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Authors: Montoya, Pablo, Flores, Salvador, and Toledo, Jorge

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EFFECT OF RAINFALL AND SOIL MOISTURE ON SURVIVAL OF ADULTS AND IMMATURE STAGES OF *ANASTREPHA LUDENS* AND *A. OBLIQUA* (DIPTERA: TEPHRITIDAE) UNDER SEMI-FIELD CONDITIONS

Pablo Montoya[1], Salvador Flores[1] and Jorge Toledo[2]
[1]Subdirección de Desarrollo de Métodos, Programa Mosca del Mediterráneo, SAGARPA. Central Poniente 14, Col. Centro, Tapachula, Chiapas, 30700 México

[2]Departamento de Entomología Tropical, El Colegio de la Frontera Sur., Apartado Postal 36, Tapachula, Chiapas, 30700 México

Abstract

In this work we report the effect of rainfall on survival of pupae and adults of *Anastrepha ludens* (Loew) and *A. obliqua* (Macquart) under semi-field conditions. The influence of 2 soil textures and soil moisture on depth of pupation and pupal survival of both species was studied. There was no statistical difference on depth of pupation between larvae of *A. ludens* and *A. obliqua* in both types of soils. Adult emergence of *A. ludens* was higher than *A. obliqua* from soils with low moisture, while no significant difference was observed in soils at field capacity and saturation point. In the farm "Alianza" locality (760 masl, 1219 mm of rainfall), adult emergence decreased in direct relation to rainfall (r = 0.956 for *A. ludens*; r = 0.952 for *A. obliqua*), but this was not observed in Metapa de Dominguez (120 masl, 1114 mm of rainfall). Rainfall did not have any significant effect on adult mortality (r = 0.038 for *A. ludens*; r = 0.051 for *A. obliqua*), even under intense precipitation (120-160 mm/day), which indicates that fruit fly adults are able to find adequate refuge during heavy rain. These results are evidence that rainfall does not exert a significant impact on emergence and survival of adults of these species, and that the yearly fluctuations of their populations are mainly correlated to other factors such as host fruiting phenology.

Key Words: fruit flies, survival, rainfall, soil humidity, *Anastrepha ludens, A. obliqua*

Resumen

En este trabajo reportamos el efecto de la lluvia en la supervivencia de pupas y adultos de *Anastrepha ludens* (Loew) y *Anastrepha obliqua* (Macquart) en condiciones de semi-campo. La influencia de la textura y humedad del suelo en la profundidad de pupación y supervivencia (respectivamente) de las dos especies fue también estudiada. No se presentaron diferencias significativas en la profundidad de pupación entre las larvas de *A. obliqua* y *A. ludens*. La emergencia de adultos fue mayor en *A. ludens* que en *A. obliqua* en suelos con baja humedad, pero no se observaron diferencias significativas en suelos a capacidad de campo y punto de saturación. En la localidad "Finca Alianza" (760 msnm, 1219 mm de precipitación) la emergencia de adultos disminuyó en relación directa con la precipitación (r = 0.956 para *A. ludens*; r = 0.952 para *A. obliqua*), pero esto no fue observado en Metapa de Domínguez (120 msnm, 1114 mm de precipitación). La lluvia no tuvo efecto sobre la mortalidad de adultos (r = 0.038 para *A. ludens*; 0.051 para *A. obliqua*), incluso bajo intensa precipitación (120-160 mm/día), lo cual indicó que los adultos fueron capaces de encontrar refugios adecuados durante lluvias torrenciales. Estos resultados son evidencia de que la lluvia no ejerce un impacto significativo en la emergencia y supervivencia de adultos de estas especies, y que las fluctuaciones anuales de sus poblaciones están correlacionadas principalmente con otros factores como la fenología de sus hospederos.

Translation provided by the authors.

Fruit flies in the genus *Anastrepha* Schinner (Diptera: Tephritidae) are among the most important fruit pests in Mexico. Both *A. ludens* (Loew) and *A. obliqua* Macquart attack mango (*Mangifera indica* L.) in practically all the regions where it is grown, and *A. ludens* also is the key pest in most cultivated *Citrus* fruits. This situation gave rise the national campaign against fruit flies launched by the federal government in 1992 (Reyes et al. 2000).

Despite the abundance of research dealing with the behavior and rearing of these species (e.g., Aluja 1994; Dominguez et al. 2000; Artiaga-López et al. 2004), gaps remain in the ecological understanding of various climatic factors affecting development and adult fly. According to Bateman (1972) the range of environments to which these species are exposed is extremely broad, and there is no single environmental component which stands out as the determining factor in their population abundance.

Population fluctuations of fruit flies have often been correlated to host fruit phenology (Malavasi & Morgante 1981; Vargas et al. 1983; Harris & Lee 1986; Tan & Serit 1994). However, fruit flies are also influenced by environmental factors, although the relative importance of each factor varies among populations, or even within a population over time (Huffaker et al. 1984; Celedonio-Hurtado et al. 1995). Physical conditions in nature, such as temperature, relative humidity, and rainfall are easy to measure, but their impact on insect populations is generally difficult to determine.

In regions where fruit flies maintain consistent populations, mainly small-scale studies have been performed to test the effects of environmental conditions, such as in field cages, a particular tree, or one single and small field (Israely et al. 2005). Thus, our knowledge about the indirect effects of a particular climatic factor remains incomplete. The simple question by Celedonio-Hurtado et al. (1995), "Does the rain act as a direct killing factor by droplet impact on adult flies, or indirectly by depleting adult food?" has still not been answered. In addition, we found a similar situation regarding the impact of rainfall and soil moisture on immature development and the survival of these insects, where the data are scarce and related to specific circumstances and species (Liu 1983; Eskafi & Fernandez 1990; Serit & Tan 1990).

The depth to which the larva burrows into the soil for pupation is affected by soil texture, moisture, compaction and temperature (Dimou et al. 2003). Additional knowledge about the interaction of physical factors on pupation depth in nature, may aid in developing alternative soil control methods, pupal sampling designs, and assessment of natural mortality factors (Hou et al. 2006; Hennessey 1994). The depth of pupation also plays an important role in pupal predation by natural enemies such as ants, staphilinid beetles and chickens (Hodgson et al. 1998). Aluja et al. (2005) reported that the presence of ants influences significantly the pupal depth in *A. ludens.*

With these topics in mind, we performed four manipulative experiments in nature and in the laboratory, to better understand the response of *Anastrepha ludens* and *A. obliqua* fruit flies to different environmental factors. Our main objective was to determine the impact of rainfall on the mortality of pupae and adult *A. ludens* and *A. obliqua*; but we also studied the effect of soil moisture on pupal survival, and the effect of two types of soil on pupation depth in both fruit fly species. We then discuss abiotic factors independent of host fruit phenology, sufficiently to understand variations in fruit fly population density.

MATERIALS AND METHODS

Study Area

This study was performed in the Soconusco region in southern Chiapas, Mexico, near the border with Guatemala. This region has great ecological diversity, and a humid-warm to subhumid-warm climate. The average temperature is 26°C, and the rainy season extends from May to October, with an annual rainfall range of 1400-5000 mm. There is a gradient for both temperature and rainfall, from higher temperature and lower rainfall in the lowlands (García 2004).

Two sites were selected: (1) The Farm "Alianza"—in the county of Cacahoatan, Chiapas, located at 760 masl is—a coffee plantation (*Coffea arabiga* L.) that grows *Inga* spp. as shade trees, and (2) Metapa de Dominguez, Chiapas, located at 120 masl, where backyard orchard of sapodilla (*Manilkara zapota* (L.), previously called *Achras zapota* L.) was mixed with guava (*Psidium guajava* L.) and citrus (mainly *Citrus cinnensis* L).

Prior to conducting the tests, a sample of soil (500 g) was analyzed to determine the physicochemical parameters in each locality. The results for each parameter are shown in Table 1.

Biological Material

Third-instars and mature pupae of *Anastrepha ludens* and *A. obliqua* were provided by the Moscafrut facility in Metapa de Dominguez, Chiapas. The mass-rearing methods for both species have been described by Dominguez et al. (2000). Larvae were used immediately in the different tests before they could begin pupation. Pupae were kept in Plexiglas cages (30 × 30 × 30 cm) until adult emergence.

Test 1. Pupation depth of *A. ludens* and *A. obliqua* in 2 localities.

To determine the soil depth selected by the larvae for pupation, we used open bottom trays of 25 × 17 × 5 cm that were carefully inserted into the soil. Previously, we dug in the soil along the perimeter of the tray with a knife (reaching 4 cm of depth), without disturbing the soil structure. Two d later, 25 third instars were released in the center of each tray so that they might burrow at will and, 3 d later, the soil of each tray was removed to find the pupae. Once a pupa was located, we measured the depth of pupation in relation to soil surface, tacking advantage of the guide-level offered by the tray. Ten repetitions were performed in each locality for both species.

TABLE 1. TEXTURE AND PHYSICO-CHEMICAL PARAMETERS OF SOIL SAMPLES FROM FARM "ALIANZA" AND METAPA DE DOMÍNGUEZ, CHIAPAS, 2005.

Physical and Chemical Parameters	Localities	
	Farm "Alianza"	Metapa de Domínguez
Texture	Loamy Sand	Loamy Sand
Clay (%)	18.5	15.0
Silt (%)	45.3	39.3
Sand (%)	36.2	45.7
Saturation Point (%)	69.0	38.0
Field Capacity (%)	18.0	10.0
Wilt Point (%)	11.0	6.0
Apparent Density (g/cm^3)	0.59	0.84
Organic Matter (%)	15.23	2.74
PH	4.3	5.6

Test 2. Effect of soil moisture on adult emergence.

Based on the physico-chemical analysis of each locality's soil, the following treatments were established: (1) Dry soil "a" (dried in a low temperature incubator) with a 7.1 and 2.2% of moisture for Farm Alianza and Metapa respectively; (2) Dry soil "b" (3 days exposed to the sun), with a 9.9% (Farm Alianza) and 4.1% (Metapa) of moisture; (3) Soil at permanent wilt point (WP) (defined as retained water by soil particles at 15 atmospheres of pressure that is not available for plants (Nuñez 1985)); (4) Soil at field capacity (FC) (defined as amount of water retained in porous spaces of the soil against gravity; this water can be easily absorbed by plants (Hulthen and Clark 2006; Nuñez 1985), and (5) Soil at saturation point (SP) (defined as water occupying all porous spaces of the soil, and the pressure potential and osmotic potential are non-existent (Nuñez 1985). The percent moisture values for WP, FC and SP in each type of soil are shown in Table 1.

To get dry soil type "b", 10 kg of soil were exposed to the sun during 3 days at an average temperature of 28°C and 65-80% RH; with this procedure we reached (as pointed out before) 9.9% soil moisture for samples from Farm "Alianza" and 4.1% for Metapa, respectively. Subsequently, the soil was placed into a low temperature incubator (Fisher 307®) for 3 d at 60°C; at the end of this process we had dry soil type "a". The moisture values in these treatments were obtained with a thermo-balance Ohaus MB45®, at 200°C for a 10-g soil-sample during ~10 min.

To test the effect of soil moisture on adult emergence, we used 500-mL plastic containers (8.2 cm in diameter and 10.5 cm in height) into which 250 g of soil type "a" was placed. In each container we added water to reach the states of WP, FC and SP (Table 1). Fifty late third-instars of each fruit fly species were placed into each container, and then covered with a plastic lid. To provide a system of aeration, 4 perforations measuring 2 mm in diameter were made in each container at ground level. The emergence of adult fruit flies was quantified 25 d later. This study was carried out under lab conditions (25 ± 1°C; 60 ± 5% RH) with 10 repetitions by treatment for each species and locality.

Test 3. Effect of Rainfall on Adult Emergence.

At the onset of the rainy season, 30 PVC tubes (30 cm in height × 15.7 cm in diameter) were set up in each study zone. The tubes were sealed at the bottom with plastic mosquito netting (36 holes / cm^2) so that water could drain out. Then a 20-cm layer of soil was put into each tube. Ten d prior to the testing, the tubes were buried at a depth of 10 cm at the foot of a sapodilla tree or coffee plant (depending on the study zone), so that the soil could be naturally compacted by the effect of environmental conditions. Finally, 50 late third-instars of *A. obliqua* and 50 of *A. ludens* were placed into each tube. As a control, larvae of each species were kept in the laboratory in tubes containing soil from each locality. A field control was impractical because preliminary tests with the tube's tops covered with plastic to avoid rainfall effect under natural conditions, resulted in high mortality (> 60%).

Larvae (and/or transformed pupae) were exposed to rainfall for periods lasting 3, 7, 14, 28, 56, and 112 d. At the end of each of the rain exposure time periods, 5 tubes from each site were removed and carried to the laboratory. We observed adult emergence by counting and recording the number of adults by sex and species.

Test 4. Effect of Rainfall on Adult Mortality.

Four wire cages (60 × 60 × 60 cm, and lined with tulle netting) were placed around a coffee plant under field conditions in the locality of

Metapa. A branch from the coffee plant was introduced into each cage to provide a natural habitat and refuge for the flies, and 50 recently emerged *A. ludens* of each sex plus 50 *A. obliqua* of each sex were placed inside the cages. The flies were fed *ad libitum* with a cake consisting in a mixture of enzymatic yeast hydrolyzed (MP Biomedical, Irvine CA) and sucrose in the proportion 1:3. Water was provided in a cotton wick. Two cages to be protected from the rain were selected at random, and their roofs were covered with a piece of plastic (80 × 80 cm); the other 2 cages were left exposed. All cages were protected with stickem to prevent access to predators such as ants and spiders. Rainfall, temperature and species mortality was daily recorded for 15 d consecutively.

Statistical Analysis

The emergence data observed in each experiment were analyzed by ANOVA followed by the Tukey means separation test (SAS Institute 2003). The *A. obliqua* and *A. ludens* larvae burrowing depth was compared with a Student's t-distribution test (SAS Institute 2003). We calculated correlation (r) between rainfall and adult emergence, percent of adult emergence and percent of soil moisture, and adult mortality and rainfall magnitude. Significance of r was determined by a Student t test.

Results

Depth of Larval Burrowing

Most larvae burrowed into natural soil to a depth of 10 to 20 mm for pupation (Fig. 1). Pupae were found deeper (19.27 ± 0.52 mm) in the soil of Farm "Alianza" than in Metapa's soil (15.22 ± 0.60 mm) ($F = 26.0$, $df = 1, 410$, $P < 0.001$). However, there was no difference in the burrowing depths of the 2 species ($F = 0.6$, $df = 1, 410$, $P < 0.411$), with 17.09 ± 0.55 mm for *A. obliqua*, and 17.97 ± 0.57 mm for *A. ludens*.

Effect of Soil Moisture on Adult Emergence

In dry soil *A. obliqua* failed to emerge, while 3.2% of *A. ludens* eclosed from their puparium. For both species, the maximum percentage of emergence occurred in soils at field capacity, but emergence declined as soil humidity reached the saturation point (Fig. 2). Adult emergence was higher in Metapa`s soil than in Farm "Alianza"'s soil ($F = 24.1$, $df= 1, 144$, $P < 0.001$). In general, the emergence of *A. obliqua* was lower than that of *A. ludens* ($F = 74.6$, $df= 1, 144$, $P < 0.001$).

Effect of Rainfall on Adult Emergence

The emergence of both species was complete within 28 d after test initiation. The environmental conditions prevailing in the field had a strong impact on adult emergence when compared with the emergence of control samples in laboratory (Table 2). In the case of Farm "Alianza", emergence decreased in direct relation to precipitation ($r = 0.956$ for *A. ludens*; $r = 0.952$ for *A. obliqua* $P < 0.024$), but the opposite was observed in Metapa de Domínguez ($r = 0.329$ for *A. ludens*; $r = 0.388$ for *A. obliqua* $P > 0.306$). The time required for the first adult to emerge was not affected by any of the treatments.

Effect of Rainfall on Adult Mortality

Longevity of adults in both species was not significantly affected by precipitation. This was ob-

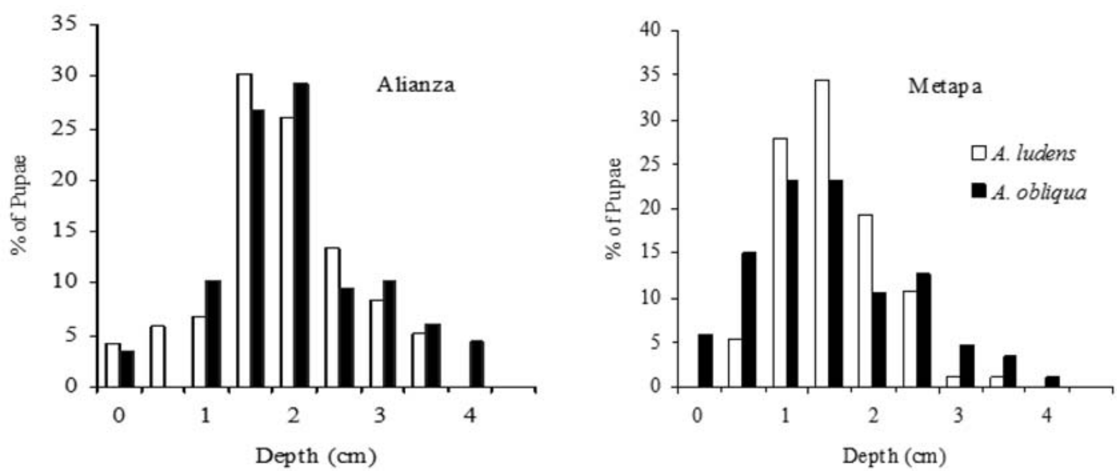

Fig. 1. Frequency distribution of pupation depth of *A. ludens* and *A. obliqua* in natural soils from 2 localities of Chiapas, Mexico.

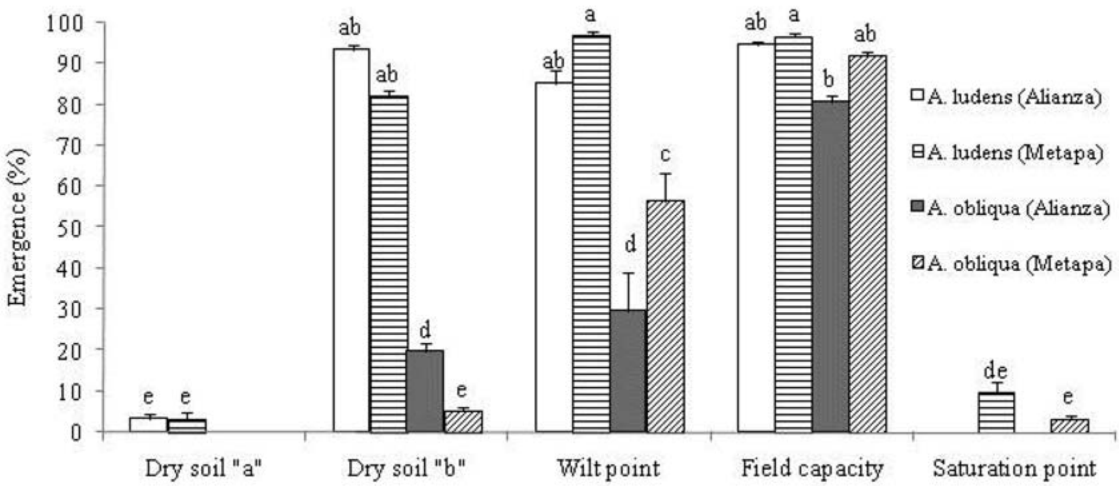

Fig. 2. Emergence of *A. ludens* and *A. obliqua* in soils from 2 localities containing different grades of moisture under laboratory conditions. Moisture values (%) correspond to: Dry soil "a": Metapa 2.2, Alianza 7.1; Dry soil "b": Metapa 4.1, Alianza 9.9; Wilt point: Metapa 6, Alianza 11; Field Capacity: Metapa 10, Alianza 18; Saturation point: Metapa 38, Alianza 69. Columns with same letter mean no statistical difference ($P > 0.05$).

served despite the fact that from the 3rd to the 5th of Oct 2005 (Fig. 3), unusually high rainfall was received (120-160 mm/day). These results also show that there was no significant relationship between the daily mortality registered for the exposed flies and rainfall ($r = 0.038$, $P = 0.320$ for *A. ludens*; $r = 0.051$, $P = 0.250$ *A. obliqua*) (Fig. 3).

Discussion

Our results showed that most *A. ludens* and *A. obliqua* larvae burrowed from 1 to 2 cm for pupation in soils, although they can eventually reach 4 cm of depth. We observed that in Metapa`s soil (with higher apparent density their burrows were generally shallower. Several authors have reported similar findings with another species of fruit flies. Dimou et al. (2003) reported that *Bactrocera oleae* (Gemel.) borrowed a maximum of 3 cm and had a mean depth of pupation of 1.16 cm in different soil types. Hennessey (1994) reported that *Anastrepha suspensa* (Loew) larvae ranged between 0.7 and 3.3 cm in their pupation depth, achieving greater depths in soils with low com-

TABLE 2. EMERGENCE PARAMETERS FOR *ANASTREPHA LUDENS* (A. L.) AND *A. OBLIQUA* (A. O.) FOR DIFFERENT EXPOSURE TIMES TO RAINFALL IN 2 LOCALITIES OF THE SOCONUSCO REGION, CHIAPAS (2005)

Period of Exposure to Rainfall (day	Precipitation (mm)	Temperature °C	Emergence (%)		Days to First Emergence		Emergence Period (days)	
			A. l.	A. o.	A. l.	A. o.	A. l.	A. o.
Metapa (120 masl)								
0	Lab (Control)	26.0 ± 0.3	94.0 a	74.0 a	18	16	1-3	1-4
3	143	27.0 ± 0.3	49.2 b	32.0 b	18	17	1-4	1-3
7	233	26.8 ± 0.2	39.2 b	21.6 b	17	16	1-4	1-4
14	334	25.9 ± 0.3	52.2 b	28.8 b	17	16	1-10	1-8
28	1144	25.3 ± 0.3	49.1 b	32.3 b	16	16	1-6	1-4
Alianza (700 masl)								
0	Lab (Control)	26.0 ± 0.3	86.8 a	62.0 a	18	16	1-2	1-4
3	95	24.8 ± 0.2	56.4 b	46.0 ab	17	17	1-5	1-3
7	268	25.1 ± 0.2	43.6 bc	46.4 ab	18	18	1-7	1-6
14	558	25.0 ± 0.1	41.6 bc	33.6 ab	20	19	1-7	1-12
28	1219	25.1 ± 0.1	26.5 c	26.0 b	17	19	1-8	1-11

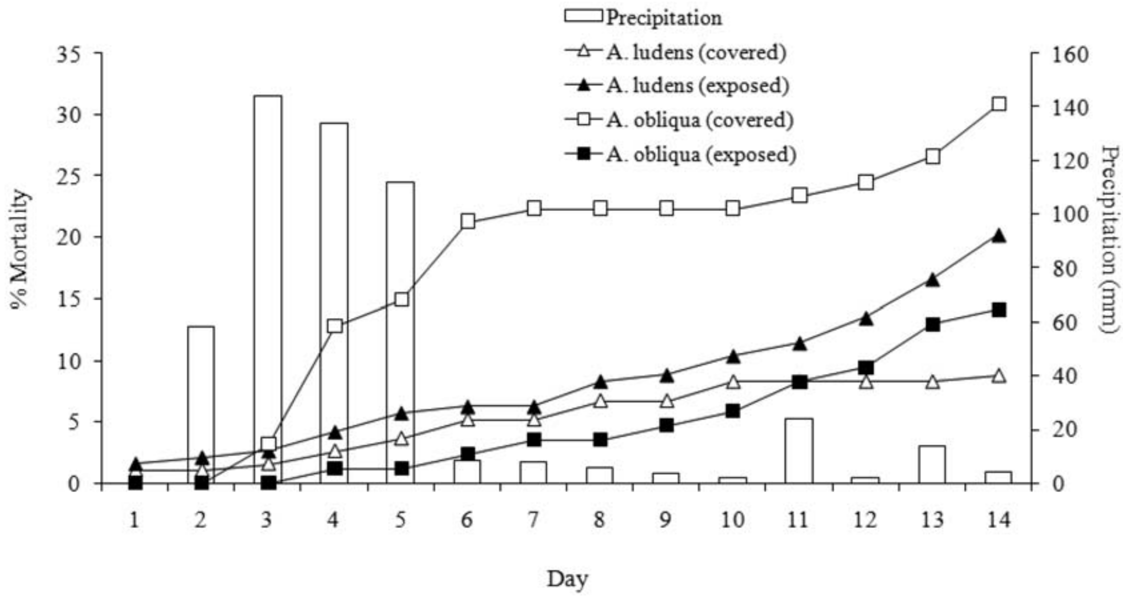

Fig. 3. Mortality of fruit fly adults held in cages exposed to natural precipitation in Metapa de Dominguez, Chiapas.

paction. Baker et al. (1944) observed that *A. ludens* puparia were normally found at a depth of 1.3 cm, and that, if the ground was hard, they would not enter the soil at all, pupating on the surface. In this respect, Hodgson et al. (1998) reported on excavations in 2 places with different soil characteristics, that larvae of *Anastrepha* spp. typically burrowed no more than 2 cm, and rarely more than 5 cm. The rate of disappearance, presumably through predation was correlated to depth in relatively shallow burrows but there was no difference in disappearing between 2.5 and 5 cm, suggesting that larvae gained no benefits from deeper pupation.

The bioassays to determine rainfall's impact on the survival of pupae and adult stages of fruit flies began with the onset of the rainy season in the region, so as to cover the longest possible period of rainfall to affect pupae of both species. However, adults complete emergence within a period of 28 d. For this reason the treatments which were to last 56 and 112 d of exposure to rain lost their significance. This homogeneity in emergence might be attributed to our using a laboratory strain, because flies that consistently emerge as early as possible would be more likely to be included in the next breeding population in a laboratory rearing program. We would intuitively expect the wild populations to present higher variability in this respect. These results demonstrate that, although there were differences in the treatments as to length of the emergence period, rainfall was not an important factor in this parameter.

The emergence of adults from soils with different grades of moisture showed that at moisture extremes, pupal survival was threatened. When moisture content reached saturation point, adult emergence dropped drastically, perhaps due to a lack of oxygen, as pointed out by Eskafi & Fernandez (1990) for *C. capitata* (Wied.). The survival of the larva-pupal stage of *Bactrocera dorsalis* (Hendel) was inhibited when soil moisture reached the field capacity (Hou et al. 2006). In our research, dry soils affected the emergence of *A. obliqua* and *A. ludens* adults. Bressan-Nascimento (2001) found that desiccation was one of the predominant causes of pupal mortality in *A. obliqua*. Similar results were reported in *B. dorsalis* (Vargas et al. 1987; Hou et al. 2006) and *C. capitata* (Jackson et al. 1998). The good rate of *A. ludens* pupal survival in soils with low moisture is most likely an adaptation to semi-desert climate in the Mexican northeast where this species originated. *Anastrepha obliqua* is abundant in the tropics and subtropical zones mainly associated with *Mangifera indica* L. and *Spondias* spp. (Hernandez-Ortiz 1992) where moisture is higher. The development of *A. ludens* pupae was adequate with high levels of emergence over the broad moisture range from wilt point to field capacity. This finding was similar to Hulthen & Clarke (2006), who reported very low levels of pupal mortality in *Bactrocera tryoni* (Froggart) at intermediate levels of soil moisture. In addition, Fitt (1981) reported that survival of *Bactrocera (Dacus) opiliae* (Drew & Ardí) and *B. tenuisfascia* (May) were drastically reduced in soils with moisture content below 10%. In this respect, Stephens et al. (2007) postulate that hot and dry stress prevents the establishment of *B. dorsalis* to Australian and African dry zones.

The effects of rainfall on the proportion of adult emergence were significant. As rainfall accumulated, the adult emergence of both species in the 2 localities declined. These results agree in part with those obtained by Eskafi & Fernandez (1990), who found that anoxia may be an important cause of mortality in pupa of *C. capitata* during the rainy season, especially in soils having a high bulk density.

The presence of rains did not increase the mortality of fruit fly adults, even during days of intense rainfall. Coincidentally, this experiment was performed while the Hurricane "Stan" wreaked its havoc in this region (Oct 2005), and was characterized by torrential rainfall but little winds. Liu (1983) pointed out that after being subjected to 4 typhoons and heavy rains for several days, *B. dorsalis* populations were depressed to low level. Our results indicate that adults of both *Anastrepha* species that we studied must be capable of finding appropriate refuge during the periods of rainfall. This result suggests than any adverse effects of rainfall on adult survival would most likely be due to the depletion of adult food by washing away or diluting it, as Celedonio-Hurtado et al. (1995) put forth for questioning. However, in this experiment, the adult flies had a constant food supply.

In summary, different environmental factors exert differential effects on the fruit flies *A. ludens* and *A. obliqua*. We found that soil humidity at saturation point inflicts the strongest negative effect on adult emergence, which in nature only can be observed under longer periods of continued rainfall. In contrast, normal rainfall did not affect the adult emergence of either species significantly. Heavy precipitation also did not impact adult mortality of either species. These findings suggest that under natural conditions, the observed fluctuation of their populations might be mainly due to host plant phenology, as has been reported for other fruit fly species by Tan & Serit (1994); Malavasi & Morgante (1981); Jiron & Hedstrom (1991); and Harris & Lee (1986).

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