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Authors: Riis, Lisbeth, Esbjerg, Peter, and Bellotti, Anthony Charles

Source: Florida Entomologist, 88(1) : 11-22

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/0015-4040(2005)088[0011:IOTASM]2.0.CO;2

INFLUENCE OF TEMPERATURE AND SOIL MOISTURE ON SOME POPULATION GROWTH PARAMETERS OF *CYRTOMENUS BERGI* (HEMIPTERA: CYDNIDAE)

LISBETH RIIS[1,2], PETER ESBJERG[1] AND ANTHONY CHARLES BELLOTTI[2]
[1]Department of Ecology and Molecular Biology
Royal Veterinary and Agricultural University (RVAU), Copenhagen, Denmark

[2]Centro International de Agricultural Tropical (CIAT), Pest and Disease Management Unit
A.A. 6713 Cali, Colombia S.A.

ABSTRACT

Abundance of *Cyrtomenus bergi* Froeschner has been reported regularly under moist and damp conditions. The influence of temperature and soil moisture on development time and mortality of first, third, and fifth instars, longevity and fecundity of *C. bergi* adult females, as well as hatching time and rate of eggs were determined under laboratory conditions at different temperature and soil moisture levels. Population growth is optimal around 26°C (constant temperature) and a soil moisture regime ranging from moist (field capacity) to wet soil (between field capacity and water saturation). Wet soil (~44% gravimetric soil water) promotes high mean fecundity in young adult females, reducing generation time and favoring population growth compared to that seen in moist soil (~33.5% gravimetric soil water, field capacity). The lower temperature threshold for development was 14.7°C. Neither egg hatching nor molting from fifth instars to adults occurred above 31°C. The lower soil moisture threshold for immature development was between dusty (~19% gravimetric soil water) and very dry soil (~22% gravimetric soil water) and between very dry and dry (~25.5% gravimetric soil water, wilting point) for adult female survival and oviposition. Third instars were most tolerant to extreme temperatures. These abiotic limitations to population growth together with other findings concerning host plant regime and movement in soil may explain patterns of local and regional abundance.

Key Words: Subterranean burrower bug, soil arthropod, population growth parameters, *Cyrtomenus bergi*

RESUMEN

Con cierta regularidad se ha reportado la proliferación de *Cyrtomenus bergi* Froeschner en condiciones de humedad. Se determinó, en condiciones de laboratorio, la influencia de diferenctes niveles de temperature y humedad del suleo en la duración del desarrollo y la mortalidad del primer, tercer y quinto instar ninfal, en la longevidad y en la fecundidad de hembras adultas de *C. bergi*, así como en el momento de eclosión y la tasa de eclosión de los huevos. El crecimiento de la población es óptimo alrededor de 26°C (temperatura constante) y un régimen de humedad del suelo que fluctúa entre suelo húmedo (capacidad de campo) y suelo saturado (entre la capacidad de campo y saturación hídrica). Suelo húmedo (~44% de agua gravimétrica del suelo) aumenta la fecundidad promedia de hembras adultas jovenes reduciendo el tiempo de procreación y favoreciendo el crecimiento de la población en el suelo saturado en comparación con el suelo húmedo (~33.5% de agua gravimétrica del suelo, capacidad de campo). El umbral de temperatura más baja para el dasarrollo fue 14.7°C. A partir de los 31°C no hubo eclosión de huevos ni muda del quinto instar a adulto. El umbral de humedad del suelo más bajo para el desarrollo de los estadios inmaduros fue entre suelo polvoriento (~19% de agua gravimétrica del suelo) y suelo muy seco (~22% de agua gravimétrica del suelo) y entre suelo muy seco y suelo seco (~25.5% de agua gravimétrica del suelo, punto de marchitez) para la superviviencia de hembras adultas y la oviposición. El tercer instar presentó la mayor tolerancia frente a las temperaturas extremas. Estas limitaciones abióticas para el crecimiento de la pobación, aunados a otros resultados en cuanto al régimen y movimiento de plantas hospedantes en el suelo pueden explicar los modelos de proliferación local y regional.

Translation provided by the authors.

Cyrtomenus bergi Froeschner is a subterranean burrower bug and polyphagous pest reported on cassava (*Manihot esculenta* Crantz), maize (*Zea Mays* L.), peanut (*Arachis hypogaea* L.), potato (*Solanum tuberosum* L.), sorghum (*Sorghum bicolor* [L.] Moench), welsh onion (*Allium fistulosum* L.), African oil palm (*Elaeis guineensis* Jacq.), coffee (*Coffea* spp. L.), sugarcane (*Saccharum* spp. L.), pasture grasses, and weeds (Bellotti & García 1983; Lacerda 1983; Herrera 1988). Since the first

description of *C. bergi* as a pest on cassava (CIAT 1980), it has become a serious problem throughout the neo-tropics (Arias & Bellotti 1985).

C. bergi feeds on roots, tubers, or subterranean fruits (e.g., peanuts) of host plants. The bug injects its stylet in the subterranean plant tissue leaving lesions that facilitate the entrance of soil pathogens such as *Fusarium*, *Aspergillus*, *Genicularia*, and *Pythium* (CIAT 1980). On peanut kernels, lesions appear as delimited dry rot spots (approximately 1-2 mm diameter), and a heavy attack can cause complete deterioration of the kernels (personal observation). On cassava roots, tissue degradation (approximately 5 mm diameter) appears on the interior white starchy and edible parenchyma 12-24 h after feeding is initiated (García 1982).

All immature stages and the imago of *C. bergi* live in the soil. Oviposition also takes place there. The five instars and the adults feed on the same host spectrum leaving similar damage symptoms. Riis et al. (2005) found that *C. bergi* has a total average life span of 380 d when feeding on peanut, 324 d when feeding on sweet cassava and 290 d when feeding on maize (25°C and 65 ± 5% RH).

The data base of *C. bergi* collections at Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia, includes collections from the northwestern part of the South American continent, with the majority (62%) reported from altitudes of 1000-1700 meters above sea level with average monthly rainfall above 85 mm throughout the year, and average monthly temperature ranges from 20-21°C (unpublished). Several reports indicate a relation between abundance of *C. bergi* and humid conditions. Clavijo (1981) showed an increased number of *C. bergi* in light traps during periods of high precipitation, and Riis (1990) observed increased cassava root damage due to *C. bergi* following increased precipitation. Cividanes et al. (1981) also related fluctuations of *C. bergi* captures to weather factors, and King and Saunders (1984) state that *C. bergi* is more frequently found under damp conditions. Highland and Lummus (1986) suggest that soil moisture and rainfall are crucial factors increasing populations of the burrower bug *Pangaeus bilineatus* (Say), also Cydnidae.

A laboratory experiment was conducted to determine the influence of temperature and soil moisture on development time and mortality of first, third, and fifth instars, longevity and fecundity of *C. bergi* adult females as well as hatching time and hatching rate of eggs. Since *C. bergi* has a very long lifecycle, second and fourth instars were left out of the experiment to reduce time.

Materials and Methods

Stock Colony

Cyrtomenus bergi was taken from a stock laboratory colony (23 ± 2°C, 65 ± 5% RH, 12 h light) maintained on germinating seeds of peanuts, *Arachis hypogaea* L. (variety 'Tatui SM-76') in unsterilized topsoil (loamy clay) kept at a moisture level approximated to the field capacity (33.5% gravimetric soil water). The colony originated from a fallow field at La Bella, Rereira (Province of Risaralda), Colombia and had been maintained in culture for one generation.

Experimental Soil

Soil of the Ah-horizon, 0-18 cm, from the CIAT Field Research Station at Santander de Quilichao in southern Colombia was used. The soil is described as a loamy clay with high content of organic matter (16.4 kg organic C/m^3) (Reining 1992) and pH ranging 4.0-5.2 (Riis 1990). The soil was passed through an M-4 hammer mill shredder (Lindig Mfg Corp., St. Paul, MN) to assure homogeneous water penetration of soil when irrigated in the laboratory.

Water retention characteristics of the experimental soil were determined on air-dried soil samples. Water content was measured at saturation (0 bar), field capacity (0.33 bar), wilting point (15 bar), and hygroscopic moisture (>32 bar) with a pressure plate apparatus (Soil Moisture Corp., Goleta, CA). The water-saturated samples were weighed and placed in plastic rings on porous ceramic plates, permeable to water. Samples were weighed when the state of equilibrium was reached, oven dried for 24 h at 105°C and reweighed. This was repeated three times for each sample. Water contents were calculated at the different pressures (Richards 1965; Scheffer & Schachtschabel 1989). A retention curve for this experimental homogenized soil could not be calculated, since we could not approximate empirical constants that affect the shape of the retention curve (Genuchten et al. 1991).

The experimental soil was desiccated at 60°C for 72 h. Subsequently, soil was placed in plastic containers, weighed, and irrigated while placed on a scale until the experimental soil water content was reached. The irrigated soil was left in closed containers for 48 h prior to use. Before use, three soil samples were taken to reconfirm the water content by weighing, drying (105°C, 24 h), and weighing again. After exposure to the bugs for 2 d (immature stages) and one week (adults), respectively, three soil samples were taken from each experimental temperature and moisture combination to record changes in soil water content during the experimental time.

Experimental Temperature Levels

Egg eclosion time and rate as well as development time and mortality of first, third, and fifth instars were assessed in temperature controlled incubators (65 ± 5% RH, 12 h light) at moisture levels that approximated wilting point (25.9% gravimetric soil water) and field capacity (33.5%

gravimetric soil water), respectively, and at the following constant temperatures (±1.5°C): 13°C, 18°C, 21°C, 23°C, 25°C, 28°C, and 31°C. Fecundity and longevity of post-teneral females of *C. bergi* were assessed under similar conditions, but only at 13°C, 21°C, 25°C, and 31°C.

Experimental Soil Moisture Levels

Eclosion time and rate of eggs, development time and mortality of first, third, and fifth instars as well as fecundity and longevity of post-teneral females of *C. bergi* were assessed in a temperature and light controlled incubator, 25 ± 1.5°C, 65 ± 5% RH, 12 h light, at the following approximated soil moisture levels of gravimetric soil water: 19.0% (dusty), 22.0% (very dry), 25.9% (dry, wilting point), 33.5% (moist, field capacity), 44.0% (wet), and 60.0%, (water saturated). The soil water content of the experimental soil was measured immediately before and after use.

Experimental Diet

The bugs fed on peanut kernels of which embryos had been removed to avoid water-consuming germination. The peanuts were wrapped in Parafilm® to avoid rapid deterioration.

Development Time and Mortality of Immature Stages

For the determination of the egg hatching time and rate, recently deposited eggs (<16 h) were recovered from soil exposed to adults by searching the soil carefully with a fine paintbrush. Each of four non-simultaneous replications comprised 50 eggs placed in groups of 25 in each of two 55-cm^2 opaque plastic vials with approximately 30 cm^3 of soil of the experimental moisture level. Egg hatch was observed daily beyond 7 d after oviposition and soil also was replaced daily. Hatching time and rate (percentage) were recorded.

Development time and mortality of first, third, and fifth instars were determined as follows: Recently emerged first instars (<16 h) were recovered from eggs placed on moist filter paper. Third and fifth instars were recovered at ecdysis (<16 h hereafter) from separate stock colonies exclusively containing second and fourth instars, respectively. Nymphs were placed individually in approximately 30 cm^3 of soil of each of the experimental moisture level in opaque plastic vials (55 cm^3 volume). Each of four non-simultaneous replications comprised 20 nymphs. Every 2 d, the plant diet and soil of experimental moisture levels were renewed after the soil of each plastic-vial had been searched for exuviae from molting nymphs. Development time and percent mortality were recorded for each instar. Each insect was withdrawn from the experiment at the time of molting or death.

Optimal Temperature for Immature Development

The optimal temperature for development of each of the immature stages was found by fitting a quadratic model (Hyams 1997) to hatching time/development time weighted against temperature. The temperature corresponding with the minimum development time of the curve was recorded as the optimal temperature for development.

Lower Temperature Thresholds and Day-Degrees Required for Development of Immature Stages

Lower temperature thresholds (T_0) for development of immature stages were estimated by linear regression on the reciprocal mean development time (y) weighted against temperature (T)

$$y = \alpha + \beta T$$

and T_0 was subsequently computed as

$$T_0 = -\frac{\alpha}{\beta}$$

Development time on a day-degree (DD) time scale was computed as

$$DD = DT(T - T_0) \text{ for } T > T_0, \text{ else } DD = 0,$$

where DT denotes the observed development time (days) at the temperature T (Frazer & Gilbert, 1976).

Female Longevity and Fecundity

Fecundity and adult female longevity of 25 females were assessed at each of the aforementioned experimental temperatures and soil moisture levels. Adults were recovered at ecdysis (<16 h hereafter) from a separate stock colony exclusively containing fifth instars. One female and two males were placed in approximately 50 cm^3 soil in an opaque plastic vial (55 cm^3 volume). Adults were transferred to a new plastic vial with new soil every week, female survival was recorded and the food diet was replaced at the same time. Dead males were replaced with males from the stock colony. The number of deposited eggs was counted every two weeks by flotation in a 20% salt solution of sodium chloride (Matteson 1966).

Statistics

An analysis of variance and subsequent REGWQ grouping (SAS Institute 1988) were run separately on each of the studied immature stages on development time and mortality, on adult female longevity, and area under the m_x-curve (fecundity weighted with time) for comparison of experimental abiotic conditions. A natural logarithm transformation was used to homogenize error of female longevity and area under the

mx-curve. The transformed data were re-tested for homogeneity by use of Taylor's Power Law:

$$s^2 = a + \bar{x}^b$$

The null hypothesis H_o: b = 0 was accepted for all transformed variable confirming homogeneity of error.

Results

Experimental Soil Moisture Characteristics

The water retention characteristics of the experimental soil are given in Table 1. Changes in soil moisture level during the experimental time are listed in Table 2. Soil moisture levels differed significantly before and after exposure to immature stages (soil replaced every 2 d) and adults (soil replaced weekly) at 25°C (see rows; Table 2). With the exception of dusty soil, the soil water content was reduced significantly by increasing temperature due to evaporation (see columns; Table 2).

Development Time and Mortality of Immature Stages as a Function of Temperature

The optimal temperature for hatching of eggs was 25.7°C. The optimal temperature for development of the first instars was 28.5-29.7°C, and 26.4°C for third and fifth instars. Third instars could develop at 13°C where other stages failed (Fig. 1).

The lower temperature threshold was 14.6°C for eggs compared with 13.7°C for first and fifth instars and 11.3°C for third instars (Table 3). If we assume that the lower temperature threshold for each nymphal instar is the same at field capacity and wilting point (*cf.* Table 3), a comparison between wilting point and field capacity of the development time on a day-degree scale of each instar showed that the development times of first and third instars on a day-degree scale were significantly longer at wilting point than at field capacity ($8.67 < F < 20.76$, $df = 6$, $P < 0.0258$) (*cf.* Table 3).

Development time and mortality decreased with temperature within the temperature regime 18-25°C (Fig. 1). The highest egg hatching rate ('inverse mortality') occurred at 25°C and no hatching occurred at 31°C. The lowest mortality of first and fifth instars occurred at 25°C, and at 28°C for third instars (Fig. 1). At temperatures where egg hatching and ecdysis of nymphs occurred, mortality did not differ significantly between wilting point and field capacity.

Exceptionally long survival times occurred at the extreme temperatures. At 13°C, below the lower temperature threshold of eggs, the mean survival time of first instars until death was 24 d (SE ± 2.98) at wilting point and 35 d (SE ± 3.86) at field capacity. The mean survival time of fifth instars until death at 13°C was 230 d (SE, ± 16.6) at wilting point and 232 d (SE, ± 13.9) at field capacity. Fifth instars could not molt at 31°C and the mean survival time of fifth instars until death at 31°C was 60 d (SE, ± 2.05) at wilting point and 69 d (SE, ± 2.27) at field capacity.

TABLE 1. GRAVIMETRIC SOIL WATER CONTENT (%) OF THE EXPERIMENTAL SOIL UNDER DIFFERENT PRESSURES (BAR).

Soil moisture level	Bar	%
Hygroscopical moisture	>32	9.9 ± 2.76
Wilting Point (WP)	15	25.9 ± 0.17
Field Capacity (FC)	0.3	33.5 ± 0.16
Saturation	0	70.2 ± 1.01

Values are means of 3 replications ± standard errors.

Development Time and Mortality of Immature Stages as a Function of Soil Moisture

Cyrtomenus bergi developed at a wide range of soil moisture levels with the exception of dusty soil. Egg hatching did not occur in very wet soil (Fig. 2). Egg hatching time was significantly shorter (by 1 d) in moist and wet soil than that in very dry soil ($F = 2889$, $df = 18$, $P < 0.0001$), and the hatching time in dry soil did not differ from any of these. The highest egg hatching rates ('inverse mortality', Fig. 2) occurred in the moisture range from dry soil (wilting point) to moist soil (field capacity) (inclusive), and were significantly higher than those in wet soil. Hatching rates in wet soil were higher than those in very dry soil ($F = 395.9$, $df = 18$, $P < 0.0001$).

Development times of nymphs (Fig. 2) did not differ significantly above wilting point (dry soil), and these were shorter than those below wilting point ($24.76 < F < 68.16$, $df = 18$, $P < 0.0001$). At all temperature levels, the development of the first instars was slightly prolonged at wilting point compared with field capacity (*cf.* Fig. 1), but these did not differ significantly. The lowest mortality of the first instars occurred in moist soil (Fig. 2) and was significantly lower than those in very wet and very dry soil ($F = 20.38$, $df = 18$, $P < 0.0001$). The lowest mortality of third and fifth instars occurred in soil moisture regime from dry (wilting point) to wet soil (Fig. 2), which did not differ significantly, and these were lower than that in very dry soil ($32.40 < F < 57,32$, $df = 18$, $P < 0.0001$).

Female Longevity and Survival by Age as a Function of Temperature

Recorded female longevity was longest at 21°C, but did not differ significantly from those at 25°C and that at 13°C at field capacity (Fig. 3a). Female survival by age (L_x) showed little mortality until

TABLE 2. SOIL WATER CONTENT (%, GRAVIMETRIC) OF EXPERIMENTAL SOIL MOISTURE LEVELS; INITIALLY AND AFTER EXPOSURE TO *C. BERGI* AT DIFFERENT TEMPERATURES.

	Soil water content (%, gravimetric)							
							ANOVA[e]	
Soil samples taken at . . .	Dusty	Very dry	Dry (WP[a])	Moist (FC[b])	Wet	Very wet	*df*	*F*
Initially	18.7 ± 0.22 a[c]A[d]	22.0 ± 0.11 aB	25.5 ± 0.08 aC	34.3 ± 0.08 aD	44.1 ± 0.22 aE	61.2 ± 0.22 aF	2714	9263****
13°C	—	—	25.2 ± 0.11 a	33.1 ± 0.10 b	—	—		
18°C	—	—	25.1 ± 0.10 a	32.9 ± 0.08 b	—	—		
21°C	—	—	24.5 ± 0.08 b	32.3 ± 0.09 c	—	—		
23°C	—	—	24.2 ± 0.17 bc	31.7 ± 0.12 d	—	—		
25°C	18.3 ± 0.54 aA	20.5 ± 0.21 bB	24.1 ± 0.07 bcC	31.5 ± 0.28 dD	42.3 ± 0.35 bE	58.7 ± 0.27 bF	790	4326****
28°C	—	—	23.8 ± 0.24 cd	31.5 ± 0.16 d	—	—		
31°C	—	—	23.4 ± 0.12 d	30.7 ± 0.28 e	—	—		
ANOVA[e]								
df	29	366	3249	2956	305	313		
F	0.75 NS	49.02****	51.35****	104.86****	17.08****	32.33****		

Values are means ± standard errors.
[a]WP denotes approximated wilting point.
[b]FC denotes approximated field capacity.
[c]REGWQ-grouping: Means with the same lower-case letter in the same column are not significantly different.
[d]REGWQ-grouping: Means with the same capital letter in the same row are not significantly different.
[e]**** denotes $P < 0.0001$; ns, not significant.

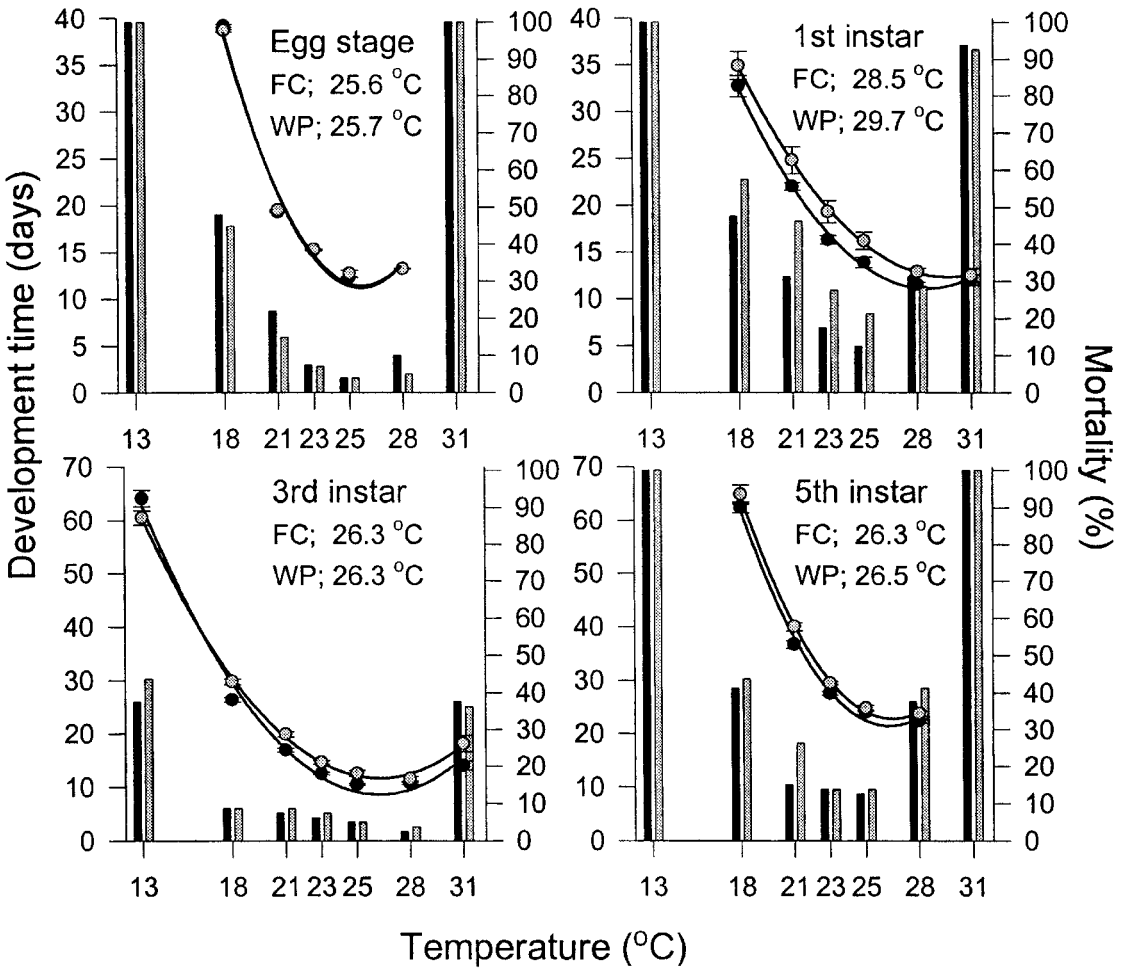

Fig. 1. Development time (dots, left axis) and mortality (bars, right axis) of some immature stages of *C. bergi* as a function of temperature and soil moisture levels approximated to field capacity (FC, black) and wilting point (WP, grey). Optimum temperatures are given at field capacity and wilting point, respectively. Dots are means and bars are percentage of 200 eggs and 80 individuals of each instar, respectively. Vertical lines denote standard errors.

approximately 180 d and then fairly steep mortality thereafter, with exception of extreme temperatures, 13°C and 31°C (Fig. 4a). Initially female survival by age (L_x) started declining more steeply at 13°C than at 31°C, both at wilting point. Nevertheless, after approximately 40 d, female survival at 13°C at wilting point declined slowly, while female survival at 31°C at wilting point declined rapidly and the population died out soon after (Fig. 4a).

Female Longevity and Survival by Age as a Function of Soil Moisture

Adult female longevity was shorter in very dry soil than at other soil moisture levels (F = 144.7, df = 120, $P < 0.0001$), which did not differ significantly from each other (Fig. 3b). Longevity did not differ significantly between field capacity and wilting point at 21-25°C. At more extreme temperatures, 13°C and 31°C, females lived longer at field capacity than at wilting point (F = 35,97, df = 192, $P < 0.0001$) (Fig. 3a).

At all soil moisture conditions female survival by age (L_x) showed little mortality until approximately 180 d and then fairly steep mortality thereafter, with exception of very dry soil in which females died out after 56 d only (Fig. 4b).

Fecundity as a Function of Temperature

Total fecundity differed significantly between temperature levels (F = 87.40, df = 192, $P < 0.0001$). It was highest at 21°C and 25°C and did not differ significantly between these two temperature levels (Fig. 3a). All females deposited eggs at 21°C and 25°C at field capacity. Between 84-92%

TABLE 3. ESTIMATION OF LOWER TEMPERATURE THRESHOLDS (T_0) AND DEVELOPMENT TIME ON A DAY-DEGREE (*DD*) SCALE OF IMMATURE STAGES OF *C. BERGI* FEEDING ON PEANUT AT APPROXIMATED SOIL MOISTURE LEVELS OF FIELD CAPACITY (FC) AND WILTING POINT (WP), RESPECTIVELY.

Instar	Soil moisture level	*n*	Regression	r^2	*P*	T_0	*DD*[a]
Egg	FC	200	$y = -0.1160 + 0.0077T$	0.998	0.0012	14.7	126.9 ± 1.75
	WP	200	$y = -0.1092 + 0.0076T$	0.996	0.0020	14.4	132.9 ± 2.21
1	FC	80	$y = -0.0939 + 0.0069T$	0.980	0.0099	13.7	153.0 ± 4.29
	WP	80	$y = -0.0798 + 0.0061T$	0.996	0.0020	13.2	186.1 ± 5.86
3	FC	80	$y = -0.0790 + 0.0069T$	0.971	0.0021	11.4	155.5 ± 7.27
	WP	80	$y = -0.0647 + 0.0058T$	0.954	0.0043	11.1	188.1 ± 8.35
5	FC	80	$y = -0.0525 + 0.0038T$	0.997	0.0018	13.7	265.8 ± 3.08
	WP	80	$y = -0.0515 + 0.0037T$	0.997	0.0018	13.9	274.4 ± 4.00

n, sample size.
[a]Values are means ± standard errors.

females deposited eggs at 21°C and 25°C at wilting point, and at 31°C at field capacity. Only 8-12% of females deposited eggs at 31°C at wilting point and at 13°C at both wilting point and field capacity (Fig. 3a), resulting in less than 0.25 eggs per female on average. At 31°C females deposited significantly more eggs at field capacity than at wilting point.

At all soil temperature and soil moisture combinations, with mean fecundity per female >1, mean fecundity by age (M_x) showed a small peak after approximately 40-55 d and a large peak after approximately 180-210 d (Fig. 5a, b), with exception of 31°C at field capacity where only one peak occurred after 112 d (Fig. 5a).

Fecundity as a Function of Soil Moisture

Total fecundity differed between soil moisture levels ($F = 51.39$, $df = 120$, $P < 0.0001$) (Fig. 3b). Most eggs were deposited in moist (field capacity) and wet soil, and significantly fewer eggs were deposited in very wet soil. Number of eggs deposited in dry soil was intermediate and did not differ significantly from moist, wet or very wet soil. No eggs were deposited in very dry soil.

All females oviposited in moist soil (field capacity). Between 84-92% of the females oviposited in wet, very wet and dry (wilting point) soil (Fig. 3b). No females oviposited in very dry soil.

Mean fecundity by age (M_x) in wet soil was high during early age of female lifespan until its large peak at approximately 182 d, and coincided thereafter with those of moist and dry soil (Fig. 5c). Mean fecundity by age in very wet soil was inferior to those of other soil moisture levels with mean fecundity per female >1.

DISCUSSION

The optimal temperature for development of first instars was 28-29°C and 26°C for other instars. The optimal temperature for the adult stage could not be determined from the few temperature levels tested, but it is likely to be within the range of that for development. Due to the lack of parameters for second and fourth instars, we could not calculate population increase rates.

In general, the development of *C. bergi* was limited to a temperature regime ranging between 14.7°C and just below 31°C. Egg hatching could not occur at 31°C. Fifth instars lived longer at 31°C than at any other temperatures above the lower temperature threshold, but were unable to molt. At high temperature, 31°C, both fecundity and longevity were reduced compared with the 21-25°C temperature regime indicating that the upper temperature threshold was between 25 and 31°C. The third instar is the most robust instar, showing high tolerance to extreme temperature conditions.

The optimal soil moisture level for development of immature stages was moist soil (field capacity) and moist to wet soil for the adult stage. The high mean fecundity in the early age of the female lifespan in wet soil reduces the generation time and favors population growth in wet soil over moist soil. Female longevity was not reduced in very wet soil, but the number of oviposited eggs was significantly less. *Cyrtomenus bergi* did not tolerate extremely dry conditions. Very dry soil reduced longevity of adult females significantly and no eggs were deposited.

Villani and Wright (1990) speculate that heavily sclerotized soil insects should be less vulnerable to moisture loss of the cuticle under dry conditions. We, on the contrary, found that the heavily sclerotized *C. bergi* adults were more sensitive to drought than less sclerotized immature stages. The lowest soil moisture threshold for adult survival and oviposition was just below dry soil (~25.5% gravimetric soil water, wilting point), whereas the lowest soil moisture threshold for the

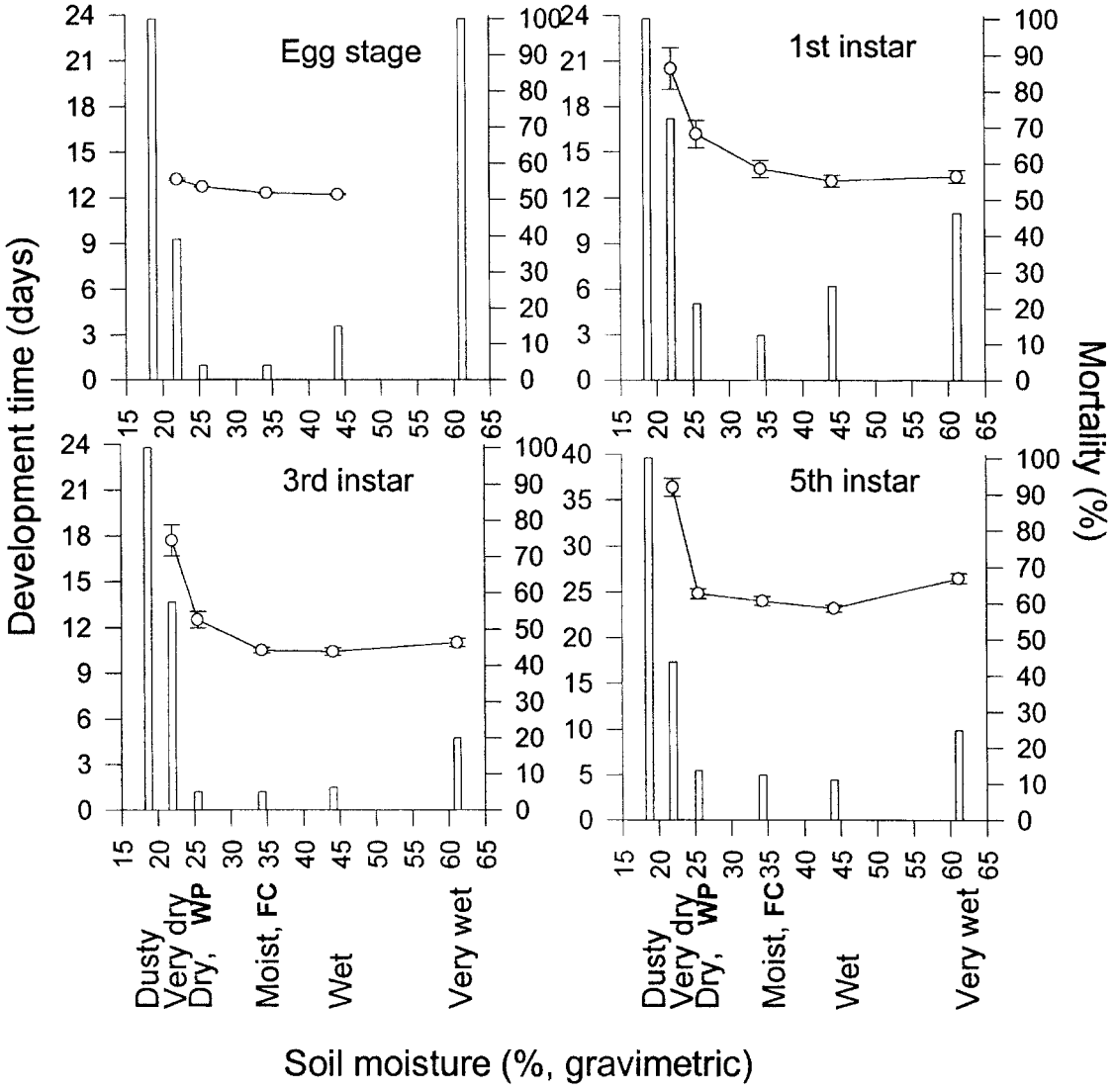

Fig. 2. Development time (dots, left axis) and mortality (bars, right axis) of some immature stages of *C. bergi* as a function of soil moisture levels and 25°C. WP and FC denote soil moisture levels approximated wilting point and field capacity, respectively. Dots are means and bars are percentage of 200 eggs and 80 individuals of each instar, respectively. Vertical lines denote standard errors.

development of immature stages was just below very dry soil (~22% gravimetric soil water). Despite the lower soil moisture threshold for immature stages compared with adults, young nymphal stages (first and third instars) did undergo some stress in dry soil as the development time on a day-degree scale was significantly longer at wilting point than at field capacity.

Although the total fecundity did not differ significantly between field capacity and wilting point within the temperature regime 21-25°C, during the initial female adult age (<150 d), we observed a higher mean fecundity at wilting point than at field capacity at 21°C opposite of what was observed at 25°C. Otherwise, soil moisture ranging from wilting point to field capacity played a significant role only for the adult stage at extreme temperatures, 13°C and 31°C. At high temperature (31°C), both total fecundity and female longevity was significantly reduced at wilting point compared to field capacity. At low temperature (13°C), longevity, but not fecundity, was significantly reduced at wilting point compared to field capacity.

Our experimental design of leaving each female individually with two males, to assure suc-

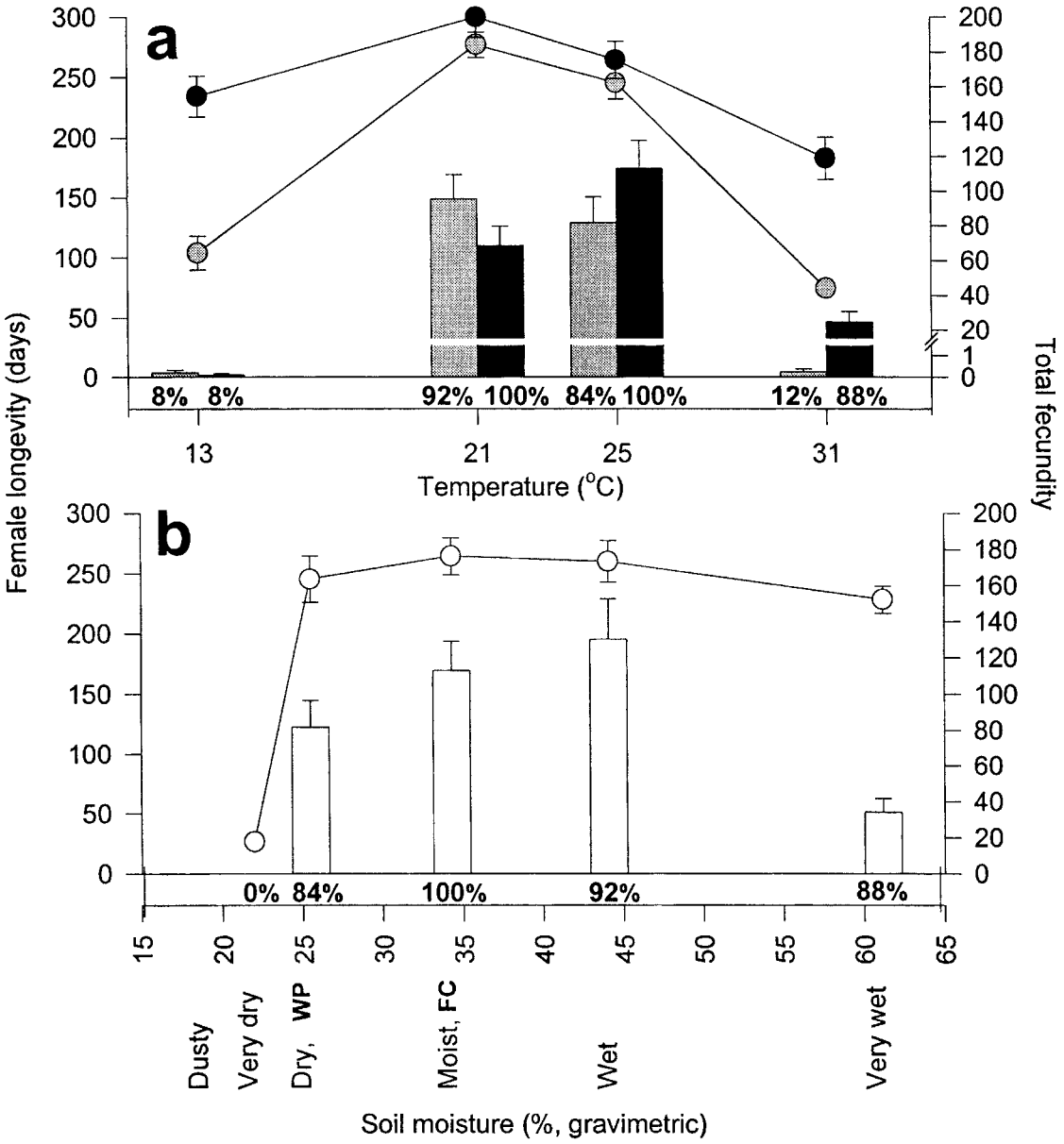

Fig. 3. Means of female longevity (dots, left axis) and total fecundity (bars, right axis) of 25 females of *C. bergi* as a function of (a) temperature at approximated field capacity (black symbols and bars) and wilting point (grey symbols and bars), and as a function of (b) soil moisture at 25°C. WP and FC denote soil moisture levels approximated wilting point and field capacity, respectively. Percentages of females ovipositing are given in bold numbers below bars. Vertical lines denote standard errors.

cessful copulation, apparently disturbed the oviposition of the female. Fewer eggs were recovered in this design compared to previous studies (Riis et al. 2005) with the same host plant and the same methodology for egg recovery, but only one male per female. The present design did not reflect the 1:1 sex ratio found in the field (Riis et al. 2005). Providing a diet of dry peanut kernels instead of germinating kernels as Riis et al. (2005) might also have influenced the ovipositional rate.

This is the first study reporting effects of soil moisture on subterranean Hemiptera. It is worth noticing that the effect of soil moisture on population growth parameters of subterranean arthropods differ remarkably among orders, for example white grubs (Cherry et al. 1990; Potter

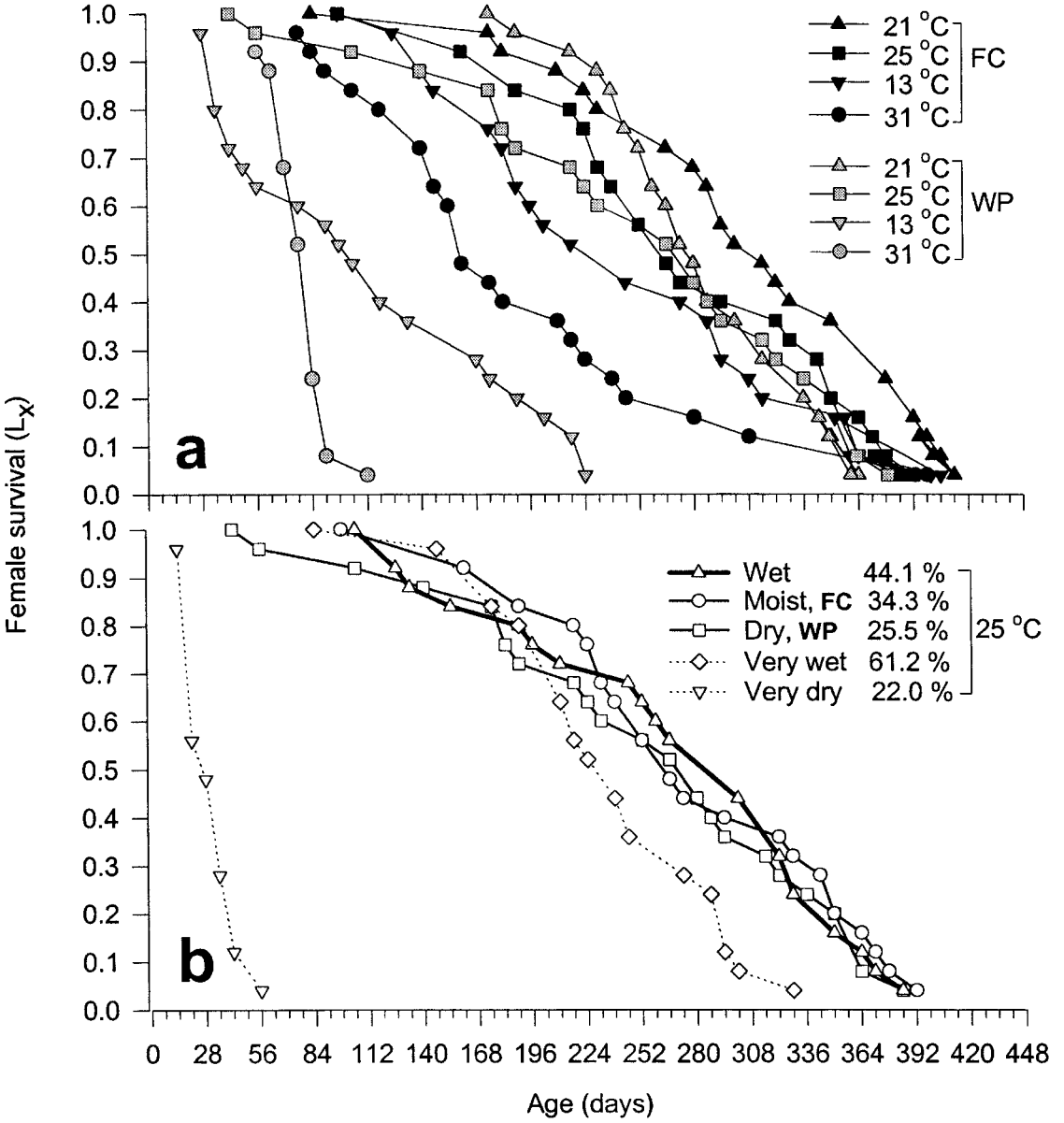

Fig. 4. Survival of 25 females of *C. bergi* during their life span as a function of (a) temperature at soil moisture levels approximated field capacity (FC, black symbols) and wiling point (WP, grey symbols), respectively, and as a function of (b) soil moisture levels (%, gravimetric) at 25°C.

1983; Règinière et al.1981), larvae of Chrysomelidae (Brust & House 1990; Lummus et al. 1983; Macdonald & Ellis 1990; Marrone & Stinner 1984), Curculionidae (Dowd & Kok 1983), and cutworms (Esbjerg 1989).

The above results, together with previous findings on active horizontal movement of *C. bergi* towards moist and wet soil, vertical emigration away from very dry soil conditions (Riis & Esbjerg 1998), and host plant regimes (Riis et al. 2005) may explain patterns of local and regional abundance.

Supported by our findings, we can conclude that *C. bergi* is well adapted for moist soil conditions, which explains its regional as well as local distribution. Moist soil conditions and a history of *C. bergi* infestation require monitoring of *C. bergi* in growers' fields and preventive treatment during early infestation.

Antagonistic soil pathogens and nematodes, which also favor moist conditions, such as the entomophilic fungi, *Metarhizium anisoplia*, and the nematodes, *Steinernema carpocapse* and *Hetero-*

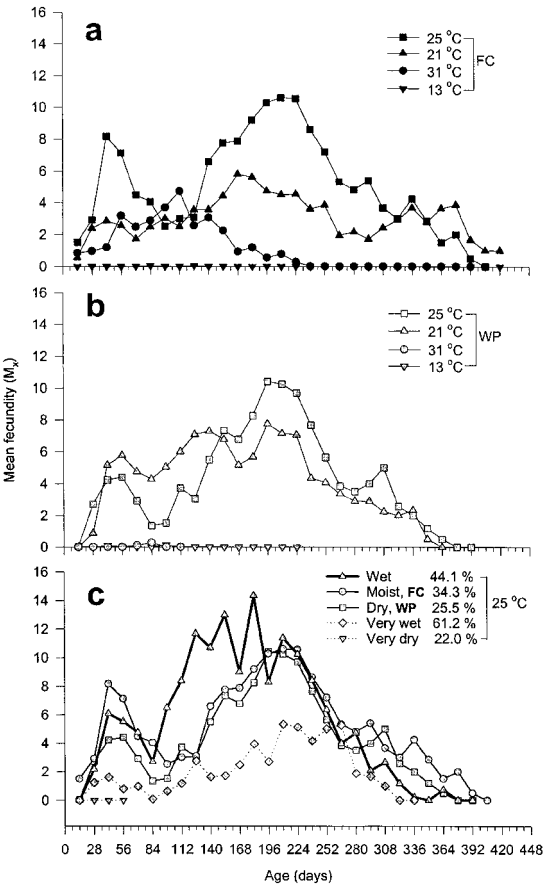

Fig. 5. Fecundity of 25 females of *C. bergi* through their life span as a function of (a) temperature at soil moisture levels approximated field capacity (FC, black symbols) and (b) wilting point (WP, grey symbols), respectively, and as a function of (c) soil moisture (%, gravimetric) at 25°C.

rhabditis bacteriophora, effectively infect *C. bergi* under laboratory conditions (Barberena 1996; Caicedo & Bellotti 1994; Sanchez 1996). Reproduction and infection rates of these differ significantly between strains depending on their climatic origin and thermal niches (Grewal et al. 1994; Kung et al. 1991; McCammon & Rath 1994). Studies for the control of *C. bergi* with such bioagents should therefore include considerations of the influence of abiotic conditions on *C. bergi*, the bio-agent strains, and their interactions.

ACKNOWLEDGMENTS

We are grateful to Héctor Morales and Gerardino Pérez (Pest and Disease Management Unit, CIAT), who assisted this work in the laboratory and to Miguel Barona (Department of Soil Physics, Universidad Nacional, Palmira, Colombia), who facilitated data on soil water retention. This project was funded by the Danish International Development Agency (Danida) and hosted by the Pest and Disease Management Unit at Centro Internacional de Agricultura Tropical in Colombia.

REFERENCES CITED

ARIAS, B., AND A. C. BELLOTTI. 1985. Aspectos ecológicos y de manejo de *Cyrtomenus bergi* Froeschner, chinche de la viruela en el cultivo de la yuca (*Manihot esculenta* Crantz). Rev. Colombiana Entomol. 11: 42-46.

BARBERENA, M. A. 1996. Capacidad Parasítica de dos Razas del Nematodo *Heterorhabditis bacteriophora* Poinar (Rhabditida: Heterorhabditidae) Sobre la Chinche de la Viruela de la Yuca *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae) en condiciones de laboratorio. B.Sc. Thesis, Universidad de Valle, Cali, Colombia.

BELLOTTI, A. C., AND C. A. GARCÍA. 1983. The subterranean Chinch Bug, a new pest of cassava. Cassava Newsletter 7: 10-11.

BRUST, G. E., AND G. J. HOUSE. 1990. Effects of soil moisture, texture, and rate of soil drying on egg and larval survival of the southern corn rootworm (Coleoptera: Chrysomelidae). Environ. Entomol. 19: 697-703.

CAICEDO, A. M., AND A. C. BELLOTTI. 1994. Evaluación del potencial del nematodo entomógeno *Steinernema carpocapse* Weiser (Rhabditida: Steinernematidae) para el control de *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae) en condiciones de laboratorio. Rev. Colombiana Entomol. 20: 241-246.

CHERRY, R. H., F. J. COALE, AND P. S. PORTER. 1990. Oviposition an survivorship of sugarcane grubs (Coleoptera: Scarabaeidae) at different soil moistures. J. Econ. Entomol. 83: 1355-1359.

CIAT. 1980. Cassava Program Annual Report. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia.

CIVIDANES, F. J., S. SILVEIRA, AND P. S. MACHADO. 1981. Flutuação populacional de cidnídeos coletados em regiões cana cieiras de São Paulo. Científica, São Paulo 9: 241-247.

CLAVIJO, S. 1981. Variaciones estacionales de poblaciones de adultos de *Spodoptera frugiperda Cyrtomenus bergi* en cinco localidades de los alrededores del lago de Valencia, medidas mediante trampas de luz. Revista de la Facultad de Agronomía (Maracay) 12: 63-79.

DOWD, P. F., AND L. T. KOK. 1983. Influence of soil conditions on *Carduus* thistles and development of the thistle head weevil, *Rhinocyllus conicus* (Coleoptera: Curculionidae). Environ. Entomol. 12: 439-441.

ESBJERG, P. 1989. The influence of soil moisture on mortality and on the damaging effect of second and 6th instar cutworms (*Agrotis segetum* Schiff, Lep.: Noctuidae). Acta Ecol./ Ecol. Appl. 10: 335-347.

FRAZER, B. D., AND N. GILBERT. 1976. Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). J. Entomol. Soc. British Columbia 73: 33-56.

GARCÍA, C. A. 1982. Biología y Morfología de *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae), Nueva Plaga de la Yuca. B.Sc. Thesis, Universidad Nacional de Colombia, Palmira, Colombia.

GENUCHTEN, M. TH. VAN, F. J. LEIJ, AND S. R. YATES. 1991. The RETC code for quantifying the hydraulic functions of unsaturated soils. USDA, Riverside, CA.

GREWAL, P. S., S. SELVAN, AND R. GAUGLER. 1994. Thermal adaptation of entomopathogenic nematodes:

niche breadth for infection, establishment, and reproduction. J. Thermal Biol. 19: 245-253.

HERRERA, J. G. 1988. Reconocimiento y manejo de la chinche subterránea *Cyrtomenus bergi* Froeschner en cultivos de 'Cebolla de rama' en Pereira. Instituto Colombiano Agropecuario (ICA), Pereira, Colombia.

HIGHLAND, H. B., AND P. F. LUMMUS. 1986. Use of light traps to monitor flight activity of the burrower bug, *Pangaeus bilineatus* (Hemiptera: Cydnidae), and associated field infestations in peanuts. J. Econ. Entomol. 79: 523-526.

HYAMS, D. 1997. CurveExpert 1.34. Starkville, MS. Web:http://www.ebicom.net/~dhyams/ cvxpt.htm.

KING, A. B. S., AND J. L. SAUNDERS. 1984. The invertebrate pests of annual food crops in Central America. Overseas Development Administration (ODA), London, UK.

KUNG, S. P., R. GAUGLER, AND H. K. KAYA. 1991. Effects of soil temperature, moisture, and relative humidity on entomopathogenic nematode persistence. J. Invertebrate Pathol. 57: 242-249.

LACERDA, J. I. 1983. Dano causados au dendê (*Elais guineesis*) por ação do *Cyrtomenus bergi* (Froeschner, 1960) (Hemiptera: Cydnidae). Rev. Floresta (Brazil) 14: 59-60.

LUMMUS, P. F., J. C. SMITH, AND N. L. POWELL. 1983. Soil moisture and texture effects on survival of immature southern corn rootworms, *Diabrotica undecimpunctata howardi* Barber (Coleoptera: Chrysomelidae). Environ. Entomol. 12: 1529-1531.

MACDONALD, P. J., AND C. R. ELLIS. 1990. Survival time of unfed first-instar Western Corn Rootworm (Coleoptera: Chrysomelidae) and the effects of soil type, moisture, and compaction on their mobility in soil. Environ. Entomol. 19: 666-671.

MARRONE, P. G., AND R. E. STINNER. 1984. Influence of soil physical factors on survival and development of the larvae and pupae of the bean leaf beetle, *Cerotoma trifurcata* (Coleoptera: Chrysomelidae). Canadian Entomol. 116: 1015-1023.

MATTESON, J. W. 1966. Flotation technique extracting eggs of *Diabrotica* sp. and other organisms from soil. J. Econ. Entomol. 59: 223-224.

MCCAMMON, S. A., AND A. C. RATH. 1994. Separation of *Metarhizium anisoplia* strains by temperature dependent germination rates. Mycol. Res. 98: 1253-1257.

POTTER, D. A. 1983. Effect of soil moisture on oviposition, water absorption, and survival of southern masked chafer (Coleoptera: Scarabaeidae) eggs. Environ. Entomol. 12: 1223-1227.

RÉGNIÈRE, J., R. L. RABB, AND R. E. STINNER. 1981. *Popillia japonica*: effect of soil moisture and texture on survival and development of eggs and first instar grubs. Environ. Entomol. 10: 654-660.

REINING, L. 1992. Erosion in Andean hillside farming: characterization and reduction of soil erosion by water in small-scale cassava cropping systems in the southern central cordillera of Colombia. Verlag Josef Margraf, Weikersheim, Germany.

RICHARDS, L. A. 1965. Physical condition of water in soil. Methods of soil analysis. C. A. Black. Madison, Wisconsin, Am. Soc. Agron. I: 128-152.

RIIS, L. 1990. The Subterranean Burrower Bug *Cyrtomenus bergi* Froeschner, An Increasing pest in Tropical Latin America; Behavioural Studies, Population Fluctuations, Botanical Control, with Special Reference to Cassava. M.Sc. Thesis, Royal Veterinary and Agricultural University, Copenhagen.

RIIS, L., B. ARIAS, AND A. C. BELLOTTI. 2005. Bionomics and population growth statistics of the subterranean burrower bug *Cyrtomenus bergi* on different host plants. Florida Entomol. 88(1): 1-10.

RIIS, L., AND P. ESBJERG. 1998. Movement, distribution, and survival of *Cyrtomenus bergi* (Hemiptera: Cydnidae) within the soil profile in experimentally simulated horizontal and vertical soil water gradients. Environ. Entomol. 27(5): 1175-1181

SANCHEZ, D. 1996. Patogenecidad de Hongos Hyphomycetes Sobre *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae) Chinche Subterránea de la Yuca en Condiciones de Laboratorio. B.Sc. Thesis, Universidad Nacional de Colombia, Palmira, Colombia.

SAS INSTITUTE. 1988. SAS/STATTM user's guide, release 6.03 ed. SAS Institute, Inc., Cary, NC, USA.

SCHEFFER, F., AND P. SCHACHTSCHABEL. 1989. Lehrbuch der Bodenkunde. Enke, Stuttgart, pp. 171-205.

VILLANI, M. G., AND R. J. WRIGHT. 1990. Environmental influences on soil macro arthropod behaviour in agricultural systems. Ann. Rev. Entomol. 35: 249-269.