

HOST PLANTS MEDIATE OMNIVORE–HERBIVORE INTERACTIONS AND INFLUENCE PREY SUPPRESSION

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Abstract. We conducted laboratory and field experiments to determine the effects of plant quality and prey abundance on the intensity of interactions involving an omnivorous insect, its two herbivorous prey, and their shared host plant. We found that variation in plant quality, prey abundance, and presence of alternative prey altered the functional response of the omnivorous big-eyed bug, *Geocoris punctipes* (Heteroptera: Geocoridae). The presence of high-quality plant parts (lima bean pods) reduced the number of prey (pea aphids and corn earworm eggs) consumed by big-eyed bugs. The results of our caged, field experiments mirrored those of the functional-response experiment. Populations of pea aphids were larger when caged with big-eyed bugs on bean plants with pods than on plants without pods. Pods, therefore, had an indirect, positive effect on the survivorship of herbivorous insects that feed on lima beans.

Because pods reduced the number of prey consumed by big-eyed bugs, and caged prey populations were larger on plants with pods, we hypothesized that herbivore populations would be larger in fields of beans with many pods than in fields of beans with few pods. To test this hypothesis, we established 20 × 30 m field plots of lima beans with many pods and with few pods. The results of this experiment forced us to reject our hypothesis: populations of herbivores were much smaller in plots of beans with many pods than in plots of beans with few pods. In an earlier study, we found that pods had a powerful, direct, positive effect on big-eyed bugs. Big-eyed bug populations were larger in plots of beans with many pods in the present study. It appears that the positive direct effects of pods on big-eyed bugs overwhelm the positive indirect effects of pods on herbivore population size, and that pod feeding by big-eyed bugs ultimately results in smaller herbivore populations. Plant quality, therefore, mediates the effect of this omnivore on prey suppression.

Key words: *Acyrtosiphum pisum*; *big-eyed bugs*; *corn earworm*; *Geocoris punctipes*; *Helicoverpa zea*; *lima beans*; *omnivore persistence*; *omnivorous insect–herbivorous prey interactions*; *pea aphid*; *Phaseolus lunatus*; *trophic cascades*.

INTRODUCTION

Under some circumstances, omnivores may be more likely to suppress prey populations than strict predators. Animals that feed at multiple trophic levels are unlikely to starve or emigrate when prey are scarce (Crawley 1975, Pimm and Lawton 1977, 1978, Walde 1994). As a result, omnivores may continue to capture and consume prey at low prey densities, and may drive them to local extinction. In contrast, typical predators either starve or emigrate when prey are scarce, allowing prey to escape predation at low densities and populations to rebound. Feeding at more than one trophic level by omnivores may deny prey density-related refugia from predation. Consequently, omnivory should promote top-down control, suppression of prey, and may increase the likelihood of trophic cascades (Dayton 1984, Holt 1984, Polis et al. 1989, Polis 1991, Holt and Lawton 1994, Polis and Strong 1996, Holt and

Polis 1997, but see Rosenheim and Wilhoit 1993, Rosenheim et al. 1993).

The potential impact of omnivores on prey, however, not only depends on their ability to persist during periods of prey scarcity, but also on the extent that feeding on plants and alternative prey decreases the consumption of a particular prey species (Abrams 1987). For example, feeding on high-quality plant food can result in relatively persistent and large omnivore populations (Eubanks and Denno 1999), but plants might also provide a highly nutritious preferred food source, and omnivores may consume fewer prey when high-quality plant food is available. Thus, the persistence afforded omnivores by feeding on multiple trophic levels may not necessarily translate into enhanced suppression of prey as predicted by theory. Few detailed studies of omnivores and their resources have addressed this and related questions, so it is difficult to say if omnivores have a greater impact on prey abundance and population dynamics than strict predators (but see Walde 1994, Morin and Lawler 1995).

Our goal was to determine if plant feeding by an omnivore ultimately increases, decreases, or does not affect the omnivore's impact on prey populations. To

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accomplish this goal, we quantified the effects of variation in host plant quality and prey abundance on the intensity of interactions between an omnivorous insect and two herbivorous prey. We studied a relatively simple, agricultural system consisting of an omnivorous "predator," two of its common prey species, and a shared host plant. Other studies of omnivory have manipulated one trophic level, and have primarily been interested in the effects of omnivores on the lowest trophic level of a food chain or web (e.g., plants) (Diehl 1992, 1995, Lodge et al. 1994, Moran et al. 1996). This study is the first to manipulate both plant quality and prey species, and to examine their interactive effects on the ability of an omnivore to suppress prey populations. The specific objectives of this study were to determine the effects of plant quality and alternative prey on an omnivorous insect's (1) functional response, (2) ability to suppress caged prey populations, and (3) ability to suppress herbivore populations in open field plots.

STUDY SYSTEM

Omnivore

Big-eyed bugs, *Geocoris punctipes* (Heteroptera: Geocoridae), are abundant in lima beans, other agricultural crops, and old fields (Crocker and Whitcomb 1980). Big-eyed bugs are active in Maryland from mid-May until early October, producing three generations per year with peak densities in late July and early August. Big-eyed bugs are omnivorous, generalist predators and their diverse range of prey species includes aphids and lepidopteran eggs (Champlain and Scholdt 1966, Lawrence and Watson 1979, Crocker and Whitcomb 1980, Cohen and Debolt 1983). We have observed big-eyed bugs feeding on both pea aphids and corn earworm eggs in Maryland lima beans (Eubanks 1997, Eubanks and Denno 1999). Big-eyed bugs also feed on the pods, seeds, and leaves of many plant species (Stoner 1970, Crocker and Whitcomb 1980, Naranzo and Stimac 1985, Thead et al. 1985).

Host plant

Lima beans, *Phaseolus lunatus* (Leguminosae), are planted in Maryland during early summer (May and June). After 20–30 growing days, lima bean plants begin to flower and produce pods in groups of three per node on an indeterminate raceme (Wooten 1994, Nesci 1996). Plants continue to produce hundreds of pods until senescence, ~60 d after planting (Wooten 1994). The presence or absence of pods is one obvious way in which lima bean plants vary in quality for the insects that feed upon them. For example, the nitrogen content of pods is often 3–5 times higher than leaves (Evans 1982, Murray and Cordova-Edwards 1984, Douglas and Weaver 1989), and the performance of many insects is enhanced by feeding on pods (Schumann and Todd 1982, McWilliams 1983). In an earlier study of

the omnivorous habits of big-eyed bugs, we found that pod feeding was more important for big-eyed bug survival than foliage feeding (Eubanks and Denno 1999). Pod feeding allowed big-eyed bugs to survive extended periods when only low-quality prey or no prey was available. The dispersal of adult big-eyed bugs from lima bean plants with pods was significantly lower than the dispersal of big-eyed bugs from plants without pods. We also found that variation in pod density was a better predictor of big-eyed bug abundance than variation in prey density, and that big-eyed bugs were more abundant in fields of beans with many pods than in fields of beans with few pods.

Herbivores

Many species of herbivorous insects feed on lima beans in Maryland, and are potential prey for big-eyed bugs. Several of these species are particularly abundant and economically important, including the pea aphid, *Acyrtosiphum pisum* (Homoptera: Aphididae) and the corn earworm, *Helicoverpa zea* (Lepidoptera: Noctuidae) (Dively 1986, Nesci 1996). Pea aphids contain a relatively low concentration of nitrogen, and much of the protein content of aphids is not digestible by big-eyed bugs (Cohen 1989). Consequently, aphids are a relatively low-quality prey species, and their consumption often results in the poor performance of big-eyed bugs (Champlain and Scholdt 1966, Cohen and Debolt 1983, Cohen 1989). In contrast, corn earworm eggs contain the developing moth embryo, its associated yolk, and extremely high concentrations of nitrogen, and are a much higher quality prey for generalist invertebrate predators (Champlain and Scholdt 1966, Cohen and Debolt 1983). We found that the survival and longevity of big-eyed bugs fed moth eggs was much higher than the survival and longevity of big-eyed bugs fed pea aphids (Eubanks and Denno 1999).

Consequences of variation in host plants and prey for big-eyed bugs

Previous results suggest that feeding at more than one trophic level furnishes big-eyed bugs with complementary resources that allow them to survive periods when resources at one trophic level are of low quality (e.g., aphids), or when resources at one trophic level are unavailable (e.g., prey) (Eubanks and Denno 1999). Furthermore, we found that the dynamics of big-eyed bugs are intimately associated with variation in their host plants, and not with changes in the density of their prey. These results suggest that the presence of pods is likely to mediate interactions between big-eyed bugs and prey. Because the presence of pods results in large and persistent big-eyed bug populations (Eubanks and Denno 1999), pods could indirectly increase predation pressure on herbivore populations, and induce a trophic cascade. In this scenario, herbivore populations would be smaller as a result of the direct, positive effects of pod feeding on big-eyed bugs (Fig.

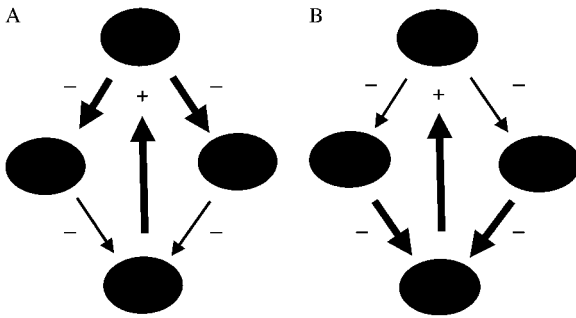


FIG. 1. Two possible ways that pods could mediate omnivore-herbivore interactions and influence prey suppression. (A) Pod feeding by omnivores results in large, persistent omnivore populations. Larger omnivore populations could translate into increased predation pressure on herbivore populations. Under this scenario, the positive direct effect of plants on omnivores drives the system. Pods, therefore, would have an indirect negative effect on the herbivores that consume them. The result would be smaller herbivore populations due to pod-feeding by omnivores. (B) In this scenario, pod-feeding by omnivores also results in large, persistent omnivore populations. Pod-feeding, however, reduces the number of prey consumed by individual omnivores to the extent that herbivore populations are larger. Pods, therefore, indirectly benefit the herbivores that are consuming bean plants, and this indirect effect drives the system. (Arrowheads indicate the recipient of the effect, line thickness indicates strength of effect, and plus and minus signs indicate positive and negative effects, respectively).

1A). Alternatively, although pod feeding results in larger big-eyed bug populations, feeding on pods could reduce the consumption of prey by individual big-eyed bugs. Pod feeding could reduce the per capita effect of big-eyed bugs to the point where their impact on herbivore populations is significantly reduced, even though the big-eyed bug population is larger as a result of pod feeding. This could result in a positive, indirect effect of pods on the herbivores that attack bean plants, ultimately resulting in larger herbivore populations (Fig. 1B). It is our aim to determine which effect is the strongest, and thus unravel the effects of host plants on the ability of omnivores to suppress prey populations.

METHODS

Effects of pods and alternative prey on the functional response of big-eyed bugs

We conducted a laboratory experiment to assess the effects of prey species (pea aphids or corn earworm eggs), prey density (20, 40, 60, or 80 individuals), plant quality (presence or absence of pods), and alternative prey (presence or absence) on prey consumption by big-eyed bugs. Immature aphids were used to prevent aphid reproduction from affecting density treatments. We manipulated the presence or absence of alternative prey by adding either 0 or 20 corn earworms or pea aphids. When focal prey were pea aphids, corn earworm eggs were alternative prey, and vice versa. We

starved field-collected, adult big-eyed bugs for 24 h and then placed a single bug onto a caged, potted lima bean plant with or without pods, and with one of the treatment combinations of focal prey and alternative prey. After 18 h, we removed the big-eyed bug and counted the number of focal prey consumed. Each treatment combination was replicated nine times.

Effects of pods and alternative prey on the ability of big-eyed bugs to suppress caged aphid populations

We conducted a field experiment in August and September of 1996 to determine the effects of the presence or absence of big-eyed bugs, initial aphid density (100 or 200 aphids), presence or absence of alternative prey (corn earworm eggs), presence or absence of pods, and their interactions on the short-term population dynamics of pea aphids. We caged either 100 or 200 pea aphids on a single lima bean plant with or without pods, with or without a single big-eyed bug, and with or without 20 corn earworm eggs. Lima bean plants were randomly selected from a 100 × 50 m field at the Central Maryland Research and Education Center located in Beltsville, Prince Georges County, Maryland, USA. Pods were removed by hand to establish the no-pod treatment. Corn earworm eggs were placed en masse (20 eggs per mass) on the upper surface of a randomly selected leaf. Cages consisted of a cylinder frame of wire mesh (60 cm tall, 20 cm diameter) tightly covered with organdy cloth. After 8 d, enough time for pea aphids to complete one generation, cages were carefully removed and all remaining pea aphids were extracted using a D-vac suction sampler with a 0.093-m² orifice (D-vac, Ventura, California, USA). The D-vac suction orifice was placed over the plant for 30 s. Collection bags were returned to the laboratory, and the number of surviving aphids was determined.

Effects of big-eyed bugs and pods on herbivore populations in the field

To determine the effect of big-eyed bugs in the presence and absence of pods, on the seasonal dynamics of pea aphids, lepidopteran larvae, and other herbivores, we conducted a large, uncaged field experiment in plots of lima beans. To establish plots of beans with many and with few pods, we planted 10 20 × 30 m plots of lima beans in early May (9–11 May) at the Central Maryland Research and Education Center. Plots contained 14 rows of beans with 90 plants per row. Ten-meter strips of bare ground separated the plots. Strips of bare ground were periodically treated with herbicide (Roundup®) and tilled. We applied a fruit thinner to five randomly selected plots on two dates (24 July and 6 August) to induce pod abscission (0.088 L/L of water) (Ethephon, produced by Rhône-Poulenc, Cranbury, New Jersey, USA). Fruit thinners, in a variety of commercial formulations, are frequently used to induce fruit abscission in fruit, cereal, and other crops (Luckwill 1977, Williams 1979). In previous

studies, the fruit thinner did not act as an insecticide nor otherwise alter the quality of bean plants for herbivores (Eubanks 1997, Eubanks and Denno 1999). To quantify the effect of fruit thinner applications on the number of pods per plant, we counted the number of pods on 10 randomly selected plants from each plot on six dates (22 July, 25 July, 30 July, 4 August, 15 August, and 20 August).

We censused insect populations in bean plots with many pods (control), and plots containing plants with few pods (treated with fruit thinner) for ~6 wk. Five suction subsamples were taken every 5–10 d, using a D-Vac suction sampler with a 0.093-m² orifice. Each subsample consisted of 30-s placements of the suction orifice over three plants. Collection bags were sealed and returned to the laboratory where we censused the numbers of big-eyed bug adults, nymphs, and other insects.

Statistical analyses

Functional response experiment.—We quantified the effects of prey species (pea aphids or corn earworm eggs), prey density (20, 40, 60, or 80 prey), plant quality (plants with pods and leaves or just leaves), alternative prey (present or absent), and their interactions on the number of prey consumed by big-eyed bugs with a four-way analysis of variance (SAS Institute 1996). Treatment combinations were randomized through time, and the experiment took ~1 mo to complete. Means were compared with the Bonferroni means separation test.

Field cage experiment.—The number of aphids in cages initiated at relatively low and high densities, with and without big-eyed bugs, pods, and corn earworm eggs were log transformed, and compared with a four-way analysis of variance. Means were compared with the Bonferroni means separation test (SAS Institute 1996). In addition, to further assess the magnitude of the impact of big-eyed bugs on caged aphid populations, we used a *G* test to compare the number of aphid populations that reached zero (i.e., became extinct) in cages with and without big-eyed bugs (Sokal and Rohlf 1981).

Field plot experiment.—We used repeated measures, one-way analysis of variance to compare the numbers of pods and flowers per lima bean plant in fruit thinner-treated and control bean plots (SAS Institute 1996). Greenhouse-Geisser-adjusted probabilities for *F* tests associated with repeated measures were used, and means were compared with the Bonferroni means separation test (SAS Institute 1996). Subsample counts of insects in the two plot types were divided by three to express results as numbers of insects per plant. We log transformed these values to meet the assumptions of analysis of variance ($\log_{10}[n + 1]$) (Sokal and Rohlf 1981). We calculated a mean of the five transformed subsample values to obtain the number of insects per plant for each plot or replicate of the experiment. We

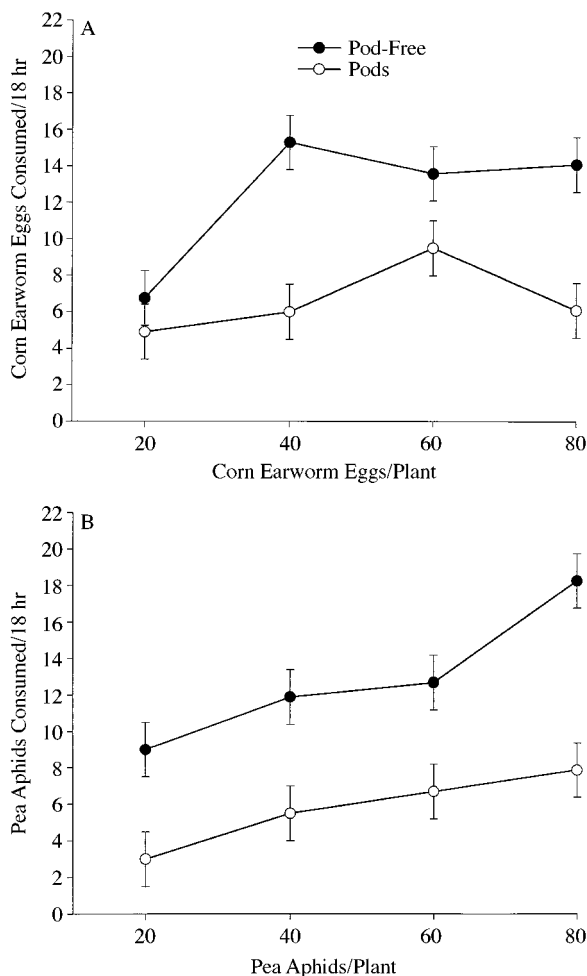


FIG. 2. The number (mean \pm 1 SE) of (A) corn earworm eggs and (B) pea aphids consumed by big-eyed bugs on plants with and without pods.

quantified the effect of pod removal on the population size of big-eyed bug, aphids, lepidopteran larvae, and other herbivores with repeated measures, one-way analyses of variances.

RESULTS

Effects of pods and alternative prey on the functional response of big-eyed bugs

The overall consumption rate of corn earworm eggs and pea aphids by big-eyed bugs was not significantly different (Fig. 2, Table 1: prey species effect). However, the presence of pods significantly reduced the consumption of both prey species by big-eyed bugs (Fig. 2, Table 1: plant part effect). The presence of aphids as alternative prey significantly reduced the consumption rate of corn earworm eggs by big-eyed bugs (Fig. 3A). The presence of corn earworm eggs, however, did not significantly reduce aphid consumption (Fig. 3B, Table 1: prey species \times alternative prey interaction). Pods, therefore, had an indirect, positive ef-

TABLE 1. Analysis of variance for the effects of prey species, prey density, plant part, and alternative prey on the number of prey consumed by big-eyed bugs.

Source of variation	df	MSE	F
Prey species	1	54.31	1.12
Prey density	3	605.57	12.48***
Plant part	1	1069.04	22.04***
Alternative prey	1	962.84	19.85***
Prey species × Prey density	3	73.64	1.52
Prey species × Plant part	1	46.68	0.96
Prey species × Alternative prey	1	663.20	13.67**
Prey density × Plant part	3	89.16	1.84
Prey density × Alternative prey	3	30.26	0.62
Plant part × Alternative prey	1	37.21	0.77
Prey species × Prey density × Plant part	3	38.23	0.79
Prey species × Plant part × Alternative prey	1	54.25	1.12
Prey species × Prey density × Alternative prey	3	53.80	1.11
Prey density × Plant part × Alternative prey	3	90.76	1.87
Error	304	48.51	

** $P < 0.01$; *** $P < 0.001$.

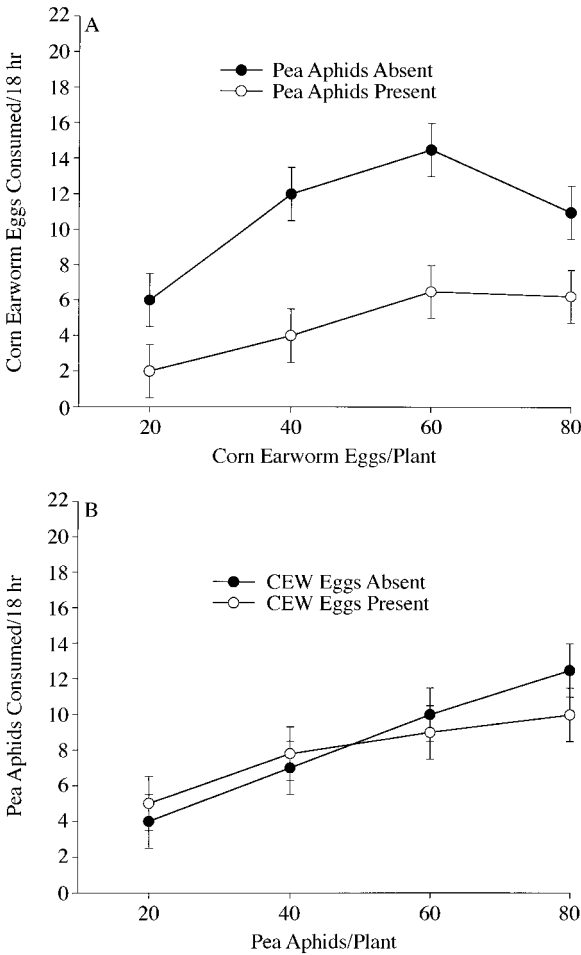


FIG. 3. The number (mean \pm 1 SE) of (A) corn earworm eggs and (B) pea aphids consumed by big-eyed bugs on plants with and without alternative prey.

fect on both prey species because the presence of pods reduced the consumption of prey by big-eyed bugs. Likewise, pea aphids had an indirect, positive effect on corn earworm eggs because big-eyed bugs essentially ignored corn earworm eggs when pea aphids were present. Corn earworm eggs, however, did not affect the consumption of pea aphids. As expected, the consumption of both prey species increased as prey density increased, but prey density did not interact with the other factors (Figs. 2 and 3, Table 1: density effect and respective interactions).

Effects of pods and alternative prey on the ability of big-eyed bugs to suppress caged aphid populations

Big-eyed bugs significantly reduced the size of caged pea aphid populations (Figs. 4 and 5, Table 2: big-eyed bugs). Moreover, the impact of big-eyed bugs on aphid populations was less on plants with pods than on plants without pods (Fig. 4A, Table 2: big-eyed bug \times pod). The presence of corn earworm eggs as alternative prey did not influence the impact of big-eyed bugs on pea aphid populations (Fig. 4B, Table 2: big-eyed bug \times alternative prey). The effect of bugs on pea aphid populations, however, was not independent of initial aphid density (Table 2: big-eyed bug \times initial aphid density). Bugs were more effective at suppressing aphid populations when the aphid populations were initiated at low densities (Fig. 5A). The effect of big-eyed bugs on caged aphid populations was often dramatic: caged aphid populations were frequently driven to extinction by big-eyed bugs (Fig. 5B, $G = 17.94$, $P < 0.01$). There was also a significant pod \times pod density interaction (Table 2), suggesting that pods positively affected aphids at high densities, independent of the effect of big-eyed bugs (Fig. 5C).

Effects of big-eyed bugs and pods on herbivore populations in the field

Fruit thinner reduced the number of pods per lima bean plant by 71% within 2 d of application, and the

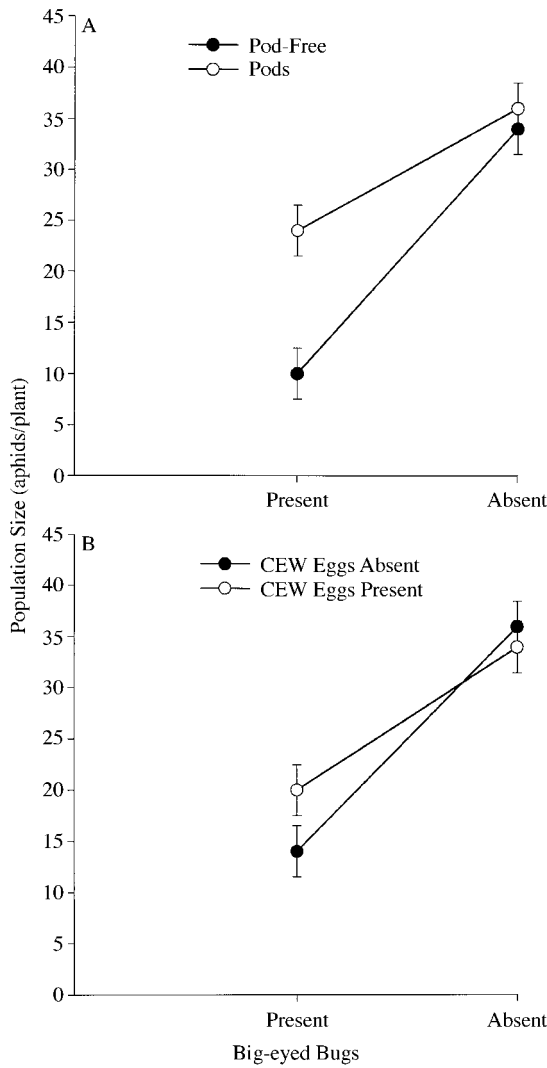


FIG. 4. The impact of big-eyed bugs on aphids caged on (A) plants with and without pods and (B) plants with and without alternative prey (mean number of aphids \pm 1 SE).

number of pods per plant in treated and control plots was significantly different throughout the growing season (treatment \times date interaction, $F_{1,5} = 6.83$, $P < 0.05$). The fruit thinner did not have a direct, insecticidal effect on insects. Densities of big-eyed bug adults and nymphs, other omnivores, strict predators, aphids, lepidopteran larvae, and other herbivores did not differ in samples taken in control and treated plots 24 h after application (25 July and 7 August; Figs. 6 and 7). Reductions in the number of insects in treated plots occurred only after pod loss (~ 5 d after treatment). The loss of lima bean pods due to fruit thinner-induced abscission did result in fewer big-eyed bugs in treated plots. By the third sampling date following treatment, the densities of big-eyed bug nymphs in plots of beans with many pods was significantly higher than in plots of beans with few pods (Fig. 6A, $F_{1,5} = 4.58$, $P < 0.05$,

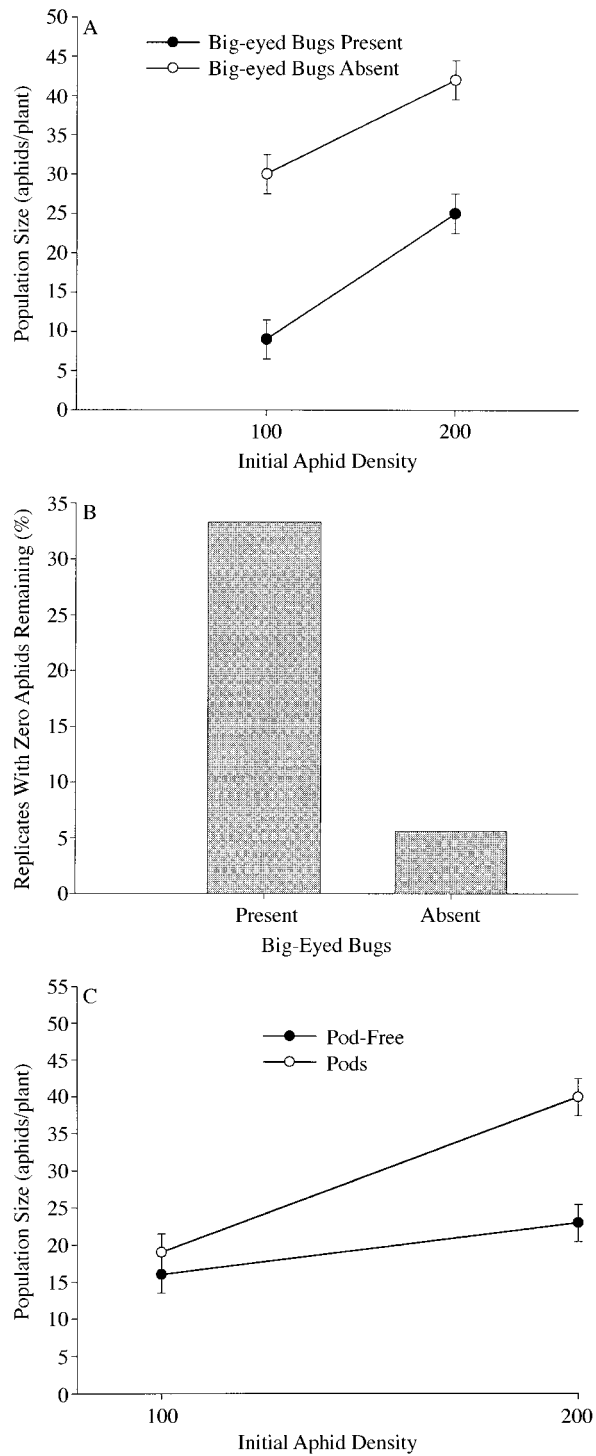


FIG. 5. (A) The impact of big-eyed bugs on aphid populations initiated at densities of 100 or 200 per plant (mean number of aphids \pm 1 SE). (B) The number of aphid populations that went extinct when caged with or without big-eyed bugs. (C) The effects of pods on aphid populations independent of big-eyed bug effects (mean number of aphids \pm 1 SE).

TABLE 2. Analysis of variance for the effects of big-eyed bugs, initial aphid density, alternative prey, and pods on the size of caged aphid populations.

Source of variation	df	MSE	F
Big-eyed bugs	1	11 949.50	41.95***
Initial aphid density	1	10 523.07	36.94**
Alternative prey	1	202.09	0.71
Pods	1	2033.64	7.14**
Big-eyed bugs × Initial aphid density	1	1191.27	4.18*
Big-eyed bugs × Alternative prey	1	574.27	2.02
Big-eyed bugs × Pods	1	1338.87	4.70*
Initial aphid density × Alternative prey	1	2.89	0.01
Initial aphid density × Pods	1	2108.98	7.40**
Alternative prey × Pods	1	121.03	0.42
Big-eyed bugs × Initial aphid density × Alternative prey	1	506.52	1.78
Big-eyed bugs × Initial aphid density × Pods	1	503.80	1.77
Initial aphid density × Alternative prey × Pods	1	20.30	0.07
Big-eyed bugs × Alternative prey × Pods	1	170.65	0.60
Error	141	284.88	

P < 0.05; ** P < 0.01; *** P < 0.001.

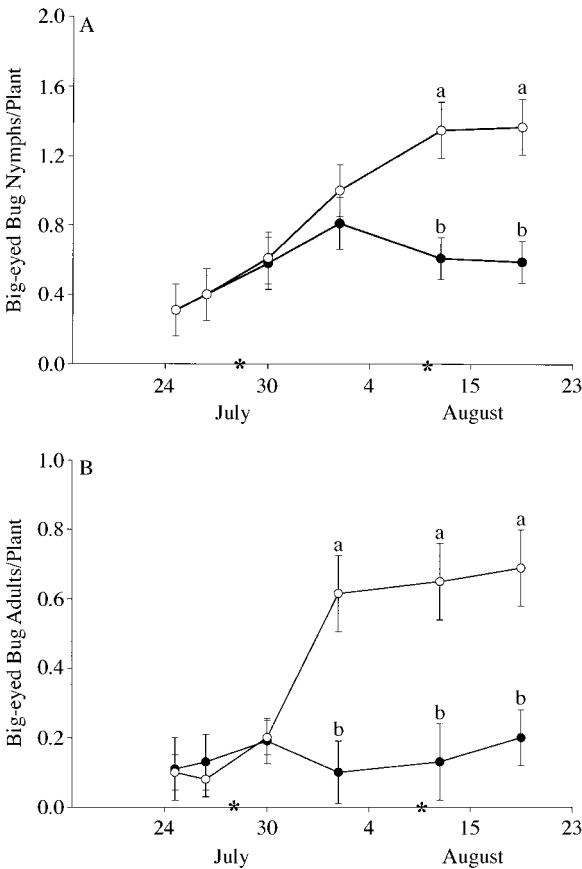


FIG. 6. The number of (A) big-eyed bug nymphs and (B) adults, per plant, in plots of lima beans with many pods (open circles) and with few pods (solid circles) (mean ± 1 SE). Means with different letters are significantly different (Bonferroni means separation test, P < 0.05). Asterisks indicate applications of fruit thinner.

date × treatment interaction for nymphs). Likewise, by the second sampling date after treatment, the density of big-eyed bug adults was significantly higher in plots of beans with many pods than in beans with few pods (Fig. 6B, $F_{1,5} = 6.55$, $P < 0.05$, date × treatment interaction for adults). Fruit thinner applications, therefore, resulted in plots of bean plants with dramatically fewer pods, and with low densities of big-eyed bugs.

Aphid populations were significantly larger in plots of beans with few pods, and with low densities of big-eyed bugs, than in plots of beans with many pods, and high densities of big-eyed bugs (Fig. 7A, $F_{1,5} = 4.44$, $P < 0.05$, treatment × date interaction for aphids). A similar pattern was observed for lepidopteran larvae (Fig. 7B, $F_{1,5} = 3.88$, $P < 0.05$, treatment × date interaction for lepidopteran larvae), and other herbivorous insects (primarily leafhoppers and tarnished plant bugs; Eubanks 1997, Eubanks and Denno 1999) (Fig. 7C, $F_{1,5} = 3.62$, $P < 0.05$, treatment × date interactions for other herbivores). Overall, plants with many pods fostered high densities of big-eyed bugs, which adversely affected the densities of aphids and most other herbivorous insects.

DISCUSSION

Indirect effects of plant quality on herbivore populations

In this omnivore–herbivore–plant interaction, the presence of high-quality plant parts (i.e., pods) had an indirect, positive effect on herbivores in functional response and field cage experiments. Individual big-eyed bugs consumed fewer prey when bean plants had pods, and aphid populations were larger when caged with big-eyed bugs on lima bean plants with pods than on pod-free plants (Figs. 2 and 4A). Because we frequently saw big-eyed bugs feeding on lima bean pods, it seems likely that fewer prey were consumed on plants with pods because big-eyed bugs spent considerable time feeding on pods instead of hunting and consuming prey.

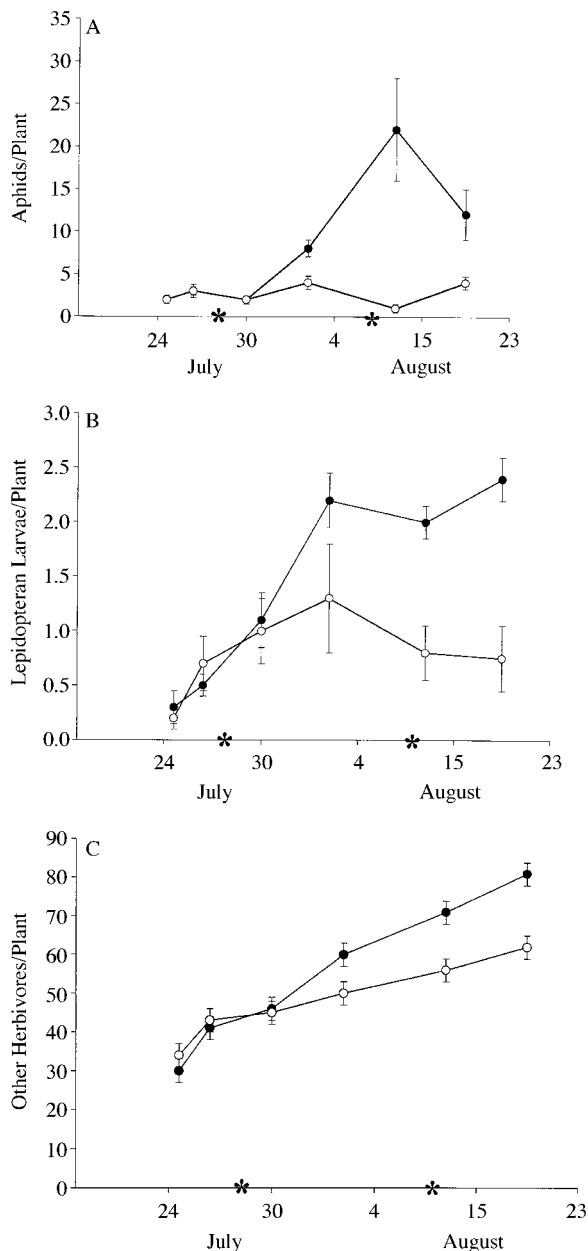


FIG. 7. The number of (A) aphids, (B) lepidopteran larvae, and (C) other herbivores per plant in plots of lima beans with many pods (open circles) and with few pods (solid circles) (mean \pm 1 SE). Means with different letters are significantly different (Bonferroni means separation test, $P < 0.05$). Asterisks indicate applications of fruit thinner.

Big-eyed bugs may become satiated as a result of pod feeding. Satiation as a result of prey feeding often reduces the consumption rates of big-eyed bugs, and other invertebrate predators (Dyck and Orlando 1977, Chow et al. 1983, Döbel and Denno 1994, Toft 1995). Regardless of the mechanism underlying reduced consumption, pods had a positive, indirect effect on prey. Pods, therefore, serve as preferred alternative prey for

big-eyed bugs in this system (Murdoch 1969, Holt and Lawton 1994). Although other studies have shown that the presence of alternative prey can reduce the impact of omnivores on focal prey species (Diehl 1992, 1995), this is the first study, of which we are aware, to demonstrate that high-quality plant food can have the same effect.

Indirect effects of alternative prey on herbivore populations

The indirect effects of alternative prey on focal prey species were species specific: pea aphids indirectly benefited corn earworm eggs, but corn earworm eggs did not benefit pea aphids. Our results are consistent with other studies of complex trophic interactions involving omnivores. Diehl (1992, 1995) found that the impact of omnivorous perch on invertebrate prey was dependent on species-specific characteristics such as prey mobility. Lawler and Morin (1993) also found that the intensity of omnivore-prey interactions appears to vary as the identity of prey and alternative prey vary. These results suggest that it will be difficult to predict the impact of a given omnivore on a given prey species without prior knowledge of the omnivore's foraging ecology, especially the omnivore's prey preferences.

Although it is not surprising that the effects of alternative prey on focal prey consumption were species specific, it was unexpected that the presence of pea aphids reduced the consumption of corn earworm eggs by big-eyed bugs, and not vice versa. The longevity and survival of big-eyed bugs was higher when fed corn earworm eggs than when fed pea aphids in a previous study (Eubanks and Denno 1999). When presented with two prey species varying in nutritional quality, big-eyed bugs, therefore, did not selectively attack the prey species whose consumption resulted in higher performance (corn earworm eggs), but instead attacked the nutritionally inferior prey (pea aphids). Big-eyed bugs must use criteria other than nutritional quality to select prey. Invertebrate predators often preferentially attack mobile prey (Atim and Graham 1984, Freed 1984, Chesson 1989, Heong et al. 1991, Döbel and Denno 1994). In a related study of big-eyed bug predation, we simultaneously presented starved big-eyed bugs with immobilized and fully mobile pea aphids, and found that big-eyed bugs selectively attacked the more mobile aphids (Eubanks 1997). Based on this companion study, we conclude that prey mobility is an important criterion for big-eyed bug prey selection, and that mobile prey can indirectly, but positively, affect less mobile prey species when they co-occur with big-eyed bugs, regardless of nutritional quality.

Foraging theory predicts that the effects of alternative prey on prey consumption should be frequency dependent (i.e., as the relative density of alternative prey increases, the predator should consume more of the alternative prey and less of the focal prey species)

(Stephens and Krebs 1986). At some ratio of alternative prey to focal prey, the predator should essentially stop feeding on the focal prey species, and feed instead on alternative prey. This behavior is often referred to as prey switching or density-dependent switching (Murdoch 1969, Murdoch and Marks 1973, Oaten and Murdoch 1975, Colton 1987). Although the presence of pea aphids as alternative prey did reduce the consumption of corn earworm eggs, this effect occurred at all corn earworm egg densities, and was not apparently density dependent (Fig. 3A). Accordingly, the ratio of pea aphids to corn earworm eggs (alternative prey : prey) had no effect on big-eyed bug prey consumption.

*Direct effects of plant quality
on herbivore populations*

Our cage experiment suggests that pea aphids benefit from pod feeding. Pea aphid populations initiated at relatively high densities were positively affected by pods to a greater degree than those initiated at relatively low densities (Fig. 5C). It appeared that pea aphids were much more likely to feed on pods at high densities than at low densities, perhaps because stems, usual feeding location of aphids, were crowded (M. D. Eubanks, *personal observation*). Studies of other aphid species have reported that pods are higher quality plant food than leaves (Srikanth and Lakkundi 1990). Likewise, pod feeding by corn earworm larvae increases larval survival, decreases larval development time, and increases the size of pupae (Biever et al. 1983, McWilliams 1983). Pods probably have a positive, direct effect on the performance of both pea aphids and corn earworm larvae.

*Direct effect of big-eyed bugs
on herbivore populations*

The results of this study demonstrate that big-eyed bugs suppress herbivore populations. Big-eyed bugs consumed relatively large numbers of pea aphids and corn earworm eggs in the laboratory (Figs. 2 and 3), reduced the size of caged aphid populations in the field (Figs. 4 and 5), and the densities of pea aphids, lepidopteran larvae, and other herbivores in lima bean plots were higher in plots of beans with relatively few big-eyed bugs (Fig. 7). The magnitude of the direct effect of big-eyed bugs on herbivores was often very strong: big-eyed bugs frequently drove caged aphid populations extinct (Fig. 5B). We attributed the decrease of herbivores in plots of beans with relatively high densities of big-eyed bugs primarily to big-eyed bug predation. We have previously shown that the density of strict predators (spiders, assassin bugs) in lima beans was positively correlated with herbivore density. Thus, strict predators were more abundant in plots of beans with few pods, few big-eyed bugs, and relatively high densities of herbivores (Eubanks and Denno 1999). The densities of omnivorous insects other than big-eyed bugs, such as minute pirate bugs, were strongly cor-

related with flower density, and not pod density. As a result, their densities were less affected by pod loss in treated plots, and herbivore density was not negatively correlated with the density of these omnivores (Eubanks and Denno 1999). Although omnivory did disperse the consumptive effect of big-eyed bugs throughout the relatively simple food web that we studied (e.g., prey consumption was reduced when plants had pods), the present study strongly supports the contention that omnivores can have powerful, negative effects on populations of their prey (Polis 1991, Diehl 1992, 1995, Polis and Holt 1992, Polis and Strong 1996).

*Coupling omnivore and herbivore
population dynamics*

Variation in plant quality mediated the impact of big-eyed bugs on prey populations through complicated, and often conflicting, direct and indirect effects. First, pods indirectly reduced the consumption of prey by big-eyed bugs (i.e., reduced their per capita effect). Thus, pods indirectly benefit the herbivores that eat lima bean plants. Pod feeding also increases the performance of many herbivores (including corn earworms and probably pea aphids). These results suggest that populations of aphids, corn earworms, and other herbivores should be larger in plots of beans with many pods than in plots of beans with few pods. We found the opposite result in our field experiment: densities of pea aphids and corn earworm larvae were lower, not higher, in plots of beans with many pods (Fig. 6). To explain this apparent paradox, one must consider the direct effect of bean plants on big-eyed bugs. Big-eyed bug survival was higher, and emigration was lower, when lima bean plants had pods than when they did not (Eubanks and Denno 1999). Increased survival and decreased emigration results in larger big-eyed bug populations in plots of beans with many pods (Fig. 6). Even though the presence of pods dampens the direct effects of big-eyed bugs on prey populations (i.e., lowers prey consumption in laboratory and field cages), the retention of big-eyed bugs in plots of beans with pods increases the overall negative effect of this omnivore on prey populations. The direct, positive effects of pods on big-eyed bugs, therefore, overwhelmed the positive direct and indirect effects of pods on herbivores. Herbivore populations were suppressed such that plants should experience significantly less damage. The direct effects of plant quality on omnivores is, therefore, likely to induce a trophic cascade whereby plant feeding by the omnivore ultimately benefits the plant.

Our results are consistent with the verbal model presented by Polis and Strong (1996). Omnivory does disperse the direct effects of consumption throughout the food web rather than focusing them at particular trophic levels (e.g., pod feeding reduced the consumption of prey by big-eyed bugs). However, because the ability to feed at multiple trophic levels can result in relatively large, persistent, and often less variable omnivore pop-

ulations (Lawler and Morin 1993, Eubanks and Denno 1999, this study), omnivory ultimately produces intense omnivore-prey interactions, and promotes prey suppression.

Implications for biological control

The importation of specialist natural enemies to target individual, exotic pests in classical biological control programs is coming under increasing criticism on both environmental (Howarth 1991, Simberloff and Stiling 1996, Kareiva 1996), and theoretical grounds (Murdoch et al. 1985, Murdoch 1990, Döbel and Denno 1994). There is a growing concern that introduced natural enemies are having deleterious effects on populations of non-target, native herbivores (Howarth 1991, Simberloff and Stiling 1996), and are competitively displacing native predators (Kareiva 1996). The efficacy of introduced, specialist natural enemies relative to native, generalist predators has also come under recent attack (Murdoch et al. 1985, Murdoch 1990, Döbel and Denno 1994). This study demonstrates that retention of native, omnivorous natural enemies in agricultural fields via plant feeding can result in the suppression of pest populations. Not only can omnivores suppress established populations of pests, they may also thwart colonization attempts of invading pests since they can persist at such low pest densities (Eubanks 1997). One of the major benefits of using omnivorous predators as biological control agents is the potential for predicting and promoting their efficacy. Several studies have now demonstrated that omnivorous insects track plant resources, and that the availability of high-quality plant resources in the form of pollen or pods is an excellent predictor of their abundance, and their ability to suppress insect pest populations (Coll and Bottrell 1991, 1992, Eubanks and Denno 1999). This is analogous to situations where the availability of nectar for adult wasps is a predictor of their abundance and attack rate (Idris and Grafius 1995, 1996). Understanding the role of plants in the population dynamics of native, omnivorous "predators" may allow biological control workers to manipulate agricultural systems in order to increase the efficacy of omnivores as biological control agents.

The use of omnivores as biological control agents, however, may have other complications. Most omnivores are generalists that attack a wide range of prey species, including predators and other omnivores (e.g., Guillebeau and All 1989, 1990, Polis et al. 1989). If intense, intraguild predation can interfere with biological control, and significantly reduce predation pressure on pest populations (Rosenheim and Wilhoit 1993, Rosenheim et al. 1993). Hence, predicting the impact of an omnivore on prey populations may not be as simple as understanding the role of plant quality in their population dynamics. To fully predict the efficacy of omnivores as biological control agents, we will need to know the role of plants in their population dynamics,

and their prey preferences, and their susceptibility to other omnivores and predators.

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