

## Explaining differences in flea beetle *Phyllotreta cruciferae* Goeze densities in simple and mixed broccoli cropping systems as a function of individual behavior

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### Abstract

Diversification of habitat has proved to be an efficient way to reduce insect pest levels in agroecosystems. Some general theories used to explain this fact, such as the natural enemies and the resource concentration hypotheses, do not always clearly apply because, in many cases, pest individuals and population response seem controlled by more specific insect-plant interactions. In non replicated plots, we found substantially lower flea beetle densities in mixed broccoli-*Vicia* cropping systems compared to broccoli monoculture. These results were consistent with those from controlled experiments reported in the literature. To investigate if beetle behavior was related to such population reduction, the movement behavior of marked individuals of *Phyllotreta cruciferae* Goeze released in plots composed solely of broccoli plants and of broccoli mixed with *Vicia faba* or *Vicia sativa* plants, was followed and analyzed. The mean tenure time of beetles was longer in simple than in mixed cultures. Also, more beetles tended to fly out and leave mixed cultures compared to monoculture. This resulted in faster reduction of artificially introduced flea beetle populations in the mixed systems.

Flea beetles landing on cover crop plants spent considerable time entangled in *Vicia sativa* branches or attempting to reach the upper part of the tall *Vicia faba* plants from which they could fly away. It is possible that the beetles characteristic movement on these two species of cover crops increased their risk of predation and the time and energy expended before they reached suitable host plants. Nevertheless, it seems that the detected flea beetle emigration rates were more than sufficient to account for the population trends observed.

### Introduction

Spatial and temporal distribution of host plants in agroecosystems are closely related to the behavior and population biology of herbivorous insects (Witman, 1988). Evidence documenting

greater colonization rates, reproduction and population density of herbivorous insects in simple and homogeneous agroecosystems has accumulated in the last three decades (see for instance Pimentel, 1961, 1977; Van Emden, 1965; Tahvanainen & Root, 1972; Root, 1973; Altieri *et al.*,

1978; Bach, 1980; Cromartie, 1981; Risch, 1981; Altieri & Letourneau, 1982; Stanton, 1983; Liss *et al.*, 1986; Pauer *et al.*, 1987; Andow, 1990). These observations inspired many researchers to explore in more detail insect behavioral and population responses to habitat structure and diversity in crop fields.

Of key importance are studies on insect movement, aimed at exploring the process of pest outbreaks in agricultural systems (Ferro, 1987; Risch, 1987). Most researchers used the natural enemies and resource concentration hypothesis, proposed by Root (1973) to explain differences in herbivorous populations between simple and complex habitats. There are however, controversies about the suitability of those general theories to explain the dynamics as well as the structure of arthropod pests and associated natural enemy communities in agroecosystems (see for instance Goodman, 1975; Murdoch, 1975; Price, 1976, Garcia, 1990).

Analyses of the movement behavior of phytophagous insects, and specifically of the flea beetle *Phyllotreta cruciferae* on diversified versus simple or homogeneous crop habitats have shown that herbivore emigration rates are greater and their tenure times are shorter in complex systems (Bach, 1980; Risch, 1981; Kareiva, 1982, 1983, 1985; Bergelson & Kareiva, 1987; Elmstron *et al.*, 1988; Andow, 1990). Despite the valuable contributions of these studies, additional research on insect emigration and immigration behavior is required, mainly for evaluation of the factors involved in movement tendencies within monocultures and polycultures. One factor that has been suggested as having great importance in the behavior and hence movement of phytophagous insects is vegetation structure (Bach, 1980, 1984). In order to test the effect of vegetation structure on flea beetle behavior, movement, and population size, we conducted the following study in simple and diversified broccoli systems, where significant differences in flea beetle densities have already been reported (Altieri & Gliessman, 1983; Altieri & Smith, 1986). We specifically examined the movement behavior and the rate at which marked flea beetles released in broccoli plot and

broccoli-*Vicia* plots tended to either leave or stay in the system, or even migrate from one system to the other.

## Materials and methods

*Study components.* The study had three components. First, we measured the size of flea beetle populations in plots with a different vegetation structure. Second, we employed mark-recapture and depletion techniques to measure beetle migration. Third, we observed the behavior of individual beetles in each system.

*Study area.* Experimental plots were established at the Division of Biological Control at Albany, California in a total area of 1000 m<sup>2</sup>. Three parallel rectangular 10 × 15 cm plots, separated by 4 m bare soil borders between were set up in August 1990. One plot was seeded with fava bean (*Vicia faba*), one was planted with vetch (*Vicia sativa*) and the central plot was left vegetation free, to later simulate broccoli-*faba* diculture, broccoli-vetch diculture and broccoli monoculture treatments respectively.

When the cover crops were about 30 cm high, four 60 cm wide parallel drills were opened 1.5 m apart in the three plots, using a rototiller. Two weeks later, 40-day old broccoli seedlings were transplanted at 56 cm intervals along each row for a total of 100 plants per plot.

*Measurement of infestation levels.* The densities of flea beetles were estimated by aspirating all broccoli plants in all plots. The material collected with a portable vacuum was transferred to plastic Ziploc® bags and placed in a cool styrofoam ice box to slow the flea beetles so that they could be separated from debris and other insects. The flea beetles were counted and used in mark-recapture experiments described below. This procedure was repeated on three occasions, one week apart, during the season.

*Mark-recapture experiments.* Three groups of 350 beetles were placed in separate plastic bags into which a small amount of a colored fluorescent

powder (either blue, orange or pink) was added. The bags were shaken gently until the beetles were coated with the powder. The bags of beetles were placed in individual boxes and taken to the field. A box was placed in the middle of each plot, at soil level and the bag inside was opened, allowing the beetles to escape slowly during the course of an hour. In all instances, beetles successfully left the box.

The number of marked beetles remaining in each plot was estimated visually by inspecting all broccoli plants, the surrounding soil, and/or cover crop plants as appropriate. Marked insects were counted six and 24 h after release. The total number of beetles present in each plot was estimated after 24 h, by vacuuming all broccoli plants. Dvac is a fast and efficient way to estimate total beetle numbers per plot, but is an ineffective tool for recapture experiments because beetles lose the powder.

Control tests were repeated twice to evaluate the length of time for flea beetles to lose their fluorescent powder.

For each color, 20 marked beetles were put in a half liter vial, containing a bouquet of broccoli leaves. The marked beetles were counted six and 24 h after marking. The results showed that in six hours,  $5 \pm 3\%$  of the beetles lost all evidence of the powder and  $25 \pm 5\%$  lost it after 24 h. The percentage of beetles having lost their marks was used as a correction factor to correct estimates of the percentage of recapture.

The combination of initial aspiration, release of marked beetles, counting of remaining beetles and final aspiration was repeated three times.

These repetitions will be referred to as experiments I, II and III. (see Table 3).

*Individual movement behavior.* In this study, individual beetles were immobilized in a cold box, and marked with a small amount of fluorescent powder on the dorsum, and then carefully transferred to the surface of a broccoli leaf in the field. The sequence of release of beetles in the plots was done at random. Flea beetles were mostly absent from the diculture plots; hence they were collected from monoculture border plants and re-

leased in the middle of the diculture plots. During the afternoons of October 15th and October 20th, a total of 20 flea beetles were marked, released and followed in each treatment. Each insect was observed until it moved onto another plant, flew out of the field of vision, or jumped to the ground or into a cover crop plant. In these cases, the movements were timed and whenever possible, the next landing place as well as insect behavior were recorded. The maximum limit of time each beetle was observed was 20 min.

*Statistical analysis.* Likelihood ratio G-test was used to analyze the differences shown in Figure 3, among broccoli, broccoli-fava and broccoli-vetch plots concerning the frequencies at which marked beetles moved onto another broccoli plant, flew out of the plot, went down to the soil, went to the cover crop, and/or remained on the same plant. The same test was used to compare the flux of marked and unmarked beetles in the three plots represented in Figure 1. The Bartlett test for homogeneity of group variances and Tukey multiple comparisons were used to compare broccoli and mixed broccoli plots concerning the time of permanence of marked beetles released on broccoli plants before the first movement (Fig. 2). All analyses were run using Systat (Wilkinson, 1988).

## Results

*Measurement of infestation levels.* Naturally occurring adult flea beetle populations were lower in broccoli-*Vicia faba* and broccoli-*Vicia sativa* plots than in broccoli monoculture plot on three sampling occasions (Table 1).

*Beetle migration.* Three types of migration were observed among the plots: an emigration from the mixed to the monoculture plot and surrounding environment, an emigration from the monoculture plot to the surrounding environment, and an immigration from the surrounding environment mainly to the monoculture plot (Fig. 1). When marked beetles were placed in the mixed plots,

Table 1. Total number of flea beetles in three broccoli cropping systems before releasing marked individuals, as estimated by vacuum sampling\*

Sampling date	Monoculture Broccoli	Diculture	
		Broccoli-Fava	Broccoli-Vetch
9/05/90	860	1	43
9/10/90	341	1	10
9/17/90	675	6	3

\* Although the data come from non replicated plots, subjected to homogeneous conditions, and flea beetle density differences were not statistically tested, from an applied entomological perspective we considered these differences dramatic, and in our opinion would guide us in recommending control actions.

Table 2. Total number of flea beetles 24 h after vacuuming all plants and releasing 350 marked individuals in each cropping system\*

Date	Monoculture Broccoli	Diculture	
		Broccoli-Fava	Broccoli-Vetch
9/05/90	214	1	17
9/10/90	128	6	9
9/17/90	559	4	7

\* See Table 1.

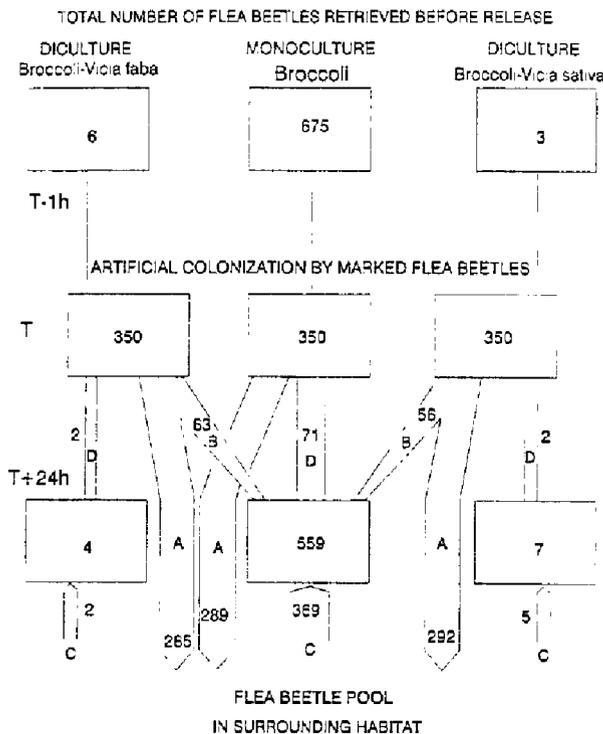


Fig. 1. Flux of *Phyllotreta cruciferae* in three different cropping systems. The results of the third experiment are used as example. A = Beetles emigrating out of crop habitat, B = Beetles moving from mixed plots to broccoli plot, C = Beetles colonizing plots from surrounding habitats, D = Beetles remaining in the plots.

only a few were found back there 24 h after release. This contrasted with the large number found in monoculture (Table 2). Total population

and marked beetles counts, six and 24 h after release, showed that the broccoli monoculture plot attracted marked flea beetles from the mixed culture plots. On the other hand, the broccoli-Vicia system seemed to have a deterrent effect that resulted in massive emigration of the released beetles. Some of the emigrants from the mixed culture plots were later recaptured in the broccoli plot (Table 3). However, beetles released in monoculture were never found in mixed cultures although many of them had emigrated out of the plot. There is evidence that emigration from monoculture tends to happen less rapidly when compared to the mixed cultures (Table 4). The broccoli-Vicia treatments lost almost all of the introduced marked beetles within 24 hours, but ca 15% still remained in monoculture after this time (Table 3). In addition, more beetles were recruited from the pool of flea beetles in the surrounding habitat to broccoli monoculture than to broccoli-Vicia dicultures (Fig. 1). Differences in beetle movement tendency as shown in Figure 1 were highly significant ( $G = 608.091$ ,  $df = 4$ ,  $P = 0.000$ ) when the three plots were compared with respect to the frequency of beetles remaining in the plot (D), emigrating out of the system (A), and immigrating from the surrounding habitat (C). When the same analysis was used to compare the number of marked beetles migrating towards (B) or remaining in monoculture (D for monoculture) and the frequency leaving the system (A), here were no significant differences ( $G = 1.592$ ,  $df = 2$ ,  $P = 0.451$ ). All these tendencies seemed to contribute to the observed high

Table 3. Influence of marked beetle release habitat and differential attractiveness of monoculture systems on the percentage of recaptured flea beetles. Data are from experiments I, II, and III, corrected for the proportion of beetles losing marks after 24 h

Release	Percent recaptured beetles								
	Monoculture			Broc-Fava			Broc-Vetch		
	I	II	III	I	II	III	I	II	III
Habitat									
Monocult.	8.4	16.4	20.2	0	0	0	0	0	0
B-Fava	7.1	14.9	17.9	0	0.4	0.8	0	0	0
B-Vetch	6.9	9.1	16.0	0	0	0	0	0.8	0.8

Table 4. Variation in absolute number of marked flea beetles recaptured in broccoli monoculture 6 and 24 h after release in broccoli monoculture, broccoli-*V. faba* or broccoli-*V. sativa* diculture habitats; expected frequencies if there was no movement considering only the proportion losing marks during the period (EF) and quantification of movement tendency (- = emigration, + = immigration) calculated as (number after 24 h - EF)

Release habitat	Beetles recaptured in monoculture							
	Experiment II				Experiment III			
	6 hrs	24 hrs	(EF)	Movement	6 hrs	24 hrs	(EF)	Movement
Monocult.	54	43	43	0	74	53	59	- 6
B- <i>V. faba</i>	30	39	24	+ 15	38	47	30	+ 17
B- <i>V. sativa</i>	25	24	20	+ 4	34	42	27	+ 15

*P. cruciferae* population density on the broccoli monoculture plot and the low population on mixed plots.

*Individual beetle movement behavior.* Observations on flea beetles' movement behavior showed that *P. cruciferae* tended to leave more quickly broccoli host plants mixed with vetch in the polyculture than those within the monoculture plot (Fig. 2). Analysis of variance revealed significant differences in time of beetles' permanence on host plants in the monoculture plot compared to the broccoli-vetch plot ( $F = 5.105$ ,  $P = 0.009$ , Tukey multiple comparison  $p = 0.007$ ), but not for monoculture plot compared to broccoli-fava plot (Tukey multiple comparison  $P = 0.465$ ) or for broccoli-fava compared to broccoli-vetch (Tukey multiple comparison  $P = 0.128$ ). However, there were clear differences in another aspect of the marked beetles' behavior in the monoculture plot

and mixed plots - The destination of the first flight - away from the broccoli plant where they were initially placed (Fig. 3). The frequency of beetles landing on next broccoli plant, on soil, emigrating from plot, or remaining on the same host plant in the three systems, is statistically different ( $G = 12.942$ ,  $df = 6$ ,  $P = 0.044$  for data from 15 October and  $G = 15.763$ ,  $p = 0.015$  for data from 20 October). In the broccoli-*Vicia faba* plot, 90% and 60% of the beetles observed on the first and second dates, respectively, initially flew over the broccoli plant up to around 50 cm and then flew horizontally, predominantly zigzagging, and were lost in the air. During the same dates, in the broccoli monoculture plot, only 40% and 10% of the beetles showed similar behavior, whereas 50% and 70% of the beetles moved to the next broccoli plant and some did not disperse at all (Fig. 3). Finally, on the broccoli-*Vicia sativa* plot (Fig. 3), more than half of the beetles jumped

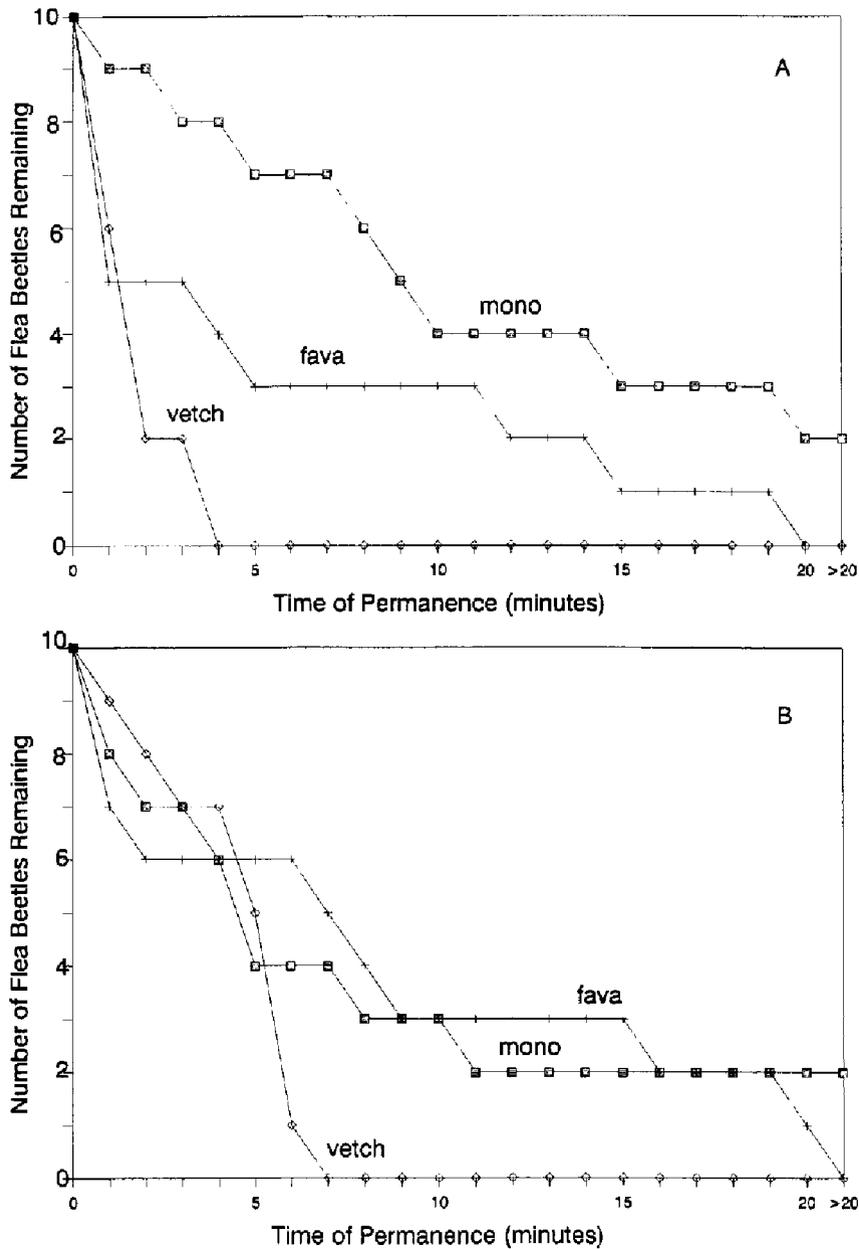


Fig. 2. Distribution of flea beetles frequencies relative to time remaining on the same broccoli host plant before dispersing. Data are for broccoli monoculture and mixed with fava or vetch.

or landed on *V. sativa* plants, while the other beetles were lost in the air after exhibiting the same behavior observed in the broccoli-*V. faba* plot. Differences between broccoli-fava and broccoli-vetch plots concerning frequencies of beetles landing on cover crop plants were significant for the group observed on 15 October  $G = 5.936$ ,

$df = 1$ ,  $P = 0.015$ ), but not for the 10/20 group ( $G = 2.470$ ,  $df = 1$ ,  $P = 0.116$ ). The beetles which landed on vetch spent a long time walking back and forth over the entangled branches of this plant before emerging on the surface of the vegetation, from which they usually flew and were lost.

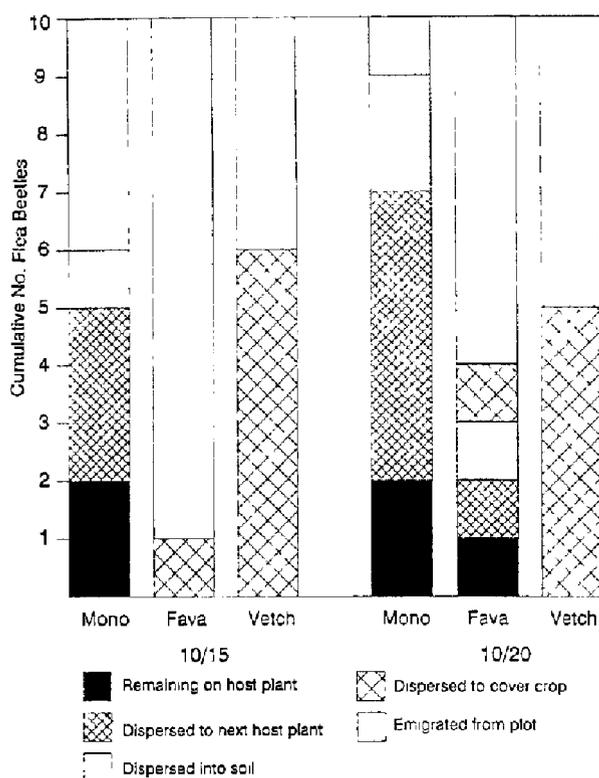


Fig. 3. Movement of marked flea beetles after introduction into different broccoli cropping systems.

## Discussion

Although an equivalent number of marked flea beetles left the simple and mixed plots (Fig. 1), broccoli either attracted or arrested a larger beetle population. On the other hand, the mixed systems not only tended to attract or arrest less flea beetles, but also tended to quickly loose them. It seems reasonable to assume that the signals emitted by monoculture and the favorability of the physical and chemical characteristics of the habitat may represent properties that strongly attract, increase the permanence or even reattract the leaving flea beetles (Fig. 4). This suggests that *P. cruciferae* may not respond positively to the same signal when there is dilution, in part because of the presence of other plants in the same area, since their odors, colors and shape-forms may represent disruptive signals in the system (Fig. 4).

There is also a tendency to continuous movement of the flea beetles that results in a certain

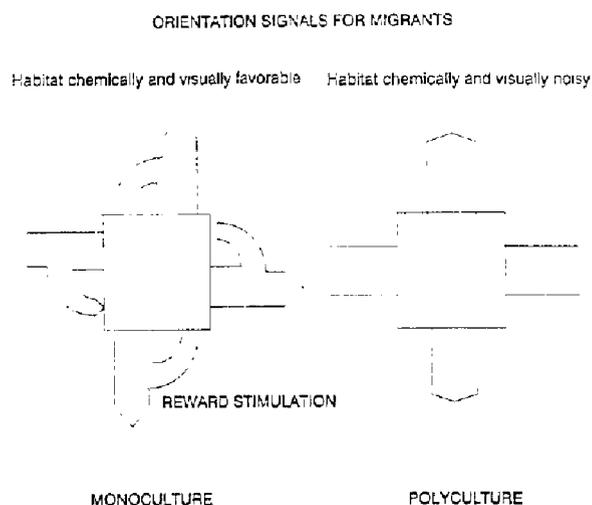


Fig. 4. A conceptual model indicating movement tendencies of flea beetle in broccoli monoculture ad polyculture.

emigration rate (Table 4 and Fig. 1). Kareiva (1985) also observed this wandering behavior of flea beetles, even when the experimental patches were composed of luxurious food plants.

The role of vegetation texture on herbivore populations has been extensively reported and analyzed (see for instance Kareiva, 1983; Bach, 1984; Andow, 1990). However, our detailed observations on *P. cruciferae* behavior suggest that, beyond the differences in attractiveness for colonization and capability to keep the insects, broccoli monoculture and mixed culture broccoli-*Vicia* elicit different movement patterns that can affect the time and energy allocation as well as survival of the insect in the system. When a flea beetle jumps or flies off a broccoli plant in the mixed system, it usually lands on a non-host plant. Here, the tendency is to walk towards the upper part of the plant from where it will leave the plant. Nevertheless, the structure of the *Vicia* plants imposes some obstacles. In the special case of *Vicia sativa*, with a complex architecture of entangled branches, the flea beetles have to allocate time and energy walking forward and backward before emerging onto the superficial foliage or before jumping and getting lost in the *Vicia* forest. It is possible to consider that in this structurally more complex habitat, flea beetles may be more vulnerable to predation, mainly by ants (as was ob-

served once) and spiders which were very common in the mixed plots. Although *V. faba* can be considered to have a more simple architecture than *V. sativa*, it also has extra floral nectaries and associated ants which may attack the beetles, interfere with the upwards movement behavior, and eventually accelerate emigration.

Finally, we conclude that the mixed crops of broccoli-*Vicia* have two main attributes that affect the colonization and establishment rates of flea beetles: 1- the low attractiveness, that results in a low immigration rate; 2- The 'hostility' of the habitat which tends to a) increase the emigration rate; b) increase expenditure of time and perhaps energy. Behavior patterns seem to explain to a large degree the small number of *P. cruciferae* arriving and staying in mixed broccoli cultures. Consequently, from our point of view, factors other than resource concentration and natural enemies effects have to be examined to explain the lower densities of flea beetle on these mixed cultures. In our study, emigration rate seem to be more than sufficient to account for the population data in these short-term experiments. More long term experiments are needed to test whether flea beetles experience lower survival and reproduction rates in broccoli-*Vicia* crops.

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### References

- Altieri, M. A. & S. R. Gliessman, 1983. Effects of plant diversity on the density and herbivory of the flea beetle *Phyllotreta crucifera* Goeze, in California collard (*Brassica oleracea*) cropping systems. *Crop protection* 2: 497–501.
- Altieri, M. A., C. A. Francis, A. van Schoonhoven & J. D. Doll, 1978. A review of insect prevalence in maize (*Zea mays* L.) and bean (*Phaseolus vulgaris*) Polycultural systems. *Field Crop Research* 1: 33–49.
- Altieri, M. A. & D. Letourneau, 1982. Vegetation management and biological control in agroecosystems. *Crop Protection* 1: 405–430.
- Altieri, M. A. L. Smith, 1986. Population trends and feeding preferences of flea beetles (*Phyllotreta cruciferae* Goeze) in collard-wild mustard mixtures. *Crop Protection* 5: 170–175.
- Andow, D. A. 1990. Population dynamics of an insect herbivore in simple and diverse habitat. *Ecology* 71: 1006–1017.
- Bach, C. E., 1980. Effects of plant diversity and time of colonization on an herbivore-plant interaction. *Oecologia* 44: 319–326.
- Bach, C. E., 1984. Plant spatial pattern and herbivore population dynamics: Plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma innubum*). *Ecology* 65: 175–190.
- Bergelson, J. & P. Kareiva, 1987. Barriers to movement and the response of herbivores to alternative cropping patterns. *Oecologia* 71: 457–460.
- Cromartie J., 1981. The environmental control of insects using crop diversity, pp 223–250. In: D. Pimentel (ed.), *CRC Handbook of Pest Management in Agriculture*. CRC Press, Boca Raton Florida.
- Elmstrom, K. M., D. A. Andow & W. W. Barclay, 1988. Flea beetle movement in a broccoli monoculture and diculture. *Environ. Entomol.* 17: 299–305.
- Feeney, P., 1976. Plant apparency and chemical defense. *Recent Adv. in Phytochem.* 10: 1–40.
- Ferro, D. N., 1987. Insect pest outbreaks in agroecosystems, pp 195–215. In P. Barbosa and Shultz (eds.), *Insect Outbreaks*, Academic Press, London.
- Garcia, M. A., 1990. Arthropods in a tropical corn field: Effects of weeds and insecticides on community composition, pp 611–634. In P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson (eds.), *Plant-Animal interactions: Evolutionary Ecology in Tropical and Temperate Regions*. Wiley & Sons Inc., New York.
- Goodman, D., 1975. The Theory of diversity-stability relationships in ecology. *The Quarterly Review of Biology* 50: 234–266.
- Kareiva, P., 1982. Experimental and mathematical analysis of herbivore movement: Quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52: 261–282.
- Kareiva, P., 1983. Influence of vegetation texture on herbivore population: resource concentration and herbivore movement. pp 259–289. In R. F. Denno & M. S. MaClure (eds.), *Variable Plants and Herbivores in Natural and Managed Systems*. Academic press, New York.
- Kareiva, P., 1985. Finding and losing host plants by *Phyllotreta*: patch size and surrounding habitat. *Ecology* 66: 1809–1816.
- Liss, W. J., L. J. Gut, P. H. Westigard & C. E. Warren, 1986.

- Perspective on arthropod community structure organization and development in agricultural crops annual Review of Entomology 31: 455-478.
- Murdoch, W. W., 1975. Diversity, complexity, stability and pest control. *Journal of Applied Ecology* 12: 795-804.
- Pawer, A. G., P. M. Rosset, R. J. Ambrose & A. J. Hruska, 1987. Populations response of bean insect herbivores to inter- and intraspecific plant community diversity: experiments in a tomato and bean agroecosystem in Costa Rica. *Turrialba* 37: 219-226.
- Pimentel, D., 1961. Species diversity and insect population outbreaks. *Annals of The Entomological Society of America* 54: 76-86.
- Pimentel, D., 1977. The ecological basis of insect pest, pathogen and weed problems, pp 3-31. In: J. M. Cherrett & G. R. Sagar (Eds.), *Origin of Pest, Parasite, Disease and Weed Problems*. Blackwell Scientific Publications. London, England.
- Price, P. W., 1976. Colonization of crops by arthropods: Non-equilibrium communities in soybean fields. *Environmental Entomology* 5: 605-611.
- Risch, S. H., 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology* 62: 1325-1340.
- Risch, S., 1987. Agricultural ecology and insect outbreaks, pp 217-238. In P. Barbosa and J. C. Schultz (eds.), *Insect Outbreaks*. Academic Press, New York.
- Root, R. B., 1973. Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *ecological Monographs* 43: 95-124.
- Stanton, M. L., 1983. Spatial patterns in the plant communities and their effects upon insect search, pp 197-210. In: S. Ahmad (ed.), *Herbivorous insects: Host seeking behavior and mechanisms*. Academic Press, New York.
- Tahvanainen, J. O. & R. B. Root, 1972. The influence of vegetation diversity on the population ecology of a specialized herbivore *Phyllotreta crucifera* (Coleoptera:Chrysomelidae). *Oecologia* 10: 321-346.
- Van Emden, H. F., 1965. The role of uncultivated land in the biology of crop pests and beneficial insects. *Scientific Horticulture* 17: 121-136.
- Wilkinson, L., 1988. *Systat: The System for Statistics*. Evanston, IL: System, INC.
- Witman, D. W., 1988. Allelochemical interactions among plants herbivores and their predators, pp 11-64. In P. Barbosa and D. Letorneau (Eds.), *Novel Aspects of Insect-Plant Interactions*. Wiley & Sons, New York.