

Host Plant Alters the Shape of the Functional Response of an Aphid Predator (Coleoptera: Coccinellidae)

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ABSTRACT The response of the lady beetle *Propylea quatuordecimpunctata* (L.) to the density of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), was measured in petri dish arenas as well as on plants with divergent leaf architectures. Logistic regression was used to distinguish the shape of the functional response (type II or III), and nonlinear least-squares regression was used to estimate attack coefficients (a) and handling times (T_h). In dishes, the behavior of both beetle larvae and adults closely conformed to a type II response. Estimates of a and T_h on whole plants were considerably different from those obtained from dishes, and they also depended on plant species. Beetle adults consumed more aphids on the slender-leaved Indian ricegrass, *Oryzopsis hymenoides* (Roemer & Schultes) Ricker, than on the broad-leaved crested wheatgrass, *Agropyron desertorum* (Fisher ex Link) Schultes, at each aphid density. Moreover, logistic regression suggested a type II response on Indian ricegrass versus a type III (sigmoidal) response on crested wheatgrass. The complex response on crested wheatgrass may have been caused by density-dependent changes in the proportion of aphids in refuges (such as rolled leaves). By modifying the shapes and parameters of functional responses, plant traits can influence the stability of predator-prey dynamics and the success of biological control.

KEY WORDS *Diuraphis noxia*, *Propylea quatuordecimpunctata*, functional response, tritrophic interactions, biological control

INTERACTIONS BETWEEN ARTHROPOD predators and their prey can be modified by the chemical and physical properties of the prey's host plant (Price 1986, Hare 1992). Simple changes in plant morphology (e.g., trichome density) or architecture (e.g., stem and leaf dimensions) can affect the search patterns and residence times of predators as well as the tendency of prey to occur in spatial refuges (Obrycki 1986, Kareiva and Sahakian 1990, Geitzenuer and Bernays 1996). By altering foraging efficiency, plant traits may also affect a predator's functional response (i.e., the way it responds to variation in prey density [Solomon 1949, Holling 1966]). In this study, we examined whether differences in leaf architecture influence the functional response of a lady beetle attacking aphid prey.

Results of cage experiments in the field and greenhouse indicate that the lady beetle *Propylea quatuordecimpunctata* (L.) is more effective in reducing populations of Russian wheat aphid, *Diuraphis noxia* (Mordvilko), on the slender-leaved Indian ricegrass, *Oryzopsis hymenoides* (Roemer & Schultes) Ricker, than on the broad-leaved crested wheatgrass, *Agropyron desertorum* (Fisher ex Link) Schultes (Messina et al. 1997). Behavioral observations suggest that this difference depends on prey refuges. Beetle adults and larvae are less likely to encounter and capture *D. noxia* on crested wheatgrass because aphids often feed in protective locations, such as within furled, immature leaves (Clark and Messina 1998). We therefore measured the beetle's functional response on each plant to

determine whether the greater susceptibility of *D. noxia* on Indian ricegrass was consistent across different aphid densities.

Functional responses of arthropod predators have typically been measured in simple laboratory arenas (Hassell 1978, Luck et al. 1988), and few studies have considered effects of host-plant variation (Carter et al. 1984, Da Silva et al. 1992, Coll and Ridgway 1995). Yet plant effects on the functional responses of arthropod predators are probably common; even in artificial arenas, capture rates can depend on the particular dispersion of prey or the complexity of the "habitat" (Kaiser 1983, Parajulee et al. 1994, Ryoo 1996, van Alebeek et al. 1996). Ritchie (1998), for example, showed how the fractal dimensions of barriers affect capture rates of predatory mites in the laboratory. We used the interaction between *P. quatuordecimpunctata* and *D. noxia* to answer the following 2 questions: (1) How does the beetle's functional response in petri dish arenas compare with that on whole plants? (2) Do the shapes or parameters of the functional response vary between plant species in a way that is consistent with the earlier, population-level studies?

Materials and Methods

Plants and Insects. Seedlings of 'Nordan' crested wheatgrass and 'Paloma' Indian ricegrass were grown in a greenhouse until they bore several leaves on the main shoot plus 3-5 tillers (see Messina et al. [1993]

for details). At this stage, crested wheatgrass and Indian ricegrass display similar bunchgrass-type architectures (Stubbenieck et al. 1992), but crested wheatgrass leaves are much wider than those of Indian ricegrass (≈ 4.5 versus 1.5 mm). More importantly, the grasses differ in the dimensions of the preferred feeding sites of *D. noxia*. Both the junctions of leaf blades and sheaths (leaf junctions) and the diameters of furled, immature leaves are wider on crested wheatgrass than on Indian ricegrass (≈ 2.5 mm versus 1.0 mm for leaf junctions; ≥ 2.0 mm versus ≤ 1.0 mm for leaf-roll diameters; Messina et al. 1997).

Aphids were obtained from an anholocyclic colony maintained on winter wheat, *Triticum aestivum* L. (Messina et al. 1993). Adults of *P. quatuordecimpunctata* were supplied by the USDA-APHIS National Biological Control Laboratory at Niles, MI. This coccinellid has been released throughout western North America for control of *D. noxia*, but it has become established only in northeastern North America (Day et al. 1994). Beetle adults were fed aphids in a growth chamber at 23°C and under constant light for 7 d, but were starved in petri dishes containing moist cotton for 16 h before an experiment. Test larvae were the 1st-generation progeny of adults supplied by the Niles laboratory. They were obtained within 20 h after the molt to the final instar (IV), and they were starved in the same manner as adults.

Petri Dish Experiments. We first measured predation rates of beetle adults and larvae in inverted petri dishes (100 by 15 mm) lined with moist filter paper. We used a camel's-hair brush to add the requisite number of aphids through a 5-mm hole that had been drilled into the lid of the dish. This step prevented the escape or injury of aphids already in the dish as more aphids were added. We added only nymphs of *D. noxia* (instars II-IV) to preclude reproduction during the experiment. We established densities of 5, 10, 20, 40, or 80 aphids per dish, with 12-13 replicates per density in an experiment using adult beetles ($n = 63$ dishes) and 13-18 replicates per density in an experiment using beetle larvae ($n = 85$ dishes).

A single predator was added to each dish 1 h after aphids were introduced; this interval ensured that aphids had dispersed throughout the dish. We did not identify the sexes of beetle adults, but selection of larger individuals probably led to a female bias. Although male and female coccinellids differ in foraging behavior (Hemptinne et al. 1996), our failure to control for beetle gender merely increased variation among replicates within each level of aphid density. Dishes were arranged randomly in an illuminated growth chamber at 23°C, and surviving aphids were counted after 1 h.

Whole Plant Experiment. We measured predation rates on grasses for adult beetles only. Indian ricegrass and crested wheatgrass plants were arranged randomly on a laboratory bench, and a cylindrical cage was placed over each plant (Messina et al. 1993). We matched surface areas of test plants by selecting the largest individuals of the Indian ricegrass. Aphids were introduced through the top of a cage at densities of 5,

10, 15, 20, 30, or 40 nymphs per plant, with 9-14 replicates for each combination of plant species and aphid density ($n = 152$ plants).

Aphids were allowed to settle for 5 h before a single predator was added to each plant. Our observations confirmed that the locations of aphids at the time of predator introductions were similar to those of colonies that developed in situ (Messina et al. 1997). Although the duration of the experiment was not long enough for aphids to induce leaf rolling (Burd and Burton 1992), aphids readily entered existing leaf rolls. We harvested each plant into 70% ethanol 3 h after the introduction of predators and counted surviving aphids. Ambient temperature during the experiment was 21-22°C.

Data Analyses. We analyzed predator functional responses in 2 stages (Juliano 1993). To determine the shape of the functional response, we performed a logistic regression of the proportion of aphids eaten as a function of initial density. Logistic regression is appropriate because the dependent variable is dichotomous (an aphid is either alive or dead at the end of a trial) and the errors associated with such a variable are likely to be distributed binomially rather than distributed normally (Trexler and Travis 1993). The logit transformation explicitly assumes binomially distributed errors (Agresti 1990). For predator functional responses, logistic regression is particularly useful for distinguishing between Holling's (1966) type II and III responses, which are not easily discriminated by nonlinear regressions that use the number of prey eaten as the dependent variable (Trexler et al. 1988). The proportion of prey eaten (i.e., the per capita risk) declines monotonically with prey density in a type II response but is positively density-dependent over some region of prey density in a type III response.

We first fit a polynomial function (Juliano 1993):

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad [1]$$

where N_e = the number of aphids eaten, N_0 = initial density, and N_e/N_0 is therefore the probability an aphid is eaten. Maximum-likelihood estimates of parameters P_0 to P_3 were obtained by applying the LOGIT module of SYSTAT (Wilkinson et al. 1996) to a dichotomous variable that equals 0 for surviving aphids and 1 for consumed aphids. The signs of the linear, quadratic and cubic coefficients from equation 1 can then be used to distinguish the shape of the functional response (Juliano 1993).

After fitting equation 1, we used the likelihood-ratio test (Trexler and Travis 1993, Hilborn and Mangel 1997) to determine if this equation fit the data better than a simpler model without a cubic expression. In this test, the difference in the log-likelihoods of the 2 models is a chi-square value with 1 df. Including a cubic expression never produced a significantly better fit than a model with only linear and quadratic expressions ($\chi^2 < 3.84$; $P > 0.10$); we therefore reestimated P_0 , P_1 , and P_2 with the simpler model. We also

Table 1. Mean proportion (SE) of aphids eaten by *P. quatuordecimpunctata* adults or larvae in petri dishes and by adults on 2 host plants as a function of initial aphid density

Aphid density	Habitat			
	Petri dish (adults)	Petri dish (larvae)	Indian ricegrass	Crested wheatgrass
5	0.82 (0.05)	0.81 (0.05)	0.75 (0.07)	0.43 (0.08)
10	0.71 (0.08)	0.72 (0.05)	0.65 (0.06)	0.37 (0.06)
15	—	—	0.64 (0.06)	0.31 (0.04)
20	0.54 (0.07)	0.51 (0.04)	0.65 (0.05)	0.52 (0.03)
30	—	—	0.54 (0.06)	0.42 (0.03)
40	0.36 (0.05)	0.30 (0.02)	0.41 (0.04)	0.32 (0.06)
80	0.22 (0.03)	0.19 (0.02)	—	—

—, No data.

used *t*-ratios to confirm whether a coefficient was significantly different from 0 (Wilkinson et al. 1996).

Once the shape of the functional response was determined, we used nonlinear least-squares regression to estimate conventional parameters associated with Holling-type models (Holling 1966). Because aphid prey were depleted during the experiment, the appropriate type II model is the "random-predator" equation (Rogers 1972):

$$N_e = N_0(1 - \exp[a(T_h N_e - T)]) \quad [2]$$

in which *a* = the attack coefficient or instantaneous searching rate, *T_h* = handling time, and *T* = the total time aphids were exposed to predators. For a type III response, *a* is no longer assumed to be constant, but increases with prey density. We fit a model in which *a* increases asymptotically with *N₀*: $a = (d + bN_0)/(1 + cN_0)$, and *b*, *c*, and *d* are fitted constants (Juliano 1993). With prey depletion:

$$N_e = N_0(1 - \exp[(d + bN_0)(T_h N_e - T)/(1 + cN_0)]) \quad [3]$$

Parameter estimates for equations 2 and 3 were obtained by iterative application of Newton's method (Juliano 1993), as performed by PROC NLIN in SAS (SAS Institute 1990). This method is preferable to the familiar linearization of the random-predator equation (Carter et al. 1984), which can produce biased estimates (Juliano and Williams 1987, Williams and Juliano 1996). In addition to estimating the functional response, we used 2-way analysis of variance (ANOVA) to compare the effects of plant species and prey density on the proportion of aphids eaten (angular-transformed) in the whole-plant experiment.

Results

Petri Dish Experiments. The proportion of aphids eaten by adult beetles in petri dishes declined monotonically with initial aphid density (Table 1). A type II functional response was also suggested by logistic regression because the estimate of the linear coefficient was significantly <0 (i.e., the proportion eaten declined even at lower aphid densities) and the quadratic coefficient was positive (Table 2). We therefore used equation 2 to estimate *a* and *T_h* (Table 3). This

Table 2. Maximum-likelihood estimates from logistic regressions of the proportion of aphids eaten by *P. quatuordecimpunctata* as a function of initial aphid density

Habitat	Parameter	Estimate (SE)	<i>t</i> -ratio	<i>P</i>
Petri dishes (adults)	Constant	1.54714 (0.20888)	7.41	<0.001
	Linear	-0.07288 (0.01060)	-6.87	<0.001
	Quadratic	0.00047 (0.00011)	4.50	<0.001
Petri dishes (larvae)	Constant	1.69991 (0.17773)	9.56	<0.001
	Linear	-0.09015 (0.00912)	-9.88	<0.001
	Quadratic	0.00063 (0.00009)	6.86	<0.001
Indian ricegrass	Constant	1.22096 (0.14270)	8.56	<0.001
	Linear	-0.03762 (0.00505)	-7.45	<0.001
Crested wheatgrass	Constant	-1.08420 (0.29614)	-3.66	<0.001
	Linear	0.07792 (0.02614)	2.98	0.003
	Quadratic	-0.00174 (0.00051)	-3.38	<0.001

model fit the observed data reasonably well (Fig. 1); the raw *R*² (= 1 - residual sum of squares/total sum of squares) = 0.85, and the observed versus predicted *R*² (= the square of the correlation between observed and predicted values) = 0.50.

Predation rates of larvae in dishes were similar to those of adults (Table 1). A type II model was again suggested by logistic analysis (Table 2), and the fit of equation 2 to observed data for larvae was slightly better than it was for adults (raw *R*² = 0.93; observed versus predicted *R*² = 0.63). The estimate of *T_h* was 25% larger for larvae than for adults because larvae consumed fewer aphids when dishes were stocked with 40 or 80 nymphs (Table 3; Fig. 1). We did not compare the stages statistically because they were tested in separate experiments, but the 95% CI of both *a* and *T_h* for adults overlapped with those for larvae.

Whole Plant Experiment. Responses of adult beetles to aphid density were more complex on whole plants. On Indian ricegrass, the proportions of aphids eaten suggested a type II functional response, except that predation risk was independent of prey density across the range of 10–20 aphids per plant (Table 1). This region thus resembled a type I response, which is expected if the effect of handling time is negligible until a critical prey density is reached. Although including a quadratic coefficient significantly improved the fit of equation 1 to observed data in both petri dish experiments, it did not do so when beetles foraged on Indian ricegrass (likelihood-ratio test: $\chi^2 = 2.31$; *df* = 1; *P* > 0.10). We therefore performed the regression with only a linear coefficient, which was significantly <0 (Table 2).

Table 3. Attack coefficients (*a*), handling times (*T_h*) and their asymptotic standard errors from nonlinear regressions of the number of aphids eaten by *P. quatuordecimpunctata* as a function of initial aphid density

Habitat	Model	<i>a</i> (min ⁻¹)	<i>T_h</i> (min)
Petri dishes (adults)	Type II	0.028 (0.009)	2.910 (0.357)
Petri dishes (larvae)	Type II	0.034 (0.007)	3.832 (0.240)
Indian ricegrass	Type II	0.010 (0.003)	7.092 (1.384)
Crested wheatgrass	Type III	— ^a	10.989 (1.222)

^a In the best-fit type III model, $a = bN_0$, $b = 3.556 \times 10^{-4}$ (asymptotic SE = 0.799×10^{-4}) and *N₀* = initial aphid density.

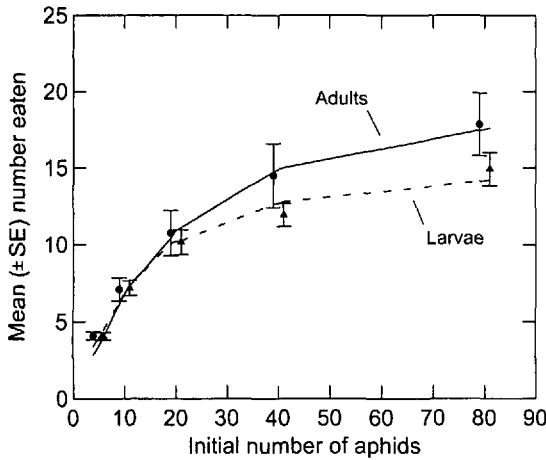


Fig. 1. Observed (symbols) versus predicted (lines) number of Russian wheat aphids eaten by *P. quatuordecimpunctata* adults (●) or larvae (▲) in petri dishes. Observed data are presented as means ± SE for clarity, but predicted values were generated from regressions that fit individual points to a type II functional response. *n* = 12–18 replicates per aphid density.

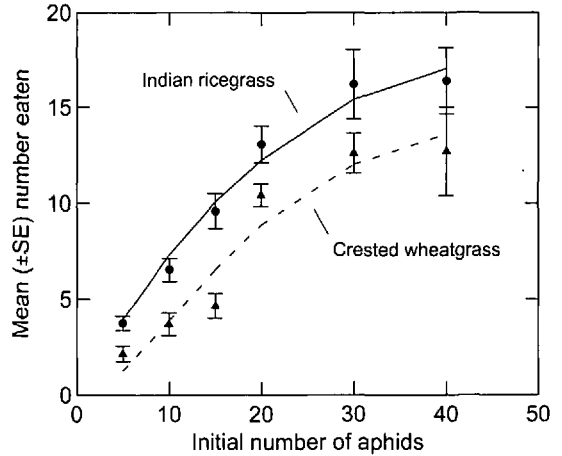


Fig. 2. Observed (symbols) versus predicted (lines) number of Russian wheat aphids eaten by *P. quatuordecimpunctata* adults on Indian ricegrass (●) or crested wheatgrass (▲). Observed data are presented as means ± SE for clarity, but predicted values were derived from regressions that fit individual points to a type II (Indian ricegrass) or type III (crested wheatgrass) functional response. *n* = 9–14 replicates per aphid density.

Both a negative linear coefficient and a nonsignificant quadratic term are compatible with a type II response (Trexler et al. 1988); equation 2 was therefore used to estimate functional-response parameters for beetles on Indian ricegrass. The fit of the model was similar to that obtained from beetles in petri dishes (raw $R^2 = 0.89$; observed versus predicted $R^2 = 0.55$). Not surprisingly, the attack coefficient was much lower when beetles foraged on Indian ricegrass plants rather than in petri dishes, but estimates of T_h also depended on "habitat" (Table 3). Beetles consumed similar maximum numbers of aphids on Indian ricegrass plants and in petri dishes (Figs. 1 and 2) even though available foraging time was longer on plants (3 h versus 1 h). Hence, the estimate of T_h for beetles on Indian ricegrass was much higher than that for beetles in dishes (Table 3).

Aphid predation risk was lower on crested wheatgrass than on Indian ricegrass at each level of aphid density (Table 1). Consequently, there was a highly significant effect of plant species on the proportion of prey eaten ($F = 38.86$; $df = 1, 140$; $P < 0.001$) in addition to the expected effect of aphid density ($F = 4.06$; $df = 1, 140$; $P = 0.002$). Although the effect of grass species appeared to be greater at low aphid densities than at high aphid densities (Table 1; Fig. 2), the host-plant × density interaction was not quite significant ($F = 1.98$; $df = 1, 140$; $P = 0.09$).

Prey consumption on crested wheatgrass did not closely resemble any of the classic Holling-type models, because the proportion of aphids eaten initially decreased with increasing aphid density, rose sharply, and then decreased again at the highest densities (Table 1). In contrast to the previous analyses, the linear coefficient of the logistic regression was significantly positive and the quadratic coefficient was negative

(Table 2). This result, and the apparent sigmoidal relationship in Fig. 2, led us to fit a type III model (equation 3) to observed data. Application of the initial model ($a = [d + bN_0] / [1 + cN_0]$) indicated that parameter c was not significantly different from 0 (i.e., its asymptotic 95% CI overlapped 0). Fitting a 2nd model omitting this parameter indicated that parameter d was also not significantly different from 0. The best-fit type III model (raw $R^2 = 0.86$; observed versus predicted $R^2 = 0.59$) was thus one in which the attack coefficient (a) is a simple linear function of N_0 , with slope $b = 3.556 \times 10^{-4}$ (asymptotic SE = 0.799×10^{-4}). The estimate of T_h on crested wheatgrass was greater than that on Indian ricegrass (Table 3), which reflects lower consumption rates on crested wheatgrass even at high prey densities (Fig. 2).

Figure 2 suggested that the reduced type III model ($a = bN_0$) did not provide a good fit to observed data in the region where the number of aphids eaten on crested wheatgrass increased sharply. Yet this model was at least marginally better than a type II model. Fitting equation 2 instead of the reduced version of equation 3 increased the residual sum of squares and reduced the observed versus predicted R^2 from 0.59 to 0.56 (direct comparisons are appropriate because both models estimate 2 parameters). Moreover, the asymptotic standard error of T_h from the type II model was so large that its 95% CI overlapped 0.

Discussion

Most investigations of tritrophic interactions have been restricted to a single spatial or temporal scale (but see Kareiva and Sahakian 1990). The short-term functional response of *P. quatuordecimpunctata* in this

study was consistent with longer-term field experiments in which *D. noxia* populations experienced a higher probability of local extinction on the slender-leaved Indian ricegrass than on the broad-leaved crested wheatgrass (Messina et al. 1997). Our results also agree with 15-min behavior trials in which beetles encountered and captured *D. noxia* at higher rates on Indian ricegrass than on crested wheatgrass (Clark and Messina 1998). Such consistency across scales suggests that functional-response experiments can provide a relatively rapid way to assess the effects of plant morphology or chemistry on the efficacy of a natural enemy.

The host-plant effect on the functional response of *P. quatuordecimpunctata* probably depended on the availability of prey refuges rather than a modification of predator searching behavior or residence time (Carter et al. 1984, Da Silva et al. 1992). On Indian ricegrass, most individuals of *D. noxia* feed on open leaf blades because rolled leaves and leaf junctions are simply too narrow to permit aphid aggregations. These microsites on crested wheatgrass usually harbor significant numbers of aphids and yet are too small to permit entry of predators as large as *P. quatuordecimpunctata* adults (Messina et al. 1997). Further support for the role of prey refuges is the lack of a plant effect on beetle time budgets or residence times in the absence of aphid prey (Clark and Messina 1998). Hawkins et al. (1993) suggested that the availability of prey refuges may affect the success of a natural enemy for biological control (see also Gross 1991). If so, the efficacy of *P. quatuordecimpunctata* adults may be limited on cereals, which have leaf architectures resembling that of crested wheatgrass (Kauffman and LaRoche 1994).

The whole-plant experiment also suggests that plant traits can modify the shape of a functional response curve in addition to altering capture rates at a given prey density. Logistic regression revealed a substantial effect of grass species on the relationship between prey density and the per capita risk of predation (Tables 1 and 2) regardless of which Holling-type model best described variation in the absolute number of prey eaten (Fig. 2). We can only speculate as to the mechanism underlying the complex, sigmoidal response observed on crested wheatgrass (Table 1; Fig. 2). One explanation is that most aphids are protected within rolled leaves at low densities, but proportionally more aphids are forced to feed outside these refuges as the number of aphids per wheatgrass seedling rises. Traditional explanations for sigmoidal response curves, such as learning and prey switching, are unlikely or impossible under our conditions, and any explanation must account for the absence of a sigmoidal response on Indian ricegrass. Regardless of underlying mechanisms, plant traits that affect the likelihood of positively density-dependent mortality could obviously influence predator-prey dynamics (Taylor 1984).

The functional response of *P. quatuordecimpunctata* on Indian ricegrass was reasonably well described by a type II model, but estimates of both a and T_h on this

host were quite different from estimates obtained from petri dish experiments (Table 3). Parameters estimated in simple arenas are therefore not easily extrapolated to more realistic conditions (Spitze 1985, Luck et al. 1988). Part of the discrepancy between functional responses measured in the laboratory versus in the field can be explained by the use of unrealistically high densities in the laboratory (O'Neil 1989, 1997). Our results demonstrate that varying the complexity of the foraging substrate can yield large differences in attack coefficients and handling times even when all parameters are estimated in the laboratory and similar prey densities are used (Table 3). It is not obvious why the estimate of T_h should be longer on whole plants than in petri dishes, but the comparison is complicated by the different durations of the 2 experiments (Figs. 1 and 2). Artificial arenas are probably most appropriate when the intention is merely to compare physiological capacities between predator species or stages, as in our comparison of beetle larvae and adults.

If functional-response experiments are to be used to evaluate potential biological control agents, they should incorporate as much realism as possible and should be considered in conjunction with numerical (aggregative) responses (Kareiva and Odell 1987). Host plants represent only 1 source of variation in the way predators respond to variation in prey density. Another likely source is the presence of alternative prey (Colton 1987). Populations of the Russian wheat aphid typically co-occur with a suite of other aphids on both crop and noncrop hosts, and most of these cereal aphids feed in microsites that appear to be readily accessible to generalist predators (Feng et al. 1992). One study has suggested that presence of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), reduces the efficiency of lacewing predators against *D. noxia* on crested wheatgrass (Bergeson and Messina 1997). This effect of alternative prey should also be evident in a predator's functional response, and can be estimated by a multispecies extension of the random-predator equation (Chesson 1989) or by more complex models that do not assume constant parameters (Abrams 1990).

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