

EFFECTS OF DROUGHT STRESSED COTTON ON BEET ARMYWORM OVIPOSITION PREFERENCE AND LARVAL GROWTH

A.T. Showler

Kika de la Garza Subtropical Agricultural Research Center
USDA-ARS
Weslaco, TX

Abstract

The beet armyworm, *Spodoptera exigua* (Hübner), has been anecdotally reported to lay more eggs on drought stressed cotton plants than on non-stressed cotton plants. This study demonstrated that, using potted cotton plants grown in well watered conditions, and on water-deficit regimes of 1,500, 1,000, and 750 ml water/wk, beet armyworms deposited 3.3, 4.6, and 2.3 times more ($P < 0.05$) eggs on plants in the three respective water deficit regimes in a cage choice assay than on the well watered cotton plants. Third instars raised on the well watered cotton plants were 1.5, 2.3, and 2.6 times heavier than those raised on cotton plants grown in the 1,500, 1,000, and 750 ml water/wk regimes ($P < 0.05$), respectively. Pupal weights followed the same trend ($P < 0.05$). Although beet armyworms preferred to oviposit on water deficit stressed cotton plants, the larvae fared poorly.

Introduction

The beet armyworm, *Spodoptera exigua* (Hübner), originated in southern Asia and was introduced to the United States in 1876 (Wilson 1932). It is known to feed on more than 50 plant species from over 10 families worldwide (Wilson 1932, Smits et al. 1987). In cotton, the beet armyworm can be economically important especially when pesticide applications disrupt populations of natural enemies (Eveleens et al. 1973).

Showler (2001) reported that the nutritive value of host plants, based to some extent on foliar free amino acid diversity and abundances, appeared to play a role in the beet armyworm's selection of pigweed, *Amaranthus hybridus* L., over cotton, *Gossypium hirsutum* L., for oviposition and feeding by third instars. Drought stress is associated with higher populations of some herbivorous insects on plant foliage (White 1984, McQuate and Connor 1990), and leaves are often sinks for elevated levels of nutritious compounds, including free amino acids and soluble proteins (Brodbeck and Strong 1987, Shen et al. 1989, Showler 2002). Host plant free amino acid accumulations have been associated with greater numbers of some phytophagous nematodes (Showler et al. 1990) and arthropods (Jayaraj and Seshadri 1967, Blua et al. 1994).

Beet armyworm eggs have been anecdotally reported as being most abundant on water deficit stressed cotton plants in fields (Ruberson et al. 1994, Ruberson 1996). Feeding behaviors of tobacco budworm, *Heliothis virescens* (F.); corn earworm, *Heliothis armigera* (Hübner); and *Spodoptera littoralis* (Boisduval) adults were correlated with the electrophysiological response of sensilla on the proboscis. Responses of the sensilla to amino acids and sugar were correlated with feeding behavior of each of these species (Blaney and Simmonds 1988). However, Huffman and Mueller (1983) found no differences between levels of beet armyworm larval establishment in irrigated and dryland soybean, *Glycine max* (L.) Merr. The purpose of this study is to determine the relationships of water deficit stressed cotton plants on beet armyworm oviposition preference and larval growth.

Materials and Methods

All assays in this study involved cotton plants (var. C-208) grown in a greenhouse in 7.6-liter pots with Sunshine™ mix no. 1 nursery potting soil (~ 75% sphagnum peat moss, perlite, dolomitic limestone, and gypsum; Sungro Horticulture, Bellevue, Washington) in late 2001 and spring of 2002 at the USDA-ARS Kika de la Garza Subtropical Agricultural Research Center, Weslaco, TX. Seedlings were thinned to three per pot at the cotyledon stage and 200 ml of Peters Professional® (Scotts-Sierra Horticultural Products Company, Marysville, Ohio) water soluble general purpose 20-20-20 N-P-K fertilizer at 15.8 g/liter of water was applied to each pot at the two true leaf stage. All pots were irrigated with one liter of water once every week until the cotton plants reached the four true leaf stage. Then, four groups of 20 pots/group were maintained on separate irrigation regimes: 4,000 ml water/wk (saturation), 1,500 ml/wk, 1,000 ml/wk, and 750 ml/wk, each delivered at one time per week. All of the pots were placed in 4-cm deep plastic dishes to retain any water that might have run through the soil and out the holes in the bottoms of the pots.

After eight weeks, when the cotton plants had reached the 7-mm diameter stage, measurements of stem diameters 6 cm above the soil surface and plant heights were taken on 25 randomly selected cotton plants in each treatment. Twenty upper (top four fully expanded) leaves, from separate unsampled plants in each treatment were excised and their water potentials were measured with a Model 610™ (PMS Instrument Co., Corvallis, Oregon) pressure bomb.

Beet armyworm larvae in this and all other assays were obtained from a laboratory colony at the USDA-ARS SARC, and reared on a soybean-wheat germ diet (Shaver and Raulston 1971). The insects were maintained in environmental chambers at 30°C, 85% relative humidity, and 13L:11D photoperiod. Pupae were sexed and placed in individual cups until adult emergence. On the day of emergence, females were paired individually with single males in 0.5-liter cardboard containers. The next day, females were placed alone in a container lined with wax paper as oviposition substrate. Each container was monitored daily for the appearance of the first egg cluster, which signified the presence of a gravid female moth. Different females were used for each replication.

Gravid beet armyworm females were provided a choice between one well watered pot of cotton plants and another pot of cotton grown on 1,500, 1,000, or 750 ml water per week in 1.8 by 1.8 by 1.1-m cages. Since maximum egg laying occurs during the first and second nights of oviposition activity (Fye and McAda 1972), only females that had initiated oviposition activity on the previous night were used in this assay. One gravid beet armyworm female was placed in each cage and allowed to oviposit for 48 hr, then each plant, and the inner cage and outer pot surfaces were inspected for egg clusters. Each of the three sets of choices was replicated 35 times.

In another assay, wax paper was used as a substrate for female beet armyworms to deposit eggs. The wax paper was cut with a razor blade so that there were 25-30 eggs on 3 by 3 cm pieces of wax paper. Thirty pots of cotton plants were grown on the four irrigation regimes. One square of wax paper with beet armyworm eggs was stapled to one upper cotton leaf on a cotton plant in each of the 30 pots. When the eggs hatched, the larvae were allowed to feed on the cotton plants until pupation. Surviving third instars were weighed and pupae were dug from the potting soil and weighed.

Statistical differences between treatment means were determined using one way ANOVA for the cotton plant phenology measurements, and the larval development assay data, and the means were separated using Tukey's HSD. The oviposition preference choice assays were analyzed with the χ^2 test, but the numbers of eggs per cluster were analyzed using the two sample t test (Analytical Software 1998).

Results

Cotton plant stem diameters and plant heights grown in well watered conditions were ≥ 1.2 ($F = 24.67$; $df = 3, 96$; $P < 0.001$) and ≥ 1.2 ($F = 50.07$; $df = 3, 96$; $P < 0.001$) times greater, respectively, than any of the three water deficit regimes (Table 1). Leaf water potentials in the four treatments were significantly different from one another ($F = 1025.74$; $df = 3, 76$; $P < 0.001$). The 750 ml water/wk leaf water potentials were 1.1, 2.7, and 3.1 times higher than leaf water potentials in the 1,000 and 1,500 ml water/wk and the well watered regimes, respectively (Table 1).

Beet armyworm eggs on the 1,500, 1,000, and 750 ml water/wk cotton plants were 3.3, 4.6, and 2.3 times, respectively, more abundant ($P \leq 0.05$) than on the well watered cotton plants (Table 3). Also, egg clusters on the cotton plants in the three water deficit regimes were 2.5, 5.8, and 1.6 times, respectively, more numerous ($P \leq 0.05$) than on the well watered cotton plants, but treatment effects on the numbers of eggs per cluster were not detected (Table 2). Differences in the numbers of egg clusters found on the cage walls and plant pots were also not detected.

Third instar beet armyworms raised on the well watered cotton plants were 1.5, 2.3, and 2.6 times ($F = 251.92$; $df = 3, 100$; $P < 0.001$) heavier than third instars raised on the 1,500, 1,000, and 750 ml water/wk cotton plants, respectively (Table 3). Pupae in the well watered regime were 1.3, 1.5, and 1.7 times ($F = 27.46$, $df = 3, 96$, $P < 0.001$) heavier than the pupae in the 1,500, 1,000, and 750 ml water/wk regimes, respectively (Table 3). Larval mortalities, observed as mostly resulting from cannibalism, occurred at rates that were not significantly different between treatments.

Discussion

Anecdotal reports of greater numbers of beet armyworm eggs on drought stressed cotton than on non-stressed plants (Ruberson et al. 1996, Ruberson 1996) are supported by the findings of this study. Infestations of some herbivore pest arthropod species are associated with crop plants growing under some degree of drought stress (White 1984). Foliar FAAs, especially those that are essential for insect growth and development (Vanderzant 1958), are readily available for utilization by leaf feeding insects, being unbound to more complex molecules such as proteins and presumably saving energy costs associated with proteolysis (Helms et al. 1971, Brodbeck and Strong 1987).

Responses of the proboscis sensilla to amino acids and sugar were correlated to feeding behavior in three noctuid species (Blaney and Simmonds 1988). Assuming that beet armyworms can detect amino acids, that such detection has a role in determination of host plants for oviposition, greater levels of important unbound amino acids helped to explain the beet armyworm's preference for oviposition on pigweed, *Amaranthus hybridus* L., which has greater quantities and diversity of free amino acids than cotton (Showler 2001). Severe drought stress, however, can reduce the nutritional quality of the host plant

(Rhoades 1983) and this could negatively influence oviposition by some lepidopterans. It has been suggested that improved host plant quality and altered crop environment, as when irrigation is used during conditions of drought, may influence oviposition behavior by some insects (Wolfson 1982, Myers 1985).

The beet armyworm larvae in our study developed poorly and mortality was greater on the water deficit stressed cotton plants than on the well watered controls. Similarly, cecropia moth, *Hyalophora cecropia* L., larvae reared on drought stressed wild cherry, *Prunus serotina* Ehrh., leaves grew more slowly and were less efficient at utilizing plant biomass, energy, and nitrogen than larvae fed on plants fully supplemented with water (Scribner 1977). It was suggested that the cecropia larvae were more desiccated, and metabolized greater portions of assimilated energy, perhaps to supplement body water with metabolic water derived from respiration. This also helps to explain why the cecropia larvae's increasing consumption rate of the drought stressed leaves did not increase their growth rates. Also, fall armyworm, *Spodoptera frugiperda* (J. E. Smith), soybean looper, *Pseudoplusia includens* (Walker), and beet armyworm larval survivorships were higher in irrigated than dryland soybean, and development was faster (Huffman and Mueller 1983, Felland and Pitre 1991), though the degree of water deficit stress to the soybeans were not assessed.

This study demonstrates that when given a choice between drought stressed and non-stressed cotton plants, the beet armyworm prefers stressed plants for oviposition, but the larvae fare poorly on the stressed plants. Berdegué et al. (1998) showed that beet armyworm choice of oviposition host is not necessarily governed by the nutritional quality of host plants. The incongruity between some of the beet armyworm's choices of host plants for its progeny can be explained by the absence of evolutionary time to select away from detrimental behavior (Thompson 1988). Both cotton and the beet armyworm were introduced to the United States (Wilson 1932, Reynolds et al. 1975), and despite cotton's chemical defenses (e.g., gossypol) against herbivorous arthropods (Hedin et al. 1991), the beet armyworm will oviposit on it even in the presence of a nutritionally superior and less toxic host plant (Ali and Gaylor 1992, Showler 2001).

Acknowledgments

Thanks to Jaime Cavazos, Raúl Cantú, Martín Porras, Raúl Vallejo, Daniel de la Fuentes, and Martín Avila for technical assistance, and to Mamoudou Sétamou and Tong-Xian Liu for critical reviews.

References

- Ali, A. and M.J. Gaylor. 1982. Effects of temperature and larval diet on development of the beet armyworm (Lepidoptera: Noctuidae). *Environ. Entomol.* 4:780-786.
- Analytical Software. 1998. Statistix for Windows. Analytical Software, Tallahassee, FLA.
- Berdegué, M, S.R. Reitz and J.T. Trumble. 1998. Host selection and development in *Spodoptera exigua*: do mother and offspring know best? *Entomol. Exp. Appl.* 89:57-64.
- Blaney, W.M. and M.S.J. Simmonds. 1988. Food selection in adult and larvae of three species of Lepidoptera: a behavioral and electrophysiological study. *Entomol. Exp. Appl.* 49:111-121.
- Blua, M.J., T.M. Perring and M.A. Madore. 1994. Plant virus-induced changes in aphid population development and temporal fluctuations in plant nutrients. *J. Chem. Ecol.* 20:691-707.
- Brodbeck, B. and D. Strong. 1987. Amino acid nutrition of herbivorous insects and stress to host plants, pp. 346-364, in P. Barbosa and J. C. Schultz (eds.), *Insect Outbreaks*. Academic Press, London.
- Eveleens, K.G., R. Van Den Bosch and L. Ehler. 1973. Secondary outbreak induction of beet armyworm by experimental insecticide applications in cotton in California. *Environ. Entomol.* 2: 497-503.
- Felland, C. M. and H.M. Pitre. 1991. Survivorship and development of noctuid larvae (Lepidoptera: Noctuidae) on irrigated and dryland soybean. *Environ. Entomol.* 20:1315-1321.
- Fye, R.E. and W.C. McAda. 1972. Laboratory studies on the development, longevity, and fecundity of six lepidopterous pests of cotton in Arizona. USDA Technical Bulletin, no. 1454.
- Hedin, P.A., W.L. Parrott and J.W. Jenkins. 1991. Effects of cotton plant allelochemicals and nutrients on behavior and development of tobacco budworm. *J. Chem. Ecol.* 17:1107-1121.

- Helms, J.A., F.W. Cobb, Jr. and M.S. Whitney. 1971. Effect of infection by *Verticicladdella wagnerii* on the physiology of *Pinus ponderosa*. *Phytopathol.* 61:920-925.
- Huffman, F.R. and A.J. Mueller. 1983. Effects of beet armyworm (Lepidoptera: Noctuidae) infestation levels on soybean. *J. Econ. Entomol.* 76:744-747.
- Jayaraj, S. and A.R. Seshadri. 1967. Preference of the leafhopper *Empoasca kerri* Pruthi (Homoptera: Jassidae) to pigeon pea [*Cajanus cajan* (L.) Milsp.] plants infected with sterility mosaic virus. *Curr. Sci.* 36:353-355.
- McQuate, G.T. and E.F. Connor. 1990. Insect responses to plant water deficits. 1. Effect of water deficits in soybean plants on the feeding preference of Mexican bean beetle larvae. *Ecol. Entomol.* 15:419-431.
- Myers, J.H. 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae*. *J. Anim. Ecol.* 54:193-204.
- Reynolds, H.T., P.L. Adkisson and R.F. Smith. 1975. Cotton pest management, pp. 379-443, in R.L. Metcalf and W.H. Luckman (eds.). *Introduction to Insect Pest Management*. John Wiley & Sons, New York.
- Rhoades, D.F. 1983. Herbivore population dynamics and plant chemistry, pp. 155-220, in R.F. Denno and M.S. McClure (eds.), *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York, NY.
- Ruberson, J.R. 1996. Environmental conditions and biological control of the beet armyworm, pp. 116-118, in *Proc. Beltwide Cotton Conf., Natl. Cotton Council, Memphis, Tennessee*.
- Ruberson, J.R., G.A. Herzog, W.R. Lambert and W.J. Lewis. 1994. Management of the beet armyworm: integration of control approaches, pp. 857-858, in *Proc. Beltwide Cotton Conf., Natl. Cotton Council, Memphis, Tennessee*.
- Scribner, J.M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hylophora cecropia*. *Oecologia* 28:269-287.
- Shaver, T.N. and J.R. Raulston. 1971. A soybean-wheat germ diet for rearing the tobacco budworm. *Ann. Entomol. Soc. Amer.* 64:1077-1079.
- Shen, L., J.G. Foster and D.M. Orcutt. 1989. Composition and distribution of free amino acids in flatpea (*Lathyrus sylvestris* L.) as influenced by water deficit and plant age. *J. Exp. Bot.* 40:71-79.
- Showler, A.T., T.E. Reagan and P.K. Shao. 1990. Nematode interactions with weeds and sugarcane mosaic virus in Louisiana sugarcane. *J. Nematol.* 22:31-38.
- Showler, A.T. 2001. *Spodoptera exigua* oviposition and larval feeding preferences for pigweed, *Amaranthus hybridus*, over squaring cotton, *Gossypium hirsutum*, and a comparison of free amino acids in each host plant. *J. Chem. Ecol.* 27:2013-2028.
- Showler, A.T. 2002. Effects of water deficit stress, shade, weed competition, and kaolin particle film on selected foliar free amino acid accumulations in cotton, *Gossypium hirsutum* (L.). *J. Chem. Ecol.* 28:615-635.
- Smits, P.H., M.C. Van Velden, M.C. Van Devrie and J.M. Vlak. 1987. Feeding and dispersion of *Spodoptera exigua* larvae and its relevance for control with a nuclear polyhedrosis virus. *Entomol. Exp. Appl.* 43:67-72.
- Thompson, J.N. 1988. Evolutionary ecology of the relationship between oviposition preference and quantitative analysis of the volatile substances emitted by maturing cotton in the field. *Entomol. Exp. Appl.* 47:3-14.
- Vanderzant, E.S. 1958. The amino acid requirements of the pink bollworm. *J. Econ. Entomol.* 51:309-311.
- White, T.C.R. 1984. The abundance of invertebrate herbivories in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63:90-105.
- Wilson, J.W. 1932. Notes on the biology of *Laphrygma exigua* Hübner. *Fla. Entomol.* 16:33-39.
- Wolfson, J. L. 1982. Developmental response of *Pieris rapae* and *Spodoptera eridania* to environmentally induced variation in *Brassica nigra*. *Environ. Entomol.* 11:207-213.

Table 1. Cotton plant stem diameters, numbers of stem nodes and leaves, heights, grams leaf water/dry leaf biomass, and leaf water potentials of cotton plants grown in continuously well watered (4,000 ml/wk) potting soil, and 1,500, 1000, and 750 ml water/wk.

Treatment	Stem diameter (cm) ^a	Plant height (cm) ^b	Water potential (barr) ^c
Well watered	6.4 ± 0.1 a	45.7 ± 0.6 a	10.1 ± 0.1 d
1,500 ml/wk	5.2 ± 0.1 b	37.9 ± 0.7 b	11.8 ± 0.2 c
1,000 ml/wk	5.2 ± 0.2 b	34.7 ± 1.1 c	29.4 ± 0.5 b
750 ml/wk	4.9 ± 0.1 b	32.6 ± 0.8 c	31.3 ± 0.4 a

Means followed by different letters in the same column are significantly different ($P \leq 0.05$). Cotton plants were at the 7 – 10 mm square diameter square stage when the plants were eight weeks old.

^aStem measurements were taken 6 cm from the soil level, $n = 25$.

^b $n = 25$.

^cLeaves taken from the top four fully expanded leaves, $n = 20$.

Table 2. Mean numbers (\pm SE) of eggs, clusters, and eggs/cluster oviposited by beet armyworms on cotton plants grown in continuously well watered potting soil, and 1,500, 1,000, and 750 ml water/wk.

Choice	Eggs ^a	Clusters ^a	Eggs/cluster ^b
Well watered	41.3 ± 10.4	0.8 ± 0.2	59.0 ± 5.9
1,500 ml/wk	137.2 ± 16.6	2.0 ± 0.3	77.7 ± 7.9
χ^2	4,057.8	65.16	
t			1.89
P	0.001	< 0.001	0.064
Well watered	37.5 ± 9.9	0.5 ± 0.1	66.9 ± 4.2
1,000 ml/wk	170.9 ± 23.6	2.9 ± 0.4	75.1 ± 9.8
χ^2	3,189.0	49.51	
t			0.77
P	< 0.001	0.049	0.445
Well watered	52.5 ± 11.3	1.0 ± 0.2	58.8 ± 4.1
750 ml/wk	122.2 ± 25.0	1.6 ± 0.3	95.1 ± 20.9
χ^2	4,741.8	64.37	
t			1.71
P	< 0.001	0.013	0.094

^a $n = 35$.

^b $n = 25$.

Table 3. Third instar and pupal beet armyworm mean weights and lengths (\pm SE) after being raised from eggs on cotton grown on continuously well watered potting soil, and 1,500, 1,000, and 750 ml water per week.

Treatment	Larval weight (g)	Pupal weight (g)
Well watered	0.02 ± 0.0005 a	0.11 ± 0.004 a
1,500 ml/wk	0.01 ± 0.0003 b	0.08 ± 0.003 b
1,000 ml/wk	0.009 ± 0.0002 c	0.07 ± 0.003 bc
750 ml/wk	0.008 ± 0.0003 c	0.06 ± 0.003 c

Means followed by different letters in the same column are significantly different ($P \leq 0.05$); means not followed by different letters are not significantly different, larvae $n = 26$, pupae $n = 25$.