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EFFECTS OF SOIL MOISTURE ON THE PUPATION BEHAVIOR OF *ALTICA SUBPLICATA* (COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

The effects of soil moisture on the pupation behavior of a willow flea beetle, *Altica subplicata*, were studied with two laboratory experiments. To test the effect of soil moisture on the number of larvae pupating and pupal survival, we set up pupation chambers filled with sand with three different soil moistures: dry, moist, and wet. The number of larvae pupating was much greater in the moist sand and wet sand treatments than in the dry sand treatment. Pupal survival, as measured by the proportion of adults successfully emerging, was greater in the moist treatment than in the wet or dry treatments. Thus, overall pupation success (number of adults successfully emerging) was greater in the moist treatment than in the wet treatment and greater in the wet treatment than in the dry treatment.

To examine the effect of soil moisture on choice of pupation site, we provided the larvae with a choice of two soil moistures in each pupation chamber. More larvae chose wet over dry conditions and more chose moist over dry conditions, but larvae did not discriminate between moist and wet conditions.

The improved pupation in areas with higher soil moisture is consistent with the field distribution pattern of greater beetle densities on dunes with greater soil moisture.

Flea beetles in the genus *Altica* represent a group of herbivores that are capable of causing extensive damage to their host plants (Woods 1917, Port and Guile 1986). At Grass Bay on Lake Huron in northern Michigan, the flea beetle, *Altica subplicata* LeC. feeds exclusively on sand-dune willow, *Salix cordata*. At this location *S. cordata* grows on sand dunes of various ages (Bach 1990). Despite the wide distribution of *S. cordata* at Grass Bay, the population of *A. subplicata* exhibits a strong distributional bias at this site. Bach (1990) found that *A. subplicata* is present on young sand dunes but absent from older dunes.

The feeding and reproductive behaviors of *A. subplicata* suggest that young sand dunes, with younger *S. cordata* plants (and thus a greater proportion of young leaves), are most beneficial for reproductive success. Cassin (1989) observed a greater larval to pupal survival rate when the diet consisted of young *S. cordata* leaves compared with old *S. cordata* leaves. Cassin (1989) also reported a higher percentage of egg laying on young *S. cordata* leaves. *Altica bimarginata* Say, another willow flea beetle, concentrates its feeding efforts on developing buds and young leaves of the willow *S. exigua* (Barstow and Gittins 1971). *Haltica* (=*Altica*)

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lythri Aube also prefers young over senescent leaves of its host plant, *Epilobium hirsutum* (Phillips 1976).

Despite the relationship observed between the food supply, conditions for egg laying and the population density of *A. subplicata*, we propose that other variables may influence this relationship, one of these potential variables being soil moisture. The location of the young sand dunes, close to the water's edge, results in greater soil moisture. Other studies report increased development and survival of soil insects in moderately wet soil (Lummus et al. 1983, Marrone and Stinner 1984). Barstow and Gittins (1971) suggested that moist sand facilitates the successful pupation of *A. bimarginata*, but they did not experimentally test this.

The purpose of this experiment was to examine the effects of soil moisture on the pupation behavior of *A. subplicata*. Specifically, we examined the number of larvae pupating, pupal survival (proportion of adults successfully emerging out of those pupating), pupation success (number of adults successfully emerging), and selection of a pupation site by *A. subplicata* as a function of soil moisture.

MATERIALS AND METHODS

Two laboratory experiments were conducted at the University of Michigan Biological Station, Cheboygan County, MI. We collected last-instar *A. subplicata* between 25 – 27 July 1990 from 2 sites: (1) Grass Bay Nature Conservancy Property on Lake Huron, Cheboygan County, MI, and (2) Pte Aux Chenes lake shore property on Lake Michigan, Mackinac County, MI. We utilized 16 oz deli dishes as pupation chambers for both laboratory experiments. To each deli dish we added dry sand (collected from Pte Aux Chenes) to a depth of 4.5 cm, ten *A. subplicata* larvae, and two *S. cordata* sprigs, each 6–8 cm in length, recently collected from the field. To maintain a fresh food supply, we provided a water supply to the sprigs via one dram vials and replaced the *S. cordata* sprigs every three days. Each dish was covered with 1mm x 1mm mesh nylon cloth.

The soil moisture experiment consisted of 5 replicate dishes of each of three treatments: dry, moist, and wet sand. On 27 July 1990, we added 60 ml and 120 ml of water to the moist and wet treatments, respectively. Every six days thereafter, we added 30 ml of water to the moist treatment and 60 ml of water to the wet treatment, to maintain a difference in soil moisture.

The *S. cordata* and larvae were placed in the dishes after the water was added on the first day of the experiment. To eliminate possible environmental differences in the lab room, we arranged the treatments in 5 blocks, with treatments within blocks in an alternating order (i.e., block 1: moist, dry, wet; block 2: wet, moist, dry; etc.). We counted the number of larvae that had not burrowed into the sand to pupate periodically between 31 July and 14 August and from that, calculated the number of larvae that had pupated (= burrowed into the sand). We also recorded the number of adult beetles that successfully emerged from the sand periodically between 18 August and 9 September. From this, we calculated pupal survival as the proportion of adults successfully emerging out of the number that had pupated, and pupation success as the number of adults successfully emerging. Data on pupal survival were arcsin transformed before analysis. Data were analyzed with repeated-measures ANOVAs (because data from different dates were not independent) testing for effects of soil moisture, treatment, time, and an interaction between treatment and time. Pairwise comparisons between individual treatments were conducted with individual contrasts (SYSTAT; Wilkinson 1988).

To calculate the percentage soil moisture in these experiments, we set up an additional set of experiments with identical conditions, but without adding larvae. We took soil samples each day for the first 7 days of the experiment and calculated percentage soil moisture (dry weight) as (wet weight – dry weight)/dry weight.

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The soil moisture choice experiment consisted of 5 replicate dishes of each of three paired treatments: dry vs. moist, moist vs. wet, and dry vs. wet sand. We divided the sand into halves with a plexiglass divider and then applied the appropriate moisture treatment to each half; each side of the divider supported one *S. cordata* sprig. We maintained the moisture treatments by adding 30 ml and 60 ml of water to the moist and wet choices, respectively, on 2 August 1990 and 15 ml and 30 ml of water, respectively, every 6 days thereafter. As described previously the treatments were arranged in an alternating order within each of 5 blocks. Final counts of the number of larvae choosing to pupate in each side of each dish were obtained by excavating the soil at the conclusion of the experiment on 12 August 1990. Data from each choice experiment were analyzed with Chi-square (χ^2) tests.

To compare soil moisture values from the laboratory experiments with those found in the field, 5 soil samples were taken on each of 2 dates from a young dune and an older dune at Grass Bay. Percentage soil moisture was calculated as described previously.

RESULTS

The number of *Altica subplicata* larvae that pupated was very strongly influenced by soil moisture ($F=63.2$, $df=(2,12)$, $p<<.001$), Fig. 1), time ($F=97.3$, $df=(4,48)$, $p<<.001$), and an interaction between treatment and time ($F=11.7$, $df=(8,48)$, $p<<.001$). This significant interaction indicates an increasing difference between treatments with time (Fig. 1). The number of larvae that pupated was much lower under dry sand conditions than under moist and wet sand conditions ($p<.05$ for all dates for both comparisons), but did not differ for moist vs. wet conditions ($p>.05$ for all dates); a total of only 12 larvae from the dry treatments burrowed into the sand versus 48 and 47 in the moist and wet treatments, respectively.

Pupal survival, measured as the proportion of adults that successfully emerged out of the number that pupated, was higher in the moist treatment (0.91 ± 0.4) than in the wet treatment (0.61 ± 0.9) or the dry treatment (0.42 ± 0.25). Soil moisture treatment significantly affected pupal survival ($F=22.7$, $df=(2,11)$, $p<<.001$), with greater proportions of adults emerging in the moist treatment than in the wet treatment ($p<.05$ for all except the last date) or the dry treatment ($p<.05$ for all dates). There was no significant difference between the proportion of adults emerging in the wet and dry treatments ($p>.05$ for all dates).

Pupation success, which combines number pupating and pupal survival, was also significantly affected by soil moisture treatment ($F=48.4$, $df=(2,12)$, $p<<.001$, Fig. 2) with greater numbers of adults successfully emerging in the moist treatment than in the wet treatment ($p<.05$ for all dates) and greater emergence in the wet treatment than in the dry treatment ($p<.05$ for the last date; Fig. 2). Again, pupation success increased with time ($F=37.1$, $df=(6,72)$, $p<<.001$), and there was an increasing difference between treatments with time ($F=8.2$, $df=(12,72)$, $p<<.001$).

The percentage soil moistures in each of the treatments over the 7-day period were the following: dry (5.4 ± 0.5 SEM, 5.7 ± 1.0, 2.4 ± 0.2, 3.4 ± 0.2, 3.1 ± 0.2, 2.9 ± 0.2, 3.1 ± 0.2, respectively), moist (32.4 ± 1.1, 24.8 ± 0.5, 15.2 ± 1.0, 12.3 ± 0.8, 11.2 ± 0.6, 9.1 ± 0.6, 18.3 ± 0.6, respectively), and wet (32.1 ± 0.8, 24.8 ± 2.3, 14.5 ± 0.7, 13.1 ± 0.6, 11.3 ± 0.6, 11.0 ± 0.4, 28.8 ± 0.5, respectively). Thus, the dry treatment had much lower soil moisture than either the moist or wet treatments throughout the study. In addition, although the soil moistures were similar in the moist and wet treatments for the first six days of the experiment, the addition of water on the seventh day resulted in a much higher soil moisture in the wet treatment (29%) than in the moist treatment (18%).

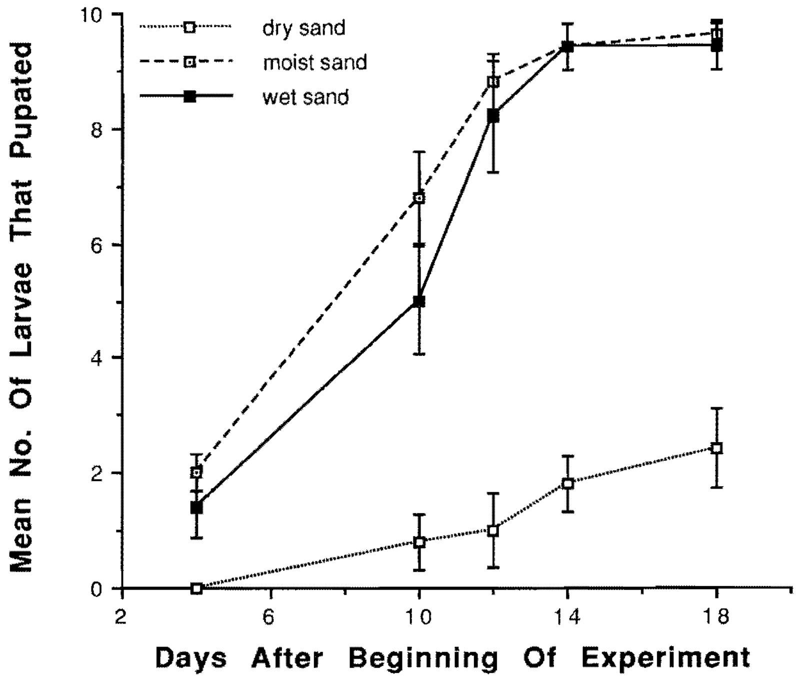

Figure 1. Mean number of larvae that pupated in containers with dry, moist, and wet sand. Data presented are means ± standard errors for the 5 replicate containers of each treatment.

The soil moisture choice experiment resulted in a highly significant difference between the number of larvae that chose a wet as opposed to a dry soil in which to pupate (Fig. 3). More larvae chose wet sand over dry sand ($\chi^2 = 17.1$, df = 1, $p <$ .001) and more larvae chose moist sand over dry sand ($\chi^2 = 31.2$, df = 1, $p < .001$). The difference between the number of larvae choosing moist vs. wet sand was not significant ($\chi^2 = 0.24$, df = 1, $p > .05$).

DISCUSSION

Results from this experiment suggest that soil moisture strongly affects pupation behavior. Since we controlled for the quality of *Salix cordata* and other environmental factors, the variable most likely influencing pupation was soil moisture. Moderately wet soil also facilitated the development and increased the survival of the bean leaf beetle (Marrone and Stinner 1984) and the southern corn rootworm (Lummus et al. 1983).

Results from both laboratory experiments showed that larvae consistently chose to pupate under moist and wet sand conditions (and did not distinguish between these conditions), but larvae avoided pupating under dry sand conditions. Marrone and Stinner (1984) suggest that high pupal mortality in dry soils results from an inability to make pupal cells and an inhibition of emergence.

The highest pupation success in the moist sand treatment clearly results both

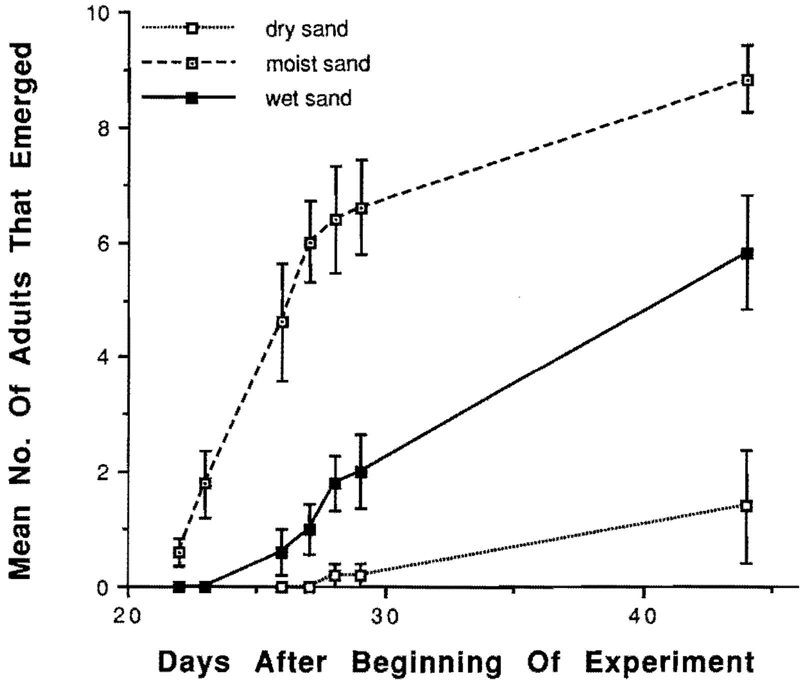

Figure 2. Mean number of adults that successfully emerged in containers with dry, moist, and wet sand. Data presented are means ± standard errors for the 5 replicate containers of each treatment.

from a greater number of larvae pupating and greater survival of pupae in that treatment. The lower adult emergence in wet sand is caused by a detrimental effect of wet sand on pupal development, not from fewer larvae burrowing into the sand to pupate. The lowest pupation success in the dry sand treatment appears to result primarily from the larvae not choosing to pupate under dry conditions, but pupal survival was also lowest in dry sand.

The improved pupation in areas with higher soil moisture is consistent with field distribution patterns of this beetle. Bach (1990) reports that beetles are abundant on young dunes nearer to the water's edge and absent from older dunes, even with similar densities of *S. cordata*. Young dunes at Grass Bay had an average soil moisture of 18.2±1.1 % and 19.1±1.3 % (which corresponds to the moist sand treatment in the laboratory experiments), whereas older dunes had an average soil moisture of 3.3±0.1 % and 3.6±0.6 % (which corresponds to the dry sand treatment). Thus, increased soil moisture, and thus increased pupation success, may be an important explanation for the high population densities on younger dunes.

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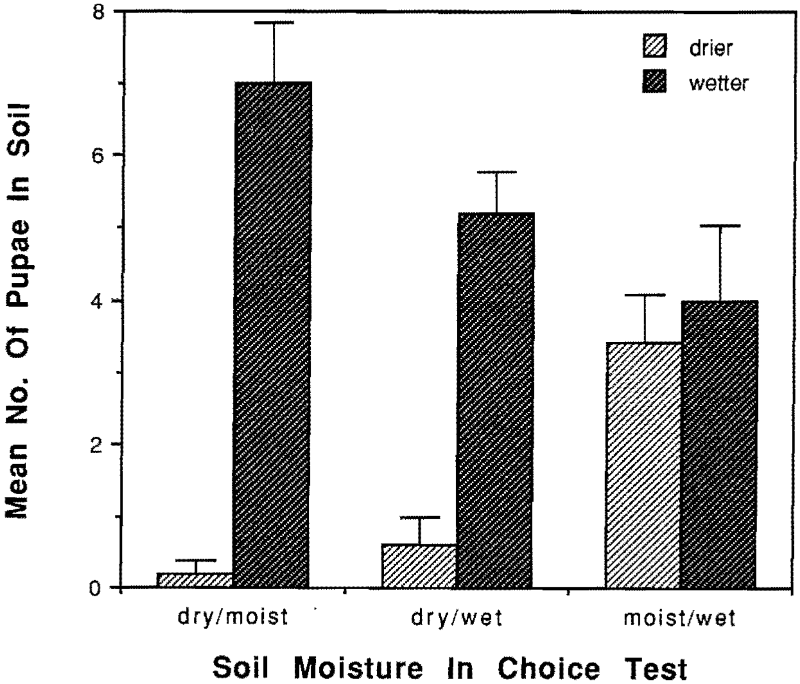

Figure 3. Mean number of pupae excavated from the drier and wetter sides of each soil moisture choice test. Data presented are means ± standard errors for the 5 replicate dishes for each of 3 choices: dry vs. moist, dry vs. wet, and moist vs. wet.

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