Effect of a Seed-Mix Deployment of Cry3A-transgenic and Nontransgenic Potato on the Abundance of *Lebia grandis* (Coleoptera: Carabidae) and *Coleomegilla maculata* (Coleoptera: Coccinellidae)

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ABSTRACT We estimated the relative abundance of 2 important natural enemies of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), in seed-mixed and pure fields of Cry3A-transgenic and nontransgenic potato. Sampling techniques included sweeping foliage, making timed visual counts of predators on foliage, and by trapping soil-dwelling predators in pitfall traps. Adults of *Lebia grandis* Hentz were less abundant in seed-mixed and pure 100% transgenic potato fields than in nontransgenic potato fields. In contrast, adults of *Coleomegilla maculata* (De Geer) were not affected by the treatments. We predict that *L. grandis* will rapidly disperse from seed-mixed and 100% transgenic potato fields because of the low densities of *L. decemlineata* in these fields. However, *C. maculata* will thrive and flourish in fields containing transgenic potato, especially when alternative prey or plant pollen are available.

KEY WORDS *Coleomegilla maculata, Lebia grandis, Leptinotarsa decemlineata, Bacillus thuringiensis,* transgenic plants

Bacillus thuringiensis BERLINER subsp. *tenebrionis*-derived Cry3A proteins are selectively toxic to coleopterans, particularly chrysomelids (Krieg et al. 1983, Herrnstadt et al. 1986, Bauer 1990, MacIntosh et al. 1990, Eckberg and Cranshaw 1994). In susceptible species, the Cry3A toxins bind to receptors on the midgut epithelium and cause cytolysis of the midgut cells, which leads to paralysis and subsequent death (Slaney et al. 1992, Federici 1993). Cry3A has insecticidal activity against the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Ferro and Gelernter 1989). Transgenic potato (*Solanum tuberosum* L.) containing the Cry3A δ-endotoxin cause paralysis within 24 h, once ingested by *L. decemlineata* instars and adults (Perlak et al. 1993).

The best method of deploying transgenic plants, such as Cry3A-transgenic potato, has been a concern, because the method of deployment will affect the selection pressure against the target insects (Daly 1994, Whalon and Wierenga 1994). Growing of homogeneous commercial stands has not been recommended because of the threat that pests will readily develop resistance (Gould 1988, 1994). One suggested method of managing resistance could be the deployment of mixtures of transgenic and nontransgenic plants (McGaughey and Whalon 1992). A mix deployment, in which susceptible individuals in the pest population could survive on nontransgenic plants, and mate with resistant individuals, may prevent rapid buildup of resistant individuals in the population (Hoy and Head 1995). However, this deployment strategy has been challenged by others who believe that the nontransgenic plants in the mixture could suffer unacceptable levels of damage (see Mallet and Porter 1992, McGaughey and Whalon 1992, Wierenga et al. 1996). Pest individuals might be able to sense that they are on a transgenic plant; hence, they might move off of the toxic plant before ingesting any foliage (Gould 1994). When selecting a deployment strategy, some consideration must be given to the ones that best incorporate biological control as an additional means of suppressing primary and secondary pests (see Johnson and Gould 1992). Biological control may play a pivotal role in resistance management because natural enemies may affect the rate of pest adaptation to transgenic host plants (Gould et al. 1991, Arpaia et al. 1997).

Increasing the abundance and effectiveness of natural enemies in a potato crop has been a challenge (Hough-Goldstein et al. 1993). Specialist and generalist natural enemies could respond differently, based on the presence or absence of the target insect pest (Jervis and Kidd 1996, Van Driesche and Bellows 1996). Fields planted to 100% transgenic potato may alter the abundance of indigenous natural enemies of *L. decemlineata* because of the low densities of this pest. Specialists may tend to disperse from the crop in the absence of their prey or host. Generalists likely will respond differently than specialists to 100% transgenic potato fields. Because they are not dependent solely on the target pest for their survival, they may persist in these fields by using alternate prey which are not affected by the plant toxins (Hoy et al. 1998). In fields

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containing seed mixtures of transgenic and nontransgenic potato, densities of *L. decemlineata* may or may not be high enough to arrest the specialist enemies in these fields. But the seed-mixed fields would provide an ideal situation for generalist enemies because the target pest-prey and alternate prey would reside in the same field.

We investigated the seasonal abundance of a generalist and a specialist natural enemy of *L. decemlineata*. They were *Lebia grandis* Hentz (Coleoptera: Carabidae) and *Coleomegilla maculata* (De Geer) (Coleoptera: Coccinellidae). *L. grandis* adults forage on potato plants during the day (E.W.R., unpublished data) and the soil surface primarily during the night, in late spring and summer (Chaboussou 1939, Groden 1989). In the potato ecosystem, adults are specialist predators of eggs and all instars of *L. decemlineata*, whereas *L. grandis* larvae are specialist ectoparasitoids of pupae of *L. decemlineata* in soil chambers. *C. maculata* are primarily active during the day on potato foliage (and also on foliage of corn, alfalfa, and other neighboring crops) during the spring and summer. Adults and larvae are predators of eggs and 1st and 2nd instars of *L. decemlineata* in addition to other prey and pollen (Groden et al. 1990, Hough-Goldstein et al. 1993).

In this article, we tested whether the relative abundance of *L. grandis* and *C. maculata* adults differed between mixed and uniform stands of transgenic and nontransgenic potato. This research will help to define the complex interactions that occur between transgenic plants, target and nontarget herbivores, and natural enemies.

Materials and Methods

Description of Experimental Fields. Field sites were located on 3 experimental farms of the Central Maryland Research and Education Center. These farms were the Upper Marlboro Facility, Upper Marlboro (Prince Georges County); the Beltsville Facility, Beltsville (Prince Georges County); and the Clarksville Facility, Ellicott City (Howard County).

On each farm, 4 isolated fields of 'Russet Burbank' potato were planted in 1994 and 1995. Treatments assigned to these fields included 100% nontransgenic (n1), 50% nontransgenic and 50% transgenic (n.5/t.5), 30% nontransgenic and 70% transgenic (n.3/t.7), and 100% transgenic (t1) potato fields. Each isolated field on all farms was ≈0.05 ha and consisted of 24 rows, each 23 m long, with seed pieces spaced at 0.3 m apart. In the seed-mix fields, nontransgenic and transgenic seed pieces were planted as a random mix by machine.

The distance between treatment fields on each farm was ≈0.50 km. The 3 farms served as replicates in space to test treatment effects. During both years, all fields were planted in early April and received the same crop management practices. Each field was assigned the same treatment for both years.

Experimental Design. Colorado potato beetle populations were established at these sites using individuals collected from commercial potato farms, with no previous history of *B. t. tenebrionis* use. Before the initiation of our experiments, beetles were distributed equally, at a density of 1 beetle per plant cluster, in the nontransgenic field at each farm in 1992 and 1993. This allowed time for the resident populations to become acclimated to each site. To further equalize densities, newly emerged beetles were collected in May 1994 from the pure stand of normal potato and distributed to the other treatment fields at a density of 1 beetle per plant cluster. In 1995, this re-allocation method was repeated only in the seed mixtures, because all adults died shortly after being placed in the 100% transgenic field in the 1994 season.

Broad-spectrum insecticides were administered to the treatment fields in both seasons using a standard, tractor-driven boom sprayer. Esfenvalerate (Asana, DuPont, Palo Alto, CA), was applied twice during the season at a rate of 0.025 kg (AI)/ha in the 100% nontransgenic fields to prevent total defoliation by *L. decemlineata*. Dimethoate (Cygon 400, American Cyanimid, Havre de Grace, MD), was applied once at a rate of 0.58 liters (AI)/ha to suppress potato leafhopper, *Empoasca fabae* (Harris), in all treatment fields. Both insecticides are toxic to coleopteran predators (Hurej and Dutcher 1994, Jepson et al. 1995, Duffield et al. 1996, Çilgi et al. 1996, Cho et al. 1997, Hamilton and Lashomb 1997). Note that sampling ceased for several days after a given field had been sprayed with either insecticide.

Estimating Predator Abundance. Predator populations were monitored in the treatment fields during both years using sweep net and timed visual count techniques. These procedures have been used previously to monitor populations of foliar predators, including lady beetles (Lapchin et al. 1987; Michels et al. 1996, 1997). At approximately weekly intervals, 3 sets of 20 standard 180° sweeps with a 38-cm beating net were taken in each field. Sampling initiation and termination dates varied among farms because of differences in crop–insect phenology. Also, dates were staggered within a week to distribute the work load. The sampling occurred from 21 June to 9 August 1994, and from 16 May to 20 July 1995. At each collection date, swept insects were stored in plastic bags and brought to the laboratory. Insects were identified to genera and species and counted. A number of predator species were captured and counted, but only the data for *L. grandis* and *C. maculata* are presented herein. Target and nontarget herbivores were represented in the samples.

Visual counts of *L. grandis* and *C. maculata* on the uppermost surfaces of plant foliage were made by walking between rows in each field and recording the number of species seen in a period of 10 min. These counts were made only in 1995 between 22 May and 28 July. Eleven counts were recorded at Upper Marlboro and Beltsville; 8 were taken at Clarksville.

Pitfall traps were used to estimate the abundance of surface-active carabids in treatment fields. Numerous studies have used this standard technique for monitoring carabids in agroecosystems (Greenslade 1964, Ericson 1979, Hokkanen and Holopainen 1986, Halsall

and Wratten 1988). Traps consisted of plastic cups (473 ml, 9 cm diameter opening) sunk into the ground with the rim flush with the soil surface. Leaf litter within 8–10 cm of the perimeter of each trap was removed and the soil smoothed to facilitate the movement of carabids around the traps (Greenslade 1964, Powell et al. 1985). Traps were filled to the ¼ mark with a solution of water and liquid detergent so that captured beetles sank to the bottom of the trap.

Pitfall traps were deployed for 48 h during 1994, but for only 24 h during 1995. In 1994, sampling occurred at intervals of ≈7 d from 23 May to 2 August at Upper Marlboro, 23 May to 9 August at Beltsville, and 15 June to 9 August at Clarksville. In 1995, sampling occurred at intervals of ≈10 d from 22 May to 18 July at Upper Marlboro, 30 May to 26 July at Beltsville, and 30 May to 27 July at Clarksville. Pitfall collections were taken to the laboratory and insects were stored in vials of alcohol, to be identified and counted at a later date. A number of carabid species were collected in the samples, but only the data for *L. grandis* are presented herein.

Statistical Analyses. Data collected by the 3 techniques were square-root transformed to normalize variances before data analysis. Data were pooled and means computed for each season because of the low abundance of both predators on many of the sampling dates in 1994 and 1995. The Kruskal–Wallis test, a nonparametric analysis of variance (ANOVA) was used to test for significance, and the Dunn test, a nonparametric multiple comparisons method, was used to detect any differences between treatment means (see Sokal and Rohlf 1981). Means were considered significantly different when $P \leq 0.05$. The Spearman Rank Correlation coefficient (r_s, see Glantz 1992), was used to identify any trends between species abundances. All data analyses were performed with Sigma Stat software (1994).

Results

Abundance of *L. grandis* and *C. maculata*. In 1994, *L. grandis* adults were significantly more abundant on potato foliage in the 100% nontransgenic field (n1) and in the n.5/t.5 mixture than in the n.3/t.7 mixture or the 100% transgenic (t1) field, as determined by sweeping foliage (Table 1). In 1995, adults were significantly more abundant in the 100% nontransgenic field than in both seed mixtures and 100% transgenic field. In contrast, *C. maculata* adults showed no preference for any treatment field in either year.

Visual counts of predators on the foliage indicated that *L. grandis* were more abundant in the 100% nontransgenic field than in the other treatments, and that *C. maculata* were not affected by the treatments (Table 2). *L. grandis* were seen on foliage during the morning hours in direct sunlight, and often were perched on the upper leaf surface in full view in the 100% nontransgenic potato in both seasons. Others were seen feeding on all instars of *L. decemlineata* on the foliage. Similarly, *C. maculata* were quite visible on the uppermost portions of the potato plant, particularly in the morning.

Table 1. Mean ± SEM number of *L. grandis* and *C. maculata* adults captured per sweep sample per day in treatment fields

Treatment[a]	1994 season	1995 season
	L. grandis	
n1	0.25 ± 0.07a	0.49 ± 0.15a
n.5/t.5	0.07 ± 0.03a	0.04 ± 0.02b
n.3/t.7	0.00 ± 0.00b	0.01 ± 0.01b
t1	0.00 ± 0.00b	0.00 ± 0.00b
	$H = 23.7$, df = 3, $P < 0.0001$	$H = 39.8$, df = 3, $P < 0.0001$
	C. maculata	
n1	0.20 ± 0.05a	0.22 ± 0.06a
n.5/t.5	0.16 ± 0.05a	0.32 ± 0.09a
n.3/t.7	0.27 ± 0.06a	0.19 ± 0.05a
t1	0.16 ± 0.05a	0.18 ± 0.05a
	$H = 3.32$, df = 3, $P = 0.34$	$H = 0.84$, df = 3, $P = 0.84$

In 1994, 252 sweep samples; in 1995, 312 sweep samples. *H*, statistic for Kruskal–Wallis test. Means followed by a different letter in a column are significantly different ($P \leq 0.05$, Dunn test).

[a] See *Description of Experimental Fields* for definitions.

The mean number of *L. grandis* captured in pitfall traps was significantly greater in the 100% nontransgenic field than in the seed mixtures or 100% transgenic field in both seasons (Table 3). *L. grandis* were observed on the ground during the day, attacking and consuming 4th instar *L. decemlineata* burrowing into the soil to pupate.

Abundance of *L. decemlineata* and *E. fabae*. Small larvae of *L. decemlineata* (1st and 2nd instars <5.0 mm long) also were captured in the sweep nets, although this method was a rough estimate of prey density. Significantly more *L. decemlineata* were present on foliage in the 100% nontransgenic field than in both seed mixtures and 100% transgenic field in 1994 and 1995 (Table 4). In addition, adult and nymphal leafhoppers, primarily *E. fabae*, were significantly more abundant on foliage in the seed mixtures and 100% transgenic field, than in the nontransgenic field.

Correlation of Predator and Pest Abundances. A significant correlation was detected between the abundance of *L. grandis* and the abundance of both pests, *L. decemlineata* and *E. fabae* (Table 5). Correlation coefficients (r_s) were rather low for both *L.*

Table 2. Mean ± SEM number of *L. grandis* and *C. maculata* adults observed on plant foliage during timed visual counts made in 8 rows per day in treatment fields (1995 season)

Treatment[a]	*L. grandis*	*C. maculata*
n1	1.19 ± 0.39a	0.74 ± 0.21a
n.5/t.5	0.13 ± 0.08b	1.16 ± 0.26a
n.3/t.7	0.06 ± 0.04b	2.45 ± 0.90a
t1	0.00 ± 0.00b	1.74 ± 0.72a
	$H = 18.1$, df = 3, $P = 0.0004$	$H = 3.91$, df = 3, $P = 0.27$

In total, 124 replicate counts were taken. *H*, statistic for Kruskal–Wallis test. Means followed by a different letter in a column are significantly different ($P \leq 0.05$, Dunn test).

[a] See *Description of Experimental Fields* for definitions.

Table 3. Mean ± SEM number of *L. grandis* adults captured in pitfall traps per row per day in treatment fields

Treatment[a]	1994 season	1995 season
n1	0.08 ± 0.03a	0.10 ± 0.05a
n.5/t.5	0.00 ± 0.00b	0.01 ± 0.01b
n.3/t.7	0.01 ± 0.00b	0.01 ± 0.01b
t1	0.00 ± 0.00b	0.00 ± 0.00b
	$H = 27.9$, df = 3, $P < 0.0001$	$H = 21.4$, df = 3, $P < 0.0001$

In 1994, 264 replicate plant rows; in 1995, 180 replicate plant rows. *H*, statistic for Kruskal–Wallis test. Means followed by a different letter in a column are significantly different ($P \leq 0.05$, Dunn test).

[a] See *Description of Experimental Fields* for definitions.

Table 5. Summary of correlation analysis between predator (*L. grandis* or *C. maculata*) and pest (*L. decemlineata* or leafhoppers)

Predator	Pest	1994 season		1995 season	
		r_s	*P*	r_s	*P*
L. grandis					
	L. decemlineata	0.37	0.001	0.41	0.001
	Leafhoppers	−0.18	0.005	−0.12	0.04
C. maculata					
	L. decemlineata	0.08	0.22	0.10	0.07
	Leafhoppers	0.06	0.32	0.01	0.79

r_s, correlation coefficient for the Spearman rank test (Glantz 1992). Statistics generated from sweep sample data described previously (see Tables 1 and 4). In 1994, $n = 242$ samples; in 1995, $n = 295$ samples.

grandis pest associations, which meant that factors other than the abundance of the 2 species influenced both associations. Nevertheless, a positive correlation occurred between *L. grandis* and *L. decemlineata* for both years, indicating that the abundance of both species tended to decrease together as the percentage of transgenic plants increased in a treatment field (see Tables 1 and 4). In contrast, a negative correlation was detected between *L. grandis* and *E. fabae;* the abundance of *L. grandis* tended to decrease as the abundance of the leafhoppers increased.

No significant correlation was detected between the abundance of *C. maculata* and *L. decemlineata* nor between *C. maculata* and *E. fabae* (Table 5).

Discussion

Lebia grandis are specialist enemies of *L. decemlineata* in cultivated potato (Hough-Goldstein et al. 1993). The adults are predators of eggs and all instars; in addition, the larvae are ectoparasitoids of mature *L. decemlineata* larvae and pupae in soil chambers (Chaboussou 1939, Groden 1989). For this reason, the low abundance or absence of *L. grandis* in the seed-mixed and 100% transgenic fields in our study largely can be explained by the effectiveness of the Cry3A-transgenic potato, which eliminated the prey or hosts of this natural enemy. As a result, *L. grandis* were abundant only in the fields that harbored substantial numbers of *L. decemlineata* (the 100% nontransgenic fields). *L. grandis* aggregate where *L. decemlineata* occur and disperse from fields harboring few or no *L. decemlineata*. *L. grandis* also could have been encouraged to disperse from fields containing transgenic potato if Cry3A-intoxicated 1st instars of *L. decemlineata* were unpalatable. However, intoxicated *L. decemlineata* were just as palatable as nonintoxicated ones (E.W.R., unpublished data).

Table 4. Mean ± SEM number of small larvae of *L. decemlineata* and leafhoppers (primarily *E. fabae*) nymphs and adults captured per sweep sample per day in treatment fields

Treatment[a]	1994 season	1995 season
	L. decemlineata	
n1	12.42 ± 1.46a	14.27 ± 2.31a
n.5/t.5	1.70 ± 0.78b	3.77 ± 1.00b
n.3/t.7	0.76 ± 0.32b	1.27 ± 0.38bc
t1	0.02 ± 0.02b	0.08 ± 0.05c
	$H = 155.5$, df = 3, $P < 0.0001$	$H = 66.1$, df = 3, $P < 0.0001$
	Leafhoppers	
n1	3.73 ± 0.77b	2.58 ± 0.58c
n.5/t.5	32.89 ± 2.50a	12.28 ± 1.71b
n.3/t.7	30.40 ± 2.39a	11.60 ± 1.30b
t1	32.06 ± 2.41a	18.16 ± 1.89a
	$H = 91.6$, df = 3, $P < 0.0001$	$H = 76.6$, df = 3, $P < 0.0001$

In 1994, 252 sweep samples; in 1995, 312 sweep samples. *H*, statistic for Kruskal–Wallis test. Means followed by a different letter in a column are significantly different ($P \leq 0.05$, Dunn test).

[a] See *Description of Experimental Fields* for definitions.

The impact of spraying insecticides did not confound the effect of the potato deployments on *L. grandis* abundance. Dimethoate was applied just once for *E. fabae* control in all treatment fields, and esfenvalerate was applied twice for *L. decemlineata* suppression in the 100% nontransgenic fields during both seasons. Despite the fact that both insecticides are toxic to coleopteran predators (Hurej and Dutcher 1994, Jepson et al. 1995, Duffield et al. 1996, Çilgi et al. 1996, Cho et al. 1997, Hamilton and Lashomb 1997), we contend that the low abundance of *L. grandis* in the seed-mixed and pure transgenic fields cannot be explained by the toxic activity of dimethoate alone, because the latter also was used in the 100% nontransgenic fields where *L. grandis* abundance was highest.

If stands of high-dose 100% transgenic potato completely replace all acreage previously planted with nontransgenic potato, the survival of *L. grandis* will depend upon their ability to locate *L. decemlineata* residing on *S. tuberosum* in abandoned fields or on the closely related *Solanum carolinense* L. (horsenettle). *L. decemlineata* adults and larvae feed on horsenettle and *L. grandis* have been found on the plant (Hemenway and Whitcomb 1967, Mena-Covarrubias et al. 1996). In addition, *L. grandis* could potentially switch to another prey or host closely related to the Colorado potato beetle, considering that this natural enemy has no historical association with this herbivore on ancestral host plants in central Mexico (see Logan et al. 1987, Cappaert et al. 1991). A potential alternate prey or host for *L. grandis* on horsenettle could be the false potato beetle, *Leptinotarsa juncta* (Germar), which is found in Maryland and other eastern states (Jacques, 1988). However, it has not been determined whether

L. juncta pupae are suitable hosts for proper development of *L. grandis* immatures.

The abundance of the generalist lady beetle, *C. maculata*, was not influenced by the deployment of 100% or seed-mixed fields of transgenic potato. *C. maculata* are generalist predators (Hodek 1993) that readily attack eggs and 1st and 2nd instars of *L. decemlineata* (Groden et al. 1990, Hazzard et al. 1991, Ciroux et al. 1995, Hilbreck and Kennedy 1996), and nymphs and adults of green peach aphids, *Myzus persicae* (Sulzer) (Smith 1965, Hazzard and Ferro 1991). Other prey found on potato include eggs of the European corn borer, *Ostrinia nubilalis* (Hübner) (Andow and Risch 1985). Apparently, *C. maculata* utilize a broad spectrum of alternate prey, such as *M. persicae*, residing on transgenic or nontransgenic foliage, which suggests that this lady beetle will be able to persist in seed-mixed and 100% transgenic fields despite the low density or lack of *L. decemlineata*. In addition, *C. maculata* consumed transgenic-fed *L. decemlineata* without any adverse effects on their preimaginal development or fecundity (Riddick and Barbosa 1998). Other published research has demonstrated that the abundance of *C. maculata* was not altered by the deployment of transgenic corn (Orr and Landis 1997, Pilcher et al. 1997), or by the deployment of intraplot mixtures of transgenic and nontransgenic collard plants (Riggin-Bucci and Gould 1997).

The abundance of *L. decemlineata* was much reduced in fields containing transgenic potato in comparison with the nontransgenic fields in both seasons. A decline of >75% in *L. decemlineata* density from the nontransgenic treatment to the 50/50% seed-mix treatment was not expected. Perhaps some of the decline resulted from predation by generalists such as *C. maculata*. However, *C. maculata* did not show any preference for the seed-mixed fields in the current study, so the likelihood that a synergistic (additive) interaction occurred between *C. maculata* predation and transgenic plant resistance was remote, based on our data.

A similar scenario was presented by Riggin-Bucci and Gould (1997). They predicted that densities of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), would decline after 2 generations in intraplot mixtures of transgenic collards and nontransgenic collards because of the plant resistance alone. They concluded that predation or parasitism by generalist natural enemies did not contribute significantly to the decline of *P. xylostella* populations.

Our experiments were not designed to identify any synergestic interactions between predators and transgenic plants. But such experiments have been conducted by Johnson (1997) and Johnson and Gould (1992). They found that in fields of 100% transgenic tobacco expressing low levels of resistance to *Heliothis virescens* (F.) (Lepidoptera: Noctuidae), certain natural enemies did, in fact, contribute to the reduction of *H. virescens* density.

Another unexpected result of the current study was the increased densities of leafhoppers (primarily potato leafhoppers, *E. fabae*) in the seed-mixed and 100% transgenic potato fields. Despite the fact that dimethoate was applied for *E. fabae* suppression in all fields, leafhopper densities remained rather high. One explanation for the differences in leafhopper abundance could be that both dimethoate and esfenvalerate were sprayed in the nontransgenic field. Esfenvalerate was used to reduce *L. decemlineata* populations, but this chemical was toxic to *E. fabae* as well. Another explanation could be that indirect competition between *L. decemlineata* and *E. fabae* was relaxed in the fields containing transgenic foliage. Tomlin and Sears (1992) demonstrated that a decrease in the quality of potato foliage resulted in indirect competition between these 2 species. They showed that potato leafhoppers produced fewer eggs on plants that were partially defoliated by *L. decemlineata* or coated with *L. decemlineata* excrement. In the current study, the low density of *L. decemlineata* in the fields containing transgenic potato could have released the leafhoppers from competition for suitable plant foliage, thereby allowing unrestricted feeding and ovipositing on an unlimited resource. As a result, leafhopper density increased rapidly in the fields containing transgenic potato. In addition, it appears that indigenous natural enemies of *E. fabae* were not effective in suppressing the high densities of this pest. The potato leafhopper is a serious pest in the eastern and northcentral United States (Walgenbach and Wyman 1985) that is not effectively controlled by indigenous natural enemies. In nontransgenic potato, they have been somewhat suppressed, indirectly, by insecticides targeted for the Colorado potato beetle in addition to possible competition, as stated above. But in transgenic potato fields, *E. fabae* must be controlled, preferably, without using broad-spectrum insecticides that disrupt the natural control of other pests (Hoy et al. 1998).

In conclusion, we have demonstrated that the specialist carabid, *L. grandis*, will not persist in seed-mixed and 100% transgenic potato fields. We predict that *L. grandis* will rapidly disperse from these fields because of the low densities of *L. decemlineata* inhabiting them. However, *C. maculata* likely will thrive and flourish in fields containing transgenic potato, especially given the generalist feeding preferences of this predator. More interestingly, the predatory behavior of *C. maculata* could decrease the rate at which *L. decemlineata* adapt to transgenic potato in plot-to-plot mixtures (Arpaia et al. 1997). Further research should seek to define clearly the complex relationship between resistance management, target and nontarget herbivores, and their natural enemies in mixtures of transgenic and nontransgenic crops.

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