

Population Dynamics of the Colorado Potato Beetle in an Agroecosystem with Tomatoes and Potatoes with Management Implications to Processing Tomatoes

CHRIS L. HARDING,¹ S. J. FLEISCHER, AND P. E. BLOM

Department of Entomology, Pennsylvania State University, University Park, PA 16802

Environ. Entomol. 31(6): 1110–1118 (2002)

ABSTRACT We evaluated the population dynamics of Colorado potato beetle in processing tomatoes and potatoes using immigration profiles, density through time, rates of development and survivorship. We also evaluated the beetle's influence on yield of processing cultivars. Colorado potato beetle immigrated into both crops. The first available crop had the earliest immigration event and higher immigrating adult and egg mass densities. Length of time that overwintering adults spent in the field, and duration of oviposition, were more closely related to accumulated degree days than time of immigration. Later in the season there was a trend toward fewer eggs per egg mass from overwintered adults. Rates of development suggested that large larvae developed more quickly in potatoes in 1998, but not in 2000, and small larvae developed at similar rates in either crop. Egg-to-adult survivorship ranged from 0.02 to 0.06, even though initial egg densities varied by approximately an order of magnitude. Survivorship varied more between years than between crops. Colorado potato beetle did not influence yield of processing tomatoes. Our field studies estimated similar life table parameters and population dynamics of Colorado potato beetle in two solanaceous crops, and concurred with laboratory bioassays in the literature suggesting that this beetle has the potential to achieve similar fitness on both tomatoes and potatoes. However, beetle densities did not influence yield, and thus may have little effect on pest management in processing tomato cultivars.

KEY WORDS Colorado potato beetle, population dynamics, life table, potatoes, tomatoes

COLORADO POTATO BEETLE feeds on solanaceous hosts, and the particular host influences its fitness, feeding behavior, diapause, and reproduction (Hsiao 1982, 1981, 1978, Hsiao and Fraenkel 1968, Hare and Kennedy 1986, Kennedy and Farrar 1987). Nonagricultural hosts influenced larval mass, survival, development time, size, and tendency to enter diapause in laboratory bioassays, with populations displaying higher fitness on the most available or predictable local host (Horton and Capinera 1988). The variation occurred on both large and small scales: between geographically separated populations, and among individuals within a local population. In feeding bioassays, adults discriminated among closely related solanaceous hosts (Harrison 1987). Beetles feeding on tomatoes, as opposed to potatoes, devoted more resources to maintenance than to growth, resulting in longer feeding bouts but lower survival and fecundity (Latheef 1972). Beetles collected from potato had reduced fecundity (Latheef 1972) and larval weight gain (Overney et al. 1997) when placed on tomato in no-choice bioassays. In field settings, recruitment rates were highest on potatoes, *Solanum dulcamara*

and *S. rostratum*, and lowest on tomatoes, *S. nigrum*, *S. eleagnifolium*, *Physalis heterophylla*, and *Datura stramonium*; three additional species were intermediate in recruitment rate (Weber et al. 1995).

These studies suggest reduced fitness and lower densities of Colorado potato beetle on tomato. Lu et al. (1997), however, showed a genetic component to variation in beetle fitness on tomato and potato. Selection from populations with high larval fitness on potato showed increased larval fitness on tomato within 4–12 generations when they were reared on tomatoes. Resulting populations did not have reduced fitness on potato. Because of the rapid adaptation to tomatoes in the laboratory, and no decrease fitness on potatoes, Lu et al. (1997) speculated that Colorado potato beetle has the potential to become a more widespread pest of tomato. Supporting data come from bioassays of beetles collected from eggplant in an agricultural environment that also included tomato (Jansson et al. 1989). Offspring of these beetles had the same female longevity and survivorship on tomato as on potato, and higher fecundity on tomato in one of two experiments. Kennedy and Farrar (1987) also reported greater larval survivorship on tomato from bioassays of populations collected from tomatoes.

¹ Naval Facilities Engineering Command, 10 Industrial Highway MS 82, Lester PA 19113 2090.

However, these laboratory findings have not been evaluated under field settings.

Similar fitness of Colorado potato beetle on potatoes and tomatoes does not necessarily translate into similar pest status on the two crops. While there has been extensive research on yield effects on potato (Ewing et al. 1994, Logan and Casagrande 1980), studies in tomato are less prevalent. Schalk and Stoner (1979) showed dramatic reductions in tomato yield and height arising from a natural infestation by 1st-generation beetles. Cantelo and Cantwell (1983) used mechanical leaf removal, based on models of leaf area consumed per life stage, to predict yield reductions in fresh market varieties. Hare (1980), however, estimated that defoliation from herbivores might be only 65–70% as debilitating as mechanical defoliation. Herbivores may selectively feed on specific plant tissues which have less effect on yield than other tissue, and some defoliation stimulates plant growth beyond what is removed (Dyer and Bokhari 1976, Harris 1974) or increases photosynthetic activity rate in the remaining leaves (Maggs 1964). Additionally, cultivars affect defoliation-yield relationships. Fresh market varieties grow on long distended vines with a relatively indeterminate fruiting pattern. Processing varieties are compact plants with multiple layers of dense vegetation; they ripen more uniformly and are harvested in a single event.

In the northeastern U.S., many farms produce both potatoes and tomatoes, and processing tomatoes are an important crop in parts of the northeast. Also, fields tend to be relatively small, resulting in a mosaic of crop species in close proximity. Understanding Colorado potato beetle ecology in agroecosystems containing both potatoes and tomatoes is relevant to these northeastern landscapes. We studied Colorado potato beetle population dynamics in agroecosystems in which populations have had access to both potatoes and processing tomatoes for multiple generations, and we estimated the influence of this beetle on yield of processing tomatoes.

Materials and Methods

Field studies were conducted over three years on a private farm adjacent to the Russell E. Larson Experimental Research Station at Rock Springs, PA. In 1998, two adjacent 0.6-hectare processing tomato fields were planted on 27 May and a 0.9-hectare potato field that was adjacent to the tomato fields was seeded 21 May. Data from the two tomato fields were pooled. In 1999, a 0.7-hectare processing tomato field was planted 28 May. Unfortunately, because of field procurement difficulties, the potato crop could not be located near the tomato plot in 1999 and was not available for study. In 2000, a 0.2-hectare processing tomato field was planted nine June ≈ 1.5 kilometers from a 0.8-hectare potato field that was seeded 15 May. Varieties were Peto 696 and Katahdin for tomatoes and potatoes, respectively. Potato pieces were planted with ≈ 0.9 m between rows and ≈ 0.3 m between pieces. Processing

tomatoes were transplanted with ≈ 1.5 m between rows and ≈ 0.2 m between plants. We replaced transplants that died during the first two weeks. Fields were rotated each year into areas that supported a non-solanaceous crop the previous year. Temperature was recorded at the KPSU Automated Surface Observing System at Rock Springs, PA.

We collected samples at least twice per week. We counted all beetles in sampling units consisting of whole plants in tomatoes and whole stem samples in potatoes, in all years and crops. Beetles were classified as adults, small larvae (first and second instar), large larvae (third and fourth instar), or egg masses. Sampling in tomato consisted of monitoring all the plants in ten to twenty 6-m row segments in 1998, thirty 6-m row segments in 1999, and ten 4-m row segments in 2000. In potatoes, we manually searched all the stems in a 10-m row segment in a predesignated hexagonal pattern consisting of 16–48 segments in 1998, and ten 4-m row segments in 2000. This change in number and placement of sampling units enabled the collection of yield data in tomatoes in 1999 and 2000, and maintained the consistency in the sample number and placement among crops in 2000. Samples were used to calculate density per meter for each life stage, which was plotted over time. For our calculations the first observance of beetles in the field marked the onset of the overwintering adult population, and it concluded when adult density dropped below 0.075 per meter. Adults observed after this time were considered to be first generation adults from in-season reproduction. We counted the number of eggs per mass in 25–84 randomly sampled eggmasses from each field using a hand lens. We compared mean eggs per eggmass among crops using analysis of variance (ANOVA), and determined the relationship of eggs per eggmass with degree days using correlation (PROC CORR, SAS Institute 1997).

Population development time for small and large larvae was determined on potatoes and tomatoes. Mean density per meter of small and large larvae were plotted against degree days from one January using the sigmoid method (Higley et al. 1986) with a base of 10°C (Logan and Casagrande 1980, Logan et al. 1985). The area under the curve was estimated with Euler's method of integration. The cumulative proportion of the total area under the curve was plotted against degree days from one January. The data followed the exponential sigmoid

$$y = \frac{A}{1 + Be^{nx}},$$

where A , B and n are coefficients, x is the number of degree days from one January and y is the predicted cumulative proportion of the population. We partitioned the data to preserve only the exponential phase by removing sampling intervals with cumulative proportions of zero or >0.9965 . Data were transformed to express the proportion of development as a linear function of increasing degree days (Spain 1982):

$$-\ln\left(\frac{A}{y} - 1\right) = \ln B + nx.$$

Populations were compared among hosts (potato and tomato) using type I sum of squares in a test for heterogeneity of slope (Littell et al. 1991).

We also estimated life table statistics from the field data. We used the graphical method to estimate survivorship (Southwood 1978). In contrast to methods that estimate the population at the beginning of a life stage, this method estimates the population density that passes through the median age of the life stage. Therefore, this method provides an estimate of density between life stages rather than mortality during a life stage and can be expressed as:

$$N_j = \frac{\sum_{i=1}^n \left(\frac{x_{ij} + x_{ij+1}}{2}\right) (d_{i+1} - d_i)}{D_j},$$

where x_{ij} is the beetle density per meter of row for life stage j on sampling date i , d_i is the accumulated degree days from one January on sample date i , D_j is the required number of degree days for life stage j (Logan and Casagrande 1980, Logan et al. 1985), and n is the number of sampling dates for life stage j . For this analysis we assumed that a similar number of degree days were required per stage for both hosts although the data were developed on potato (we are not aware of degree-day estimates collected on tomato). We estimated $N_{\text{first generation adults}}$ using peak density per meter (adults do not have a degree-day requirement for development). We multiplied the average number of eggs per mass by the density of egg masses to estimate egg density per meter. The difference in the number of individuals between life stages is the result of mortality and emigration. Emigration of small and large larvae was assumed to be negligible and percent survivorship between life stages was estimated as:

$$\% \text{Survivorship} = \frac{N_{j+1}}{N_j} 100.$$

We evaluated yield by weighing all usable fruit within thirty 6-m and ten 4-m samples evenly distributed in a hexagonal pattern throughout the processing tomato fields for 1999 and 2000 respectively. Yield was estimated from one harvest 73 and 66 d from planting in 1999 and 2000, respectively. To be considered useful for processing, fruit had to be free of insect damage. We determined beetle density using whole plant counts (described above) of all plants within each six or 4 m sample. Care was taken to minimize plant and beetle disturbance during sampling. Sampling was initiated after transplanting and continued twice a week until senescence of the beetle population. Plant growth stage was evaluated at each sampling date as vegetative (no buds or fruits), budding and fruiting (initiation of budding through flower drop) or fruit maturation (fruiting through harvest). Mean density was plotted against calendar day, and Euler's method of integration was used to calculate the area under the

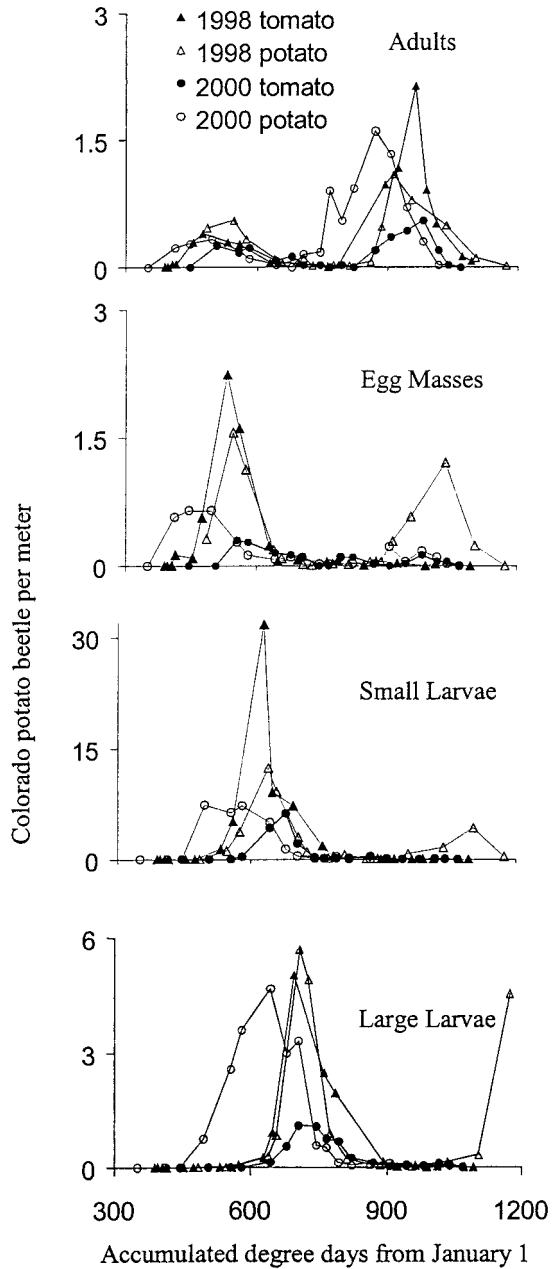


Fig. 1. Population dynamics of Colorado potato beetle in tomatoes and potatoes in 1998 and 2000

curve for each plant growth stage. Beetle pressure was considered to be equivalent to the area under the density-time curve. Tomato yields for each segment were regressed against beetle pressure (Proc GLM, SAS Institute 1997) for the vegetative stage (transplanting to 26 and 16 d for 1999 and 2000, respectively), budding and flowering stage (24–34 d posttransplanting in 1999, and 11–28 d posttransplanting in 2000), fruit maturation stage (27 and 22 d posttransplanting to harvest, in 1999 and 2000, respectively), and for the time of total plant growth.

Table 1. Duration of crop infestation by overwintering adult Colorado potato beetles in processing tomatoes and potatoes

	1988				2000			
	Date		Degree Days		Date		Degree Days	
	Tomato	Potato	Tomato	Potato	Tomato	Potato	Tomato	Potato
Population initiation ^a	June 8	June 18	406	485	June 22	June 13	506	412
Population senescence ^b	June 24	June 30	559	639	July 10	June 29	678	580
Total time (days or degree-days)	16	12	153	154	18	16	172	168

^a First sighting of beetles.

^b When population density dropped below 0.075 beetles per meter.

Results

Colorado potato beetle immigrated into both potato and tomato fields in every year of the study (Fig. 1). In 1998, tomato foliage was available immediately after transplanting on 27 May while the potatoes did not emerge until approximately 18 June at which time ≈ 50% of the potato crop had shoots above the soil. In 2000, foliage from both crops was available at approximately the same time: 50% of the potatoes emerged above the soil by eight June and tomatoes were transplanted nine June. The time and order of initial immigration varied between crops. In 1998, beetles immigrated into tomatoes between 396 (4 June) and 406 (8 June) accumulated degree days. Colorado potato beetle was observed on potatoes as the crop emerged from the soil at 485 accumulated degree days (18 June), which was 10 to 14 d after immigration occurred in tomatoes. In 2000 the order of immigration was reversed, with beetles immigrating first into potatoes between 350 (8 June) and 412 (13 June) accumulated degree days, and immigrating into tomatoes between 445 (16 June) and 506 (22 June) accumulated degree days.

In both years the host crop with the earliest immigration was also the first to have the overwintering adult population senesce. Moreover, the duration of crop infestation by overwintering adults was fairly constant among hosts for a given year, especially when expressed on a degree-day scale (Table 1). Despite differences among hosts in the time of initial immigration (10–14 d in 1998, and 9 d in 2000), the accumulated degree-days between immigration and senescence was similar for both crops in both years (153 and 154 in 1998, and 172 and 168 in 2000, for tomatoes and potatoes, respectively). The number of calendar days was also similar (16 and 12 d in 1998, and 18 and 16 d in 2000) for tomatoes and potatoes, respectively.

In all fields, oviposition began within four days after initial immigration of overwintered adults. There was no significant difference in the number of eggs per mass between egg masses deposited in tomatoes (24.5 ± 0.70, n = 204) and potatoes (25.9 ± 1.12, n = 100) (F = 1.19; df = 1, 303, P = 0.27). There was a significant trend (r = -0.87; df = 6; P = 0.01) toward decreasing eggs per mass with increasing accumulated degree days (Fig. 2).

Despite large numbers of second generation adults in all fields, their oviposition behavior differed between host crops and years. In 1998, second genera-

tion oviposition occurred in potatoes but not adjacent tomatoes. In 1999, there was oviposition in tomatoes, and in 2000 second generation adults did not oviposit in either crop.

We compared larval developmental rate between hosts by comparing the proportion of population development as a function of degree-days. The slopes were significantly different for large larvae in 1998 (F = 9.44, df = 1,16, P = 0.01 in 1998) but not in 2000 (F = 0.52; df = 1, 22; P = 0.47). The slopes for small larvae were not significantly different in either 1998 (F = 2.01; df = 1,18; P = 0.17) or 2000 (F = 0.00; df = 1,18; P = 0.97) (Fig. 3). The intercepts were significantly different for large larvae in 1998 (F = 6.79; df = 1,18; P = 0.01), but not for small larvae in 1998 (F = 1.72; df = 1,18; P = 0.20). However, intercepts were significantly different for both small (F = 58.89; df = 1,18; P = 0.01) and large larvae (F = 60.20; df = 1, 22; P = 0.01) in 2000.

The number of eggs estimated to have passed through the stage's midpoint varied widely, ranging from 10–98 eggs per row-meter (Table 2). However, population survivorship from egg to adult stage varied only from 0.02 to 0.06. The field with the highest egg density (tomatoes in 1998) had the lowest egg-to-adult survivorship (0.02). Mortality was not consistently concentrated within any one stage (Table 2). For the five fields evaluated, peak beetle mortality occurred once between eggs and small larvae (tomatoes 1999),

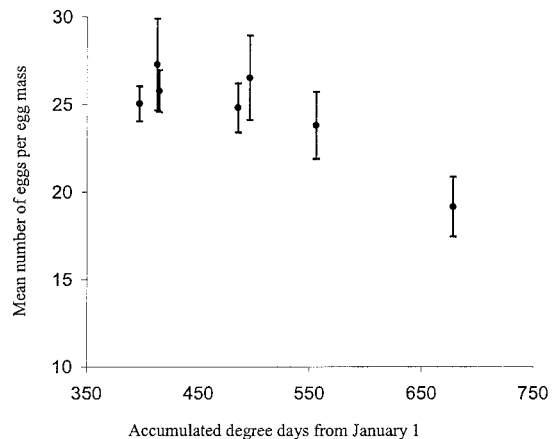
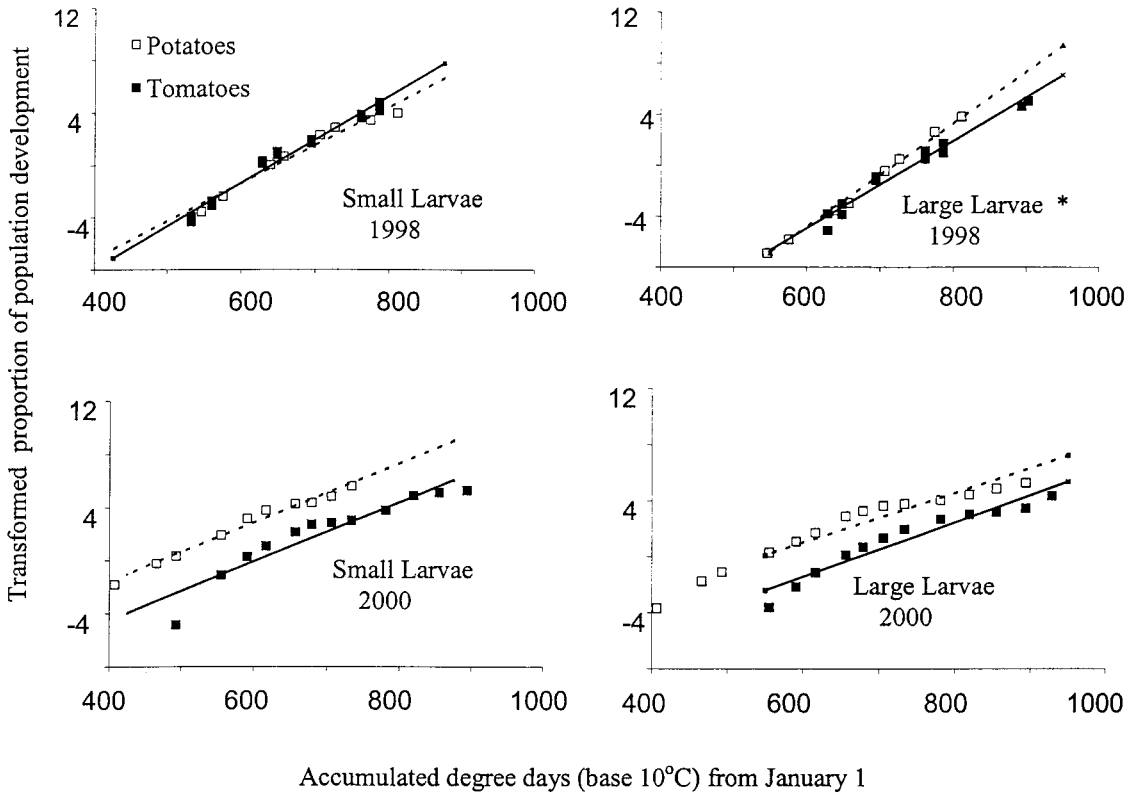


Fig. 2. Number of eggs per mass as a function of accumulated degree days in tomatoes.



Accumulated degree days (base 10°C) from January 1

Fig. 3. Transformed proportion of population development as a function of accumulated degree days from one January (base 10°C). Significant difference between slopes at $P < 0.05$ is indicated (*).

three times between small and large larvae (tomatoes in 1998 and 2000 and potatoes in 1998), and once between large larvae and adult (potatoes in 2000) (Table 2). Survivorship from egg to adult stage was more similar between crops for a given year (0.021–0.036, and 0.057–0.064, for tomato and potato in 1998 and 2000, respectively) than between years for a given

crop (0.021–0.057 for tomato, and 0.036–0.064 for potato, in 1998 and 2000, respectively).

Tomato yields ranged from 21 to 35 kg/m (132–220 metric tons/ha) and mean yields were similar in 1999 (175 ± 3.7 metric tons/ha) and 2000 (159 ± 8.5 metric tons/ha). Pressure from combined adult and large larvae averaged 3.0 (SE ± 0.6) and 2.7 (SE ± 0.6) for

Table 2. Colorado potato beetle survivorship from egg through adult stage on processing tomatoes and potatoes

Year	Life stage _x	Processing Tomato			Potato		
		Density per row meter at midpoint of stage _x a _x	Proportion of stage _(x-1) surviving to stage _x	Proportion of egg stage surviving to stage _x l _x	Density per row meter at midpoint of stage _x a _x	Proportion of stage _(x-1) surviving to stage _x	Proportion of egg stage surviving to stage _x l _x
1998	Egg	98.5			29.8		
	Small larvae	42.3	0.42	0.43	10.2	0.34	0.34
	Large larvae	7.2	0.17	0.07	2.9	0.28	0.10
	Adult	2.1	0.29	0.02	1.1	0.37	0.04
1999	Egg	61.4					
	Small larvae	17.8	0.29	0.29			
	Large larvae	9.6	0.54	0.16			
	Adult	3.9	0.40	0.06			
2000	Egg	10.4			26.4		
	Small larvae	4.8	0.46	0.47	11.0	0.41	0.42
	Large larvae	1.0	0.19	0.09	4.9	0.44	0.19
	Adult	0.6	0.60	0.06	1.7	0.34	0.06

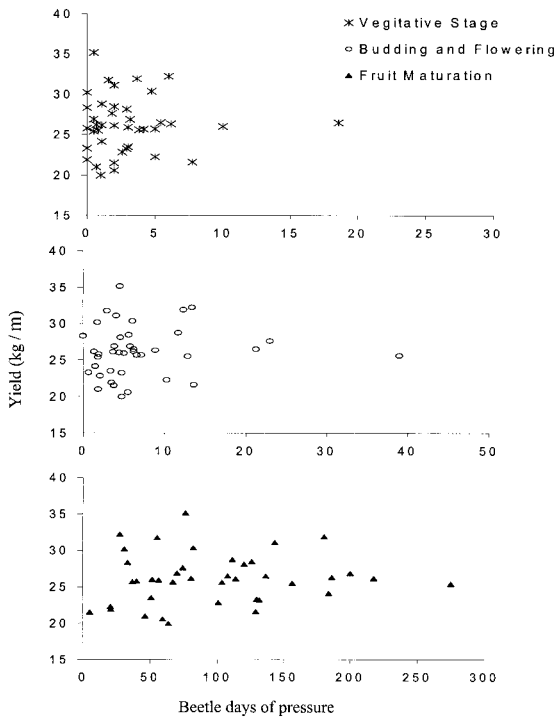


Fig. 4. Influence of Colorado potato beetle combined adult and large larval pressure during the vegetative, budding and fruiting, and fruit maturation stages on tomato yield in 1999 and 2000. Note difference in axes expressing beetle days of pressure among the plant growth stages.

the vegetative stage, 7.4 (SE \pm 1.5) and 5.8 (SE \pm 1.5) for the budding and fruiting stage, and 117.6 (SE 10.5) and 37.1 (SE \pm 6.2) for the fruit maturation stage for 1999 and 2000 respectively. Pressure was higher in 1999 than in 2000 because of a larger first generation of adults and the initiation of a second summer generation. For both years there was no significant relationship between beetle pressure and yield (Fig. 4) during the vegetative stage (1999: $F = 0.22$; $df = 1, 28$; $P = 0.64$; 2000: $F = 1.11$; $df = 1, 8$; $P = 0.32$), the budding and flowering stage (1999: $F = 0.00$; $df = 1, 28$; $P = 0.96$; 2000: $F = 1.15$; $df = 1, 8$; $P = 0.31$), or the fruit maturation stage (1999: $F = 0.24$; $df = 1, 28$; $P = 0.63$; 2000: $F = 0.25$; $df = 1, 8$; $P = 0.63$). When all plant growth stages were combined, there was no significant relationship between beetle pressure and yield for small larvae (1999: $F = 0.2$; $df = 1, 28$; $P = 0.7$; 2000: $F = 1.4$; $df = 1, 28$; $P = 0.3$), large larvae (1999: $F = 0.7$; $df = 1, 28$; $P = 0.4$; 2000: $F = 1.1$; $df = 1, 28$; $P = 0.3$), overwintering adults (1999: $F = 0.02$; $df = 1, 28$; $P = 0.9$; 2000: $F = 4.89$; $df = 1, 28$; $P = 0.06$) and overwintering adults and large larvae (1999: $F = 0.7$; $df = 1, 28$; $P = 0.4$; 2000: $F = 0.1$; $df = 1, 28$; $P = 0.7$). Additionally, we could not detect a significant relationship in 1999 (which had a F_2 generation) by combining overwintering adults, first generation adults and large larvae ($F = 0.4$; $df = 1, 28$; $P = 0.8$) or overwintering adults,

first generation adults plus all larvae ($F = 0.4$; $df = 1, 28$; $P = 0.5$).

Discussion

Colorado potato beetle immigrated, oviposited, and established populations in both tomato and potato fields that were in close proximity, regardless of which crop was available first. However, in both years, the crop that was available first (tomatoes in 1998, potatoes in 2000) had the earliest immigration event and higher immigrating adult and egg mass densities (Fig. 1). Delayed immigration reduced immigrating population densities in potatoes (Weisz et al. 1994, Hough-Goldstein and Whalen 1996), and our data suggest the same would hold true in tomatoes. However, despite differences in the timing of initial immigration (10 d earlier in tomatoes in 1998, 9 d earlier in potatoes in 2000), overwintering adults infested fields for a similar number of degree days (153 and 154 in 1998 and 172 and 168 in 2000, for tomatoes and potatoes, respectively) (Table 1). Thus, immigrating into the field earlier did not result in a longer period of adult infestation or oviposition. While some laboratory bioassays suggest that Colorado potato beetle has similar adult longevity when reared on potato or tomato (Jansson et al. 1989), in the current study it is unclear if oviposition ended because of beetle mortality, emigration, or because the beetles had exhausted their egg supply. The number of eggs per mass for immigrating adults was similar irrespective of host, however there were fewer eggs per mass late in the season (Fig. 2). This is consistent with Jansson et al. (1989) who observed a decline in fecundity over time in laboratory bioassays on tomato and potatoes. While delaying immigration may lower immigration densities, it did not result in a shorter duration of overwintering adult infestation or oviposition.

Oviposition behavior of first generation adults differed dramatically between host and years. First generation adults initiated a second generation in two of three years: once in potatoes (1998) and once in tomatoes (1999). We did not observe visual differences in foliage and crops when second generation adults were present. In cases where late season oviposition did not occur, we believe that the majority of adults were entering diapause, because few adults were observed dying or exiting the field during ≈ 20 h of field work per week. Oviposition behavior by late season Colorado potato beetle is primarily influenced by photoperiod (Tauber 1988), but Horton et al. (1988) found that host crop also influenced the tendency to diapause in populations feeding on potato, buffalo bur (*Solanum rostratum*) and hairy nightshade (*S. sarachoides*). Senanayake et al. (2000) showed geographic variation in oviposition and diapause behavior over fairly small geographic scales. Our work suggests that Colorado potato beetle populations are capable of having either one or two generations a year in processing tomatoes in central Pennsylvania, and that beetle response to diapause cues may vary between tomatoes and potatoes.

The difference in the time of initial immigration did not result in asynchrony of later life stages between hosts in 1998, but did result in asynchrony in 2000, (Fig. 1). Timing of larval and F_1 adult life stages may have been influenced by timing of peak oviposition by the preceding overwintering adults. This first oviposition peak was more tightly synchronized between hosts in 1998 than in 2000.

The test for slope heterogeneity suggests that large larvae developed at a slightly faster rate in potato than tomato in 1998 (Fig. 3), but there was no difference in the development rate of small larvae in that year, or of either larval stage in 2000. The difference in intercepts in 2000 reflects the asynchrony of larval population development in that year (Fig. 1). The intercepts were also significantly different for large but not small larvae in 1998, suggesting that small larvae were synchronized in 1998, but that the large larval population was not, which is consistent with the different developmental rates in large but not small larvae in that year.

Survivorship from egg to adult was more similar between crops in the same year than within a crop across years (Table 2). In both 1998 and 2000 survivorship was equal or higher in potatoes than tomatoes, but the percent difference in mortality between potatoes and tomatoes decreased from 41% in 1998 to 11% in 2000. This may reflect adaptation to tomato as a host crop, which would be consistent with the laboratory findings of Lu et al. (1997). Our survivorship estimates in tomatoes were considerable higher than those in Latheef and Harcourt (1974) from fresh-market cultivars in Ottawa, Canada, which may reflect variation among geographic populations or cultivars. It is also possible that tomatoes were a more common antecedent host for the beetle population in central Pennsylvania. Our survivorship estimates in potato, however, were considerable lower than those in Harcourt (1971). In Harcourt's (1971) study "hilling operations were completed early in the season to avoid disturbing the populations," whereas we conducted hilling during late vegetative growth, just before row closure. This is consistent with commercial practices in central Pennsylvania, and tends to occur when first generation larvae are present. It is possible that disturbances from the tractor contributed to the lower survivorship by knocking larvae off the plant, and geographic and cultivar variation also exists among these studies. Sources of mortality were not evaluated in this study, and further work would be needed to determine what caused the differences in survivorship.

Colorado potato beetle did not have a significant influence on yield of processing tomatoes (Fig. 4) during the vegetative, budding and flowering, or fruit maturation stages, or when all plant growth stages were combined. While Colorado potato beetles are a threat to newly transplanted tomatoes (by clipping off the stems at the ground), their influence on established processing tomato plants is poorly documented. Plants had the opportunity to grow for 10, 10 and 13 d after transplantation but before infestation in 1998,

1999, and 2000 respectively. No-choice bioassays suggest that Colorado potato beetle engages more in tasting than feeding on less-preferred hosts (Harrison 1987). Adults and fourth instars can consume tremendous amounts of potato foliage, 10 and 12 cm² per day, respectively (Ferro et al. 1985), but, we observed only limited defoliation of processing tomatoes under field conditions despite densities exceeding 12 adults per 6 m. Presumably, defoliation reduces yield by reducing photosynthesis and nutrient translocation, but this relationship is not linear. Defoliation may not influence yield at low levels and must exceed 5–30% before yield is impaired in some crops (Mattson and Addy 1975). Processing tomatoes are the result of a directed breeding program to produce a tomato high in soluble solids that is compatible with mechanical harvest and peeling. This selected breeding combined with the horticultural management system for processing tomatoes may have resulted in a high defoliating threshold before yield reduction, and may explain the difference we observed compared with the dramatic influence on yield in older cultivars (Schalk and Stoner 1979). Additionally, the structure of the processing tomato plant may influence the relationship of beetle feeding and yield. The majority of the feeding we observed occurred in the upper canopy. The processing tomato plant is very compact with multiple layers of leaves. Interior leaves are shaded from direct sunlight by the canopy leaves. It may be possible that canopy defoliation allowed greater sunlight penetration, and interior leaves compensated with increased photosynthetic output.

Our sampling methods may have influenced measures of beetle influence on yield. Sampling beetle densities required manipulation of leaves and stems, and plants were occasionally injured. Sampled row segments had a 10–15% reduction in usable fruit when compared with adjacent nonsampled segments. Future experiments should include methods that estimate yield and beetle pressure without damaging plants. However, this source of error was distributed randomly among samples. If beetle pressure were a strong determinant of yield, we would still expect to find a significant relationship, which was not observed for any life stage.

The Colorado potato beetle accepted processing tomatoes as both a food source and an oviposition substrate when given the choice of ovipositing in nearby potatoes under field conditions. Additionally, life table statistics were similar, or appeared to converge, between beetles on tomatoes and beetles on potatoes. However, the observed immigration and fitness on both crops may not indicate a need for increased control in processing tomatoes. Colorado potato beetle did not influence the yield of processing tomatoes. This study illustrates that Colorado potato beetle will use tomatoes in a landscape containing potatoes, and estimates life table parameters for both solanaceous crops. The Colorado potato beetle may achieve similar fitness on both crops, affecting their population dynamics at a landscape level, while not

significantly affecting pest management concerns in processing tomato cultivars.

Acknowledgments

We thank P. Tobin and anonymous reviewers for earlier reviews, and the technical assistance of K. Arrington, J. Avila, L. Fang, J. Ferentz, K. Fordney, E. Friedrichsen, T. Grove, G. Krum, K. Martin, J. Munroe, N. Myers, J. Pedrick, P. Rebarchak, M. Reynolds, K. Turner and B. Weidenboerner. Support was received from USDA 97-3465-5032 and PDA ME 400487.

References Cited

- Cantelo, W. W., and G. E. Cantwell. 1983. Tomato yield loss as a result of simulated Colorado potato beetle (Coleoptera: Chrysomelidae) feeding. *Environ. Entomol.* 12: 1646–1651.
- Dyer, M. I., and U. G. Bokhari. 1976. Plant animal interactions: Studies of the effects of grasshopper grazing on blue grama grass. *Ecology* 57: 762–772.
- Ewing, E. E., K. P. Sandlan, and A. G. Nicholson. 1994. Modeling the effects of Colorado potato beetle and early blight defoliation on potato growth and yield, pp. 461–473. In G. W. Zehnder, M. L. Powelson, R. K. Jansson, and K. V. Raman. [eds.] *Advances in potato pest biology and management*. The American Phytopathological Society, St. Paul Minnesota.
- Ferro, N. D., 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.
- Harcourt, D. G. 1971. Population dynamics of *Leptinotarsa decemlineata* in Eastern Ontario. *Canadian Entomologist*. 103: 1049–1061.
- Hare, D. J. 1980. Impact of defoliation by the Colorado potato beetle on potato yields. *J. Econ. Entomol.* 73: 369–373.
- Hare, J. D. and G. G. Kennedy. 1986. Genetic variation in plant/insect associations: survival of *Leptinotarsa decemlineata* populations on *Solanum carolinense*. *Evolution* 40: 1031–1043.
- Harris, P. 1974. A possible explanation of plant yield increases following insect damage. *Agro-Ecosystems* 1: 219–225.
- Harrison, G. D. 1987. Host plant discrimination and evolution of feeding preference in the Colorado potato beetle *Leptinotarsa decemlineata*. *Physiological Entomology* 12: 407–415.
- Higley, L. G., L. P. Pedigo, and K. R. Ostlie. 1986. DEGDAY: a program for calculating degree-days, and assumptions behind the degree-days approach. *Environ. Entomol.* 15: 999–1016.
- Horton, D. R., and J. L. Capinera. 1988. Local differences in host use by two populations of the Colorado potato beetle. *Ecology* 69: 823–831.
- Hough-Goldstein, J. A., and J. M. Whalen. 1996. Relationship between crop rotation distance from previous potatoes and colonization and population density of Colorado potato beetle. *J. Ag. Entomol.* 13: 293–300.
- Hsiao, T. H., and G. Fraenkel. 1968. Selection and specificity of the Colorado potato beetle for solanaceous and nonsolanaceous plants. *Ann. Entomol. Soc. of Am.* 61: 493–503.
- Hsiao, T. H. 1978. Host plant adaptations among geographic populations of the Colorado potato beetle. *Entomol. Exp. Appl.* 24: 437–447.
- Hsiao, T. H. 1981. Ecophysiological adaptations among geographic populations of the Colorado potato beetle in North America, pp. 69–85. In J. Lashomb and R. Casagrande [eds.], *Advances in Potato Pest Management*. Hutchinson and Ross Publ. Co, Stroudsburg, PA.
- Hsiao, T. H. 1982. Geographic variation and host plant adaptation of the Colorado potato beetle, pp. 315–324. In P.T.I. Symp. [eds.], *Insect-plant Relationships*. Pudoc, Wageningen, Netherlands.
- Jansson, R. K., A.E.J. Zitzman, and J. H. Lashomb. 1989. Effects of food plant and diapause on adult survival and fecundity of Colorado potato beetle (Coleoptera: Chrysomelidae). *Environ. Entomol.* 18: 291–297.
- Kennedy, G. G., and R. R. Farrar. 1987. Response of insecticide-resistant and susceptible Colorado potato beetles, *Leptinotarsa decemlineata* to 2-tridecanone and resistant tomato foliage: the absence of cross resistance. *Entomol. Exp. Appl.* 45: 187–192.
- Latheef, M. A. 1972. A quantitative study of food consumption, assimilation, and growth in *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) on two host plants. *Can. Entomol.* 104: 1271–1276.
- Latheef, M. A. and D. G. Harcourt. 1974. The dynamics of *Leptinotarsa decemlineata* populations on tomato. *Entomol. Exp. Appl.* 17: 67–76.
- Littell, R. C., R. J. Freund, and P. C. Spector. 1991. SAS System for Linear Models, 3rd Ed. SAS Institute. Cary, NC.
- Logan, P. A., and R. A. Casagrande. 1980. Predicting Colorado potato beetle (*Leptinotarsa decemlineata* Say) density and potato yield loss. *Environ. Entomol.* 9: 659–663.
- Logan, P. A., R. A. Casagrande, H. H. Faubert, and F. A. Drummond. 1985. Temperature-dependent development and feeding of immature Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *Environ. Entomol.* 14: 275–283.
- Lu, W., G. G. Kennedy, and F. Gould. 1997. Genetic variation in larval survival and growth and response to selection by Colorado potato beetle (Coleoptera: Chrysomelidae) on tomato. *Environ. Entomol.* 26: 67–75.
- Maggs, D. H. 1964. Growth rates in relation to assimilate supply and demand. *J. Exp. Bot.* 15: 574–583.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515–522.
- Overney, S., A. Fawe, S. Yelle, and D. Michaud. 1997. Diet-related plasticity of the digestive proteolytic system in larvae of the Colorado potato beetle (*Leptinotarsa decemlineata* Say). *Archives of Insect Biochemistry and Physiology* 36: 242–250.
- Schalk, J. M., and K. Stoner. 1979. Tomato production in Maryland: effect of different densities of larvae and adults of the Colorado potato beetle. *J. Econ. Entomol.* 72: 826–829.
- SAS Institute. 1997. JMP, Version 3, Statistics and graphics guide. SAS Institute, Cary, NC.
- Senanayake, D., E. Ratcliff, and N. J. Holliday. 2000. Oviposition and diapause behavior in Colorado potato beetle (Coleoptera: Chrysomelidae) populations from east central Minnesota and the valley of the Red River of the north. *Environ. Entomol.* 29: 1123–1132.
- Southwood, T. R. 1978. Ecological methods with particular reference to the study of insect populations. Chapman & Hall, London.

- Spain, J. D. 1982. Basic microcomputer models in biology. Addison-Wesley, London.
- Tauber, M. J. 1988. Voltinism and the induction of aestival diapause in the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 81: 748-754.
- Weber, D. C., F. A. Drummond, and D. N. Ferro. 1995. Recruitment of Colorado potato beetle (Coleoptera: Chrysomelidae) to solanaceous hosts in the field. *Environ. Entomol.* 24: 608-622.
- Weisz, R., Z. Smilowitz, and B. Christ. 1994. Distance, rotation, and border crops affect Colorado potato beetle (Coleoptera: Chrysomelidae) colonization and population density and early blight (*Alternaria solani*) severity in rotated potato fields. *J. Econ. Entomol.* 87: 723-729.

Received for publication 18 March 2002; accepted 9 August 2002.
