

# Reproduction and Dispersal of Summer-Generation Colorado Potato Beetle (Coleoptera: Chrysomelidae)

ANDREI V. ALYOKHIN AND DAVID N. FERRO

Department of Entomology, University of Massachusetts, Amherst, MA 01003

Environ. Entomol. 28(3): 425-430 (1999)

**ABSTRACT** Colorado potato beetle dispersal and reproduction was investigated under field and laboratory conditions. Movement and mating of newly emerged summer-generation Colorado potato beetle adults was monitored in the field using a mark-recapture technique, and beetle mating within experimental plots was recorded. The number of degree-days (DD) required for the beetles to become reproductive was tested in an environmental chamber using 10°C as a developmental threshold. A computer-linked flight mill system was used to quantify the influence of mating on the flight behavior of male and female beetles. Adult dispersal started within the first 24 h after eclosion from the pupae, but a significant proportion of newly emerged beetles stayed close to the place of their larval development until reaching reproductive maturity. The beetles required at least 34 DD before mating produced viable offspring, and females did not start laying eggs until a minimum of 51 DD after eclosion. Mating had a pronounced effect on beetle flight, decreasing flight activity of the females and increasing flight activity of the males. Enhancing gene flow between beetles surviving on transgenic plants and susceptible beetles in refugia should be advantageous in managing beetle resistance to transgenic plants.

**KEY WORDS** Colorado potato beetle, mating, flight, resistance management, transgenic plants

COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), is the major insect defoliator of potato in North America (Weber and Ferro 1994a). This pest has a complicated and diverse life history, which is well-suited to agricultural environments. Migration, closely connected with diapause, feeding, and reproduction, allows Colorado potato beetle to employ "bet-hedging" reproductive strategies, distributing its offspring in both space (within and between fields) and time (within and between years), and minimizing the risk of its catastrophic loss from insecticides or crop rotation (Solbreck 1978, Voss and Ferro 1990a). Furthermore, Colorado potato beetle has a remarkable ability to develop resistance to a wide variety of chemicals, with some insecticides failing as soon as 1 yr after application (Forgash 1985). As a result, indiscriminate use of insecticides or simple crop rotation does not provide adequate control of this pest (Whalon and Ferro 1998). However, successful development of more sophisticated techniques largely depends on understanding beetle life history, including the relationship between its dispersal and reproduction.

Colorado potato beetle is a highly mobile species, capable of moving both by flight and by walking. Summer generation adult beetles start walking soon after they complete pupation in the soil (Voss and Ferro 1990a); however, they need to feed for 5-10 d before they finish flight muscle development and become capable of initiating flight (Voss and Ferro 1990a, Yang 1994, Weber and Ferro 1996). Once flight muscles are fully developed, the beetles can easily fly

several kilometers (Weber and Ferro 1994a). Beetle incursions across the Baltic Sea to Scandinavia show that under favorable meteorological conditions beetles can fly >100 km (Wikteliuss 1981). Flight activity continues throughout the season, and resumes in the spring after adult beetles complete diapause development (Weber and Ferro 1994a).

Both beetle sexes are capable of flying (Weber and Ferro 1994a). However, information on the relative flight activity of male and female beetles is somewhat controversial. Voss and Ferro (1990b) showed that significantly more males than females engaged in local flight activity, possibly in the search of mates. In the experiments by Weber and Ferro (1994b), overwintered males departed from a nonhost habitat more readily than females, but were more likely than females to remain in a potato field. Conversely, Zehnder and Speese (1987) reported a 50:50 sex ratio of beetles caught in windowpane traps throughout the growing season. All the beetles used by Voss and Ferro (1990b), Weber and Ferro (1994b), and Zehnder and Speese (1987) were collected in the field, and their exact mating history was unknown.

Reproductive activity is an important factor affecting insect flight (Johnson 1969), and flight behavior of virgin and mated individuals is often distinctly different (Milne 1960, Green 1962, Dingle 1966, Sappington and Showers 1992, King 1993). Our recent experiments (unpublished data) did not show any influence of spring mating on the flight behavior of the overwintered Colorado potato beetle females. However, these females normally overwinter

sperm from the previous season, and do not need to mate after diapause to produce viable offspring (Ferro et al. 1991). Little is known about the movement of recently emerged summer-generation Colorado potato beetles, or about the possible influence of their mating status on dispersal. A good understanding of this issue is of practical importance. Commercial potato growers in North America increasingly rely on transgenic potato plants expressing *Bacillus thuringiensis* (Berliner) subsp. *tenebrionis* Cry3A toxin in their foliage (Whalon and Ferro 1998). Persistence, dosage, and coverage by the toxin is maximized in such plants. As a result, we should expect rapid resistance development as a result of increased selection pressure on beetle populations (Ferro 1993). Only resistant larvae will be able to survive to adulthood on transgenic plants, and pupation normally takes place in the soil under a plant where larval development was completed. Therefore, if adult beetles mate before moving away from the site of emergence, there is a high probability that resistant beetles will mate with each other, produce and disperse homozygous resistant offspring.

### Materials and Methods

**Effect of Beetle Age on the Viability of Mating.** Two hundred teneral virgin beetles (100 males and 100 females) were collected from the laboratory colony within 24 h after emergence from the soil. The colony currently maintained in our laboratory originated in 1982 by collecting beetles from the University of Massachusetts Vegetable Research Farm, South Deerfield, MA. However, large colony size and annual infusions of field-collected individuals allowed us to keep genetic composition of the colony close to that of local field populations. Collected beetles were placed into separate ventilated plastic Nalgene containers (12 by 7 by 5.5 cm), and provided with potato foliage (excised leaflets inserted into floral pics containing tap water). Potato plants, *Solanum tuberosum* L., used in the current experiment were nontransgenic, belonged to 'Atlantic', and had been grown in plastic pots in a greenhouse for  $\approx 4$  wk before the beginning of the experiment. The foliage in Nalgene containers was checked daily and replaced as needed, so that the beetles were always supplied with food. Containers were maintained in an environmental chamber at  $+27^{\circ}\text{C}$  and a photoperiod of 16:8 (L:D) h. The beetles were separated into the following 5 groups based on when females and males were paired in the same container: (1) on the 1st d after emergence from the soil, (2) on the 2nd d after emergence from the soil, (3) on the 3rd d after emergence from the soil, (4) on the 4th d after emergence from the soil, and (5) on the 5th d after emergence from the soil. The beetles were allowed to mate for 24 h, after which the males were removed from the containers. The number of degree-days (DD) accumulated by the beetles at the time of mating was calculated, assuming a linear relationship between the rate of development and temperature and using  $10^{\circ}\text{C}$  as a developmental threshold (Tauber et al. 1988). As a whole, relationship of the Colorado potato beetle development rate to temperature is nonlinear

(Ferro et al. 1985, Logan et al. 1985). However, at the temperatures ranging from  $+15.6$  to  $+29.4^{\circ}\text{C}$ , the linear model used in the current study gives a good approximation to the actual rate of development (Tauber et al. 1988). Beetle oviposition was checked daily for a 10-d period after the day of mating. Egg masses were collected and incubated at  $+27^{\circ}\text{C}$  and a photoperiod of 16:8 (L:D) h to check their viability.

**Movement of Newly Emerged Beetles Under Field Conditions.** Eight potato plots ('Katahdin') were planted on 5 May 1994 at the University of Massachusetts Vegetable Research Farm, South Deerfield, MA. Each plot consisted of 8 rows (each 10 m long) of plants, with 0.9 m spacing between the rows and 25 cm spacing between the plants in a row. The plots were arranged in a  $2 \times 4$  grid and isolated from each other by a 5-m fallow area. The experiment was carried out between 8 August and 31 August 1994. The plots were treated earlier in the season with foliar applications of M-Trak (Mycogen, San Diego, CA) for Colorado potato beetle larval control and Maneb (Elf Atochem North America, Philadelphia, PA) for early and late blight control. All applications stopped 10 d before the beginning of the current experiment. Potato foliage at the experimental plots did not begin senescing until early September.

A metal screen cage was fitted over a single potato plant at the center of each experimental plot. All naturally occurring Colorado potato beetle adults, larvae, and eggs were removed from the caged plants before the beginning of the experiment. Forty 4th instars were obtained from the University of Massachusetts laboratory colony, placed onto each of the caged plants, and allowed to complete development to adulthood. As teneral adults emerged from the soil, they were removed from the cages and marked according to the elytral puncture method described by Unruh and Chauvin (1993). This technique allowed us to mark beetles permanently without affecting their survivorship or propensity to fly (Unruh and Chauvin 1993). Each mark in the current study was unique, allowing us to distinguish between individual beetles. Marked adults were released next to the cage of their emergence. All plants in each plot were thoroughly checked for marked beetles daily over a 2-wk period, and the identity of each beetle, location, and distance traveled, along with the number of dead beetles were recorded. Missing beetles were assumed to have migrated outside of the experimental field. The number of beetle pairs in which a male was mounted on top of a female was recorded, but no attempt was made to determine if paired beetles actually copulated. Hourly temperature readings were obtained from the weather station located  $\approx 800$  m from the experimental field. Because the temperatures above  $+29^{\circ}\text{C}$  were recorded only twice during the study, the number of degree-days accumulated by the beetles at each day of the experiment was calculated as described by Tauber et al. (1988) (see above). Experimental data were analyzed using logistic regression (PROC LOGISTIC, SAS Institute 1989), Student *t*-tests (PROC *t*-test, SAS Institute 1989), and Mann-Whitney rank sum test (PROC NPARIWAY, SAS Institute 1989).

**Effect of Mating Status on Colorado Potato Beetle Flight Behavior.** Teneral adults were collected from the laboratory colony within 24 h after emergence from the soil and separated into 4 groups: virgin males, virgin females, mated males, and mated females. To obtain virgin beetles, teneral females and males were placed individually into ventilated plastic Nalgene boxes containing a 1-cm layer of soil. To obtain mated beetles, the beetles were paired in similar containers (1 female + 1 male per container) for the duration of the experiment. All the beetles were provided with cut potato leaflets inserted in floral pics containing tap water. The boxes were placed into an environmental chamber at  $+23 \pm 1^\circ\text{C}$  and a long-day photoperiod of 16:8 (L:D) h. The foliage was checked daily and replaced as needed, so that the beetles were always supplied with food.

Starting on the 7th d after emergence from the soil, the beetles were repeatedly placed on a flight mill system for 1 h every other day for 2 wk. The number of beetles that flew, duration of each flight, and the number of flights for each beetle were recorded. Five males and 5 females per treatment were tested at a time. The experiment was replicated 10 times, with a total of 50 males and 50 females per treatment tested. The flight mill system used in the current study was similar to the system described by Weber et al. (1993). The beetles were suspended on turnabouts by their pronotae using hot melt glue sticks as an adhesive. The turnabouts were propelled in a horizontal plane by the flying beetles, with each turnabout rotation detected by an infrared sensor and recorded by an IBM PC-compatible computer. Between the flights, the beetles were allowed to grip on the globular pieces of styrofoam to simulate tarsal contact with a substrate. To increase system reliability, we used a PC-DIO-96 interface board (National Instruments, Austin, TX) instead of a custom made interface board used by Weber et al. (1993). Flight mill data on the number and duration of flights were transformed using rank transformations (Conover and Iman 1981) to equalize variances and normalize their distribution, and then Huynh-Feldt adjusted repeated measures analysis of variance (ANOVA) was applied to the transformed data (PROC GLM, SAS Institute 1989). Means and standard errors reported in the article were calculated using nontransformed data.

**Results**

**Effect of Beetle Age on Viability of Mating.** All tested females laid eggs during the experiment. However, none of the eggs were fertile unless the beetles accumulated at least 34 DD (3 d after eclosion) before being paired in the containers (Table 1). Further degree-day accumulation did not affect the proportion of beetles producing viable offspring ( $\chi^2 = 2.67$ ,  $df = 2$ ,  $P = 0.2636$ ). Regardless of the beetle age at mating, females did not start laying eggs until they had accumulated a minimum of 51 DD. Although oviposition was significantly delayed for the beetles that were paired at 51 DD ( $\chi^2 = 13.38$ ,  $df = 4$ ,  $P = 0.0096$ ) (Table 1), the observed difference could probably be attributed to an experimental artifact caused by the interference of mating with oviposition. When the beetles from that particular group were dropped from

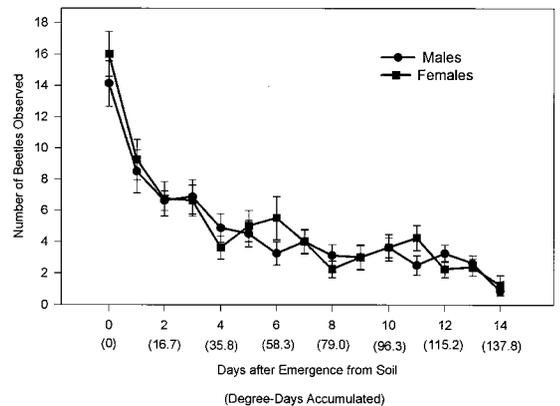
**Table 1. Colorado potato beetle oviposition as a function of physiological age at the time of mating**

	Age at mating, (d)				
	1	2	3	4	5
Degree-days accumulated (based on a 10°C threshold)	0-17	17-34	34-51	51-68	65-85
% beetles laying fertile eggs	0	0	75	70	80
Mean number of degree-days accumulated before oviposition (SE)	59.50 (1.95)	55.47 (1.76)	56.10 (1.79)	65.45 (2.23)	60.84 (2.37)

the analysis, the difference among the remaining groups became insignificant ( $\chi^2 = 4.66$ ,  $df = 3$ ,  $P = 0.1987$ ).

**Movement of the Newly Emerged Beetles Under Field Conditions.** A total of 231 beetles emerged from the soil between 8 August and 17 August 1994; 19 of the emerged beetles died during the experiment. Within the first 24 h after emergence from the soil, only about half of the originally released beetles were observed, and  $\approx 5\%$  of the beetles remained within the plots until the end of the experiment (Fig. 1). Logistic regression model provided a good fit for the collected data ( $\chi^2 = 532.13$ ,  $df = 2$ ,  $P = 0.0001$ ). The number of accumulated degree-days had a highly significant effect on the proportion of marked beetles leaving the experimental site ( $\chi^2 = 472.28$ ,  $df = 1$ ,  $P = 0.0001$ ), and there was no difference in the departure rate of males and females ( $\chi^2 = 2.55$ ,  $df = 1$ ,  $P = 0.1103$ ). The beetles that did not move away from the experimental site tended to stay close to the place where they emerged from the soil. After accumulating between 35.8 and 58.3 DD after emergence (the amount of degree-days sufficient to become reproductive), males traveled  $\approx 1.33$  m (SE = 0.12), and females traveled  $\approx 0.95$  m (SE = 0.40) (Fig. 2). The difference between sexes was statistically insignificant ( $t = 0.9096$ ,  $df = 46.03$ ,  $P = 0.3681$ ).

Fifty beetles were observed pairing with the opposite sex during the experiment. On average, the 1st pairing



**Fig. 1.** Number of marked Colorado potato beetles observed after being released in experimental plots, South Deerfield, MA. Because adults eclosed from the pupae over an 11-d period, degree-days accumulated at each day after release are calculated as means of degree-days accumulated by individual beetles at that particular day.

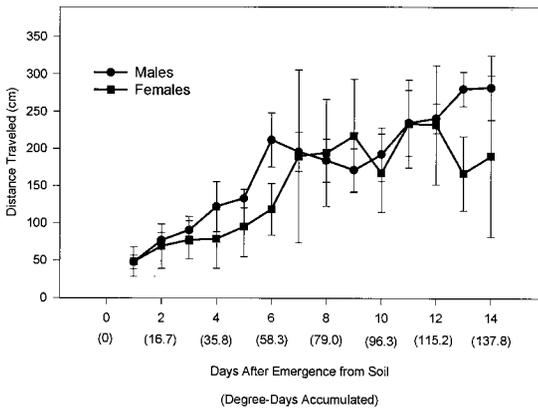


Fig. 2. Distance traveled by the Colorado potato beetles released in experimental plots, South Deerfield, MA. Because adults eclosed from the pupae over an 11-d period, degree-days accumulated at each day after release are calculated as means of degree-days accumulated by individual beetles at that particular day.

was recorded after the beetles accumulated 53.12 DD. However, 8 females and 5 males paired as early as 19.75 DD after their emergence from the soil. The age at 1st pairing did not differ significantly between the sexes ( $U = 238.5$ ,  $df = 48$ ,  $P = 0.3169$ ). Ten beetles were observed pairing more than once, with 9 of them associated with multiple partners.

**Effect of Mating Status on Colorado Potato Beetle Flight Behavior.** Beetles from all 4 treatments tested in the experiment flew after being placed on the flight mill system (84.0% of unmated males, 94.0% of unmated females, 100.0% of mated males, and 91.67% of mated females). Proportion of flying beetles did not differ significantly among the treatments ( $\chi^2 = 0.37$ ,  $df = 3$ ,  $P = 0.9472$ ) or between the days of experiment ( $\chi^2 = 6.59$ ,  $df = 6$ ,  $P = 0.3607$ ). The number of flights performed by the beetles depended heavily on their sex and mating status, as well as on the sex-mating status interaction (Table 2). Unmated males flew on average 1.3 (SE = 0.1) times, unmated females flew on average 3.7 (SE = 0.2) times, mated males flew on average 2.4 (SE = 0.2) times, and mated females flew on average 1.8 (SE = 0.2) times. When the sexes were analyzed separately, the effect of

mating was significant both for males ( $F = 9.62$ ;  $df = 1$ ,  $98$ ;  $P = 0.0025$ ) and females ( $F = 33.82$ ;  $df = 1$ ,  $98$ ;  $P = 0.0001$ ). Similar to the number of flights, mean flight duration was also influenced by beetle sex, mating status, and by the interaction of these 2 factors (Table 2). An average flight lasted  $\approx 35.1$  s (SE = 4.4) for unmated males, 72.7 s (SE = 5.6) for unmated females, 31.7 s (SE = 3.7) for mated males, and 18.9 s (SE = 2.8) for mated females. Separate analysis of beetle sexes did not reveal any differences between mated and unmated males ( $F = 2.91$ ;  $df = 1$ ,  $98$ ;  $P = 0.0914$ ), but the flights performed by unmated females were significantly longer than the flights performed by mated females ( $F = 61.71$ ;  $df = 1$ ,  $98$ ;  $P = 0.0001$ ). Both number of flights and mean flight duration changed over time (Fig. 3). The difference between the days of experiment was statistically significant, and there was a significant 3-way interaction between the day of flight, beetle sex, and beetle mating status (Table 2).

Discussion

Colorado potato beetle is a highly mobile species. Adult dispersal starts at the moment of beetle eclosion, with the newly emerged beetles walking from the place of their emergence from the soil. As soon as the beetles develop flight muscles, they engage in local and migratory flights, allowing for further dispersal within the field of origin, as well as for colonization of new host habitats. Initial increase in flight activity after completion of flight muscle development (Yang 1994) is followed by a gradual decline in beetle flight (Fig. 3). However, we did not observe a distinct peak of flight activity characteristic of the overwintered beetles. Overall, our results agree with the earlier findings of Voss and Ferro (1990a) and Weber and Ferro (1996).

The data from the current study indicate that some of the beetles moved away from the site of larval development before completing maturation of the reproductive system and flight muscles. Unfortunately, it was hard to determine the exact proportion of individuals dispersing before becoming reproductive. The numbers reflected in Fig. 1 might underrepresent the actual number of beetles staying within the experimental plots because some of the beetles remained unnoticed during the ob-

Table 2. ANOVA table for mean number of flights and mean flight duration of summer-generation mated and unmated male and female Colorado potato beetles

Source	df	Mean no. of flights			Mean flight duration		
		Mean square	F	P	Mean square	F	P
Between subjects							
Sex	1	2,812,141.26	9.54	0.0023	2,856,731.49	10.58	0.0013
Mating status	1	1,488,548.68	5.05	0.0257	5,253,902.64	19.47	0.0001
Sex $\times$ mating status	1	12,057,596.82	40.92	0.0001	12,481,002.12	46.24	0.0001
Error	196	294,664.49			269,906.77		
Within subjects							
Day	6	1,668,977.36	16.88	0.0001	1,597,308.77	16.61	0.0001
Day $\times$ sex	6	60,944.28	0.62	0.7118	44,496.85	0.46	0.8348
Day $\times$ mating status	6	218,804.80	2.21	0.0396	223,619.35	2.33	0.0312
Day $\times$ sex $\times$ mating status	6	430,661.54	4.36	0.0002	507,876.51	5.28	0.0001
Error	1,176	98,879.33			96,155.45		

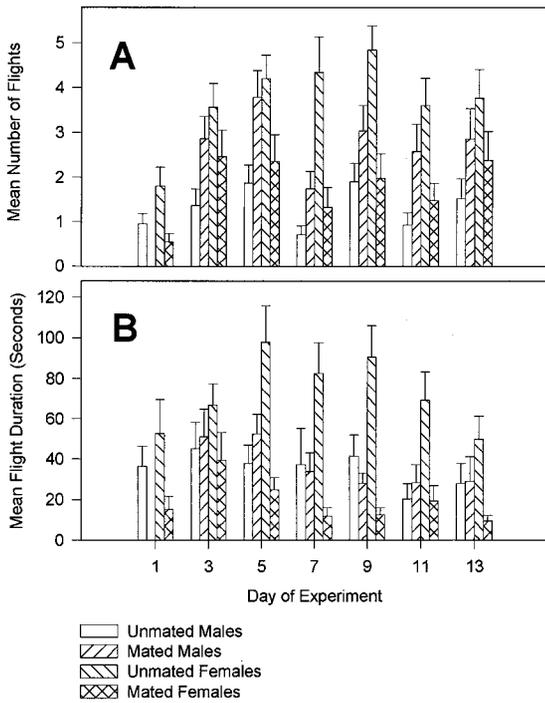


Fig. 3. Flight activity of summer-generation Colorado potato beetles on the consecutive days of experiment. (A) Mean number of flights. (B) Mean flight duration.

servations. This could also explain a dramatic decrease in the number of encountered beetles on the day after release (Fig. 1). Furthermore, it was difficult to calculate the precise number of degree-days accumulated by the beetles in the field. Degree-day accumulation depends on the microclimate of the potato field, especially because the beetles are known to exhibit behavioral thermoregulation (Lactin and Holliday 1994). Therefore, degree-day estimates from the weather station only provided rough estimates of temperatures witnessed by the beetles. However, we can conclude that a significant part of the beetle population remains in the vicinity of emergence sites, accumulating enough degree-days to initiate reproduction. These beetles are likely to mate with each other and then either move away or stay near the place of their larval development. Because only *Bacillus thuringiensis*-resistant larvae are able to survive and develop to adulthood on transgenic plants, there is a high probability that resistant beetles will mate with each other and leave homozygous resistant offspring.

Mating status has a pronounced effect on the flight activity of beetles, and this effect is expressed differently in males and females. Mated females fly less than unmated females. This is not unexpected because both migration and reproduction are physiologically demanding for females, and these 2 processes are known to interfere with each other (Rankin et al. 1986). From the resistance management perspective, decrease in the female flight activity after mating might indicate decreased probability that homozygous resistant alleles will be carried to other potato fields. Conversely,

we might expect an increase in the frequency of resistant alleles in the local populations. However, we did not observe a complete cessation of flight in gravid females, a phenomenon described as "oogenesis-flight syndrome" for a number of insect species (Johnson 1969, Dingle 1985). Continuation of flight by reproductive females allows them to distribute offspring in space, thus reducing risk of offspring being killed because of some catastrophic event (Solbreck 1978, Voss and Ferro 1990a). Additional studies quantifying distances flown by mated and unmated females under more natural conditions are required for a better understanding of the gene flow between beetle populations in the system of transgenic crops and refugia of nontransgenic plants.

Unlike mated females, mated males increase their flight activity, probably in an attempt to find another mate. Our results support a hypothesis proposed by Szentesi (1985), who suggested that male reproductive strategy in the Colorado potato beetle is directed toward maximizing the number of matings with different females. Similarly, Voss and Ferro (1990b) concluded that elevated local flight activity displayed by the males was connected to the search for mates. An obvious advantage of such a strategy for a male is an increased genetic diversity of its offspring (McCauley and Reilly 1984). From the resistance development perspective, multiple matings at different locations are likely to promote gene flow between resistant and susceptible populations, and increase the number of individuals heterozygous for the resistant allele.

A high dose/refugia strategy, currently recommended for resistance management in the Colorado potato beetle, is based on curtailment of mating between resistant individuals (Whalon and Ferro 1998). Although insecticide resistance is almost never completely dominant (Roush and Daly 1990), it is improbable that heterozygous progeny of resistant  $\times$  susceptible crosses will survive high concentrations of the Cry3A toxin expressed in transgenic plants. Unfortunately, results of the current study indicate that there is a high probability of resistant beetles mating with each other before dispersing from the area of their larval development, thus compromising the proposed strategy (Gould 1998). Therefore, an overall success in managing beetle resistance might depend on our ability to enhance movement between resistant and susceptible beetle populations. This could be achieved through close integration of transgenic crops with nontransgenic refugia (Whalon and Ferro 1998) combined with early planting of nontransgenic plants. This way, at the time when resistant beetles emerge from the pupae, the main crop will be already colonized by the susceptible adults immigrating from refugia, and the probability of 2 resistant beetles mating with each other will be diminished.

#### Acknowledgments

We thank Andy Slocombe, Tuan Dang, Chris Mercier, Eli Fanning, and Richard Ferro for providing technical assis-

tance. This work was supported by NE-178 from the University of Massachusetts Agricultural Experiment Station. UMASS Publication No. 3236.

### References Cited

- Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35: 124–129.
- Dingle, H. 1966. Some factors affecting flight activity in individual milkweed bug, *Oncopeltus*. *J. Exp. Biol.* 44: 335–343.
1985. Migration, pp. 375–415. In G. A. Kerkut and L. I. Gilbert [eds.], *Insect physiology, biochemistry, and pharmacology*, vol. 9. Pergamon, Oxford, England.
- Ferro, D. N. 1993. Potential for resistance to *Bacillus thuringiensis*: Colorado potato beetle (Coleoptera: Chrysomelidae)—a model system. *Am. Entomol.* 39: 38–44.
- Ferro, D. N., J. A. Logan, R. H. Voss, and J. S. Elkinton. 1985. Colorado potato beetle (Coleoptera: Chrysomelidae) temperature-dependent growth and feeding rates. *Environ. Entomol.* 14: 343–348.
- Ferro, D. N., A. F. Tuttle, and D. C. Weber. 1991. Ovipositional and flight behavior of overwintered Colorado potato beetle (Coleoptera: Chrysomelidae). *Environ. Entomol.* 20: 1309–1314.
- Forgash, A. G. 1985. Insecticide resistance in the Colorado potato beetle, pp. 33–52. In D. N. Ferro and R. H. Voss [eds.], *Proceedings, Symposium on the Colorado Potato Beetle*. XVIIth International Congress of Entomology. Research Bulletin 704. Mass. Agric. Exp. Stn. Circ. 347.
- Gould, F. 1998. Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Annu. Rev. Entomol.* 43: 701–726.
- Green, C. W. 1962. Flight and dispersal of the European pine shoot moth, *Rhyacionia buoliana* (Schiff). I. Factors affecting flight, and the flight potential of females. *Can. Entomol.* 94: 282–299.
- Johnson, C. G. 1969. *Migration and dispersal of insects by flight*. Methuen, London.
- King, B. 1993. Flight activity in the parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *J. Insect Behav.* 6: 313–321.
- Lactin, D. J., and N. J. Holliday. 1994. Behavioral responses of Colorado potato beetle larvae to combinations of temperature and insolation, under field conditions. *Entomol. Exp. Appl.* 72: 255–263.
- Logan, P. A., R. A. Casagrande, H. H. Faubert, and F. A. Drummond. 1985. Temperature-dependent development and feeding of immature Colorado potato beetles, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *Environ. Entomol.* 14: 275–283.
- McCaughey, D. E., and L. M. Reilly. 1984. Sperm storage and sperm precedence in the milkweed beetle, *Tetraopes tetrapterthalmus* (Forster) (Coleoptera: Cerambycidae). *Ann. Entomol. Soc. Am.* 77: 526–530.
- Milne, A. 1960. Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). VII. The flight season: male and female behavior, and concluding discussion. *Bull. Entomol. Res.* 51: 353–378.
- Rankin, M. A., M. L. McAnelly, and J. E. Bodenhamer. 1986. The oogenesis-flight syndrome revisited, pp. 27–38. In W. Damthararayana [ed.], *Insect flight: dispersal and migration*. Springer, Berlin.
- Roush, R. T., and J. C. Daly. 1990. The role of population genetics in resistance research and management, pp. 97–152. In R. T. Roush and B. E. Tabashnik [eds.], *Pesticide resistance in arthropods*. Chapman & Hall, New York.
- Sappington, T. W., and W. B. Showers. 1992. Reproductive maturity, mating status, and long-duration flight behavior of *Agrotis ipsilon* (Lepidoptera: Noctuidae) and the conceptual misuse of the oogenesis-flight syndrome by entomologists. *Environ. Entomol.* 21: 677–688.
- SAS Institute. 1989. *SAS/STAT user's guide*, version 6, 4th ed. SAS Institute, Cary, NC.
- Solbreck, C. 1978. Migration, diapause, and direct development as alternative life histories in a seed bug, *Neocoryphus bicrucis*, pp. 195–217. In H. Dingle [ed.], *Evolution of insect migration and diapause*. Springer, New York.
- Szentesi, A. 1985. Behavioral aspects of female guarding and inter-male conflict in the Colorado potato beetle, pp. 127–137. In D. N. Ferro and R. H. Voss [eds.], *Proceedings, Symposium on the Colorado Potato Beetle*. XVIIth International Congress of Entomology. Research Bulletin 704. Mass. Agric. Exp. Stn. Circ. 347.
- Tauber, C. A., M. J. Tauber, B. Gollands, R. J. Wright, and J. J. Obrycki. 1988. Preimaginal development and reproductive responses to temperature in two populations of the Colorado potato beetle (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 81: 755–763.
- Unruh, T. R., and R. L. Chauvin. 1993. Elytral punctures: a rapid, reliable method for marking Colorado potato beetle. *Can. Entomol.* 125: 55–63.
- Voss, R. H., and D. N. Ferro. 1990a. Phenology of flight and walking by Colorado potato beetle (Coleoptera: Chrysomelidae) adults in western Massachusetts. *Environ. Entomol.* 19: 117–122.
- 1990b. Ecology of migrating Colorado potato beetles (Coleoptera: Chrysomelidae) in western Massachusetts. *Environ. Entomol.* 19: 123–129.
- Weber, D. C., D. N. Ferro, and J. G. Stoffolano, Jr. 1993. Quantifying flight of Colorado potato beetles, *Leptinotarsa decemlineata* Say, with a microcomputer-based flight mill system. *Ann. Entomol. Soc. Am.* 86: 366–371.
- Weber, D. C., and D. N. Ferro. 1994a. Colorado potato beetle: diverse life history poses challenge to management, pp. 54–70. In G. W. Zehnder, R. K. Jansson, M. L. Powelson, and K. V. Raman [eds.], *Advances in potato pest biology and management*. APS, St. Paul, MN.
- 1994b. Movement of overwintered Colorado potato beetles in the field. *J. Agric. Entomol.* 11: 17–27.
1996. Flight and fecundity of Colorado potato beetles (Coleoptera: Chrysomelidae) fed on different diets. *Ann. Entomol. Soc. Am.* 89: 297–306.
- Whalon, M., and D. N. Ferro. 1998. Bt-potato resistance management, pp. 107–136. In M. Mellon and J. Rissler [eds.], *Now or never: serious new plans to save a natural pest control*. UCS, Cambridge, MA.
- Wiktelius, S. 1981. Wind dispersal of insects. *Grana* 20: 205–207.
- Yang, B. 1994. Muscle development, energy source utilization and metabolism hormone activity in Colorado potato beetle, *Leptinotarsa decemlineata* (Say). M.S. thesis, University of Massachusetts, Amherst.
- Zehnder, G., and J. Speese III. 1987. Assessment of color response and flight activity of *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) using window flight traps. *Environ. Entomol.* 16: 1199–1202.

Received for publication 6 July 1998; accepted 9 February 1999.