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The impact of weed diversity on insect population dynamics and crop yield in collards, *Brassica oleraceae* (Brassicaceae)

Abstract Vegetational diversity within agricultural fields is often suggested as a means to reduce insect herbivore populations and to increase their natural enemies. In this paper we compare population densities of herbivores, predators, and parasitoids on collards in monocultures and on collards interplanted with two different groups of weeds, one with weed species from the same plant family as the collards (Brassicaceae) and one with weed species from unrelated plant families (non-Brassicaceae). The collards in the Brassicaceae weed polyculture had higher densities (number of herbivores/mean leaf area (cm^2) per plant) of specialist herbivores than collards in the non-Brassicaceae weed polyculture and in collard monoculture. The "resource concentration" hypothesis is supported by the observation of higher populations of *Phyllotreta* spp., acting as facultative polyphages, in the Brassicaceae weed polyculture than in the non-Brassicaceae weed polyculture where *Phyllotreta* spp. are facultative monophages. Population densities of natural enemies (mostly coccinellids, carabids, and staphylinids) were higher in the polycultures than in the monoculture: carabid and staphylinid predators may be responsible for larval mortality in the imported cabbage worm, *Pieris rapae*, and in the diamondback larvae, *Plutella xylostella*. In spite of differences in densities of specialist herbivores across treatments, crop yield, leaf area (cm^2), the proportion of leaf area damaged, and the number of leaves undamaged did not differ. These findings suggest that plant competition may interfere with attempts to reduce herbivore damage. We conclude that the use of weedy cultures can provide effective means of reducing herbivores if the crop and weed species are not related and plant competition is prevented.

Introduction

Vegetational diversity and density in agroecosystems may influence the abundance of herbivorous insects and their natural enemies (Andow 1983). In temperate agricultural settings, several experiments have demonstrated that crop systems grown with a high diversity of weeds (i.e., non-crop plants) are more likely to have lower population densities of insect herbivores and higher densities of natural enemies than monocrop systems (Pimentel 1961; Dempster 1969; Root 1973; Speight and Lawton 1976; Altieri and Whitcomb 1979; Altieri and Letourneau 1982; Shelton and Edwards 1983; Andow 1988, 1990, 1991a). Despite problems known to be caused by weeds (e.g., negative impact on crop yield, costly chemical herbicides, increased population densities of insect pest), a careful analysis of the literature suggests that the presence of weeds in crop fields is not necessarily always damaging (Dempster 1969; Smith 1976a, b; Andow 1988, 1991a). Since weeds are always part of an agroecosystem and can never truly be eliminated, it is important to consider their effect on insect populations.

Weeds that are closely related to the crop plant can encourage specialist herbivores by increasing the number of host plants or concentrating resources (Root 1973), making the habitat more attractive than a weed-free one. Weeds that are more distantly related to the crop plant can interfere with specialist herbivores, visually or chemically for example, making the habitat less attractive (Andow 1988). Weeds can also encourage generalist herbivores (defined here as insects that consume a variety of plants from several families) that move freely back and forth between the host and weed species or sequentially from weed to crop or vice versa (Andow 1988). Similarly, weeds can interfere with or encourage natural enemies (Andow 1988). Some studies have

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demonstrated that a particular weed species (Altieri and Gliessman 1983; Latheef and Ortiz 1984; Altieri et al. 1985; Altieri and Schmidt 1986; Andow et al. 1986; Kloen and Altieri 1990), or various mixtures of weed species (Dempster 1969; Tahvanainen and Root 1972; Cromartie 1975; Horn 1981) can influence insect herbivores of the associated crop species, and the predators and parasitoids of the insect pest. However, none of the studies have simultaneously distinguished between weed diversity and weed relatedness. Most importantly, in all of the studies on vegetational diversification within agricultural fields, little research has shown whether or not the reduction in herbivore populations results in crop yield gain (Andow 1991b). Of the few studies that have measured crop yield and cosmetic damage, some have found that weeds frequently reduce crop yield (Dempster 1969; Dempster and Coaker 1974; Altieri et al. 1985) because weeds are encouraged to grow within the field and directly compete with the crop, or that although yield is reduced, cosmetic damage is also reduced (Altieri and Schmidt 1986), but not enough to defer economic loss (Latheef and Ortiz 1984). Other examples have shown weeds to increase crop plant yield (Pitre and Boyd 1970; Altieri et al. 1985) or to have no effect on yield (Kloen and Altieri 1990; Altieri and Gliessman 1983). Determining whether a particular weed-crop combination results in higher or lower insect populations and changes in yield or cosmetic damage can provide valuable benefits to the crop plant, such as reducing herbivore damage and pest control costs, and enhancing crop yield (Pitre and Boyd 1970; Dempster and Coaker 1974; Andow 1991b).

The goal of this study was to test whether specific combinations of weed species, both within a single plant family and among several plant families, differentially affect insect herbivore, predator and parasitoid populations, and crop yield. Specifically, this study had two related objectives: (a) to evaluate herbivore, predator, and parasitoid response in a collard monoculture, and in collards interplanted with two different groups of weeds, one with weed species from the same plant family as the cultivar and one with weed species from unrelated plant families, and (b) to measure the direct herbivore impact in terms of cosmetic damage and crop yield of the cultivar.

Materials and methods

Study species

This study was conducted using collards (*Brassica oleraceae* Brassicaceae; var. "Georgia Southern", Hummerts Seed Company). The common herbivore species on collards in the St. Louis area consist of six species that preferentially use plants in the family Brassicaceae and four groups whose diet breadth is more general (Feeny et al. 1970; Davidson and Lyon 1987). The major lepidopteran species present include: the imported cabbage worm, *Pieris rapae* (Linn.) (Pieridae); the cabbage looper, *Trichoplusia ni* (Hubner) (Noctuidae), and the diamondback moth, *Plutella xylo-*

stella (Linn.) (Plutellidae). All three species specialize on cole crops (Brassicaceae), but the cabbage looper can feed on beans, celery, cotton, and plants in the Cucurbitaceae family. The other specialist herbivores include two species of flea beetles, *P. striolata* (Fabricius) and *P. cruciferae* (Goeze) (Coleoptera: Chrysomelida: Alticinae), and the harlequin bug, *Murgantia histrionica* (Hahn) (Pentatomidae). All these species can be serious pests to the collard cultivar.

The generalist herbivore species include *Philaenus* spp. (Hemiptera: Auchenorrhyncha: Cercopidae) and several species of the Cicadellidae (Hemiptera: Auchenorrhyncha), mostly belonging to the subfamilies Ledrinae, Cicadellinae, and Deltocephalinae. Because of the difficulty separating the taxa while making observations for data collection, the cicadellid species were grouped together. Surprisingly few aphids were present; however, of these, most were *Myzus persicae* (Sulzer) (Hemiptera: Sternorrhyncha: Aphididae), a generalist. In addition, a weevil, *Phyxelis rigidua* (Say) (Curculionidae: Brachyrhininae) was present on several plants in various families in the experimental plots.

Experimental design and methods

This study was conducted during spring and summer 1990 at Shaw Arboretum near Gray Summit, Franklin County, MO., USA. In a fallow field of old field vegetation, an area of 1200 m^2 was plowed, cultivated, and divided into 12 6-m^2 plots with a vegetation-free 3 m distance between each of the plots. Three treatments, each replicated four times arranged in a systematic design (Fig. 1) included: (a) weed-free collard monoculture (MONO); (b) collard planted with four Brassicaceae weed species (B-POLY), and (c) collard planted with four weed species from several plant families, excluding Brassicaceae (N-POLY). The Brassicaceae weeds were *Barbarea vulgaris* (R.) (yellow rocket), *Brassica nigra* (L.) Koch (black mustard), *Brassica kaber* (DC.) L.C. Wheeler (wild mustard), and *Raphanus raphanistrum* (L.) (wild radish). The non-Brassicaceae weeds were *Trifolium pratense* (L.) (sweet clover; Fabaceae), *Polygonum persicaria* (L.) (smart weed; Polygonaceae), *Taraxacum officinale* (Weber) (dandelion; Asteraceae), and *Phy-*
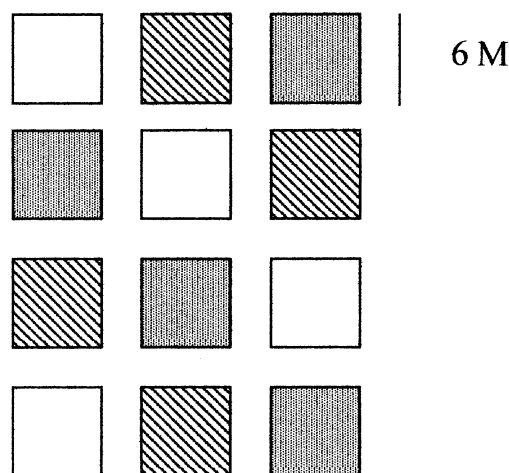
SHAW ARBORETUM

Fig. 1 Layout of the 6-m^2 experimental plots at Shaw Arboretum, Gray Summet, Franklin County, Mo., USA. Each plot was surrounded by a 3-m vegetation-free border [*open box* collard monoculture (MONO), *striped box* collard and Brassicaceae weed polyculture (B-POLY), *hatched box* collard and non-Brassicaceae weed polyculture (N-POLY)]

tolacca americana (L.) (poke weed; Phytolaccaceae). These weeds all occur naturally throughout Missouri.

Brassicaceae and non-Brassicaceae weeds were sown at equal seed volume among seven rows of collards of the respective plots between 23 March and 1 April 1990. On 29 April, 35-day-old greenhouse-grown collards (8–13 cm tall) were transplanted at a density of 91 plants per replicated treatment, and irrigated. The rows were spaced 1 m apart with 50 cm between plants. The *Brassica* weeds bloomed first, in mid-spring, and senesced by mid-summer. *P. persicaria* from the non-Brassicaceae group flowered by late spring, with *T. pratense* and *T. officinale* flowering in early summer. Weeds not intended for the study were removed by frequent hoeing.

To quantify the effect of the three treatments on herbivore abundance, population densities of the herbivore species (both larvae and adults) were measured by direct visual counts on 15 collards (hereafter denoted as focal collard plants) in each replicated experimental plot throughout the season. These 15 plants were selected by choosing every other plant in the center five rows, excluding the two perimeter rows. The 15 focal collard plants were repeatedly sampled on nine dates at approximately weekly intervals throughout the season starting on 13 May through 7 July 1991. We also recorded the abundance of arthropod predators at the same time.

Parasitism of lepidopteran larvae was estimated in two ways. (1) Field inventory data were collected during the herbivore density census by recording the number of larvae that had been parasitized. During the season, several parasitized larvae were removed from the experimental side plot and brought back to the laboratory for further identification. (2) At harvest, yellow water pan traps (ca. 40 × 20 cm) were placed in each of the plots for 24 h 1 day prior to harvesting collards. Parasitoids and predators were identified to family; for a few species, more precise identification was possible.

We assessed the impact of herbivores on collards by measuring the leaf area (cm^2) damaged and the dry weight crop yield (g) at the end of the season. Leaf area damage was measured on 25, 40, and 65 days after planting (DAP) on the 15 focal collard plants using a grid (20 cm^2) to count the missing or eaten leaf area for each plant. Leaf area was estimated by multiplying the length and width of each leaf at the widest part on the focal collard plants. To guage the accuracy of this method, we measured leaf area by directly counting squares of a grid from 30 leaves in four categories ranging from small to very large. Pearson's correlation of estimated leaf area on observed leaf area yield was 0.87.

Crop yield (above-ground biomass) was measured at harvest, 70 DAP (9 July 1991). The 15 focal collard plants from each of the twelve plots were harvested, weighed before drying, placed in drying ovens at 60°C, and then weighed after water loss was complete (usually 24–36 h).

To examine the effect of non-crop plant diversity and density on insect populations, we quantified specialist and generalist herbivore densities on the weeds. These estimates were accomplished by selecting 15 locations evenly spaced in the center five weed rows (excluding the perimeter). A 10 cm × 10 cm frame was placed over these 15 locations in the eight weed treatment plots to give a total of 120 locations. Herbivores were repeatedly sampled on the weeds (hereafter denoted as focal weeds) throughout the season at the same time as collard sampling. Weed density was measured using the same 15 focal weeds on three dates, approximately 22 days apart, by counting the number of plants present and assigning them to height class (class 1 = 0.01–5 cm, class 2 = 5.1–10 cm, and so on) in the 10-cm^2 frame. Weed density was then calculated by multiplying the number of individuals by their height class. Although weed seeds were sown at equal volume, above-ground plant density differed both within and among treatment replicates or plots.

Statistical analysis

We tested the effects of treatment on two dependent variables, number of specialist herbivores per mean leaf area (cm^2) and number of generalist herbivores per mean leaf area (cm^2) per plant.

The data were square root transformed to equalize error variance. To remove the effect of plant size on herbivore density, we conducted an ANCOVA with leaf area (cm^2) as a covariant. These analyses were done separately for each of three sampling periods: early (0–28 days after planting), mid (29–49 days after planting), and late (50–70 days after planting) season. The ANCOVA provides an analysis of herbivore load [number of herbivores per mean leaf area (cm^2) per plant]. ANCOVAs are presented if the model meets the assumption that the regression coefficients are constant over all treatment groups resulting in homogeneity of slopes. If the assumptions were violated, the treatment effects are not the same at different levels of the covariate. Then, the slopes were plotted to observe the interaction between the treatment groups and/or the covariate (Huitema 1980).

Using a repeated-measures ANOVA with season as the repeated measure, we tested the effect of treatment on the number of herbivores (both specialist and generalist) on weeds, and on the number of predators and parasitoids on both collards and weeds using a repeated-measures ANOVA on the mean values per plant (square root transformed to equalize variance). A general regression significance test was used as an a posteriori hypothesis test for the ANCOVA to separate mean differences in herbivore numbers across all treatments (Montgomery 1991). Orthogonal planned comparisons (using a per-comparison error rate) were analyzed between monoculture and weedy cultures for the repeated-measure model (Day and Quin 1989).

The effects of treatment on the plant parameters of proportion damaged, number and percentage of leaves without damage, crop yield, and weed density were examined using separate one-way ANOVA for early, mid, and late season. All plant parameters were log(value + 1) transformed except for proportion damaged which was arcsine square root transformed. Additionally, a priori planned comparisons contrasting monoculture versus weedy culture were used (Day and Quin 1989).

Results

Herbivore population densities on collards

The ANCOVA results indicated a significant effect of treatment for specialist herbivore abundance in early, mid, and late seasons (Table 1). Because the interaction term was significant for early season data, the significant early season treatment main effect must be interpreted cautiously. When the slopes were plotted to observe the interaction between treatment groups and the covariate (Fig. 2a), it can be seen that the mean number of herbivores per plant increased with plant area for the Brassicaceae weed and the non-Brassicaceae weed polycultures, but the slope is almost level for the collard monoculture. This finding indicates that plant area did not increase specialist herbivore loads on collard plots in the early season. However, plant area did increase specialist herbivore load on collards in the mid and late season (Fig. 2b, c).

Specialist herbivore density [number of herbivores/mean leaf area (cm^2) per plant] on the collards was higher in the Brassicaceae weed polyculture than on collards in the non-Brassicaceae weed polyculture for the entire season ($P < 0.05$; Table 2). The difference between the treatments is primarily due to a higher population of flea beetles, *Phyllotreta* spp. throughout the season, and diamondback moth larvae, *P. xylostella*, early in the season. Furthermore, the collard plants

Table 1 ANCOVA table of mean specialist herbivore numbers (square root transformed) per collard plant at each sampling date during early [0–28 days after planting (DAP), mid (29–49 DAP), and late (50–70 DAP) season for each treatment. Mean leaf area (cm^2) per plant (log transformed) is used as the covariate (see Table 4). For the mid and late season, interactions were not significant and were not included in the analayses

	df	Type III MS	F
Early season:			
Treatment	2	3.594	9.36*
Plant area	1	15.482	40.32***
Treatment × plant area	2	4.073	10.61**
Error	6		
Total	11		
Mid season:			
Treatment	2	10.495	5.10*
Plant area	1	79.229	38.51***
Error	8		
Total	11		
Late season:			
Treatment	2	21.004	5.64*
Plant area	1	121.781	32.72***
Error	8		
Total	11		

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

in the Brassicaceae weed polyculture also had more specialist herbivores/cm^2 of leaf than the collards in the monoculture during the early and mid seasons ($P < 0.05$; Table 2). By late season, flea beetle and imported cabbage worm, *P. rapae*, populations had increased in the monoculture resulting in a similar population density of specialist herbivores between the monoculture and Brassicaceae weed polyculture.

Specialist herbivore populations did not differ significantly between the monoculture and non-Brassicaceae weed polyculture during early and mid seasons (Table 2); however, the proportions of specialist herbivores comprising the totals were different. Early in the season, a flea beetle, *P. cruciferae*, made up half of the herbivore population in the monoculture with an even proportion of the other specialists making up the rest, whereas the imported cabbage worm, *P. rapae*, comprised more than half of the herbivore population in the non-Brassicaceae weed polyculture. By mid season, *P. rapae* and the *Phyllotreta* spp. comprised nearly the total specialist herbivore population in the monoculture, whereas *P. rapae* was responsible for two-thirds of the total population in the non-Brassicaceae weed polyculture.

Early in the season, the generalist herbivore density (Lerineae, Cicadellinae, Deltocephalinae, *Philaenus* spp., *M. persicae*, and *P. rigidea*), particularly *M. persicae*, was higher in the monoculture than in to the Brassicaceae weed polyculture (ANCOVA, $F_{2,8} = 6.64$, $P < 0.05$; Table 2). Mid and late season showed no treatment differences for generalist herbivore density (ANCOVA mid and late season: $F_{2,8} = 1.17$, $P > 0.10$ and $F_{2,8} = 0.64$, $P > 0.10$, respectively).
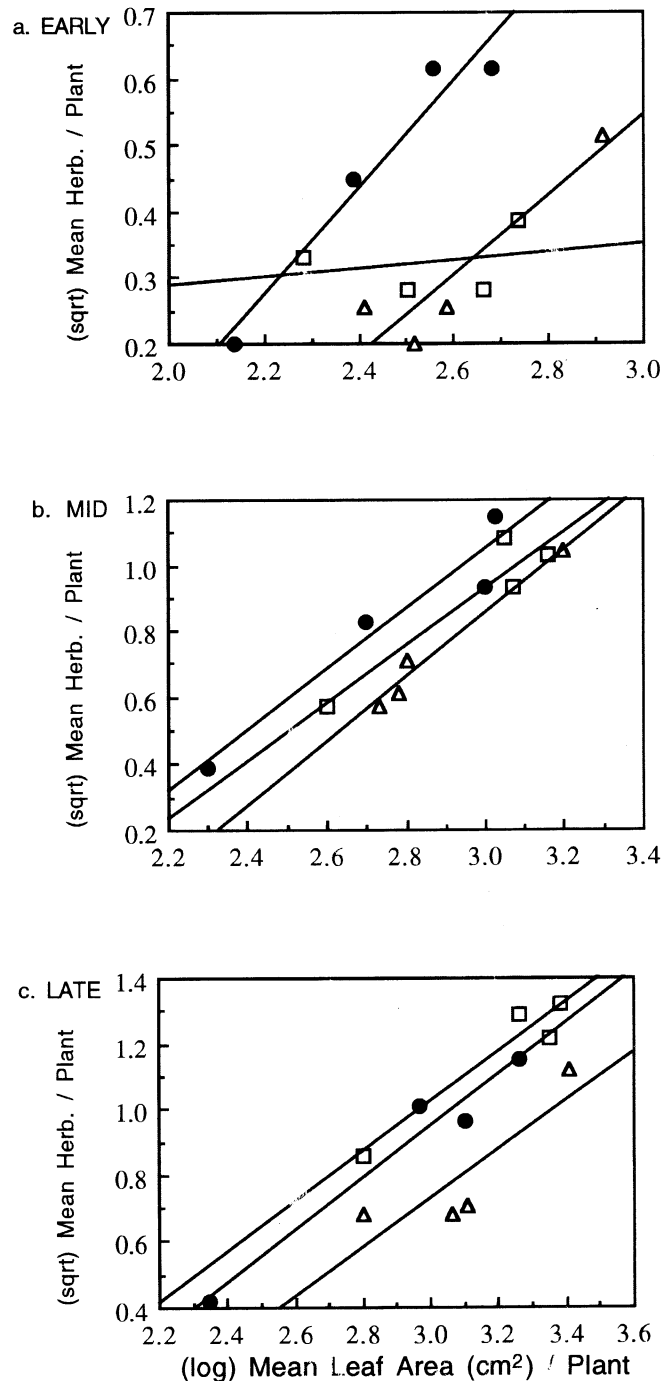

Fig. 2a–c Slopes of the interaction between the mean number of specialists (square root transformed) per collard plant and the covariate [mean leaf area (cm^2)/plant (log transformed)] (*open square* collard monoculture, *closed circle* Brassicaceae weed polyculture, *open triangle* non-Brassicaceae weed polyculture). **a** Early season, **b** Mid season, **c** Late season

Herbivore population densities on weeds

Specialist herbivore populations, primarily *Phyllotreta* spp, were higher on the Brassicaceae weeds than on the non-Brassicaceae weeds (ANOVA, $F_{1,5} = 32.38$, $P < 0.01$; Fig. 3a). However, generalist herbivore popula-
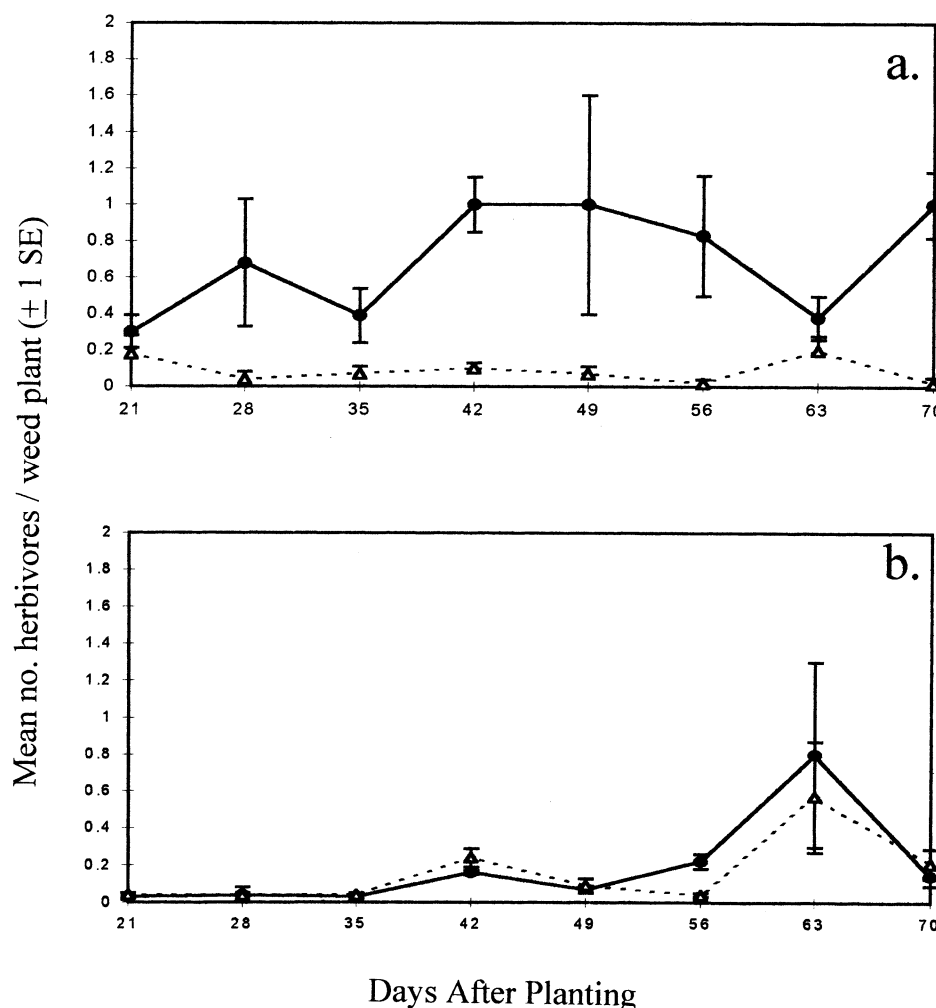
tions were very similar on the Brassicaceae and non-Brassicaceae weeds throughout the season (ANOVA, $F_{1,5} = 0.02$, $P > 0.10$; Fig. 3b).

Table 2 Mean specialist and generalist herbivore density [number of herbivores/mean leaf area (cm^2) per plant] and insect predator density (number/plot) per sampling date during the early, mid, and late season for the collard monoculture (*MONO*), Brassicaceae weed polyculture (*B-POLY*), and non-Brassicaceae weed polyculture (*N-POLY*)

	Early	Mid	Late
Specialist herbivores			
MONO	0.004[a]	0.014[a]	0.015[a]
B-POLY	0.013[b]	0.019[b]	0.013[a]
N-POLY	0.003[a]	0.010[a]	0.009[b]
Generalist herbivores			
MONO	0.005[a]	0.004[a]	0.001[a]
B-POLY	0.001[b]	0.002[a]	0.002[a]
N-POLY	0.002[ab]	0.007[a]	0.001[a]
Insect predators			
MONO	0.500[a]	0.416[a]	0.166[a]
B-POLY	1.416[b]	1.666[b]	1.166[b]
N-POLY	1.166[b]	3.416[b]	4.083[b]

Means with the same superscripts are not significantly different at $P < 0.05$

Plant parameters

Dry mass yield (g)/plant of collards did not differ significantly among the three treatments at harvest time, 70 DAP, although the trend was towards greater yield and greater leaf area (cm^2; Table 3) in the monoculture [ANOVA, $\bar{x}_{MONO} = 16.03 + 3.19$ (SE), $\bar{x}_{B\text{-}POLY} = 7.70 + 2.12$, $\bar{x}_{N\text{-}POLY} = 11.42 + 3.39$)].

The proportion of damage to the collard plants caused by herbivores was similar at harvest for the monoculture, Brassicaceae weed, and non-Brassiceae weed polycultures with damage of 6.8%, 6.2%, and 5.2%, respectively. The number of leaves remaining with no damage at harvest was also similar for all treatments.

Predator and parasitoid population densities

Repeated-measures analysis indicated a difference in population density of the major adult predators (Coccinellidae, Carabidae, Cincindelidae, Staphylinidae) on the ground and foliage among the three treatments ($F_{2,9} = 26.99$, $P < 0.001$; Table 4). Greater densities of adult predators occurred in the non-Brassicaceae weed

Fig. 3 Mean (± 1 SE) number of specialist (**a**) and generalist (**b**) herbivores per focal weed in the B-POLY (*solid circle, solid line*) and N-POLY (*open triangle, dotted line*) treatments

Mean no. herbivores / weed plant (± 1 SE)

Days After Planting

Table 3 Mean (± SD) leaf area (cm²) per plant during early, mid, and late season for the collard monoculture (*MONO*), Brassicaceae weed polyculture (*B-POLY*) and non-Brassicaceae weed polyculture (*N-POLY*). ANOVA shows no significant treatment effect ($a = 0.05$)

	Early	Mid	Late
MONO	423 (179)	1098 (488)	1891 (841)
B-POLY	326 (157)	704 (421)	1124 (686)
N-POLY	490 (260)	912 (539)	1532 (840)

and Brassicaceae weed polycultures than in the monoculture (Table 2). Nearly three times as many coccinellids occurred in the non-Brassicaceae weed polyculture compared to the Brassicaceae weed polyculture and none were found in the monoculture. Carabid densities were equal in the two polycultures and were twice as many as in the monoculture. Because only a few spiders were identified and their feeding habits were unknown, the statistical analyses was conducted including and excluding spiders. The results remained the same.

The number of parasitoids (Hymenoptera: Braconidae, Encyrtidae, Figitidae, Mymaridae, Scelionidae, Sphecidae; Diptera: Dolichopodidae, Tachinidae) captured in yellow pan traps at the end of the season was not significantly different across treatments (ANOVA, $F_{2,9} = 0.92$, $P > 0.10$). Additional analyses revealed no significant effect of treatment on hymenopteran parasitoids (ANOVA, $F_{2,9} = 1.10$, $P > 0.10$) and dipteran parasitoids (ANOVA, $F_{2,9} = 1.93$, $P > 0.10$). The field inventory data collected on parasitism rates of lepidopteran larvae throughout the growing season did not provide enough information for a statistical analysis. Parasitism of adult flea beetles, *Phyllotreta* spp., was never observed.

Density of Brassicaceae and non-Brassicaceae weeds

Although weed seeds were shown at equal volumes, weed density in the non-Brassicaceae weed polyculture

Table 4 Repeated-measures ANOVA on mean number of adult insect predators (excluding spiders) on the ground and foliage in the three treatments. *Date* is the repeated measure which takes into consideration the change in the mean predator number in the plots throughout the season for nine sampling dates

	df	SS	MS	F
Treatment	2	1.482	0.714	26.99***
Error	9	0.238	0.026	
Date	8	0.419	0.052	
Date × treatment	16	0.664	0.041	1.45
Error	72	2.601	0.036	1.15
Planned contrast:				
Mono vs. weeds	1	1.168	1.168	44.17***
Date × mono vs. weeds	8	0.294	0.036	1.02

***$P < 0.001$

was significantly greater than in the Brassicaceae weed polyculture on all three sampling dates (early season: ANOVA, $F_{1,5} = 6.89$, $P < 0.05$; mid season: ANOVA, $F_{1,5} = 6.37$, $P < 0.05$; late season: ANOVA, $F_{1,5} = 8.55$, $P < 0.05$).

Discussion

This study demonstrates that a mixed polyculture of non-related weeds can reduce the specialist herbivore load on an agricultural plant, and a mixed polyculture of related weeds can increase the specialist herbivore load on an agricultural plant. We observed that population densities of specialist herbivores were lowest in the non-Brassicaceae weed polyculture, the most taxonomically diverse treatment. This result is primarily due to fewer flea beetles, *Phyllotreta* spp., in the non-Brassicaceae weed polyculture throughout the season, but also to fewer diamondback moth larvae, *P. xylostella*, in the non-Brassicaceae weed polyculture early in the season. The non-Brassicaceae weeds might visually (Bergelson and Kareiva 1987) and chemically (Bach 1980; Stanton 1983; Andow 1988) interfere with host plant colonization. The finding of fewer flea beetles on a brassica cultivar in a diverse cropping system than on a brassica cultivar in a monoculture is consistent with the most of the published literature (Pimentel 1961; Tahvanainen and Root 1972; Root 1973; Cromartie 1975; Altieri and Gliessman 1983; Latheef and Ortiz 1984; Altieri et al. 1985; Altieri and Schmidt 1986; Andow et al. 1986; Weiss et al. 1994).

The Brassicaceae weed polyculture is an example of how closely related non-crop plants facilitate specialist herbivores, *Phyllotreta* spp., by increasing host plant density (Andow 1988). This result is consistent with the "resource concentration" hypothesis (Root 1973) where concentrated areas of host plants are easier for the specialist herbivore to find and colonize. *Phyllotreta* spp. are facultative polyphages in the Brassicaceae weed polyculture, and should be more abundant than on collards in the monoculture or on collards in the non-Brassicaceae weed polyculture where they are facultative monophages (Andow 1991a). It is not until late in the season that their population is higher in the collard monoculture than in the two polycultures when all of the Brassicaceae weeds have senesced and are no longer suitable for feeding. Furthermore, *Phyllotreta* spp. are most likely responding to the species of weeds and not to their density because their populations were highest where weed density was lowest, in the Brassicaceae polyculture. Our finding of more *Phyllotreta* spp., the specialist, on a brassica cultivar in a polyculture of closely related non-crop plants is in contrast to other studies. For example, Altieri and Gliessman (1983) and Altieri and Schmidt (1986) found that flea beetles, *P. cruciferae*, achieved lower densities on collards grown intermingled with wild mustard (*Brassica campestris* with *B. kaber*) than collards grown in monocul-

tures. They argued that flea beetles preferentially foraged on the mustard rather than adjacent collards because of the higher concentrations of the glycoside sinigrin (a powerful attractant to adult flea beetles) in the brassica weed than the collards. The contrast illustrates that the pattern of fewer flea beetles on the crop plant than on the closely related non-crop plant may not be observed when the concentration of resources is sufficiently high to stimulate their populations.

Unlike the pattern of specialist herbivores, we found that the generalist herbivores did not show population differentiation in any of the treatments. Apparently, generalists are less affected by increased plant density and diversity and their populations are not differentially affected by natural enemies. Our result that generalist herbivores show no particular response to polycultures is consistent with general conclusions from the literature (Andow 1988).

Although predator densities were highest in the polycultures, predation by natural enemies did not account for our major herbivore findings. The majority of the predators encountered in the weedy polycultures were coccinellids, carabids, and staphylinids, with coccinellid populations nearly three times higher in the non-Brassicaceae weed polyculture than in the Brassicaceae weed polyculture, and carabid populations the same in both treatments. To a large extent, higher predator populations in diverse plant assemblages are consistent with most of the published literature (Andow 1986). Using a review of published studies by Andow (1986), but considering only those studies that compared monocultures to weedy cultures, 50% (13 species) of the predator species showed higher densities in the weedy cultures, 15.38% (4 species) showed higher densities in the monocultures, 15.38% (4 species) showed no difference between the two, and 19.24% (5 species) showed a variable response. Of the 13 species with higher densities, 7 were carabids and 1 was a staphylinid, and coccinellids were found to have a variable response. Several studies have shown carabids to be a significant mortality factor of first and second instars of *Pieris* spp. (Dempster 1969; Dempster and Coaker 1974; Thiele 1977; Kristensen 1994) and coccinellids to prey on young instars of Lepidoptera (Hodek 1966). Nevertheless, none of these predators have been recorded to prey on any stage of *Phyllotreta* spp. Predator densities were highest in the treatment with the lowest prey density, the non-Brassicaceae, even when density is calculated per square centimeter of leaf area for both collards and weeds. This inverse relationship between predator and prey for the entire season demonstrates that the predators are not tracking prey densities. It is more likely that the high carabid density in the weedy cultures is due to a more favorable microhabitat (Speight and Lawton 1976; Altieri et al. 1985), and the high coccinellid density in the non-Brassicaceae weed polyculture is due to the presence of aphids on the clover (Altieri et al. 1985).

The second major finding of our study was that the treatments had no significant impact on crop yield. In spite of the significant variation in specialist herbivore populations on collards across treatments, dry mass yield, the proportion of damage to the collards, and number of leaves and leaf area without damage did not differ. Leaf damage was lowest in the non-Brassicaceae polyculture, but the difference among treatments was not large enough to detect significance. However, mean leaf area at the end of the season was the highest in the collard monoculture, indicating that the weeds negatively affected crop yield. In this experiment, the total biomass of the polycultures was much higher than the monoculture, suggesting that plant competition was also responsible for the lower crop yield.

In conclusion, whether a particular weed-crop combination facilitates or interferes with insect populations depends on the relatedness of the crop and weed species. Specifically, the Brassicaceae weeds facilitate *Phyllotreta* spp. on collards in the Brassicaceae weed polyculture, whereas the non-host weeds interfered with their collard colonization in the non-Brassicaceae weed polyculture. The "resource concentration" hypothesis (Root 1973) is supported by the observation of higher populations of *Phyllotreta* spp. acting as facultative polyphages in the Brassicaceae weed polyculture, compared to facultative monophages in the non-Brassicaceae weed polyculture (Andow 1991a). Furthermore, both polycultures had higher populations of carabid and staphylinid predators that may have been responsible for mortality of larvae of the imported cabbage worm, *P. rapae*, and the diamondback larvae, *P. xylostella*, but cannot account for the *Phyllotreta* spp. population differences. Finally, although pests reductions are found in conditions of greatest diversity, this reduction does not have a beneficial effect in raising yield or reducing cosmetic damage. Interspecific plant competition will have to be eliminated to realize the crop yield benefits from reducing herbivore populations with increasing plant diversity and density.

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