

IMPACT OF THE MIRID BUG *CAPSODES INFUSCATUS*  
(HEMIPTERA: MIRIDAE) ON FRUIT PRODUCTION OF THE  
GEOPHYTE *ASPHODELUS AESTIVUS*: THE EFFECT OF  
PLANT DENSITY

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ABSTRACT

The leaf, stalk, flower, and fruit of the geophyte *Asphodelus aestivus* Brot. (Liliaceae) in east Mediterranean mesic habitats are mainly attacked by the monophagous mirid bug *Capsodes infuscatus* Brulle (Hemiptera: Miridae). The sexual reproductive performance of *A. aestivus* was examined under natural levels of insect herbivory at three different host densities at the same site. Plants in the low and medium density plots were heavily attacked by *C. infuscatus* and failed to produce fruits, while plants from high density plots were less intensively attacked and produced some fruits. The observed inversely density-dependent damages are discussed with respect to plant compensation, population dynamics, and sexual vs. asexual reproduction.

Key Words: Insect herbivory, plant density, mirid bug, fruit production, geophyte, Israel

RESUMEN

La hoja, el tallo, la flor y el fruto de *Asphodelus aestivus* Brot. (Liliaceae) en el Mediterráneo Oriental son atacadas por el mirido monófago *Capsodes infuscatus* Brulle (Hemiptera: Miridae). La capacidad sexual reproductiva de *A. aestivus* fue examinada bajo niveles naturales de herbivoría por insectos a tres densidades diferentes de hospedante en el mismo lugar. Las plantas en las parcelas con densidades baja y media fueron fuertemente atacadas por *C. infuscatus* y no produjeron frutos, mientras que las plantas de parcelas con alta densidad fueron menos intensamente atacadas y produjeron algunos frutos. Los daños densodependientes observados son discutidos con respecto a la compensación de las plantas, dinámica de población y reproducción sexual vs. asexual.

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Crawley (1989) claimed that plants have more impact on the population dynamics of insects than insects have on the population dynamics of plants. In general, monophagous insects tend to have little impact on equilibrium plant abundance even when the insects are food-limited (Crawley 1983). However, several studies have suggested that herbivorous insects have a great impact on the evolution and population dynamics of plants (Blais 1983, Stalter & Serrao 1983, Twery & Patterson 1984, Berryman et al. 1985). In this case, herbivorous insects may reduce the reproductive success of their host-plants either by direct predation on flowers (e.g. Louda 1982, Hendrix & Trapp 1989) and seeds (e.g. Louda 1982) or indirectly by feeding on other plant parts such as foliage (e.g. Rausher & Feeny 1980) and roots (e.g. Gange & Brown 1989).

This study deals with the effects of a monophagous insect on the sexual reproductive success of its geophyte host in Mediterranean habitats. The female mirid bug, *Capsodes infuscatus* Brulle (Hemiptera: miridae), deposits eggs inside the inflorescence stalk of its host (*Asphodelus aestivus* Brot. = *A. microcarpus* Salzm. = *A. ramosus* Viv.) in spring. Developing nymphs as well as adults feed on this plant. Different structures of *A. aestivus* are consumed by the bugs including leaves, flower stalks, buds, flowers and fruits (Ayal & Izhaki 1993). *C. infuscatus* nymph feeding may kill young inflorescences, or suppress the development of the inflorescence branches and kill all its flowers while adult feeding may also kill green fruits (Ayal 1994). The geophytes also reproduce vegetatively and are distributed in clones (for more detailed description of plant phenology see Schuster et al. 1993, and for the life cycle of the bug see Ayal & Izhaki 1993).

Several authors reported that high-density host plants are subjected to greater herbivore attack than low-density plants (Dethier 1959; Orians et al. 1975). Under such circumstances, the herbivorous insect may regulate plant density. Other studies, however, point out that isolated plants have been attacked by more herbivorous insects than high-density stands (Pimental 1961, Heathcote 1969, Jones 1977). If this is true, insect attack may act to promote a local increase in plant density rather than to limit it (Rausher & Feeny 1980). In some cases there was no evidence to differentiate the degree of damage on the reproductive success between plants growing in high- and low-densities (e.g., Rausher & Feeny 1980).

The goals of this study were to: (a) estimate the damage to fruit production of the host-plant clones caused by *C. infuscatus* in its natural habitat, and (b) detect correlations between the clone density and the reduction in its reproductive success due to *C. infuscatus* feeding.

## MATERIALS AND METHODS

### Study Area

The study was conducted at the western end of Yizrael valley, 1 km south of Kiryat Tivon, Israel (32°42'N, 35°07'E, 100 m altitude). The annual mean temperature is 20°C, and the mean relative humidity is 75%. The mean annual precipitation is 600 mm, and there are 240 dew days per year (Atlas of Israel 1985). The 5000 m<sup>2</sup> study area was intensively grazed by sheep and goats before and during the study. However, these herbivorous domestic mammals did not consume *Asphodelus aestivus*, probably due to high amounts of secondary compounds in its tissues (Zohary 1962). Therefore, *A. aestivus* is common and locally dominant in large areas in the Mediterranean region which are now, and have been overgrazed for a long time (Schuster et al. 1993). The study began in December before the first nymph emerged and continued until the end of the fruiting season (March).

### Study Plots

The study area was covered by several patches of *A. aestivus* clones at different densities which were sampled along randomly-chosen transects. A total of 6 samples were taken at 30 m intervals along each of 5 transects. Each sample unit was 4 × 4 m. Clone density within the samples was categorized as: (a) low (<1 clone per m<sup>2</sup>), (b) medium (1-3 clones per m<sup>2</sup>) and (c) high (>3 clones per m<sup>2</sup>). We sampled until each of the above density categories was represented twice in each transect. Thus, 30 plots were established, 10 for each clone density. Each clone and inflorescence stalk in each plot

were marked and numbered. The diameter of each clone was measured at the beginning of the study and the surface area of each clone was calculated. The phenological status of *A. aestivus*, insect density, and damage were observed twice a month as described below.

#### Bug Density

When only a few bugs were present (<10 per plant), they were visually counted on the plant. When a large number of bugs were present, a 50 × 30 cm plastic tray was placed beneath each clone and the observer hit the clones until the bugs fell into the tray where they were counted. The bugs were relocated on the same clone immediately after counting. The average number of bugs per clone per plot was calculated and compared within each sample date among the three clone densities using one-way ANOVA followed by Duncan's Multiple Range Test ( $P < 0.05$ , SAS 1988).

#### Damage Estimation

*Leaves and flowers.* Damage to *A. aestivus* leaves was recorded for each clone and was classified into four categories: 0-no damage, 1-scattered yellow spots on the leaf area due to bug feeding, 2-the leaf end had turned yellow due to bug feeding, and 3-most of the leaf area had turned yellow due to bug feeding. The average damage category was calculated for each plot, for each date and was compared among the three densities by Kruskal-Wallis one-way ANOVA (SAS 1988).

During flowering, the number of *A. aestivus* inflorescences with flowers were counted and their proportion among all inflorescences in each plot was calculated. The mean proportion of flowering inflorescences was compared between the three densities by one-way ANOVA after arcsin square root transformation.

*Fruits.* Several *A. aestivus* clones without damage were randomly sampled at the end of the fruiting season for the number of fruits and the inflorescence stalk diam 5 cm above the ground. We assumed that the lack of attack in these plants did not represent differences in reproductive effort. On the basis of the correlation between stem diam and fruit production in these clones, a regression equation was established to predict the potential fruit production from the stalk diam. The diam of the inflorescence stalk from damaged plants in the study plots was recorded and the expected fruit production was calculated from this equation and compared to actual fruit production (Ayal & Izhaki 1993). Because fruit production in low and medium density plots was zero, this procedure was carried out for high clone density plots only. The difference between observed and predicted fruit production was used as an estimate of insect damage.

## RESULTS

#### Clone Density

The average number of *A. aestivus* clones per plot was significantly different between the three defined densities with 3.2 at low density plots, 20.8 at medium density and 73.6 at high density. The size of the clone in terms of the surface area it occupied on the ground, and the number of inflorescences per clone were independent of clone density (Table 1). However, the density of inflorescences at the high density plots was 15 and 3 times more than at the low and medium density plots, respectively.

TABLE 1. COMPARISON OF PLANT AND INFLORESCENCE DENSITY, FLOWERING, AND FRUIT PRODUCTION OF *A. AESTIVUS* IN THREE DIFFERENT CLONE DENSITIES. ALL RATIOS WERE ARCSIN SQUARE ROOT TRANSFORMED BEFORE STATISTICAL ANALYSIS.

	Plant Density Mean±SE <sup>1</sup>			df	F <sup>2</sup>
	Low n=10	Medium n=10	High n=10		
Number of clones per m <sup>2</sup>	0.2±0.03 <sup>c</sup>	1.3±0.12 <sup>b</sup>	4.6±0.31 <sup>a</sup>	2,26	228.6***
The area of clone (cm <sup>2</sup> )	1594±239 <sup>a</sup>	1082±125 <sup>a</sup>	1493±196 <sup>a</sup>	2,24	2.03 ns
Number of inflorescences per clone	4.0±0.8 <sup>a</sup>	3.1±0.1 <sup>a</sup>	2.9±0.6 <sup>a</sup>	2,24	0.77 ns
Number of inflorescences per m <sup>2</sup>	0.8±0.2 <sup>c</sup>	3.7±0.4 <sup>b</sup>	12.1±2.1 <sup>a</sup>	2,24	60.87***
Proportion of inflorescences with mature flowers	0.13±0.09 <sup>b</sup>	0.01±0.01 <sup>b</sup>	0.22±0.06 <sup>a</sup>	2,24	5.85**
Number of fruits per clone	0 <sup>a</sup>	0 <sup>a</sup>	5.4±4.6 <sup>a</sup>	2,26	2.11 ns

<sup>1</sup>Means followed by same letter in rows are not significantly different as determined by Duncan's Multiple Range Test (P<0.05).

<sup>2</sup>\*\*=0.01<P<0.05, \*\*\*0.001<P<0.01, ns= not significant.

### Bug Density

The number of *C. infuscatus* nymphs per clone was greater in the low *A. aestivus* density plots than in the high density plots during two sample dates (Fig. 1). During the first three observations, there were no differences between the number of nymphs per clone among the low and medium densities. However, at the end of January and at the beginning of February, when peak *C. infuscatus* infestation occurred, the number of nymphs in the low density plots was much higher than in the medium density plots. At the end of the study, no differences could be detected between the number of nymphs among the three densities.

### Infestation Level

The majority of the clones in low density plots were already infested at the beginning of the season, reaching 100% infestation from mid-January (Fig. 2). Although the mean proportion of infested clones in medium density plots was lower than in the low density clones, the differences were insignificant. The proportion of infested clones in high density plots was much lower (<40%) throughout most of the study. The proportion of infested clones in the high density plots decreased during the first half of the study (until January 29) but increased later on.

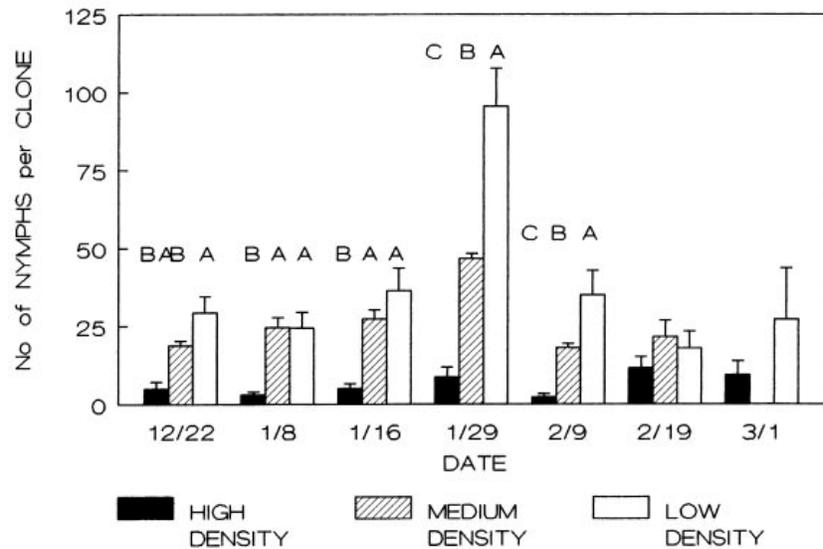


Fig. 1. Densities $\pm$ SE of *C. infuscatus* on *A. aestivus* clones at three different clone densities. Differences in densities were analyzed using one-way ANOVA. Different letters above bars indicate significant difference as determined by Duncan's Multiple Range Test ( $P < 0.05$ ).

#### Damage to Foliage

The mean damage rank to *A. aestivus* leaves increased throughout the study in the low and medium clone densities, while in the high density plots, it increased only in the second half of the study period (from February 9, Fig. 3). Leaf damage in low and medium density plots was similar and much higher than in the high density plots. There was a positive correlation between the damage rank and the number of bugs per clone when pooling the data from the three densities in different dates ( $r_s = 0.62$ ,  $P < 0.001$ ,  $n = 155$ ).

#### Damage to Flowers and Fruits

Only 1% of *A. aestivus* inflorescences at medium density and 13% at low density produced flowers, but these two values were not significantly different (Table 1). In contrast, the mean proportion of inflorescences in high density plots which produced flowers (22%) was significantly higher than the other plots. Total failure in fruit production was observed in the low and medium density plots. However, the very low and varied fruit production (Coefficient of variation=254%) detected in the high density plots was not significantly different than in the other two densities.

Two linear equations were calculated to predict the number of fruits as a function of inflorescence stalk diam in (a) uninfested clones; and (b) damaged clones in the high density plots (Fig. 4). The actual fruit production of the damaged plants was much lower than that of the uninfested clones. The significant differences between these two equations ( $t = 3.72$ ,  $d.f. = 125$ ,  $P < 0.001$ ) presumably represents the actual damage in fruit production to plants in the high density plots. Therefore, the actual damage

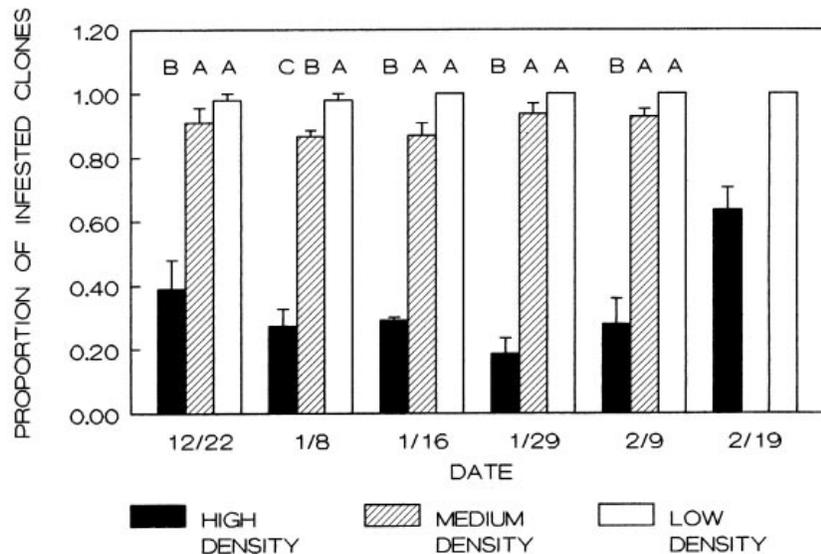


Fig. 2. Proportions of clones  $\pm$  SE of *A. aestivus* infested by *C. infuscatu* at three different clone densities. Differences in arcsin square root transformed proportions were analyzed using one-way ANOVA. Different letters above bars indicate significant difference as determined by Duncan Multiple Range Test ( $P < 0.05$ ). The proportion of infested clones in medium density was not measured in 2/19.

in terms of number of fruits per stalk (Y) was also a linear function of stalk diam (X):  $Y = 11.63X + 16.65$ .

#### DISCUSSION

##### Inverse Density Dependent Damage

The colonization behavior of an herbivore is determined by the spatial and temporal availability of its host plants and the dispersion, behavior and abundance of its enemies and competitors (Cromartie 1975). The proportion of infested *A. aestivus* clones at the beginning of the season, before *C. infuscatu* nymphs had the ability to move between clones (personal observation), was much higher in low and medium than in high density plots. Therefore, adult females at the end of the previous year probably deposited eggs in inflorescences of clones at low density but only in 40% of the clones at high density. The proportion of infested clones in high density plots increased throughout the second half of the season, when the nymphs became more mobile, but remained high at the plots of low and medium densities throughout the season.

Several studies have demonstrated that hosts of several neotropical Euptychiine butterflies (Nymphalidae: Satyrinae) are more likely to bear eggs or larvae if they are scarce and isolated than if they are clumped and abundant (Mackay & Singer 1982 and reference therein). Flower attack rates can also be inversely density dependent (De Steven 1983, Crawley & Patrasudhi 1988). These similar observations could arise from several causes such as different plant quality (size, chemistry, etc.) among

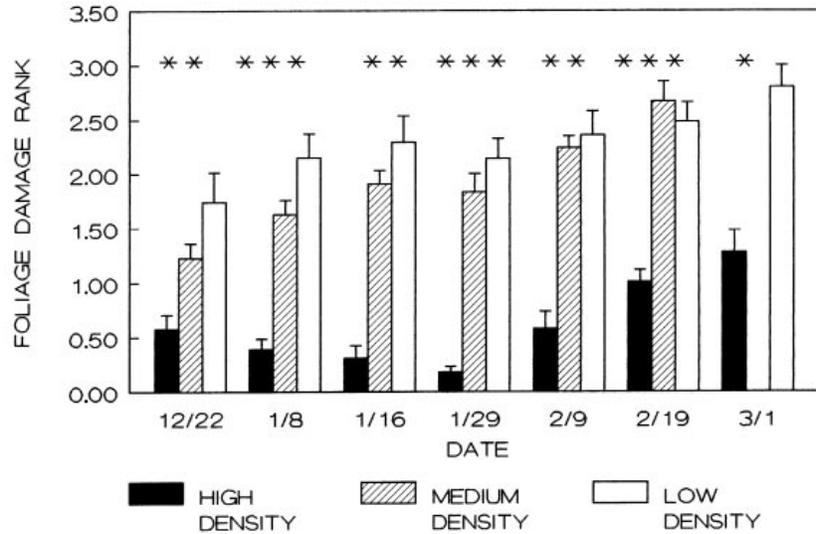


Fig. 3. Foliage damage rank  $\pm$  SE of *A. aestivus* caused by *C. infuscatus* in three different clone densities. Differences in damage ranks were analyzed by Kruskal-Wallis One-way ANOVA. Significance is indicated on each date by: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

densities or an active preference of insects for isolated clones. But, host plant search by herbivorous insects may be initiated at random, or at least without reference to local plant density. If this is the case, each plant is at high risk when an insect starts searching in an area of low density. Thus, the high risk of isolated plants may be a side effect of the random initiation of search, rather than the result of active preference on the part of the insect (Mackay & Singer 1982, Thomas 1989). Whatever the primer of insect behavior, *A. aestivus* plants at relatively low density were at high risk to be colonized by *C. infuscatus* while over 60% of the clones at high density escaped bug colonization.

#### Damage to Sexual Reproduction

This study also revealed that *A. aestivus* plants at low and medium densities could not produce fruits, presumably due to intensive bug herbivory. This failure in fruit production contrasted the success of several clones in high density plots that did produce fruits. Hence, mirid bugs may act as selective agents favoring sexual reproduction if members of *A. aestivus* clumps are more prolific sexually than isolated clones.

Herbivory by other monophagous insects on different perennials were also found to reduce the number and size of seeds produced (Louda 1982, Waloff & Richards 1977). It was also demonstrated that feeding on buds and flowers by mirid bugs can cause a heavy loss of fruit production in sainfoin (*Onobrychis viciifolia*, Morrill et al. 1984). Mirids feeding on the flower stalks of grasses can cause silver top in which an entire panicle of unfilled seeds is produced as a result of a blockage of the phloem (Wagner & Ehrhardt 1961).

Direct attack on ripening fruits by adult mirid bugs (*Lygus borealis* and *Adelphocoris lineolatus*, Hemiptera: Miridae) causes a more or less linear decline in seed pro-

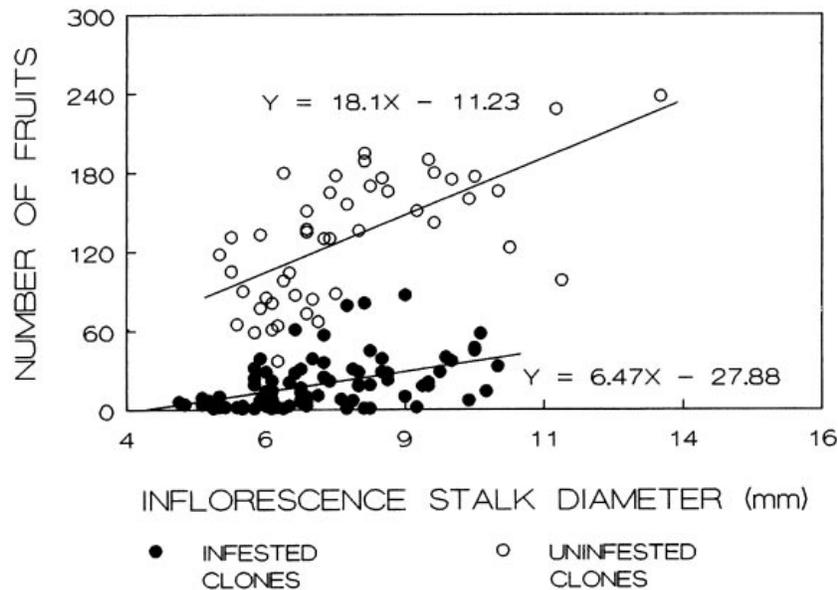


Fig. 4. Relationships between the number of mature fruits of *A. aestivus* as a function of the diameter of inflorescence stalks in (a) infested clones in high density plots ( $R^2=0.21$ ,  $n=83$ ,  $P<0.001$ ) and (b) uninfested clones in the study area ( $R^2=0.41$ ,  $n=46$ ,  $P<0.001$ ). The difference between these two lines represents the damage caused to fruit production by *C. infuscatu*s.

duction in sainfoin as the number of insects increases (Morrill et al. 1984). However, all stages of *C. infuscatu*s feed upon *A. aestivus*; nymphs consume leaves early in the season, but as they develop they feed preferably on inflorescence stalks, flowers, and fruits (Ayal & Izhaki 1993). Therefore, reduced fruit production in this study may be an indirect result of feeding damage on leaves as well as direct damage to flowers and fruits. A positive correlation between the number of young nymphs of *C. infuscatu*s per clone early in the season, long before fruit appearance, and the resulting damage to fruit production in *A. aestivus* was previously demonstrated in a desert habitat (Ayal & Izhaki 1993).

#### Compensation and Reproduction

The relation between timing of insect damage and plant phenological stage is usually critical for understanding compensation responses, at least in annual species (Trumble et al. 1993). However, *Capsodes* attacks *A. aestivus* shortly after the first leaves appear until the above ground parts dry-up. Such continuous pressure can be extremely detrimental to the plants, as they may not recover reproductive potential in the same season. However, reallocation of available assimilates from flowers and fruits to storage in the tuber may result in compensation. This can result in increased sexual and asexual reproductive efforts in the next growing season or increased life span of the individual (Hendrix 1988). Therefore, it is suggested that isolated clones which are heavily attacked by bugs reallocate more reserves to the tuber than high

density clones which suffer less massive attack. As growth continues and clones come to occupy large areas, opportunities for seedling establishment are reduced. This favors further reduction in sexual reproduction as well as increased dispersal and/or dormancy (Waller 1988). However, this study revealed that the bugs intensively attacked isolated plants and reduced their chance to disseminate seeds when the environmental conditions favored seed establishment. Only later, when the conditions favored asexual reproduction, did some plants escape the bug's herbivory and have the potential to reproduce sexually.

#### Population Dynamics of the Plant

Intense feeding by herbivores can result in a 99% reduction in host plant population reproduction (Huffaker et al. 1983); however, a selective pressure that reduces parent fitness by even 1% can be important and result in significant changes in the host population in just a few generations (Crow & Kimura 1970). Furthermore, population dynamics of other plant species have been affected by much lower percent reductions in seed yield due to insect damage (e.g., Louda 1982). Although many examples can be found in which herbivory leads to reduction or even extinction of plant species, other plants, despite visible impact on primary production, do not seem less successful than plants with less herbivore damage (Meijden et al. 1988). Because the activity of *C. infuscatus* reduces plant growth and seed production, but does not result in the mortality of the plant, the effects of their feeding may be manifested only as reductions in the population size of subsequent generations. Therefore, the actual effects of the mirid bug herbivory on population dynamics can only be assessed properly when studied over several generations. (e.g., Verkaar 1987).

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#### REFERENCES CITED

- ATLAS OF ISRAEL. 1985. Cartography, physical and human geography, 3rd edition. Tel-Aviv: Survey of Israel, MacMillan, New-York.
- AYAL, Y. 1994. Time-lags in insect response to plant productivity: significance for plant-insect interactions in deserts. *Ecol. Entomol.* 19: 207-214.
- AYAL, Y., AND I. IZHAKI. 1993. The effect of the Mirid bug *Capsodes infuscatus* on fruit production of the geophyte *Asphodelus ramosus* in a desert habitat. *Oecologia* 93: 518-523.
- BERRYMAN, A. A., B. DENNIS, K. F. RAFFA, AND N. C. STENSETH. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology* 66: 898-903.
- BLAIS, J. R. 1983. Trends in the frequency, extent, and severity of spruce bud-worm outbreaks in eastern Canada. *Canadian J. For. Res.* 13: 539-547.
- CRAWLEY, M. J. 1983. *Herbivory. The Dynamics of Animal Plant Interactions.* Oxford, Blackwell.
- CRAWLEY, M. J. 1989. Insect herbivory and plant population dynamics. *Ann. Rev. Entomol.* 34: 531-564.
- CRAWLEY, M. J., AND R. PATTRASUDHI. 1988. Interspecific competition between insect herbivores: asymmetric competition between cinnabar moth and the ragwort seed-head fly. *Ecol. Entomol.* 13:243-249.
- CROMARTIE, JR. W. J. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *J. App. Ecol.* 12: 517-533.

- CROW, J. F., AND M. KIMURA. 1970. An Introduction to Population Genetics Theory. Harper and Row, New York.
- DE STEVEN, D. 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. *Ecology* 64: 89-98.
- DETHIER, V. G. 1959. Food-plant distribution and density and larval dispersal as factors affecting insect populations. *Canadian Entomol.* 91: 581-596.
- GANGE, A. C., AND V. K. BROWN. 1989. Effects of root herbivory by an insect on a foliar-feeding species, mediated through changes in the host plant. *Oecologia* 81: 38-42.
- HEATHCOTE, G. D. 1969. Cultural factors affecting colonization of sugar beet by different aphid species. *Ann. App. Biol.* 63: 330-331.
- HENDRIX, S. D. 1988. Herbivory and its impact on plant reproduction, pp. 246-263 in J. Lovett Doust, and L. Lovett Doust [eds.] *Plant Reproductive Ecology, Patterns and Strategies*. Oxford University Press, New York.
- HENDRIX, S. D., AND E. J. TRAPP. 1989. Floral herbivory in *Pastinaca sativae*: do compensatory responses offset reduction in fitness? *Evolution* 43: 891-895.
- HUFFAKER, C. B., J. HAMAI, AND R. NOWIERSKI. 1983. Biological control of puncture-vine, *Tribulus terrestris*, in California after twenty years of activity of introduced weevils. *Entomophaga* 28: 387-400.
- JONES, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. *J. Anim. Ecol.* 46: 195-212.
- LOUDA, S. M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower-feeding and seed-feeding insects. *J. Ecol.* 70: 43-54.
- MACKAY, D. A., AND M. C. SINGER. 1982. The basis of an apparent preference for isolated host plants by ovipositing *Euptychia libye* butterflies. *Ecol. Entomol.* 7: 299-303.
- MELJDEN, E. VAN DER, M. WIJN, AND H. J. VERKAAR. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51: 355-363.
- MORRILL, W. L., R. L. DITTERLINE, AND C. WINSTEAD. 1984. Effects of *Lygus borealis* Kelton (Hemiptera: Miridae) and *Adelphocoris lineolatus* (Goeze) (Hemiptera: Miridae) feeding on sainfoin production. *J. Econ. Entomol.* 77: 966-968.
- ORIAN, G. H., R. G. CATES, D. F. RHOADES, AND J. C. SCHULTZ. 1975. Producer consumer interactions, pp. 213-217 in W. H. van Dobben and R. H. Lowe [eds.], *Unifying Concepts in Ecology, Proceedings of the First International Congress of Ecology*, Dr. W. Junk, Netherlands.
- PIMENTAL, D. 1961. The influence of plant spatial patterns on insect populations. *Ann. Entomol. Soc. Am.* 54: 61-69.
- RAUSHER, M. D., AND P. FEENY. 1980. Herbivory, plant density and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* 61: 905-917.
- SAS INSTITUTE. 1988. *Sas/Stat User's Guide*. Cary, NC, USA.
- SCHUSTER, A., I. NOY-MEIR, C. C. HEYN, AND A. DAFNI. 1993. Pollination-dependent female reproductive success in a self-compatible outcrosser, *Asphodelus aestivus* Brot. *New Phyt.* 123: 165-174.
- STALTER, R., AND J. SERRAO. 1983. The impact of defoliation by gypsy moths on the oak forest at Greenbrook Sanctuary, New Jersey. *Bulletin of the Torrey Botanical Club* 110: 526-529.
- THOMAS, C. D. 1989. Predator-herbivore interactions and the escape of isolated plants from phytophagous insects. *Oikos* 55: 291-298.
- TRUMBLE, J. T., D. M. KOLODNY-HIRSCH, AND I. P. TING. 1993. Plant compensation for arthropod herbivory. *Ann. Rev. Entomol.* 38: 93-119.
- TWERY, M. J., AND W. A. PATTERSON. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. *Canadian J. For. Res.* 14: 565-574.
- VERKAAR, H. J. 1987. Population dynamics-the influence of herbivory. *New Phyt.* 106: (Suppl.) 49-60.

- WAGNER, F., AND R. EHRHARDT. 1961. Untersuchungen am Stickanal der Graswanze *Miris dolobratus* L., der Urheberin der totalen Weissahrigkeit der Rotschwingels (*Festus rubra*). Z. Pflanzenkr Pflanzenschutz 68: 615-620.
- WALLER, D. M. 1988. Plant morphology and reproduction, pp. 203-227 in J. Lovett Doust, and L. Lovett Doust [eds.], Plant Reproductive Ecology, Patterns and Strategies Oxford University Press, New York.
- WALOFF, N., AND O. W. RICHARDS. 1977. The effect of insect fauna on growth, mortality and natality of broom *Sarothamnus scoparius*. J. App. Ecol. 14: 787-798.
- ZOHARY, M. 1962. Plant Life of Palestine. The Ronald Press Company, New York.

