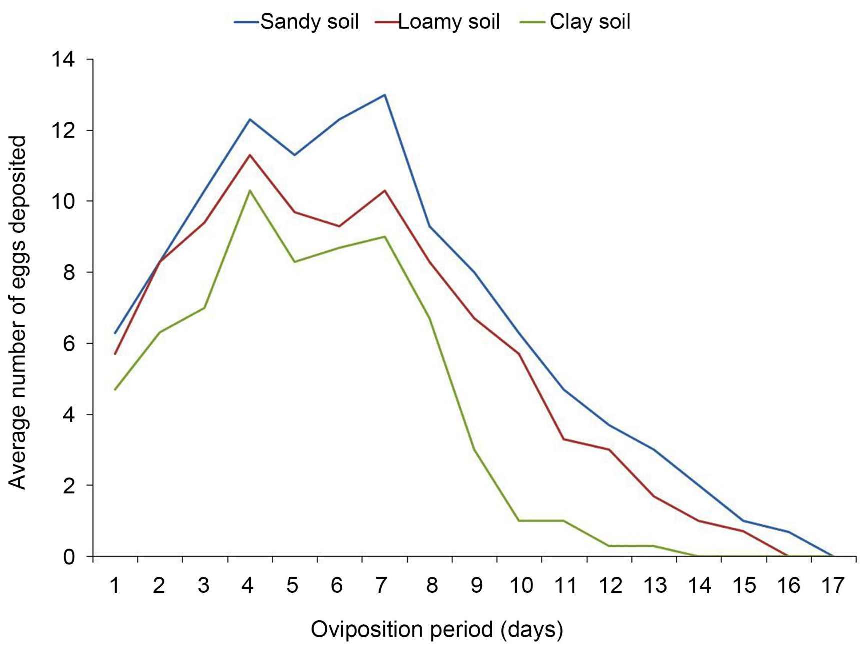

Figure 1. Mean number of eggs of *Z. variegatus* deposited on three different substrates (soil types) during the developmental period.

Table 2. Developmental parameters (mean ± SE) of *Z. variegatus* that emerged from sandy, loamy and clay soils.

Parameter	Soil/Substrate types (Mean ± SE)			*F and P values*
	Sandy	Loamy	Clay	
Net reproductive rate (R_0)	3.30 ± 0.00a	2.54 ± 0.00b	1.33 ± 0.00 c	F = 37400, P = 0.0001
Generation time (Tc)	52.90 ± 0.62c	54.80 ± 0.52b	57.75 ± 0.64a	
Intrinsic rate of increase (r_m)	0.023 ± 0.01a	0.017 ± 0.01b	0.011 ± 0.00c	
Finite rate of increase (λ)	0.063 ± 0.00a	0.036± 0.02b	0.014± 0.00c	
Doubling time (Dt)	30.14 ± 9.01c	40.76± 0.0b	138.64 ± 0.00a	

Means in the same row with the same letters are not significantly different from each other at P = 0.05 (SNK).

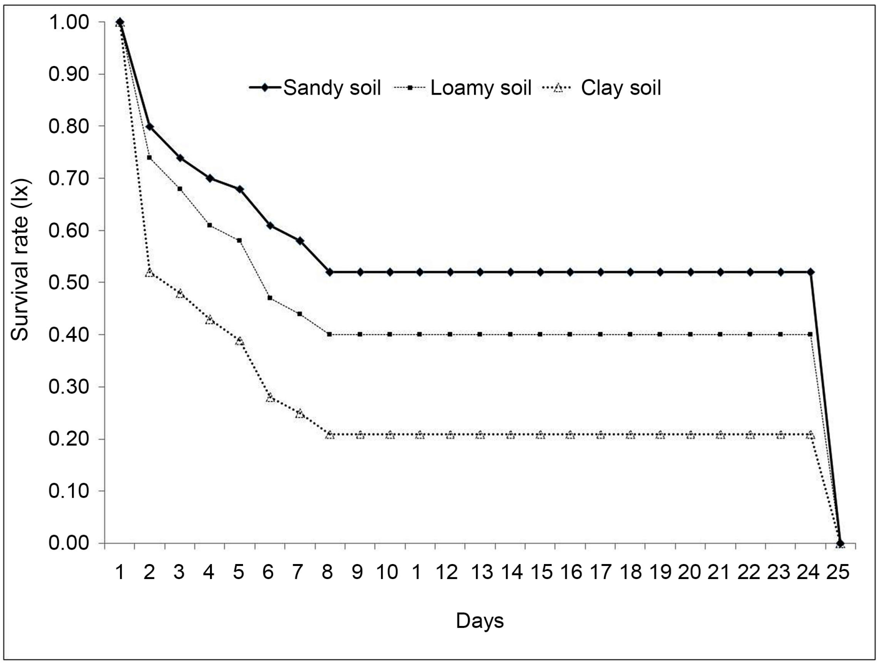

Figure 2. The comparison of survival rate (l_x) of grasshopper immature/nymphs emerging from different soil types (sandy, loamy and clayey soils, respectively).

Maximization of embryo survival necessitates that oviposition sites should minimize predation risk and maintain a microclimate suitable for embryo development. Females that oviposit in terrestrial [41] and aquatic habitats [42] prefer predator-free oviposition sites. Mitchell [43] opined reduced egg survivorship with increased density of eggs on a host plant; while Williams and Gilbert [44] found that early hatched larvae may feed on neighboring conspecific eggs. Thus, plants bearing conspecific eggs are often avoided. Maximization of maternal survival is another determining factor considered in selecting oviposition sites, especially in iteroparous species, where the lifetime reproductive success of a female depends on her survival across periodic breeding events. Proximity to suitable habitat for offspring is another critical criterion for oviposition site selection. Eggs and larval stages of insects are most often vulnerable to predation, desiccation, and/or starvation, thus suitable oviposition habitat is critical. Pöykkö [45] suggested that oviposition sites that provide suitable habitats with the highest nutritional benefits to larvae are selected by female insects. Oviposition-site selection is also done on the basis of an artifact of natal philopatry with females returning to the nest at the same site where they themselves hatched during their development. If oviposition-site choice is heritable, females that oviposit at locations that produce high-quality offspring would pass on this oviposition site choice to their daughters, thereby maintaining a lineage that produces high-quality offspring resulting from oviposition-site choice. Oviposition site choice is indirectly influenced by mate choice since offspring from eggs deposited in high-quality oviposition sites are more likely to be sired by males with high-quality phenotypes [46]. Thus, favorable habitat manipulation strategies are critical for oviposition site preference and the subsequent development of variegated grasshoppers.

4. Conclusion

This study established that soils are highly variable components of the environment that affect the life history traits of *Z. variegatus*. Soil type had significant effects on the survival times and development of nymphal *Z. variegatus*. The *Z. variegatus* insects deposited more eggs in sandy soil > loamy soil > clayey soil, respectively; and subsequent survivorship of the immature unto mature adult insect revealed a similar order. This indicates that the sandy soil is the most preferred substrate for oviposition and subsequent development into adult grasshopper insects. Adult *Z. variegatus* insects demonstrated strong oviposition preferences based on a soil substrate. The composition of the various soil substrates in *Z. variegatus* habitat has the potential to influence the development, survival, and distribution of the insects. Future studies should target exploration of the relationships between variability of soil chemical composition and *Z. variegatus* that would strengthen our understanding of this environmental variable in the ecology of the studied insect. Since the trials of the present study were done in a laboratory setting, future testing should explore how these results translate to *Z. variegatus* in field conditions. Moreover, future studies should consider how soil microbial communities and soil organic matter composition affect the variation in soils in the context of *Z. variegatus* life history traits.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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