Journal of Chemical Ecology, Vol. 15, No. 5, 1989

PREFERENCE FOR MAGNESIUM SULFATE-TREATED LEGUMINOUS SEEDS IN EGG-LAYING BEAN WEEVIL (*Acanthoscelides obtectus* Say, Col., Bruchidae)

ÁRPÁD SZENTESI

Zoology Department, Plant Protection Institute
Hungarian Academy of Sciences
Budapest, Pf. 102, H-1525, Hungary

(Received March 2, 1988; accepted July 25, 1988)

Abstract—Unlike many secondary plant substances, a wide range of concentrations (4–1000 mM) of magnesium sulfate, applied to dry beans, significantly increased egg-laying by the dry bean weevil in binary choice tests, in favor of treated seeds. No other magnesium-containing compounds studied exerted such an effect, nor was a similar response noted on treated beans in no-choice situations. The total number of eggs laid per female was in the same range in both types of test. Variably enhanced or suppressed oviposition responses were shown on magnesium sulfate-treated secondary hosts and on nonhosts or on indifferent substrates. No specific behavior by egg-laying bean weevil females on Mg-treated seeds could be detected. The results are explained by assuming the functioning of magnesium as a supernormal stimulus for egg-laying. However, a physiological effect on neuromuscular synaptic transmission, as a consequence of probable Mg uptake resulting in a decreased propensity to move, is also hypothesized.

Key Words—Magnesium sulfate, oviposition, bean weevil, *Acanthoscelides obtectus* Say, Coleoptera, Bruchidae, supernormal stimulus, neuromuscular synaptic depression.

INTRODUCTION

In many biochemical and physiological processes of various species, including man, the presence of magnesium ions is considered to be indispensable (Aikawa, 1981; Ferment and Touitou, 1985). As for insects, water-soluble magnesium compounds usually are deterrent (Dethier, 1968; Simpson, 1978). However, a

0098-0331/89/0500-1545$06.00/0

strong preference was shown by egg-laying females of egg parasitoids (*Trichogramma* spp.) for artificial host eggs containing higher or close to host hemolymph levels of magnesium and potassium acting synergistically (Nettles et al., 1982, 1983).

In the presence of plant allelochemicals and of inorganic substances applied to dry bean seeds, egg-laying by the bean weevil, *Acanthoscelides obtectus* Say (Coleoptera, Bruchidae), has been depressed to various extents (Muschinek et al., 1976; Jermy and Szentesi, 1978; Szentesi, 1983). Among the substances examined to date, only magnesium sulfate showed the opposite effect, i.e., egg-laying was enhanced by magnesium-treated beans as compared to untreated ones (Jermy and Szentesi, 1978). To our knowledge, no other data exist in the literature concerning the role of magnesium in influencing oviposition in phytophagous insects.

Jermy and Szentesi (1978) briefly indicated the preference showed by the bean weevil for magnesium-treated beans; it was the aim of the present paper to investigate the nature and extent of this preference, examining: (1) the range of compounds eliciting a similar response, (2) the stimulus situation in which the preference is manifested, and (3) whether preference is accompanied by specific behavioral patterns. There is also discussion of two possible modes of action: (1) whether magnesium-treated beans represent a supernormal stimulus, and (2) whether possible uptake of magnesium sulfate might result in changes of behavior reflecting a neurophysiological effect.

METHODS AND MATERIALS

The dry bean weevils were obtained from a mixture of wild (heterogeneous) populations maintained in the laboratory for at least three years on dry beans (Szentesi, 1972). Freshly emerged adults were sieved, kept in glass jars lined with corrugated paper strips, and supplied with 10% honey–water. Adults mated in the jar and were used at the age of 4 days.

Oviposition was measured in choice and no-choice tests on treated and untreated beans. The surface of the seeds was coated with a given compound by a method described by Muschinek et al. (1976). In short, 0.25 ml of a compound's solution or suspension was dried onto the surface of 10 g seeds by a cold or warm (about 93–96°C) airstream for 1 min.

The quantity of magnesium salts, both administered and naturally present, was determined by chemical analysis and by atomic absorption spectrophotometry (AAS). The results are given as percentage magnesium in relation to absolute dry matter (Table 1).

The uniformity of magnesium sulfate deposits on coated surfaces was assessed on 8-mm-diam. (201-mm^2 surface) glass beads, treated by the standard

TABLE 1. MAGNESIUM CONTENT OF LEGUMINOUS SEEDS AND PLANT PARTS AND MAGNESIUM SULFATE-TREATED SUBSTRATES TESTED FOR OVIPOSITION (AAS ANALYSIS)

Substance	Percentage of magnesium content[a]
Beans[b]	0.170, 0.13[c]
Soybeans[b]	0.289, 0.27[d]
Peas[b]	0.147, 0.15[e]
Lentil[b]	0.127
Bean varieties ($N = 4$)	0.185–0.214
Bean seeds treated with 111 mM or 3000 mM magnesium sulfate	0.198
Magnesium sulfate (111 mM) treatment for	
1 min	0.211
5 min	0.208
10 min	0.211
Bean seed cotyledon	0.146
Bean seed testa	0.447
Bean pods	0.427
Bean pod stem	0.413

[a] Refers to absolute dry matter content.
[b] Dry whole seeds.
[c] Nehring et al. (1972).
[d] Mándy et al. (1980).
[e] Raboy et al. (1984).

procedure with 37 mM magnesium sulfate. Microscopic examination has shown that there were 7.1 ± 0.7 (mean ± SE) magnesium sulfate crystals per square millimeter on the glass beads. The size of the crystals varied between 0.04 and 0.87 mm.

Titrimetry showed that the loss of chemicals during treatment was within the range of 5–10% and that individual seeds received, e.g., in case of 111 mM concentration, 0.103 mg magnesium sulfate per square millimeter of seed surface.

Magnesium sulfate was incorporated into pills. Pills of different kinds consisting of bean pod or seed powder, potato starch, and cellulose powder were prepared in various compositions. As sticking materials, distilled water, glycerine and soluble cellulose, to which magnesium sulfate was added to give a 100 mM concentration, were used. The 6-mm-diam. pills were prepared with a pharmaceutical device. These were dried at 45°C and used for oviposition tests. The pills of different types weighed 91 ± 2 (SD) to 165 ± 7 mg.

In choice tests, solvent-treated and coated leguminous seeds were offered in 10-cm-diam. Petri dishes divided into four sections. Opposite sections contained the same stimulus. Ten males and 10 females were confined in each dish for 10 days. For no-choice tests, 2.8 × 5-cm size vials were used, each having three or four pieces of oviposition material and three to four males and females. The vials were covered with pieces of linen cloth.

Tests were conducted in total darkness, at 23°C and 60–70% relative humidity, without food or water for the adults. The number of eggs laid per female was used for evaluation. Preference was expressed by a discrimination quotient (DQ) (David and van Herrewage, 1970) (see legend of Figure 1). Statistical evaluations were done on the basis of the number of eggs laid [Wilcoxon's signed-ranks test, Student's *t* test, or Duncan's new multiple-range (DNMR) test; Steel and Torrie, 1960; Sokal and Rohlf, 1969].

All chemicals used were of analytical grade, unless otherwise stated.

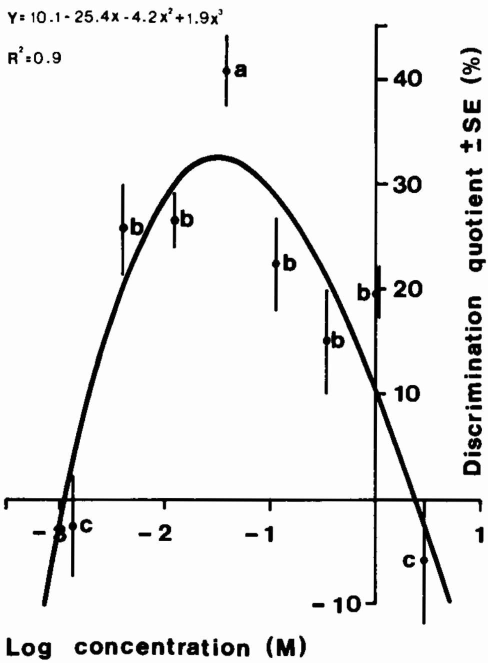

FIG. 1. Dose–response curve of egg-laying *A. obtectus* females to beans in binary choice tests treated with magnesium sulfate at different concentrations. Values are expressed as discrimination quotient (DQ) (David and van Herrewage, 1970) given by the ratio: (No. of eggs laid on control − No. of eggs laid on treated)/Total No. of eggs laid. To obtain a percentage value, the ratio is multiplied by 100. Concentrations: 1.3, 4, 12, 37, 111, 333, 1000, and 3000 mM. SE = standard error (bars). Means followed by the same letters are not significantly different at the 1% probability level (DNMR test for ESS).

Experiments with Magnesium Sulfate on Bean Seeds. Eight millimolar levels of $MgSO_4 \cdot 7H_2O$ were examined from 1.3 to 3000 (Figure 1). Magnesium sulfate of two purity grades, different lengths of treatment time, cold and warm application, as well as different exposure times of treated seeds to ovipositing adults were also tested.

Experiments with Other Magnesium or Sulfate Compounds. In addition, other magnesium compounds (Table 3) were tested at 111 mM. Some of them were applied as suspensions in 2% potato starch solution, while aqueous solutions were used for the rest. Other sulfate-containing compounds and sulfuric acid were also tried (Table 3).

Experiments with Magnesium Sulfate on Various Oviposition Substrates. Heterogeneous-type bean weevil females lay eggs on a range of substrates (Pouzat, 1975; Basky, 1977; Szentesi, 1976; Jermy and Szentesi, 1978). Occasional and secondary hosts (peas, lentils, and soybeans), and partially or totally indifferent substrates (e.g., glass beads, starch + cellulose pills, dry seed cotyledon devoid of testa) were also treated with magnesium sulfate (111 mM conc.). These substrates were offered both in choice and no-choice tests for egg-laying.

Experiments on Direct Effect of Magnesium Sulfate on Adult Behavior. Twenty 2- to 4-day-old *A. obtectus* females deprived of egg-laying but mated were allowed to oviposit on control and 111 mM Magnesium sulfate-treated seeds. Single seeds with hilum upright were stuck to the bottom of 2.8 × 5-cm glass vials. Homogeneous illumination (1900 lux) was provided. Temperature inside the open vial was 30°C. Individual mated females were put onto the beans and allowed to perform preovipositional behavior, which was observed through a binocular microscope and simultaneously tape-recorded.

Bean weevil adults can take up magnesium sulfate from treated seed surfaces, and this might affect behavior. For "voluntary" uptake, 3-day-old mated females were allowed to move and lay eggs on untreated or treated seeds, among which cotton wicks were placed containing 1 ml honey–water or honey–water + 10 or 100 mg magnesium sulfate. The cotton wicks were replaced daily (five females per Petri dish; 11 replicates). For "forced" uptake of magnesium sulfate two groups of adults were confined in cages without beans for three days. The cages were kept at 28°C, and drinking of honey–water containing the salt (100 mg/ml) was ensured. "Magnesium drunk" adults (10 males and 10 females) were transferred onto dry beans (15 replicates). In both cases locomotor activity of adults was monitored for 3–4 hr daily for four to nine days, at 15-min intervals. The eggs laid were also counted.

In a choice test, presence of a mated female in the treated or untreated section was recorded hourly, 3–8 hr/day, for 13 days. Light intensity was 600 ± 300 lux (299 replicates).

The effect of "built-in" magnesium on moving activity was examined by rearing the bean weevils both in control pills containing 0.5% magnesium sulfate (near the range occurring in whole seeds of legumes: Nehring et al., 1972, cited by Szabó, 1980; Spector, 1956, cited by Mándy et al., 1980), and in treated ones containing 1, 2.5, and 5% of magnesium sulfate. Pills were infested with a single egg each. The adults that emerged were put onto untreated bean seeds in Petri dishes. Ambulatory movement of six adults (three females and three males) per replicate was recorded for nine days for 4–8 hr/day at half-hour intervals (seven to nine replicates).

RESULTS

AAS analysis revealed that bean seed coat, bean pod, and bean pod stem contained approximately two to three times more magnesium than whole seeds of some bean varieties or than bean cotyledon alone. Leguminous seeds were in the same range as dry beans, while soybeans contained a slightly higher percentage (Table 1).

Effects of Bean Seeds Covered with Magnesium Sulfate. In choice tests beans treated with 4–330 mM magnesium sulfate were significantly preferred for egg-laying with a maximum at 37 mM (Figure 1). In no-choice tests, the number of eggs laid with a concentration spectrum of 4–3000 mM ranged between 37 $\pm$ 7 (mean $\pm$ SD) and 44 $\pm$ 8, and none of the values was significantly different. On control beans, females laid 37 $\pm$ 8 eggs. Also, beans were equally preferred whether treatment was applied warm or cold (Table 2). Preference for treated seeds gradually decreased as treatment time increased. Impurities in the compound (e.g., other unknown inorganic elements) or ways of treatment did not influence preference (Table 3).

Effects of Other Magnesium or Sulfate Compounds. No bean seeds treated with other magnesium or sulfate-containing compounds were preferred in choice tests, although some proved to be neutral. The sulfate moiety alone slightly depressed egg-laying (Table 3).

Effects of Magnesium Sulfate Administered to Various Oviposition Substrates. Generally, preference for other magnesium sulfate-treated leguminous seeds and for treated bean seed coat pills increased (Table 4). In spite of the magnesium treatment, indifferent substrates (e.g., glass beads, starch pills) were not preferred. Females laid significantly ($P = 0.5\%$) more eggs on peeled halved bean cotyledons treated with magnesium sulfate (Table 4).

Results of Behavioral Experiments. No specific behavior related to magnesium sulfate treatment was observed. The exploratory phase comprising palpation, chewing into and around the hilum, etc., as well as preoviposition and egg deposition phases, all seemed to be performed in the same manner on magnesium-treated and control beans.

Free access to 10 or 100 magnesium sulfate/ml honey–water did not result in a decrease of moving activity during the nine days of observation (Table 5).

TABLE 2. EGG-LAYING RESPONSE OF *A. obtectus* FEMALES TO EXPOSURES AND TREATMENTS OF 111 mM MAGNESIUM SULFATE ON DRY BEANS IN BINARY CHOICE TESTS (N = 9–14)

Treatments and exposure	DQ[a] (% ± SD)	Level of significance (%)
Treatments		
Warm airstream	+32 ± 12a[b]	0.5[c]
Cold airstream	+36 ± 18a	0.5
Duration of treatment		
1 min	+25 ± 17A	0.5
5 min	+4 ± 17B	NS
10 min	−8 ± 16B	NS
Exposure to treated seeds for		
2 days	+30 ± 16a	0.5
4 days	+28 ± 10a	0.5
6 days	+37 ± 13a	0.5
8 days	+32 ± 13a	0.5
10 days	+30 ± 19a	0.5

[a] Discrimination quotient (David and van Herrewage, 1970).
[b] Means in the column followed by the same lower- or uppercase letters are not significantly different at the 1% probability level (DNMR test for ESS).
[c] Denotes statistical comparison with own control and *not* within column (Wilcoxon's signed-ranks test by paired values of eggs laid).

TABLE 3. EGG-LAYING RESPONSES BY *A. obtectus* FEMALES TO MAGNESIUM COMPOUNDS, IMPURITY LEVELS OF MAGNESIUM SULFATE, AND INORGANIC SULFATES ON DRY BEANS IN BINARY CHOICE TESTS (CONC. 111 mM, N = 9–19)

Compounds	DQ[a] (% ± SD)	Level of significance (%)
Magnesium compounds		
Sulfate	+22 ± 14	0.5[b]
Hydroxide	0 ± 15	NS
Fluoride	−6 ± 13	0.5
Chloride	−14 ± 11	0.5
Nitrate	−46 ± 15	0.5
Citrate	−34 ± 15	0.5
Impurities of magnesium sulfate		
analytical vs. technical grade	+5 ± 17	NS
Inorganic sulfates		
Sulfuric acid (pH 5.5)	−14 ± 13	0.5
Nickel	−2 ± 20	NS
Zinc	−36 ± 14	1.0
Barium	−19 ± 19	2.5

[a] See Table 2 for explanation.
[b] Denotes statistical comparison with the own control, but *not* within column (Wilcoxon's signed-rank test calculated by the paired values of eggs laid).

TABLE 4. EGG-LAYING RESPONSES OF *A. obtectus* FEMALES TO MAGNESIUM SULFATE-TREATED SUBSTRATES IN BINARY CHOICE TESTS (CONC. 111 mM, $N = 7-10$)

Oviposition substrates	DQ[a] (% ± SD)	Level of significance (%)
Leguminous seeds + magnesium sulfate		
Dry beans	+22 ± 14	0.5[b]
Lentils	+33 ± 20	1.0
Peas	+20 ± 28	5.0
Soybeans	+6 ± 14	NS
Bean cotyledon (no testa)	+43 ± 15	0.5
Host constituents in pills + magnesium sulfate		
Bean seed coat	+38 ± 31	1.0
Bean pod	−11 ± 25	NS
Indifferent substrates + magnesium sulfate		
Starch pilules	−34 ± 12	2.5
Glass beads	−5 ± 53	NS

[a] See Table 2 for explanation.
[b] Denotes statistical comparisons with the own control, but *not* within column (Wilcoxon's signed-ranks test calculated by the paired values of eggs laid).

TABLE 5. MOVING ACTIVITY OF *A. obtectus* ADULTS AFTER VOLUNTARY AND FORCED UPTAKE OF MAGNESIUM SULFATE FROM DRINKING WATER (HONEY–WATER) ($N = 11-15$)

Solution	Moving activity (mean ± SD) per female per 15 min (observational units)	
	Free access	Forced uptake
10 mg magnesium/ml (untreated beans)	0.11 ± 0.09a	—
100 mg magnesium/ml (untreated beans)	0.09 ± 0.07a	0.11 ± 0.06A
Honey–water only (magnesium-treated beans)	0.12 ± 0.09a	—
Honey–water only (untreated beans)	0.11 ± 0.8a	0.19 ± 0.05B

a = NS; A and B = $P \ll 0.1\%$ (Student's t test, $t_{calc.} = 8.149$, $df = 118$).

The rate and amount of magnesium uptake by the females is unknown, although they were observed drinking honey–water containing the salt. Mortality was the same for all groups during the observation period.

"Forced" uptake of magnesium significantly decreased moving activity (Table 5). The number of eggs laid by the two groups were: 75.3 ± 2.5 (control) vs. 33.2 ± 6.1 ("magnesium-drunk") (mean ± SD) eggs per female ($P < 0.1\%$, Student's t test, $t_{calc.} = 14.08$, $df = 28$). High mortality (37.3 ± 11.8% vs. 3.0 ± 4.1%) occurred among "magnesium-drunk" adults by the third day of observation.

Mated females stayed significantly more frequently on magnesium-treated beans in choice tests. During 13 days, 200 females were found on 12,500 occasions on, under, or in the immediate vicinity of magnesium-treated beans vs. 7994 occasions on untreated ones ($P = 1\%$, Wilcoxon's signed-ranks test for paired observations). The egg-laying response reflected the same preference for magnesium-treated seeds [32.4 ± 14.7 (mean ± SD) vs. 26.6 ± 14.2 eggs, $P = 0.1\%$, $t_{calc.} = 3.43$, $N = 200$].

Adults that emerged from pills containing elevated magnesium during their larval development did not show any decreased level of moving activity following emergence.

DISCUSSION

Phytophagous insects live in a chemically extremely diverse milieu where a multitude of plant chemicals carry information. The principal components of this milieu are organic molecules. In contrast, inorganic substances are only very rarely the basic determinants of acceptance or rejection, although some insects do show characteristic responses to them (Dethier, 1968; Simpson, 1978). Earlier studies cited by Dethier (1953) on taste and oviposition perception of electrolytes by several species of insects, listed magnesium ions among the unacceptable cations, albeit not among the most unacceptable ones.

The experiments carried out in this study not only strengthened the earlier finding (Jermy and Szentesi, 1978), namely, that ovipositing females preferred magnesium-treated bean seeds, but they also revealed that a relatively wide (circa 100-fold) concentration range (4–330 mM) of magnesium sulfate "stimulated" egg-laying (Figure 1). Such direct stimulation by magnesium and other cations acting synergistically has been shown so far only in an egg-parasitoid (Nettles et al., 1982, 1983). Thus, this is the only known case of magnesium sulfate by itself enhancing oviposition of a phytophagous insect species.

The AAS analysis revealed that the distribution of magnesium is more or less specific in the host plant (Table 1). The results of whole seed analyses agree with data in the literature (see references in Table 1). Some plant parts (seed testa, pod, and stem) contain approximately twice as much magnesium as the whole seed and three times more than seed cotyledon alone. As bean weevil females come into contact with the seed coat during oviposition, the pronounced preference for the seed could be partially explained by the presence of this single influential factor, although other chemicals acting on the olfactory and gustatory systems, as well as shape or size, etc., of the oviposition substrate are also important (Avidov, 1965; Pouzat, 1974a,b, 1975; Szentesi, 1976).

As for the perception of magnesium deposits on the treated seeds, Chapman (1977) has shown that insect gustatory receptors can respond to solid substances. Uptake of magnesium deposits from the bean surface is likely to occur, since ejection and uptake of small quantities of saliva by the bean weevil, while examining the seed surface, can regularly be observed (Huignard, personal communication; Szentesi, unpublished). That magnesium ions might be able to bond to substances on the surface of dry seeds during surface treatment seems improbable. Binocular (and scanning electron) microscopic examinations have revealed no conspicuous changes on the surface of the treated seeds. A chemical alteration of the seed surface, although possible, is unlikely.

Treatment time did alter the oviposition response, namely, the longer the coating process took the less acceptable the seed became (Table 2). No explanation is suggested for this phenomenon. (Usual treatment time never exceeded 1 min.) The biased egg-laying response had occurred by two days and did not show a further change from then on (Table 2).

Other magnesium- or sulfate-containing compounds showed either oviposition inhibition, namely, the water-soluble ones, or were ineffective (the weakly or not soluble compounds) (Table 3). The anion moiety alone could not be responsible for the preference for magnesium sulfate, since sulfuric acid treatment and other sulfate-containing chemicals did not increase the acceptability of bean seeds (Table 3).

The females responded positively not only to treated dry beans, but also to other leguminous seeds following magnesium treatment. For instance, the ovipositional status of lentil, pea, and bean cotyledon devoid of testa, and pills incorporating bean seed coat improved relative to their own respective controls, although their suitability for egg-laying without magnesium treatment was relatively low (Table 4). On the other hand, although soybeans were relatively highly rated for oviposition by *A. obtectus* females (Jermy and Szentesi, 1978), magnesium sulfate treatment decreased this status. Starch pills, a poor egg-laying substrate were even inferior after magnesium treatment, while glass beads remained neutral in effect.

Direct observation of egg-laying females on magnesium sulfate-treated beans did not reveal any specific behavioral pattern related to the presence of this salt. However, an arrestant effect of magnesium sulfate was proven in choice tests in which females were found significantly more frequently staying on treated beans, resulting also in a significantly higher number of eggs laid on such seeds. This arrestment effect seems to support the notion that magnesium-treated bean seeds may function as a supernormal stimulus for the bean weevil females, as defined by Manning (1972). The natural magnesium content of seed testa, acting together with factors such as shape, specific organic substances, etc., provide the normal stimulus pattern, while an additional 20–40% increase of magnesium by treatment with the salt represents supernormality. As a result, in choice tests magnesium-treated seeds were more readily oviposited upon (Figure 1), while in a no-choice situation there was always the same number of eggs laid on both types of seeds. The latter merely refers to the maximum response possible and that magnesium sulfate alone does not stimulate egg-laying.

Supernormality presupposes a stimulus situation in which choice can be exercised, or in which essential stimuli (shape, size, coloration, etc.) are strongly emphasized (McFarland, 1981). Although, such exaggerated behavioral responses are mostly documented in insects to visual stimuli (Prokopy, 1969; Magnus, 1958), the case reported here may indicate the effect of a supernormal chemical stimulus.

The above reasoning does not exclude another explanation on physiological grounds considering that, during thorough palpation and "licking" of the treated surface, some magnesium sulfate must be ingested. Considering the many important roles of magnesium in a living organism (Bara, 1977; Aikawa, 1981; Levine and Coburn, 1984; Ferment and Touitou, 1985), it has been shown that excess magnesium ions might depress both neuromuscular and other types of synaptic transmission, as shown in insects by Hoyle (1955), Callec (1974), Fukami et al. (1984); in mollusks by Burton et al. (1987); and in vertebrates by del Castillo and Engbaek (1954), Ault et al. (1980), Artemenko and Gerasimov (1984), and others. The depression would then result in a low propensity to move. However, an observable reduction in moving activity was found only when adults of *A. obtectus* were forced to take up magnesium sulfate with drinking water (Table 5) and not in the case of free access to magnesium-containing drinking water or when having developed in pills with elevated salt concentration. Nevertheless, it cannot be excluded that a very slight decrease in propensity to move, which may easily escape direct observation, may result in longer stays on treated beans, i.e., in increased number of eggs laid on them. This is the more likely since the behaviorally active doses that were applied in the study were well within the range found effective in other studies (e.g., Nettles et al., 1982, 1983; del Castillo and Engbaek, 1954).

CONCLUSIONS

The preference of egg-laying by *A. obtectus* females for magnesium sulfate-treated beans can be explained partly by the two hypotheses, although the functioning of magnesium sulfate as a supernormal chemical stimulus seems more probable. It is also likely that females do not find a situation in nature where such a preference could be exercised; therefore, the adaptive significance of the behavior is highly questionable. However, a possible implication would be that an increase of magnesium concentration in the hemolymph or blood of hibernating or overwintering animals provides a means of freeze-resistance (Aikawa, 1981). Magnesium uptake by bean weevil adults could serve a similar purpose as they also hibernate as adults. However, both hypotheses and, especially, the latter speculation would need further investigation to clarify the details sufficiently.

Acknowledgments—I thank Drs. T. Jermy (Budapest, Hungary), J. Huignard (Tours, France), and W. Blaney (London, U.K.) for comments and suggestions and for grammatical correction of the manuscript; J. Koncz for carrying out the AAS analysis; and Mrs. M. Mydlo and T. Tihanyi for valuable assistance.

REFERENCES

AIKAWA, J.K. 1981. Magnesium: Its Biologic Significance. CRC Press, Boca Raton, Florida.

ARTEMENKO, D.P., and GERASIMOV, V.D. 1984. Effect of magnesium and calcium ions on adenosin-induced blockade of synaptic transmission in isolated hippocampal slices of the rat. *Neirofiziologiia*, 16:532–539 (in Russian).

AULT, B., EVANS, R.H., FRANCIS, A.A., OAKES, D.J., and WATKINS, J.C. 1980. Selective depression of excitatory amino acid induced depolarizations by magnesium ions in isolated spinal cord preparations. *J. Physiol.* 307:413–428.

AVIDOV, Z., BERLINGER, M.J. and APPLEBAUM, S.W. 1965. Physiological aspects of host specificity in the Bruchidae: III. Effect of curvature and surface area on oviposition of *Callosobruchus chinensis* L. *Anim. Behav.* 13:178–180.

BARA, M. 1977. Magnésium et membranes. *Ann. Biol.* 16:289–315.

BASKY, Z. 1977. Babzsizsik (*Acanthoscelides obtectus* Say) tenyésztési kisérletek szójamagvakon. (Experiments to rear the bean weevil, *A. obtectus*, on soybean seeds.) *Növényvédelem* 13:14–18 (in Hungarian).

BURTON, R.F., MORRISON, S.M., and DOUGLAS, A.M. 1987. Some effects of injected magnesium chloride in the snail, *Helix aspersa:* Narcosis, magnesium distribution and responses to infused potassium. *Comp. Biochem. Physiol.* 86A:113–116.

CALLEC, J.-J. 1974. Synaptic transmission in the central nervous system of insects, pp. 119–185, *in* J.E. Treherne (ed.). Insect Neurobiology. North-Holland Publ., Amsterdam.

CHAPMAN, R.F. 1977. The role of the leaf surface in food selection by acridids and other insects. *Coll. Int. CNRS* 265:133–149.

DAVID, J., and VAN HERREWAGE, B.O.C. 1970. Choix d'un site de ponte chez *Drosophila melanogaster:* Technique d'étude et variabilité. *Rev. Comp. Anim.* 4:82–84.

DEL CASTILLO, J., and ENGBAEK, L. 1954. The nature of the neuromuscular block produced by magnesium. *J. Physiol.* 124:370–384.

DETHIER, V.G. 1953. Chemoreception. pp. 544–576, *in* K.D. Roeder (ed.). Insect Physiology. John Wiley & Sons, New York.

DETHIER, V.G. 1968. Chemosensory input and taste discrimination in the blowfly. *Science* 161:389–391.

FERMENT, O., and TOUITOU, Y. 1985. Magnesium: metabolism and hormonal regulation in different species. *Comp. Biochem. Physiol.* 82A:753–758.

FUKAMI, J.-I., USUI, T., and SHIMIZU, T. 1984. Supressive effect of magnesium ions on the peristalsis of the gut of the American cockroach, *Periplaneta americana* L. (Orthoptera: Blattidae). *Appl. Entomol. Zool.* 19:259–260.

HOYLE, G. 1955. The effects of some common cations on neuromuscular transmission in insects. *J. Physiol.* 127:90–103.

JERMY, T., and SZENTESI, Á. 1978. The role of inhibitory stimuli in the choice of oviposition site by phytophagous insects. *Entomol. Exp. Appl.* 24:458–471.

LEVINE, B.S., and COBURN, J.W. 1984. Magnesium, the mimic/antagonist of calcium. *N. Engl. J. Med.* 310:1253–1255.

MAGNUS, D. 1958. Experimentelle Untersuchungen zur Bionomie und Ethologie des Kaisermantels *Argynnis paphia* L. (Lep. Nymph.), I. Über optische Auslöser von Auffliegereaktionen und ihre Bedeutung für das Sichfinden der Geschlechter. *Z. Tierpsychol.* 15:397–426 (in German).

MÁNDY, G., SZABÓ, L., and ÁCS, A. 1980. A borsó. *Pisum sativum* L. (The pea.) *Magyarország Kultúrflórája,* 3(17):170 (in Hungarian).

MANNING, A. 1972. An Introduction to Animal Behaviour. Edward Arnold, London.

MCFARLAND, D. (ed.). 1981. The Oxford Companion to Animal Behaviour. Oxford University Press, Oxford.

MUSCHINEK, G., SZENTESI, Á., and JERMY, T. 1976. Inhibition of oviposition in the bean weevil (*Acanthoscelides obtectus* Say, Col., Bruchidae). *Acta Phytopathol. Acad. Sci. Hung.* 11:91–98.

NEHRING, K., BEYER, M., and HOFFMAN, B. 1972. Futtermittel-Tabellenwerk. VEB D. Landw. Verlag, Berlin.

NETTLES, W.C., Jr., MORRISON, R.K., XIE, Z.-N., BALL, D., SHENKIR, C.A., and VINSON, S.B. 1982. Synergistic action of potassium chloride and magnesium sulfate on parasitoid wasp oviposition. *Science* 218:164–166.

NETTLES, W.C., Jr., MORRISON, R.K., XIE, Z.-N., BALL, D., SHENKIR, C.A., and VINSON, S.B. 1983. Effects of cations, anions and salt concentrations on oviposition by *Trichogramma pretiosum* in wax eggs. *Entomol. Exp. Appl.* 33:283–289.

POUZAT, J. 1974a. Comportement de la bruche du haricot femelle, *Acanthoscelides obtectus* Say (Col., Bruch.), soumises à différents stimulus olfactifs: mâle, plante-hôte. *C.R. Acad. Sci. Paris* 278:2173–2176.

POUZAT, J. 1974b. Electro-antennogrammes de bruches du haricot femelle (*Acanthoscelides obtectus* Say, Col., Bruch.), soumises à différents stimulus olfactifs (dont la plante-hôte, le haricot et le mâle). *C.R. Acad. Sci. Paris* 278:2323–2326.

POUZAT, J. 1975. Analyse experimentale du role de l'ovitube dans le comportement de ponte de la bruche du haricot (*Acanthoscelides obtectus* Say—Coleoptera, Bruchidae). *Behaviour* 54:258–277.

PROKOPY, R.J. 1969. Visual responses of European cherry fruit—*Rhagoletis cerasi* L. (Diptera, Tephritidae). *Pol. Pismo Entomol.* 39:539–566.

RABOY, V., DICKINSON, D.B., and BELOW, F.E. 1984. Variation in seed total phosphorus, phytic acid, zinc, calcium, magnesium, and protein among lines of *Glycine max* and *G. soja. Crop Sci.* 24:431–434.

SIMPSON, S.J. 1978. An analysis of compounds influencing larval feeding behaviour in *Lucilia cuprina* (Wied.). BSc thesis, University of Queensland, Australia.

SOKAL, R.R. and ROHLF, F.J. 1969. Biometry. W.H. Freeman, San Francisco.

SPECTOR, W.S. 1956. Handbook of Biological Data. W.B. Saunders, Philadelphia.

STEEL, R.G.D., and TORRIE, J.H. 1960. Principles and Procedures of Statistics. McGraw-Hill, New York.

SZABÓ, L.G. (ed.). 1980. A magbiológia alapjai. (An Introduction to the Biology of Seeds.) Akadémia Kk., Budapest (in Hungarian).

SZENTESI, Á. 1972. Studies on the mass rearing of *Acanthoscelides obtectus* Say (Col., Bruchidae). *Acta Phytopathol. Acad. Sci. Hung.* 7:453–463.

SZENTESI, Á. 1976. The effects of the amputation of head appendages on the oviposition of the bean weevil, *Acanthoscelides obtectus* Say (Coleoptera: Bruchidae). *Symp. Biol. Hung.* 16:275–281.

SZENTESI, Á. 1983. Inhibition of oviposition and the boring of larvae into seeds in *Acanthoscelides obtectus*: Laboratory tests. *Proc. Int. Conf. Integr. Plant Prot.* 4:176–182.