Natural Mortality of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say)

by

Eleanor Groden

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ABSTRACT

NATURAL MORTALITY OF THE COLORADO POTATO BEETLE, *LEPTINOTARSA DECEMLINEATA* (SAY)

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This study was designed to explore the potential for developing endemic biological controls for the Colorado potato beetle (CPB). A comparative study of the natural mortality of the CPB was conducted over three years in both early and late potato plantings in R.I. and Mich., including regions with high and low population pressures. Large larval and pupal mortality were most highly correlated with total mortality over all plantings and research sites. Parasitism by the tachinid, *Myiopharius doryphorae*, was correlated with pupal survival, but was inverse density dependent. In early planted potatoes, egg mortality was most highly correlated with total survival. The incidence of the coccinellid predator, *Coleomegilla maculata*, was correlated with CPB egg and small larval mortality in R.I., but not in Mich. The densities of the carabid predator, *Lebia grandis,* were correlated with the densities of preyed CPB eggs in 1987 in both R.I. and Mich.

L. grandis was found to be primarily nocturnal, and a method of trapping was developed for daytime sampling. Adult *L. grandis* densities were synchronized with CPB egg and larval population in both R.I. and Mich. The release of tethered CPB prepupae allowed for the sampling of the ectoparasitic larvae of *L. grandis*, and parasitism of CPB pupae in Mich. exceeded 50% at peak pupal densities. Laboratory development studies and field sampling indicated that this predator completes one generation per year in both regions. *L. grandis* rate of prey consumption was greater than any CPB predator studied to date.

C. maculata adult densities were synchronized with first generation CPB prey in Mich., and first and second generation in R.I. The presence of alternate prey decreased their consumption of CPB prey. *C. maculata* densities were higher in alfalfa and sweet corn, than in potatoes.

CPB adult and larval infection by *B. bassiana* was lower in Mich. than R.I. Mich. soils were more fungistatic than R.I. soils, and fungistasis was correlated with soil pH. *B. bassiana* LD_{50} levels determined for inoculated pupae incubated in the different soils increased with increased soil fungistasis.

To my father, Harold Michael Groden, M.D.,
whose dedication, values, and humor
will always be with me.

and

To women in science,
may they go forth and multiply.

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INTRODUCTION

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), (hereafter referred to as CPB) is a pest of potatoes, *Solanum tuberosum* (L.) in the United States, Canada, continental Europe, and the Soviet Union. The CPB appears to be native to Mexico, the geographic origin of the genus *Leptinotarsa* (Tower 1906), where its primary host plants are *Solanum angustifolium* Mill. and *Solanum rostratum* Dunal (Hsiao 1985). The CPB was first collected on *S. rostratum* (Buffalo bur) in 1811 in western Iowa and appears to have adapted to potato ca. 40 years after the introduction of the crop to its native range in 1820 (Casagrande 1985). The beetle rapidly spread eastward on its new host plant, and has since become the most important insect pest of potatoes throughout most of the potato producing areas in the world (Hsiao 1981).

CPB pest management has been dominated by chemical controls since the introduction of Paris green in the mid 1800's (Gauthier et al. 1981, Casagrande 1987). After 125 years of exclusive reliance on a sequence of insecticides, many regional CPB populations have developed resistance to every available compound, and the effective life of newly introduced compounds has declined (Forgash 1981, 1985). The CPB has indeed demonstrated itself to be an incredibly adaptable insect, overcoming the resistance of wild potato plants within three generations (Groden and Casagrande 1986). It is evident that the "silver-bullet" approach will not provide a long-term solution to the potato beetle problem, and future pest management programs for this insect must rely on the integration of cultural and biological controls.

Cultural control measures were recommended for management of the CPB in the 1800's, but were abandoned as sole reliance on chemical controls increased (Casagrande 1987). These included the use of early maturing varieties of potato and crop rotation. Recently, Lashomb and Ng (1984) and Wright (1984) have shown that crop rotation can substantially reduce CPB pest problems, however, rotation is not commonly practiced in many potato growing regions.

The impact of natural enemies of the CPB has been considered to be inadequate for effective suppression of pest populations (Harcourt 1964). However, as with most research on biological control of agricultural pests, studies of the impact of CPB natural enemies have been conducted within the constraints of the current crop production system. Many of these cropping practices have evolved during a period of heavy pesticide use. The evolution of agricultural production systems has led to changes in agroecosystems that frequently disrupt the life systems of natural enemies. To fully evaluate the potential of predators, parasitoids, and pathogens suppressing insect pests, it is important to study their dynamics in a broader arena than current production systems. This can be accomplished through studies on the temporal and spatial dynamics of the natural enemy species as well as studies on its interactions with the insect pest. This focus must expand the system's boundaries to include alternative hosts and their habitats, and feeding and overwintering sites.

This study represents the first steps in this process of exploring the potential and developing and integrating biological controls of the CPB into the design of future potato production systems. The natural mortality of the CPB was evaluated under a variety of conditions, which encompassed both spatial and temporal differences. These included both early and late plantings of potato in the northeast and north central regions of the U.S., and areas with high and low regional population pressures. Variations in natural mortality were examined and the role of natural enemies was investigated. As a result of this population study, some aspects of the life systems of three individual natural enemy species were explored. These included: the biology and seasonal dynamics of the carabid, *Lebia grandis* Hentz, predation of the CPB by the coccinellid, *Coleomegilla maculata* DeGeer and fungistatic effects of soils on the fungal pathogen, *Beauveria bassiana*

(Bals.) Vuill. These studies are presented in the following four manuscripts, preceded by a general review of pertinent literature.

LITERATURE REVIEW

Many aspects of the biology and economic importance of CPB have been investigated since the discovery of this insect in 1811. Due to the severity of the CPB pest problem worldwide, this is one of the most intensively studied insects. In a computerized literature search conducted in 1986, more than 900 citations were available for this insect between 1975 and 1985 (Drummond pers. comm.). In this review, I will describe the life cycle of the CPB and discuss those studies concerning the population dynamics of the CPB and the role of endemic natural enemies. For a comprehensive coverage of much of the recent research concerning the biology and management of CPB, readers are referred to Lashomb and Casagrande (1981) and Ferro and Voss (1985).

CPB LIFE HISTORY

CPB overwinters in the adult stage, generally emerging in mid to late May in Rhode Island and Michigan. Lashomb et al. (1984) developed a predictive model for CPB emergence based on the accumulation of heat units in the soil. On emergence, CPB adults walk in search of host plants, or if sufficiently starved, fly (Caprio 1987). The CPB is a primary pest of potatoes, tomatoes, and eggplants and also feeds on several wild solanaceous plants (Hsiao 1985). Overwintered beetles mate in the spring, and females oviposit eggs in masses on the underside of the host plant leaf. After hatching, the insect completes four larval instars, all of which feed on the foliage of the potato plant. When mature, the prepupae drop to the ground and burrow into the soil to pupate. Logan et al. (1986) quantified the temperature dependent development of the CPB, and based upon their results, degree-day (base 10°C) requirements for eggs, the four larval instars, and pupae (+prepupae) are: 72, 36, 32, 37, 69, and 176, respectively.

Summer adults emerge in July and August in Rhode Island and Michigan and feed on potato foliage. Voss et al. (1988) determined that in western Massachusetts the majority of females emerging before July 25 oviposit, contributing to the second generation of CPB larvae. Those females emerging after this time are in reproductive diapause, and after feeding burrow into the soil to overwinter. Thus the timing of emergence of summer adults determines the magnitude of the second generation. In most years in Rhode Island, the CPB appears capable of completing a large second generation. In Michigan, the second CPB generation is usually small (Grafius, pers. comm.).

POPULATION DYNAMICS OF THE CPB

Harcourt (1963, 1964) and Logan (1981) investigated the spatial pattern of CPB on potatoes and developed a sampling plan for adults, eggs and larvae. Harcourt (1964) recommends sampling 100 to 200 plants per sample date to estimate densities of CPB life stages. Logan (1981) presents the number of stems necessary to sample for set levels of precision as a function of density.

Harcourt (1971) investigated the population dynamics of the CPB in eastern Ontario based on 10 sets of life table data collected over nine years. He found survival of summer adults or starvation-stimulated emigration to be the key factor responsible for numerical change from generation to generation. Starvation of large larvae is a key factor of less importance. Harcourt (1971) reported cannibalism of CPB eggs by adults to be the largest source of mortality for oviposited eggs, and rainfall as the only measurable source of mortality for small larvae. He concluded that mortality due to predators was so small as to be obscured by sampling error. Harcourt (1971) found survival of all immature stages to be density-independent, except pupal survival, which was positively density-dependent (pupal survival increased with pupal density). He attributed this relationship to the failure of the tachinid parasitoid *Mylopharius doryphorae* Riley to respond to changes in host density. Harcourt's conclusion was that nothing regulates CPB densities in potatoes except CPB density itself when defoliation results in total depletion of the food source.

THE ROLE OF ENDEMIC NATURAL ENEMIES

Many endemic natural enemies have been reported attacking the CPB. From 1869 to 1876, Riley listed 26 natural enemies of the CPB in the U.S.; Bethune (1872) describes 22 (Table 1), and Wegorek (1955) lists 59 species of invertebrate predators and parasites. In addition to invertebrate predators, Karg and Mazur (1969) found CPB adults and larvae to be an important component in the diets of three species of amphibians inhabiting potato fields. Studies attempting to assess the impact of natural enemies on the CPB have been focused on the tachinid parasitoid, *M. doryphorae* , the fungal pathogen, *B. bassiana* , and the pentatomid predators, *Perillus bioculatus* F. and *Podisus maculiventris* (Say). My preliminary observations suggest that the foliar searching carabid, *L. grandis* , and some coccinellids may also contribute significantly to CPB mortality in Rhode Island and Michigan.

Mylopharius doryphorae Riley

The CPB is the sole host reported for *M. doryphorae* . Adults larviposit in the second, third and fourth instars of the CPB, but the parasitic maggots do not start development until the fourth instars enter the soil to pupate (Tamaki et al. 1983). The parasitoid kills its host during the prepupal stage and a characteristic "mummy' is formed when the maggot pupates within its host's prepupal skin. *M. doryphorae* adult emergence lags several days behind that of nonparasitized CPB, and adults have a preoviposition period of ca. 7-10 days at 25°C (Tamaki et al. 1982). The overwintering stage of *M. doryphorae* is unknown.

Riley (1869) reported *M. doryphorae* killing 10% of the second larval generation of CPB in Missouri and 50% of the third generation. Riley's observations on the effectiveness of this parasitoid have been confirmed by Kelleher (1966), Harcourt (1971), and Tamaki et al. (1983). Although Kelleher found a significant correlation

Table 1. Natural enemies of the Colorado potato beetle endemic to North America reported by Riley and Bethune (1869-1877).

Scientific Name	Stage attacked
Phalangida	
Phalangium spp.	preys on eggs and larvae
Hemiptera	
Reduviidae	
Harpactor cinctus	preys on larvae
Sinea diadema *(=Reduvius raptatorius)*	" " "
Pentatomidae	
Podisus maculiventris *(=Arma spinosa)*	preys on eggs and larvae
Perillus bioculatus	" " " " "
P. circumcinctus	" " " " "
Euschistus variolarius *(=E. punctipes)*	preys on larvae
Coleoptera	
Cicindelidae	
Tetracha virginica	preys on larvae
Carabidae	
Lebia grandis Hentz	preys on eggs and larvae, and parasitizes pupae
Lebia atriventris	preys on eggs and larvae
Calasoma calidum	preys on larvae
Pasimachum elongatus	" " "
Harpalus caliginosus	" " "
Staphylinidae	
Philonthus spp.	" " "
Coccinellidae	
Coleomegilla maculata *(= Hippodamia maculata)*	preys on eggs and small larvae
Coccinella novemnotata	" " " " " "
Hippodamia tridecimpunctata	" " " " " "
H. convergens	" " " " " "
H. glacialis	" " " " " "
Anatis quindecimpunctata *(=Mysia 15-punctata)*	" " " " " "
Diptera	
Asilidae	
Promachus bastardii	preys on adults
Tachinidae	
Myiopharus doryphorae *(=Doryphorophaga doryphorae =Lydella doryphorae)*	parasitizes larvae
Hymenoptera	
Vespidae	
Polistes rubiginosus	preys on larvae

between CPB pupal mortality and parasitism, there was no correlation between larval density and percent parasitism. Harcourt found pupal parasitism to be inversely density dependent, suggesting that *M. doryphorae* did not respond to changes in host density. Kelleher suggests that *M. doryphorae* 's main limitation in controlling CPB is its lack of synchrony with its host. In Manitoba, adult flies were most abundant as the second larval generation were declining. The majority of the first larval generation and the early portion of the second larval generation escaped attack. Tamaki et al. (1983) also reported the impact of *M. doryphorae* to be limited by its low abundance during the first generation of CPB in Washington, although maximum parasitism of the second generation reached 75%. This species has also been found parasitizing the CPB in Mexico (Logan et al. 1985).

Beauveria bassiana (Bals.) Vuill.

The endemic biological control agent most intensively studied is the entomopathogen *B. bassiana.* This fungus is the causal agent of the white muscardine disease, which infects more than 200 insect hosts (Lipra 1967). The reported North American hosts of this fungus are presented in Table 2. All stages of the CPB, except eggs, are susceptible to *B. bassiana* infection.

The germinating conidia of *B. bassiana* penetrate directly through the cuticle of its hosts (Cooke 1977). Once in the haemocoel, the mycelium breaks into hyphal bodies which circulate and proliferate in the haemolymph. The multiplication of fungal cells retards and obstructs circulation. Disease symptoms and death are thought to be caused by toxins produced by the invading fungus (Ferron 1978). After death, the fungus reverts to a filamentous form and ramifies throughout the internal organs and body of the insect. Under favorable conditions hyphae emerge through the integument and produce conidiophores and conidia (Cooke 1977).

Table 2. Known North American hosts of *Beauveria bassiana* from reports of natural incidence in the field.

Scientific Name	Common Name	Reference
Heteroptera		
Lygaeidae		
Blissus leucopterus	chinch bug	Ramoska & Todd 1985
Miridae		
Lygus lineolaris	tarnished plant bug	Humber 1986
Coleoptera		
Carabidae		
Lebia grandis		Madge 1967
Pythidae		
Pytho sp.		Humber 1986
Coccinellidae		
Coccinella septempunctata	7-spotted ladybird	Cartwright et al. 1982
Coleomegilla maculata	spotted ladybird	Humber 1986
Chrysomelidae		
Cerotoma trifurcata	bean leaf beetle	Marrone et al. 1983
Diabrotica undecimpunctata	southern corn rootworm or spotted cucumber beetle	Humber 1986
Leptinotarsa decemlineata	Colorado potato beetle	Humber 1986
Curculionidae		
Araeceris fasciculatus	coffee bean weevil	Humber 1986
Chalcodermus aeneus	cowpea curculio	Humber 1986
Conotachelus nenuphar	plum curculio	Humber 1986
Curculio caryae	pecan weevil	Gottwald & Tedders 1982
Diaprepes abbreviatus		Beavers et al. 1983
Hypera brunneipennis	Egyptian alfalfa weevil	Johnson et al. 1984
Otiorhynchus sulcatus	black vine weevil	Humber 1986
Rhinocyllus conicus		Dowd & Kok 1983
Sitona hispidulus	clover root curculio	Quinn & Hower 1985
Scolytidae		
Dendroctonus frontalis	southern pine beetle	Pabst & Sikorowski 1980
D. ponderosae		Humber 1986
D. rufipennes		Humber 1986
Dryococtis confusus	western bark beetle	Whitney et al. 1984
Ips sp.		
Scolytus scolytus	elm bark beetle	Doberski & Tribe 1980
Lepidoptera		
Pyralidae		
Ostrinia nubilalis	European corn borer	Humber 1986
Tortricidae		
Choristoneura sp.		Humber 1986

Table 2, continued.

Scientific Name	Common Name	Reference
Noctuidae		
Heliothis virescens	Tobacco budworm	Humber 1986
H. zea	bollworm/corn earworm/ tomato fruitworm	Smith et al. 1981
Lasiocampidae		
Malacosoma americanum	Eastern tent caterpiller	Humber 1986
M. disstria	forest tent caterpiller	Stark & Harper 1982

B. bassiana has been mass produced in Europe and the Soviet Union for control of the CPB. In the Soviet Union, *B. bassiana* (Boverin) sprayed in combination with a sub-lethal dose of insecticide (which weakens the insect host) has been successful for CPB control (Ferron 1981).

B. bassiana has been studied for several years in Rhode Island. This work included monitoring its natural incidence in CPB populations (Clark 1980) and evaluating several different spray formulations and methods of conidial application (Roberts et al. 1981). This pathogen has consistently been most effective late in the growing season (LeBrun pers. comm.). It caused only negligible mortality to the first generation, but over 58% mortality to the second larval generation in Clark's (1980) natural incidence study. Similar results were obtained by spraying this pathogen on the foliage. Therefore, this increased efficacy is probably not due to inoculum build-up throughout the season, but rather to changes in the abiotic environment or in CPB susceptibility.

Effects of some environmental factors on infection and disease development have been elucidated. Temperature affects the rate of disease development directly and indirectly. Clark (1980) found the time to death of inoculated CPB larvae and adults to be a function of inoculum concentration and temperature. Indirectly, temperature influences the time between successive molts CPB larvae, and hence the ability of larvae to shed germinating conidia at ecdysis.

Humidity has a greater influence on disease development than temperature (Ferron 1978). Walstad et al. (1970) observed no germination of *B. bassiana* conidia at relative humidities below 97.5%. Once conidia have successfully penetrated the host integument, ambient humidity is no longer a factor until sporulation.

Sunlight may also be a limiting factor in *B. bassiana* activity in exposed portions of the potato canopy. Clerk and Madelin (1965) showed that sunlight reduces spore viability. Tourmanoff (1933) showed that spores were inactivated by periods of sunlight in excess of 3 hours.

The humidity and sunlight limitations on *B. bassiana* spore viability and germination have stimulated research in the interactions between this pathogen and the CPB in the soil environment. Watt and LeBrun (1984) found significant reductions (74% first generation and 77% second generation) in CPB adult populations due to soil applications of *B. bassiana* conidia.

The fungistatic pressure of soils on *B. bassiana* varies with soil type and season (Sharapov and Kalvish 1984). Fungistasis, the inhibition of fungal spore germination in natural soils, is thought to be an adaptive characteristic for fungi, limiting germination of spores to times when sufficient resources are available for complete development (Lockwood and Filonow 1981). Although the viability of *B. bassiana* conidia in soil decreases as temperature and soil moisture increase, their half-lives are still relatively long (120 days under normal temperature and humidity conditions) (Lingg and Donaldson 1981). Greater understanding of the ecology of *B. bassiana* in the soil and the interactions of CPB with the soil microhabitat is necessary if any potential is to be found for manipulating this environment to increase CPB mortality.

Perillus bioculatus F.

The two spotted stink bug, *P. bioculatus* , is considered the most important predator of the CPB in most potato growing areas of the U.S. (Riley 1869, Knight 1923, Tamaki and Butt 1978) and Canada (Bethune 1911, Franz 1957, Harcourt 1971). The North American distribution of *P. bioculatus* extends east through Ontario, New York, and Quebec; south to Florida and Mexico and west to the Pacific (McPherson 1982). *P. bioculatus* has not been reported in potato growing regions in New England. *P. bioculatus* has a fairly limited host range (Table 3), with the CPB considered as its predominant prey.

Overwintered *P. bioculatus* adults emerge in the early spring and congregate in potatoes as the first CPB's appear (Knight 1923). Females lay their eggs in masses (ca.

Table 3. Known prey species of *Perillus bioculatus*.

Scientific Name	Common Name	Reference
Coleoptera		
Coccinellidae		
Epilachna varivestis	Mexican bean beetle	Howard & Landis 1936
Chrysomelidae		
Acalymma vittata	Stripped cucumber beetle	Marsh 1913
Chrysomela scripta	cotton leaf beetle	Burkot & Benjamin 1979
Leptinotarsa decemlineata	Colorado potato beetle	Knight 1922
Pyrrhalta luteola	elm leaf beetle	Beaver 1986
Trirhabda canadensis	golden rod beetle	Knight 1922
Zygogramma heterothecae		Altieri & Whitcomb 1979
Z. suturalis		Altieri & Whitcomb 1979
Lepidoptera		
Liparidae		
Unidentified species		Nash 1912
Noctuidae		
Mamestra picta		Marsh 1913

14 eggs per mass) on the upper surface of the potato leaves. Eggs hatch in 8 days at 24°C and the primarily non-feeding first instars remain on the egg cluster for ca. two days (22-24°C) before molting to second instars and searching for prey (Tamaki and Butt 1978). Nymphs pass through four predacious instars before molting to adults. Total nymphal development requires 18.2 days at 24°C and 20.7 days at 22°C (Tamaki and Butt 1978).

Adults and fourth and fifth instars of *P. bioculatus* feed on all life stages of CPB including adults. Third instars feed on all immature stages of CPB, but second instars prefer eggs and newly-hatched larvae (Knight 1923). Tamaki and Butt (1978) quantified consumption rates for all nymphal instars. Though fifth instars consumed an average of 39 CPB eggs per day when reared solely on CPB eggs, they consumed only 0.2 large CPB larvae per day.

P. bioculatus completes two generations per year in the northern U.S. (Knight 1923). The onset of diapause in 14 day-old adults is triggered by photoperiods of less than 15 hours (Shagov 1977b). Extremely high overwintering mortality has been reported in Minnesota (95%, Knight 1923) and Europe (90-96%, Jermy 1980).

Since the late 1920's, many attempts have been made to establish and study *P. bioculatus* in Europe (Jermy 1980). Although temperature and humidity regimes favored by this predator (Shagov 1977a, 1977c) exist in many European countries, the species is not established (Jermy 1980). Jermy (1980) suggested that direct control of CPB with repeated mass-rear and release programs had little potential because of cost, the predator's susceptibility to insecticides, and the inability of the predator to keep CPB populations below an economically acceptable level. Tamaki and Butt (1978) and Harcourt (1971) also suggested that endemic populations of *P. bioculatus* in Washington State and Ontario, respectively, were ineffective in suppressing CPB populations below economically damaging levels.

***Podisus maculiventris* (Say)**

Unlike *P. bioculatus* , the spined soldier bug, *P. maculiventris* , is found in all potato growing regions in North America, and it has a very broad host range. McPherson (1982) lists over 100 prey species for this predator (Table 4). The more commonly reported prey include the CPB, Mexican bean beetle (*Epilachna varivestris*), elm leaf beetle (*Pyrrhalta lateola*), greater wax moth (*Galleria mellonella*), fall webworm (*Hyphantria cunea*), bollworm (*Heliothis zea*), soybean looper (*Pseudoplusia ni*), cabbage looper (*Trichoplusia ni*), and eastern tent caterpillar (*Malacosoma americanum*).

Similar to *P. bioculatus* , *P. maculiventris* overwinters in the adult stage in the humus layer and leaf litter (McPherson 1982). Esselbaugh (1948) reported that adult females overwinter in a non-gravid state and mating occurs in the spring, three to four days after emergence. Mukerji and LeRoux (1969a) found that continued mating is not necessary for the production of fertile eggs, but the fecundity of mated females is a function of temperature and food intake. The number of eggs per mass increased from 18.5 at 21°C to 31.4 at 27°C, although egg masses per female decreased slightly with increasing temperature. Eggs hatch in ca. 9-10 days at 21°C or 5 days at 27°C (Couturier 1938).

P. maculiventris nymphal development is influenced by temperature, prey consumption, and sex. Couturier (1938) reported that males develop faster than females (1-3 days) and total nymphal development is completed in ca. 27-30 days at 23°C. Landis (1937) and Drummond et al. (1985) found that prey species strongly influence both development rates and survival of nymphs. Drummond et al. (1985) reported the CPB to be an inferior host in comparison with the Mexican bean beetle, the greater wax moth, and the eastern tent caterpillar in that both the development rate and survival of *P. maculiventris* nymphs are significantly less when reared on CPB larvae.

Table 4. Known prey species of *Podisus maculiventris* (Say). (From McPherson 1982)

Scientific Name	Common Name
Ephemoroptera	
Unidentified species	
Orthoptera	
Acrididae	
Melanoplus femurrubrum (DeGeer)	Redlegged grasshopper
Gryllidae	
Gryllus assimilis (Fabricius)	Field cricket
Phasmatidae	
Diapheromera femorata (Say)	Walkingstick
Hemiptera	
Miridae	
Lygus lineolaris (Palisot de Beauvois)	Tarnished plant bug
Tingidae	
Gargaphia solani Heidemann	Eggplant lace bug
Pentatomidae	
Acrosternum hilare (Say)	Green stink bug
Apateticus cynicus (Say)	
Euschistus tristigmus (Say)	Dusky stink bug
Nezara viridula (Linnaeus)	Southern green stink bug
Podisus maculiventris (Say)	Spined soldier bug
Homoptera	
Cercopidae	
Clastoptera obtusa (Say)	Alder spittlebug
Philaenus spumarius (Linnaeus)	Meadow spittlebug
Aphididae	
Acyrthosiphon pisum (Harris)	Pea aphid
Unidentified species	
Coleoptera	
Scarabaeidae	
Unidentified species	
Lampyridae	
Unidentified species	
Coccinellidae	
Adalia bipunctata (Linnaeus)	Two-spotted lady beetle
Anatis quindecimpunctata (Olivier)	
Coccinella sp.	
Coleomegilla maculata (DeGeer)	
Epilachna varivestis Mulsant	Mexican bean beetle
Unidentified species	
Tenebrionidae	
Bothrotes arundinis (Le Conte)	
Tenebrio molitor Linnaeus	Yellow mealworm

Table 4, continued.

Scientific Name	Common Name
Chrysomelidae	
Altica chalybea Illiger	Grape flea beetle
Anomoea flavokansiensis Moldenke	
Chrysomela scripta Fabricius	Cottonwood leaf beetle
Crioceris asparagi (Linnaeus)	Asparagus beetle
Diabrotica undecimpunctata howardi Barber	Spotted cucumber beetle
Lema trilineata (Olivier)	Threelined potato beetle
Leptinotarsa decemlineata (Say)	Colorado potato beetle
Nodonota sp.	
Pyrrhalta luteola (Muller)	Elm leaf beetle
Systena elongata (Fabricius)	Elongate flea beetle
Unidentified species	
Zygogramma heterothecae Linell	
Zygogramma suturalis (Fabricius)	
Curculionidae	
Hypera postica (Gyllenhal)	Alfalfa weevil
Unidentified species	
Lepidoptera	
Pyralidae	
Anagasta kuehniella (Zeller)	Mediterranean flour moth
Galleria mellonella (Linnaeus)	Greater wax moth
Ostrinia nubilalis (Hubner)	European corn borer
Psorosina hammondi (Riley)	Appleleaf skeletonizer
Udea rubigalis (Guenee)	Celery leaftier/ greenhouse leaftier
Olethreutidae	
Ancylis comptana fragariae (Walsh & Riley)	Strawberry leafroller
Laspeyresia pomonella (Linnaeus)	Codling moth
Spilonota ocellana (Denis & Schiffermuller)	Eyespotted bud moth
Tortricidea	
Archips argyrospilus (Walker)	Fruittree leafroller
Archips cerasivoranus (Fitch)	Uglynest caterpillar
Archips fervidanus (Clemens)	Oak webworm
Argyrotaenia velutinana (Walker)	Redbanded leafroller
Pandemis canadana Kearfott	
Pandemis lamprosana Robinson	
Cossidae	
Cossus cossus Linnaeus	
Oecophoridae	
Depressaria pastinacella (Duponchel)	Parsnip webworm
Yponomeutidae	
Plutella xylostella (Linnaeus)	Diamondback moth
Coleophoridae	
Coleophora serratella (Linnaeus)	Birch casebearer/cigar casebearer

Table 4, continued.

Scientific Name	Common Name
Gracilariidae	
Caloptilia syringella (Fabricius)	Lilac leafminer
Geometridae	
Paleacrita vernata (Peck)	Spring cankerworm
Pleuroprucha insulsaria (Guenee)	
Unidentified species	
Ctenuchidae	
Lymire edwardsii (Grote)	
Archtiidae	
Hyphantria cunea (Drury)	Fall webworm
Noctuidae	
Alabama argillacea (Hubner)	Cotton leafworm
Alypia octomaculata (Fabricius)	Eight-spotted forester
Amphipyra tragopoginus (Linnaeus)	
Anticarsia gemmatalis Hubner	Velvetbean caterpillar
Ceramica picta (Harris)	Zebra caterpillar
Euxoa scandens (Riley)	White cutworm
Heliothis virescens (Fabricius)	Tobacco budworm
Heliothis zea (Boddie)	Bollworm/corn earworm/ tomato fruitworm
Lithophane antennata (Walker)	Green fruitworm
Plathypena scabra (Fabricius)	Green cloverworm
Pseudoplusia includens (Walker)	Soybean looper
Spodoptera exigua (Hubner)	Beet armyworm
Spodoptera frugiperda (J.E. Smith)	Fall armyworm
Trichoplusia ni (Hubner)	Cabbage looper
Unidentified species	
Notodontidae	
Datana ministra (Drury)	Yellownecked caterpillar
Lymantriidae	
Orgyia leucostigma (J.E. Smith)	Whitemarked tussock moth
Unidentified species	
Lasiocampidae	
Malacosoma americanum (Fabricius)	Eastern tent caterpillar
Malacosoma californicum pluviale (Dyar)	
Saturniidae	
Anisota virginiensis (Drury)	Pinkstriped oakworm
Pieridae	
Pieris rapae (Linnaeus)	Imported cabbageworm
Phoebis sp.	
Papilionidae	
Papilio cresphontes Cramer	Orangedog
Papilio polyxenes asterius Stoll	Black swallowtail/ parsleyworm
Danaidae	
Danaus plexippus (Linnaeus)	Monarch butterfly

Table 4, continued.

Scientific Name	Common Name
Diptera	
Tephritidae	
Rhagoletis pomonella (Walsh)	Apple maggot
Anthomyiidae	
Hylemya antiqua (Meigen)	Onion maggot
Muscidae	
Musca domestica Linnaeus	House fly
Tachinidae	
Unidentified species	
Hymenoptera	
Diprionidae	
Diprion similis (Hartig)	Introduced pine sawfly
Neodiprion taedae linearis Ross	Loblolly pine sawfly
Tenthredinidae	
Fenusa pusilla (Lepeletier)	Birch leafminer
Pristophora geniculata (Hartig)	Mountain-ash sawfly
Pristiphora rifipes Lepeletier	
Tethida cordigera (Palisot de Beauvois)	Blackheaded ash sawfly
Formicidae	
Camponotus sp.	Carpenter ant
Vespidae	
Unidentified species	
Apidae	
Apis mellifera Linnaeus	Honey bee

Feeding preferences of *P. maculiventris* nymphs are similar to those of *P. bioculatus* ; the smaller nymphs prefer small hosts while the larger nymphs and adults feed on all prey life stages (Mukerji and LeRoux 1969a). Waddill and Shephard (1975) reported that due to the selection of larger prey individuals, the number of prey consumed per predator may decrease with nymphal age. However, older nymphs are able to subdue prey more quickly and consume food faster than younger nymphs (Mukerji and LeRoux 1967a)

P. maculiventris is considered a timid predator. Morris (1963) reported prey defense and density to strongly influence predation rates of adults feeding on *H. cunea* larvae. Predation of sluggish prey was greater than that of active prey. However, Iwao and Wellington (1970) found that active prey (Western tent caterpillars) were more attractive to the predators than sluggish prey, thus for smaller prey less capable of defense, predation increased with prey activity. Morris (1963) and Mukerji and LeRoux (1969b) found predation rates of adult *P. maculiventris* to decrease with age.

The seasonal dynamics of *P. maculiventris* have not been followed in the field. The predator probably completes two generations per year in the southern portion of its range (Rhode Island) and one generation per year in Michigan and northward (McPherson 1982). Its presence in potato fields in Rhode Island is not detectable until the latter part of the growing season (Casagrande, per. comm.), hence its potential for biological control of the CPB may be limited. Drummond et al. (1985) simulated development of *P. maculiventris* and the CPB under average Rhode Island temperatures and found the predator to have a considerable developmental disadvantage in the early season. CPB eggs and larvae develop more rapidly than *P. maculiventris* with the cool spring and early summer temperatures.

Several attempts have been made to introduce *P. maculiventris* into Europe (Schwartz 1941, Bjegovic 1971, and Tadic 1975), and like *P. bioculatus* introductions, these have been unsuccessful.

Lebia grandis Hentz

The foliar searching carabid, *L. grandis* was first reported as a predator of CPB by Riley in 1872. In 1936, French entomologists collected *L. grandis* along with other CPB natural enemies in upper New York State to study their potential for controlling the CPB in Europe (Bruneteau 1937). Chamboussou (1938) described the biology of *L. grandis* and succeeded in mass rearing the predator on the CPB. The life cycle of the genus *Lebia* is unusual in that while the adults are predaceous on eggs and larvae of chrysomelids, the larvae are ectoparasitoids on pupae of the same host (Madge 1967).

The CPB is the only reported host of both the adult and immature stages of *L. grandis* (Madge 1967). Adult females lay their eggs singularly in the soil. The newly-hatched larvae burrow into the soil in search of CPB pupae. After locating its host, it feeds as an external parasitoid, becoming less mobile as it feeds (Chamboussou 1938). Chamboussou (1939) noted that in the laboratory successful parasitism is achieved by parasitic larvae released in a CPB pupation chamber within 30 minutes after CPB prepupae burrow into the soil. After feeding, the bloated first instar molts into a non-feeding second stage larva, then molts into a pupa. At 25°C, *L. grandis* develops from first instar to adult in 22 to 25 days (Chamboussou 1938).

No reports of field releases of *L. grandis* have been published, although Chamboussou (1938) suggested that it had potential for biological control of CPB. *L. grandis* is one of the more abundant egg predators in potato research fields in Rhode Island, and specimens in the MSU, Department of Entomology Insect Museum indicate that it is widespread throughout the state of Michigan. No research studies concerning *L. grandis* have been published since Chamboussou (1939).

Coccinellids

Much research has been focused on the interactions between coccinellids and aphids in potato fields (Shands and Simpson 1972; Mack and Smilowitz 1978, 1980, 1982a,b; Mack et al. 1981; Shands et al. 1972 a,b,c; Tamaki 1981) with little mention of the fact that several species also feed on the CPB. Karg (1976) reported higher mortality rates for CPB eggs and larvae in areas close to shelterbelts in potato growing areas in Poland, and attributes this partially to the coccinellids which overwinter in the these protected areas. Specific species were not reported. Trojan (1968) lists several species of aphidophages, including nine species of coccinellids, found in potatoes in Poland, and reports an inverse relationship between the mortality of CPB eggs and the ratio of aphids:aphidophages. He concludes that aphids are the preferred food of these predators, but as aphids decrease, they switch to CPB eggs for prey. Of the nine species of coccinellids listed by Trojan, only one, *Hippodamia tridecimpunctata* L., has been reported to feed on the CPB in North America (Bethune 1872). Seven different species of coccinellids have been sampled in Rhode Island potato fields, and eight species in Michigan fields. Of these, the spotted ladybird, *Coleomegilla maculata* DeGeer was most frequently observed feeding on CPB eggs.

C. maculata is a polyphagous predator commonly reported feeding on aphids in many cropping systems including potatoes. The reported prey species and food of *C. maculata* is presented in Table 5. In addition to insect prey, this coccinellid has been observed to feed considerably on pollen, and Smith (1960) showed that larvae of *C. maculata* can complete development when reared solely on this food.

Wright and Laing (1978) and Obrycki and Tauber (1978) describe the temperature-dependent development of this predator and its braconid parasite, *Perilitus coccinellse* (Shrank.) Wright and Laing (1978) found that fecundity (avg. 191.5 eggs per female) but not longevity (avg. 82.3 days) varies with temperature. Smith (1961, 1965) found *C. maculata* longevity, fecundity and development to vary with diet.

Table 5. Known prey species and food of *Coleomegilla maculata*.

Scientific Name	Common Name	Reference
Plant pollen and nectar		
Barbarea vulgaris	yellow rocket	Conrad 1959
Betula populifolia[1]	gray birch	Smith 1961
Cannabis sativa[1]	hemp	Smith 1961
Carpinus caroliniana[1]	hornbean	Smith 1961
Juglans cinerea[1]	butternut	Smith 1961
Prunus perisica	peach	Putman 1964
Taraxacum officinale	dandelion	Conrad 1961
Typha latifolia[1]	cat-tail	Smith 1961
Zea mays	corn	Britton 1914
Acari		
Tetranchidae		
Tetranchus canadensis	four-spotted spider mite	Putman 1964
Heteroptera		
Lygaeidae		
Blissus leucopterus	chinch bug	Conrad 1959
Miridae		
Trigonotilus rubicornis		Conrad 1959
Pentatomidae		
Podisus placidus		Conrad 1959
Reduviidae		
Sinea diadema		Conrad 1959
Homoptera		
Aphididae		
Acrythosiphon dirhodum		Gordon 1985
A. pisum (=*Macrosiphum pisi*)	pea aphid	Conrad 1959
Aphis gossypii	melon aphid	Conrad 1959
A. rumicis		Gordon 1985
Brevicoryne brassicae	cabbage aphid	Conrad 1959
Cryptomyzus ribis	currant aphid	Conrad 1959
Hyadaphis erysimi	turnip aphid	Gordon 1985
Macrosiphum avenue	English grain aphid	Gordon 1985
M. euphoribiae	potato aphid	Gordon 1985
Myzus persicae	green peach aphid	Mack & Smilowitz 1980
Nearctaphis crataegifoliae		Gordon 1985
Pemphigus bursarius	lettuce root aphid	Gordon 1985
Schizaphis gramminum	greenbug	Conrad 1985
Phylloxeridae		
Pineus strobi	pine bark adelgid	Gordon 1985
Psyllidae		
Trioza diospyri	persimmon psylla	Conrad 1959

Table 5, continued

Scientific Name	Common Name	Reference
Coleoptera		
Chrysomelidae		
Chrysomela scripta	cottonwood leaf beetle	Conrad 1959
Crioceris asparagi	asparagus beetle	Conrad 1959
Leptinotarsa decemlineata	Colorado potato beetle	Riley 1869
Coccinellidae		
Coleomegilla maculata	spotted ladybird	Pienhowski 1965
Cycloneda munda		Conrad 1959
Lepidoptera		
Archtiidae		
Hyphantria cunea	fall webworm	Warren & Tadic 1967
Noctuidae		
Heliothus zea	bollworm	Whitcomb & Bell 1964
Pyralidae		
Ostrinia nubilalis	European corn borer	Conrad 1959

[1] From laboratory studies.

Although consumption rates have been determined for this predator in the laboratory (Mack and Smilowitz 1982), little is known of its population dynamics or the impact on prey species in the field. Conrad (1959) did track *C. maculata* predation of European corn borer eggs in corn fields in Delaware by examination of fecula. Conrad also surveyed many crop fields in Delaware on a weekly basis and reported *C. maculata* adults present in all crops, but found larvae only in clover, alfalfa, and aphid-infested corn. Conrad estimated four to five generations per year for *C. maculata* in Delaware, but as with other mobile predators, their seasonal dynamics is difficult to ascertain.

Ground-dwelling carabids

Surveys of ground-dwelling carabid species have been conducted by pitfall trapping in potato fields in the U.S. (Boiteau 1984, Evans unpublished data), Europe (Scherney 1959) and the Soviet Union (Sorokin 1981). Studies attempting to relate carabid populations with CPB mortality have been limited to Germany (Thiele 1977), Poland, and the Soviet Union (Sorokin 1981). Scherney (1959) confined two species of *Carabus* common in potato fields in Bavaria, with cohorts of CPB eggs on potatoes in containers and in 4 m^2 enclosed areas. He found a 73-95% reduction in CPB larvae and pupae after 33-40 days in both cases, and reported significant increases in potato yields over treatments with no CPB control. The densities of carabids used in Scherney's experiments were typical of those found in the research areas, but were considerably higher than those found in most potato growing areas in the rest of the country (Thiele 1977).

Sorokin (1981) used three criteria to rank commonly encountered carabid species for their importance as predators of the CPB in irrigated and nonirrigated potatoes: estimates of their relative abundance in potato fields, analysis of gut contents, and consumption rates. He determined the three species, *Pterostichus cupreus, Ophones rufipes,* and *Brocus uphalotes* to be the most effective predators. Although these particular species have not been reported in cropland in North America, other species within the genera *Carabus* (Rivard 1964) and *Pterostitchus* (Evans, unpublished data) have been recorded.

Summary

There appears to be little potential for control of the CPB with endemic natural enemies under conventional cropping systems. Several natural enemy species have been reported to be fairly abundant late in the growing season, after considerable CPB damage has been sustained. This late season activity may be a result of a build-up of natural enemy populations, or it may be due to favorable environmental conditions.

L. grandis and *M. doryphorae* are specific predators and parasitoids of the CPB. The other natural enemies monitored in this study have alternate hosts or prey. The dynamics of these natural enemy populations may be dependent on the availability of alternate prey or habitats.

MANUSCRIPT 1.

Stage-Specific Survival of the Colorado Potato Beetle in Early and Late-Planted Potatoes in Rhode Island and Michigan

ABSTRACT - The densities of adult and immature Colorado potato beetles (CPBs) and their predators were sampled in both early and late planted potatoes at one research site in Rhode Island and two sites in Michigan from 1985-1987. In each plot CPB adults and large larvae were sampled to determine the percentage infected by the entomopathogen, *Beauveria bassiana,* and prepupae were collected to determine the percentage parasitized by the tachinid, *Myiopharius doryphorae.* For each of eight plots, seasonal density estimates and stage-specific survival rates of four immature stages (eggs, small larvae, large larvae, and pupae) of CPB were calculated. Key factor analysis revealed that the large larval and pupal stages were the most highly correlated with total within-generation survival. The pupal stage was the only stage for which survival was significantly correlated with density. Pupal mortality was inverse density dependent, and of the various factors responsible for pupal mortality, parasitism by the tachinid, *Myiopharius doryphorae,* was most highly correlated. *M. doryphorae* parasitism decreased with increased host density and was positively correlated with degree-day accumulation.

Key factor analysis was conducted for the early and late planted potatoes independently, and egg survival was found to be the key factor in within-generation survival in early planted potatoes. Although no measured source of mortality was significantly correlated with egg survival over all plantings, the incidence of *Coleomegilla maculata* was inversely correlated with egg and small larval survival (total *C. maculata* prey) in Rhode Island alone. In 1987, the densities of egg masses

preyed upon by haustellate and mandibulate predators and the densities of the carabid predator *Lebia grandis* were sampled. *L. grandis* densities were positively correlated with the densities of mandibulate-preyed egg masses in both Rhode Island and Michigan. The combined action of CPB egg and larval predators accounted for greater than 96% mortality of this pest in one Michigan research plot.

INTRODUCTION

Insecticides have been used intensively against the Colorado potato beetle (CPB) since 1865 (Casagrande 1987). In the past 30 years this practice has resulted in high levels of insecticide resistance and more recently, ground water contamination (Forgash 1985, Dover and Croft 1986). CPB has demonstrated itself to be an extremely adaptable insect, overcoming the resistance of wild potato plants within two generations (Groden and Casagrande 1986). It is evident that single control strategies will not provide long-term solutions to CPB pest problems. Future pest management programs for this pest must rely on the integration of cultural and biological controls.

Crop rotation greatly reduces CPB populations (Lashomb and Ng 1984, Wright 1984), and early recommendations for controlling CPB included rotations and growing early maturing and resistant varieties (Walsh 1865, Riley 1869, Bethune 1872). These strategies are not currently practiced in many potato growing regions.

Many endemic natural enemies have been reported attacking the CPB. Riley lists 26 natural enemies of the CPB in the U.S (1869, 1871, 1872, 1873). Studies have addressed the impact of the pentatomid predators, *Podisus maculiventris* (Say) (Drummond et al. 1985), and *Perillus bioculatus* (Harcourt 1971, Tamaki and Butt 1978, Jermy 1980), the tachinid parasitoid, *Myiopharius doryphorae* (Riley) (Kelleher 1960, 1966, Harcourt 1971, and Tamaki et al. 1983), and the fungal pathogen, *Beauveria bassiana* (Bals.) Vuill. (Clark 1980, Watt and LeBrun 1984) on CPB populations under current potato production practices. Each investigation concludes that the natural enemy does not adequately suppress CPB populations. However, most of the species described by Riley have not been studied. Harcourt (1971) studied the population dynamics of the CPB in Eastern Ontario, and concluded that natural enemies do not regulate CPB populations. He found that CPB populations in unsprayed potato research fields are only limited by starvation resulting from complete defoliation of their host plant. Harcourt's study demonstrates the destructive potential of unchecked

CPB populations, and the limitations of natural enemies under current potato production practices. However, more can be learned about the interactions of natural enemies and the CPB and the potential for biological control of this pest by looking beyond the boundaries of current potato production system.

The objectives of this study were to investigate the stage-specific survival of the CPB under different planting practices, geographic regions, and regional population pressures, and examine the role of endemic natural enemies in stage-specific mortality. A comparative study was conducted with the expectation that we would gain insight into factors responsible for mortality of CPB by examining temporal and regional differences.

MATERIALS AND METHODS

Study Sites.

This study was conducted from 1985-1987 at two university research farms in Michigan and one in Rhode Island. The Michigan sites included the Michigan State University Potato Research Farm in Montcalm County, Michigan (hereafter referred to as the Montcalm site) which is in the center of Michigan's largest potato growing region, and the Michigan State University Kellogg Biological Station in Kalamazoo County, Michigan (hereafter referred to as KBS). The Rhode Island site was the University of Rhode Island's Research Farm in Kingston, Rhode Island.

In 1985 research was conducted in both early and late planted potatoes in Rhode Island, and in late planted potatoes at all other sites. In 1986 and 1987, both early and late planted potatoes were established at all sites. All early potatoes were planted during the first week or second week of May, and late potatoes were planted between June 19 - June 25 in Michigan, and July 1 - July 4 in Rhode Island. In Rhode Island, late potatoes were planted in an area isolated from the earlier plantings in order to manage the densities of colonizing CPB summer adults. At both of the Michigan sites, late potatoes were planted adjacent to earlier plantings. At the KBS site, an additional plot of late potatoes (referred to as KBS late-2) was planted in an area isolated from earlier plantings. All plots consisted of 1/4 acre of Caribe′ potatoes planted in ca. 30-50 m. rows, 0.9 m. between rows, 0.26-0.30 m. between plants within a row. Caribe′ is an early maturing potato variety with heat and drought tolerance, thus making it suitable for late plantings when soil temperatures and moisture may be unsuitable for most potato varieties.

Daily maximum and minimum temperatures were obtained from the standard weather stations at each site, and degree day accumulations were calculated with a base of 10° C (Logan et al. 1986).

CPB and Natural Enemy Sampling.

In 1985, in the early planted potatoes in Rhode Island and late planted potatoes at the Montcalm site, CPB adult and egg mass densities were sampled throughout the growing season (2 to 3 times per week in Rhode Island and once per week at Montcalm). In late planted potatoes in Rhode Island and at the KBS site, densities of egg masses, each instar, and adults were sampled 2 to 3 times per week. In 1986, all lifestages were sampled 2 to 3 times per week at the KBS and Rhode Island sites, and once per week in Montcalm. In 1987, all lifestages were sampled once per week at all sites. Samples consisted of nondestructive visual counts of 100-200 plants per plot per sample date. Harcourt (1964) and Logan (1981) determined 150-200 plants per plot to be optimal for sampling eggs, larvae and adults of CPB.

In all plots, all predators on potato plants were counted while sampling CPB. In 1987 relative densities of *L. grandis* adults were sampled at the Rhode Island site with burlap traps, and absolute densities were sampled at the KBS site with weekly midnight observation of 100-200 plants per sample date (see manuscript 2).

Daily recruitment of eggs into the plots was monitored throughout the growing season in the late planted potatoes in Rhode Island in 1985, and in all Rhode Island and

KBS plots in 1986. As the potato plants were beginning to emerge, 100-200 plants were tagged, and checked every twenty-four hours for new egg masses. All egg masses were removed daily and tags were switched to new plants every 7 to 10 days throughout the growing season.

In 1985 and 1986, the egg masses collected in the daily recruitment samples were subsampled and the number of eggs per mass determined. In plots where daily recruitment was not measured, the number of eggs per mass was determined from a subsample of egg masses observed during visual counts of CPB life stages. For each plot, an analysis of variance was performed to determine if the size of egg masses varied by week throughout the growing season.

In 1986, an attempt was made to distinguish the signs of egg mass feeding by common CPB predators and CPB adults. It was not possible to definitively distinguish feeding by the mandibulate feeders, *L. grandis, C. maculata,* and CPB adults. However, it was possible to distinguish mandibulate feeders from the haustellate feeders, *P. bioculatus* and *P. maculiventris.* The mandibulate feeders generally consumed the entire egg and only the bottom of the egg chorion where the egg was attached to the leaf remained. The haustellate feeders pierced the egg with their stylets and sucked out the contents, leaving the chorion relatively intact. In 1987 while sampling CPB lifestages, the densities of CPB egg masses eaten by mandibulate and haustellate feeders were also sampled in all plots.

In order to estimate the absolute density of preyed egg masses, it was necessary to determine the length of time that the remains of preyed egg masses are detectable on the potato leaf (the residence time). In June 1988, a plot of ca. 100 potato plants was planted at the KBS site. The plot was colonized by native CPB adults, and the plants were checked daily for newly oviposited egg masses. As eggs were oviposited, they were tagged and rechecked daily for signs of predation. Once an egg mass was preyed on, the type of feeding was noted, and the egg mass remains were examined daily to determine the point at which they would not be detected in regular sampling of potato plants. The residence time of preyed egg masses was determined in degree-days (base 10°C) for each feeding type.

Emergence of first (summer) and second generation CPB adults were monitored with twelve 1-m^3 screen field cages set in each plot ca. 150-200 degree-days after the first observance of the CPB prepupae in the field. Emergence was monitored in early and late planted potatoes in Rhode Island in 1985-1987, in early and late planted potatoes in Montcalm in 1986-1987, and in early planted potatoes at KBS in 1986-1987. (Densities were too low in the late plantings at KBS to effectively sample.) Each cage was centered over a row of potatoes and contained 3 potato plants. Cages were checked three times per week for newly emerged CPB adults.

Prepupal and pupal mortality were evaluated in cages in Rhode Island in 1985-1987 and at KBS in 1986. In 1985 in the Rhode Island late planted potato plot, 3 1-m^3 screen cages were set up in a tilled area of soil just outside the potato field. On three occasions at 5 d intervals during the pupation of second generation CPB, 50 prepupae were collected from the field and released into one of the cages. Emergence of CPB adults in the cages was monitored every 2-3 days. In 1986 in order to include the impact of soil dwelling mortality factors that may be present under the potato canopy (such as *L. grandis* larvae) prepupal cages were set up within the potato fields. Prior to the occurrence of large CPB larvae within a field, 3 m X 3 m plots were marked, and within these areas all large fourth instar larvae were removed daily. With the occurrence of prepupae in the field a 1-m^3 cage was set up in the center of each of these plots, and 25 prepupae were released per cage at 5 day intervals until 100-125 prepupae had been released per cage. Cages were checked every 2-3 days for the emergence of CPB adults. In Rhode Island in 1986, three cages per planting were inoculated with prepupae. At the KBS site in 1986, and the Rhode Island site in 1987, four cages per planting were used.

Parasitism by the tachinid, *M. doryphorae* , was evaluated by sampling CPB prepupae as they burrowed into the ground to pupate. Collections were made at regular intervals throughout the prepupal generation. Collected individuals were placed in petri dishes or pint-size containers with moist sand and vermiculite and held in the laboratory at 20-25°C. Dishes were checked daily for the emergence of CPB or parasitoid adults.

CPB adults and large larvae were sampled to determine the percentage infected with *B. bassiana* . Samples were collected at regular intervals throughout the adult and large larval generations. Collected individuals were surface sterilized by dipping them in a 1% solution of Zephran Chloride® (Clark 1980), followed by a rinse in distilled water. Insects were then transferred to petri dishes with moist paper toweling and potato foliage, and the dishes were surrounded with water-saturated paper toweling and held at 20-25°C. Samples were checked every 2-3 days for mortality and/or sporulation of *B. bassiana*, at which time the insects were transferred to clean and sterilized dishes with fresh food. Individuals were held for 10 days and if an individual died, it was held for an additional two days under high humidity to encourage sporulation of the fungus. When sampling for *B. bassiana* infection or *M. doryphorae* parasitism, no more than five percent of the larval or adult population in the field was collected.

Estimating total seasonal density and stage-specific survival.

To calculate stage-specific survival rates for a population it is necessary to estimate the absolute densities (densities per unit area) of successive life stages. In populations with overlapping life stages or where all age classes occur simultaneously, as with the CPB, field estimates at peak density cannot be assumed to reflect the true density of insects entering or surviving a stage. This is particularly the case when the development time of successive stages differ. Southwood (1966, 1976), Helgesen and Haynes (1972), and Lampert and Haynes (1985) described methods for estimating total seasonal incidence in populations with overlapping stages which involved frequent sampling of stage-specific densities. When these densities are plotted against accumulated degree-days, the integration of these incidence curves divided by the development time of the stage, estimates the total seasonal production or number of individuals entering the stage ($DENS_i$). Hence,

$$DENS_i = AREA_i / T_i \qquad [1]$$

where:

i = life stage,
$AREA_i$ = the integral of the incidence curve of stage i, and
T_i = the development time of stage i .

Stage-specific survival (S_i) is then estimated as the proportion of individuals entering successive stages:

$$S_i = DENS_{i+1} / DENS_i \qquad [2]$$

This method assumes that any mortality experienced in the population occurs at the end of the stage, thus the residence time of individuals in the field (RT_i) equals the development time of the stage (T_i). Sawyer and Haynes (1984) discuss the limitations of this assumption and present a technique for estimating the true mean residence time of a stage when mortality is experienced throughout the stage at a constant rate. The more accurate form of equation [1] is thus:

$$DENS_i = AREA_i / RT_i \qquad [3]$$

The technique presented by Sawyer and Haynes uses equations [1] and [2] to calculate preliminary estimates of stage-specific densities and survival. If, as is the case with the CPB, these estimates result in negative mortality (survival estimates > 1.0) either due to sampling error or high mortality experienced early in a stage, their technique does not yield an appropriate solution. Therefore, to estimate seasonal densities and stage-specific survival for CPB populations, it was necessary to develop modifications of their technique based on directly measured or estimated recruitment into successive stages.

Estimation of egg survival (S_E) when recruitment is known. Recruitment into the egg stage was measured directly in all Rhode Island and KBS plantings in 1986, and in the late planting in Rhode Island in 1985. Egg recruitment in the early planting in Rhode Island in 1985 and the early planting in Montcalm in 1986 was estimated with an oviposition model (see Appendix A), and observed adult densities and temperatures. Using the observed or estimated recruitment ($DENS_E$) and the observed incidence ($AREA_E$), equation [3] was solved for RT_E. With a constant rate of mortality, Sawyer and Haynes (1984) showed that RT_i is related to survival (S_i) by the equation:

$$RT_i = T_i \; [\, (S_i - 1) \,/\, \ln S_i \,] \qquad [4]$$

Using T_E = 72 DD base 10°C (calculated from Logan et al. 1985), a unique solution to equation [4] was found such that $(S_E - 1) / \ln S_E = RT_E / 72$.

Estimation of egg survival (S_E) from density of eggs preyed upon by predators. In all plantings in 1987, the densities of preyed egg masses were sampled throughout the season. From these sampled densities, incidence curves for both haustellate- and mandibulate-preyed eggs were generated by multiplying the egg mass density by the mean number of eggs per mass. The seasonal densities for preyed eggs were estimated by dividing the area under each curve by the residence time for that type of preyed egg. The sum of mandibulate-preyed eggs and haustellate-preyed eggs ($DENS_{PE}$) were assumed to represent the number of eggs dying throughout the stage. A preliminary estimate of total egg density ($DENS_E'$) was calculated using equation [1], with T_e = 72 dd. From this, a preliminary estimate of egg survival (S_E') was calculated by:

$$S_E' = 1 - (\, DENS_{PE} \,/\, DENS_E') \qquad [5]$$

Using S_E' in equation [4], a preliminary estimate of the mean residence time of eggs (RT_E') was obtained. RT_E' was then used in equation [3] to arrive at an improved estimate of total egg density, $DENS_E''$. This improved estimate of total density was used in equation [5] to calculate an improved estimate of egg survival, S_E''. This iterative process was continued until equations [4] and [5] each converged on final estimates within 0.0001 S_E and RT_E.

Estimation of CPB larval survival (S_{SL} and S_{LL}) when adult emergence and pupal survival (S_P) are known . For calculating and analyzing CPB larval and pupal densities and survival, life stages were grouped as follows: small larvae = 1st and 2nd instars, large larvae = 3rd and 4th instars, and pupae = prepupae and pupae. First instar CPB densities are the most difficult stage to estimate as these extremely small larvae are difficult to detect on the potato plant once they have dispersed from the egg mass. Therefore, it was assumed that the incidence of small larvae was underestimated, and for those plantings where pupal survival and adult emergence were measured directly, survival of large larvae (S_{LL}) was estimated most accurately by solving backwards (using the method presented by Sawyer and Haynes, 1984) as follows. The number of adults produced per plant ($DENS_A$) was determined by dividing the mean adult emergence per cage by 3 plants per cage. Survival of pupae (S_P) was determined directly as the proportion of individuals surviving in the field cages seeded with prepupae. The density of pupae (or individuals entering stage P, $DENS_P$) was calculated by:

$$DENS_P = DENS_A / S_P \qquad [6]$$

Preliminary estimates of density and survival of large larvae ($DENS_L'$ and S_{LL}') were calculated using equations [1] and [2], and S_{LL}' was used in the following equation from Sawyer and Haynes (1984) to calculate an estimate of $DENS_{LL}''$ which corrects for the difference between RT_{LL} and T_{LL}:

$$DENS_i'' = DENS_i' \, [\ln S / (S - 1)] \qquad [7]$$

The density of small larvae ($DENS_{LS}$) was calculated by:

$$DENS_{LS} = S_E * DENS_E \qquad [8]$$

and survival of small larvae (S_{LS}) was then calculated with equation [2].

Estimation of larval survival (S_{LS} and S_{LL}) with corrected estimates of first instar larval incidence. From the seven plantings where larval survival was estimated as described above, the error in sampling first instar CPB larval densities was examined and a predictive model was developed to correct for this error . It was then possible to estimate total seasonal densities and survival of successive stages with recruitment estimates generated from the previous stage (as described in the section on estimation of egg survival when recruitment is known). However, estimation of total seasonal density of small CPB larvae was complicated because the mortality rate is not constant through the stage, but is highest early in the stage. The relationship between RT_i and S_i described by Sawyer and Haynes (1984) in equation [4] is based on a constant rate of mortality, where:

$$S(t) = e^{-at} \qquad [9]$$

with:

$S(t)$ = the proportion of the initial population surviving to time t,

e = the base of the natural logarithms, and

a = a positive constant defining S at time t = 1.

The mean age of the population (μ) expressed as a proportion of the maximum life-span is defined by the definite integral:

$$\mu = \int_0^1 e^{-at}dt$$

$$= -1/a\ (e^{-a} - 1)\ . \qquad [10]$$

Solving equation [9] for a, and substituting into equation [10], Sawyer and Haynes (1984) derive equation [4].

For the small larvae of the CPB, where mortality is highest early in the stage, equation [9] was replaced with the following which describes an exponential decay in S through the stage:

$$S(t) = e^{-at^{(1/n)}} \qquad [11]$$

where n is a constant which determines the initial slope of the curve. For small larvae of the CPB, n = 2. Again, the integral of equation [11] is the mean life-span expressed as the proportion of the maximum life span:

$$\mu = \int_0^a e^{-at^{(1/2)}} dt$$

$$= (2/a^2)\ [\ -ae^{-a} - e^{-a} + 1\ ] \qquad [12]$$

Solving equation [11] for a:

$$a = -\ln S\ /\ t^{1/2}\ , \qquad [13]$$

and substituting this into equation [12] for time t = 1 gives:

$$RT = 2/(\ln S)^2\ [\ S(\ln S - 1) + 1\ ]\ . \qquad [14]$$

Equation [14] was used to described the relationship between the survival (S_{SL}) and mean residence time (RT_{SL}) of small CPB larvae, and larval densities were estimated as follows. The corrected estimate of first instar-dd was added to the observed 2nd instar-dd to determine $AREA_{SL}$. The number entering the stage ($DENS_{SL}$) was estimated with equation [8]. Equation [3] was then solved for RT_{SL}, and equation [13] was used to determine S_{SL}. With these estimates of $DENS_{SL}$ and S_{SL}, the density of large larvae ($DENS_{LL}$) was determined with equation [8] , equation [3] was then solved for RT_{LL}, and equation [4] was used to determine S_{LL}. Again, equation [8] was used to estimate the total production of pupae ($DENS_P$), and survival of pupae (S_P) was determined using adult emergence ($DENS_A$) and equation [2].

This method for estimating stage-specific survival of CPB was used for eight plantings in which adult emergence, but not pupal survival was measured directly, and recruitment into the small larval stage ($DENS_{SL}$) could be estimated from egg survival. These included late plantings at KBS in 1986, and 1987, the early planting at KBS in 1987, the early planting at Montcalm in 1986, and the early and late plantings at Montcalm in 1987.

RESULTS AND DISCUSSION

CPB Colonization and Egg Recruitment

Endemic populations of CPB colonized all plantings at the Rhode Island and Montcalm sites in 1985-1987. However, it was necessary to release CPB adults collected at Montcalm into the 1985 and early 1986 plantings at KBS. In 1985, from July 23 to August 8, 2300 CPB adults were released directly into the potato plot at KBS. In 1986, to increase the endemic population, 500 CPB adults were released into the early planted potatoes at KBS between May 25 and mid-June. In 1986 and 1987, CPB adults collected emerging from the early planted potatoes at KBS were released into the isolated late planted potatoes at the same site (KBS late-2). Beetles were released at the same densities observed in KBS late-1. In 1986, 300 CPB adults were released, and in 1987, 400 adults were released.

Degree-day accumulations for the month of May at the Michigan sites were greater than those at the Rhode Island site for the first half of the month in 1986, and throughout the month in 1987 (Table 1). Throughout the first and second CPB generations degree-day accumulations differed only slightly between the sites in 1986, with the KBS site being a little warmer. Degree-day accumulations were higher at all sites in 1987, and higher in Michigan than Rhode Island. All early plantings in 1985-1987 were colonized by overwintered CPB adults during the last few days of May or the

Table 1. Accumulation of degree-days (base 10°C) from May 1, at research sites in Rhode Island and Michigan, 1986-1987.

	Rhode Island		KBS, Michigan		Montcalm, Michigan	
	1986	1987	1986	1987	1986	1987
May 15	36	40	82	78	78	96
30	151	128	154	224	160	227
June 15	274	278	295	419	289	399
30	406	419	428	626	413	573
July 15	557	594	591	829	559	773
30	726	780	806	1035	756	996
Aug 15	900	948	958	1257	907	1196
30	1031	1097	1083	1405	1022	1325

first few days of June (Figures 1-3) coinciding with plant emergence. Differences in phenology did exist between sites, however. Daily recruitment samples in 1986, indicated that beetles were ovipositing earlier at the KBS site than in Rhode Island (Figure 4). Although the number of eggs laid in the Rhode Island planting far exceeded that in the KBS site, the initial rate of oviposition was higher at KBS, most likely due to the warmer early season temperatures.

Dramatic differences in CPB adult colonization and egg recruitment were observed between early versus late planted potatoes, and within the late plantings, egg recruitment varied between sites and years. In the late plantings at KBS, egg recruitment was much lower than that observed in either the 1985 or the 1986 late plantings in Rhode Island (Figure 4). In the KBS site, second generation beetles stopped ovipositing 20 to 30 days earlier than in the Rhode Island. In Rhode Island, oviposition ceased at ca. the same Julian day in both years. Adult densities in the Rhode Island 1985 late planting were twice that observed in the 1986 late planting, however, twice as many eggs were laid in 1986 than 1985. Figures 1 and 4 indicate that beetles colonized the planting and oviposited eight to 10 days earlier in 1986 than 1985. Voss et al. (1988) demonstrated that the magnitude of the second CPB generation in western Massachusetts was determined by the time of emergence of summer adults. The majority of adults emerging prior to July 25 oviposited, whereas, those emerging after this date entered reproductive diapause. It appears that the egg recruitment in late planted potatoes is similarly determined by the timing of colonization by summer adults.

The mean number of eggs per mass did differ throughout the season in some plantings (Table 2). Early and late plantings in Rhode Island generally had smaller egg masses in the first two weeks that the site was colonized, egg mass size increased through the oviposition period, and then declined slightly at the end of the generation. This pattern was also observed in the 1987 early planting at Montcalm. There was no significant correlation between daily degree-day accumulation and egg mass size.

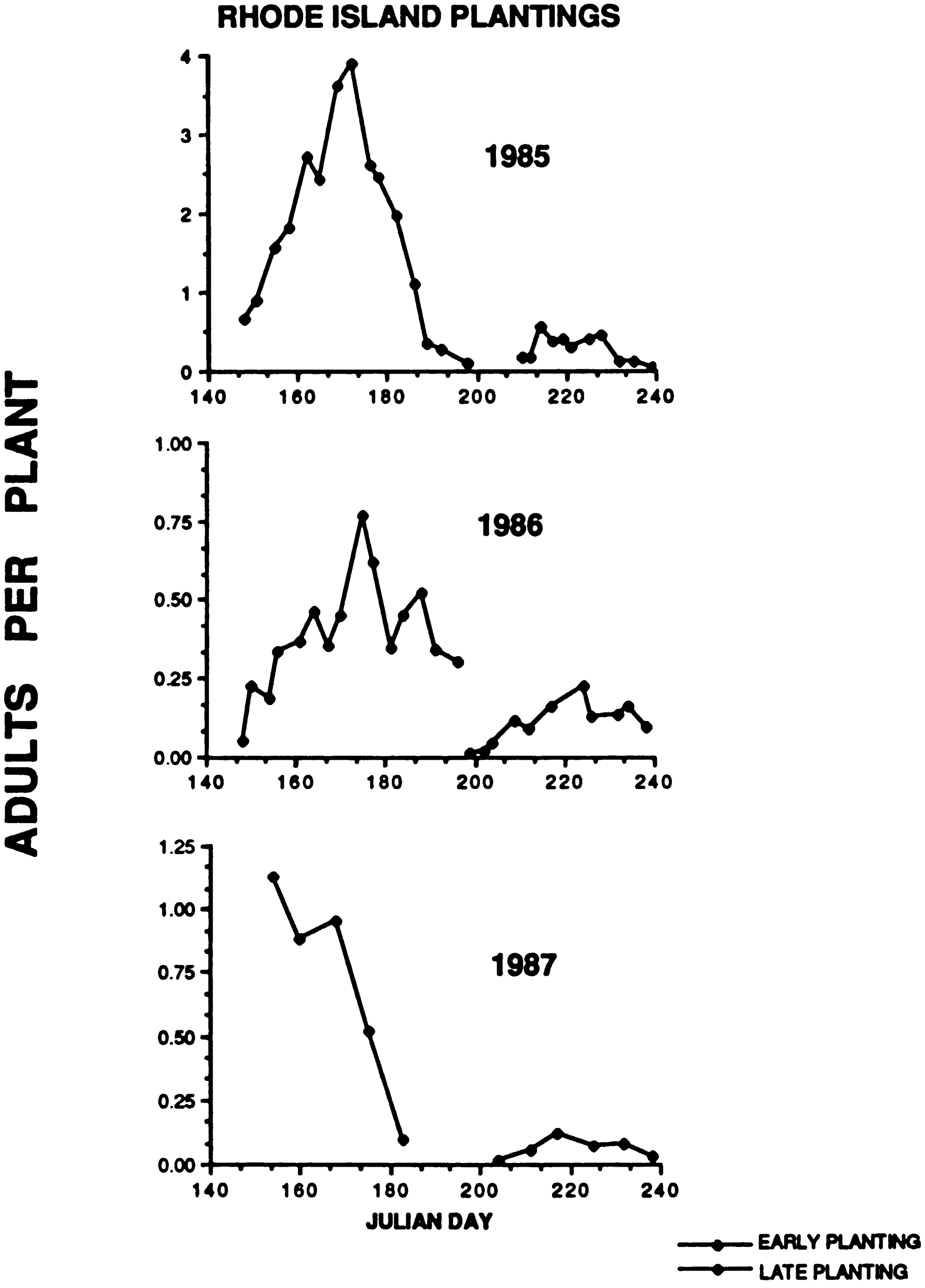

Figure 1. Densities of adult CPB in potato research plots in Rhode Island, 1985-1987.

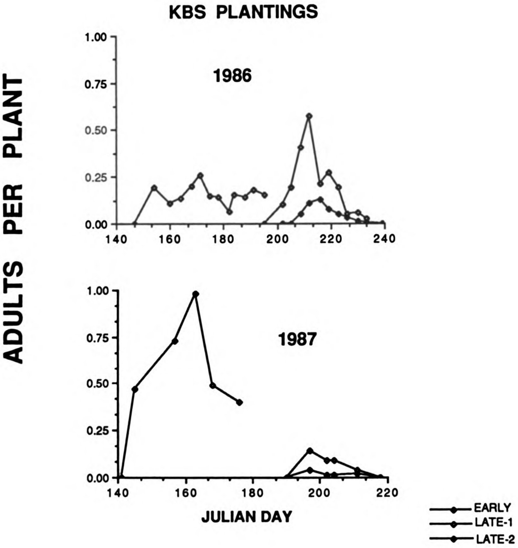

Figure 2. Densities of adult CPB in potato plots at the KBS site in Michigan, 1986 and 1987.

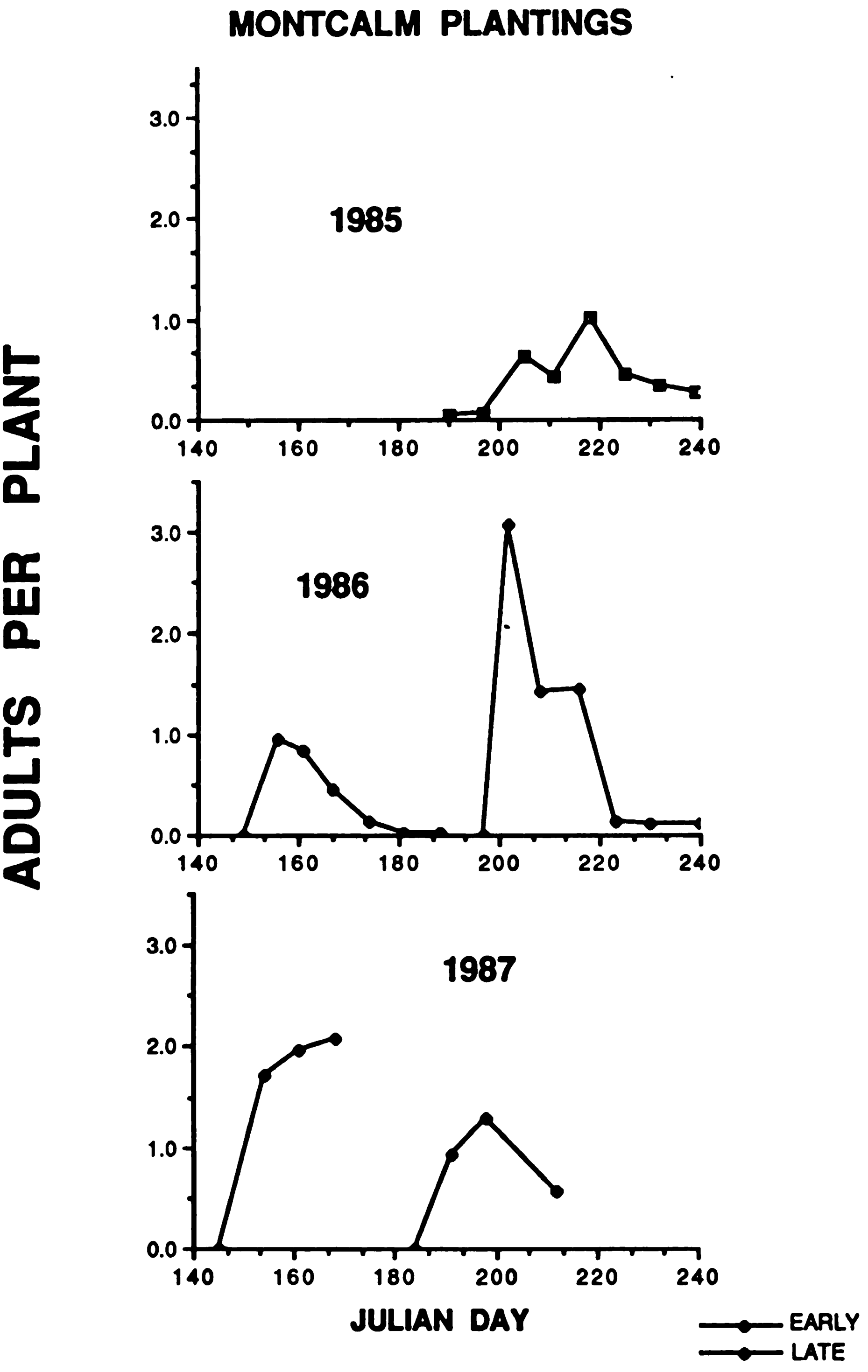

Figure 3. Densities of adult CPB in potato plots at the Montcalm site in Michigan, 1985 and 1987.

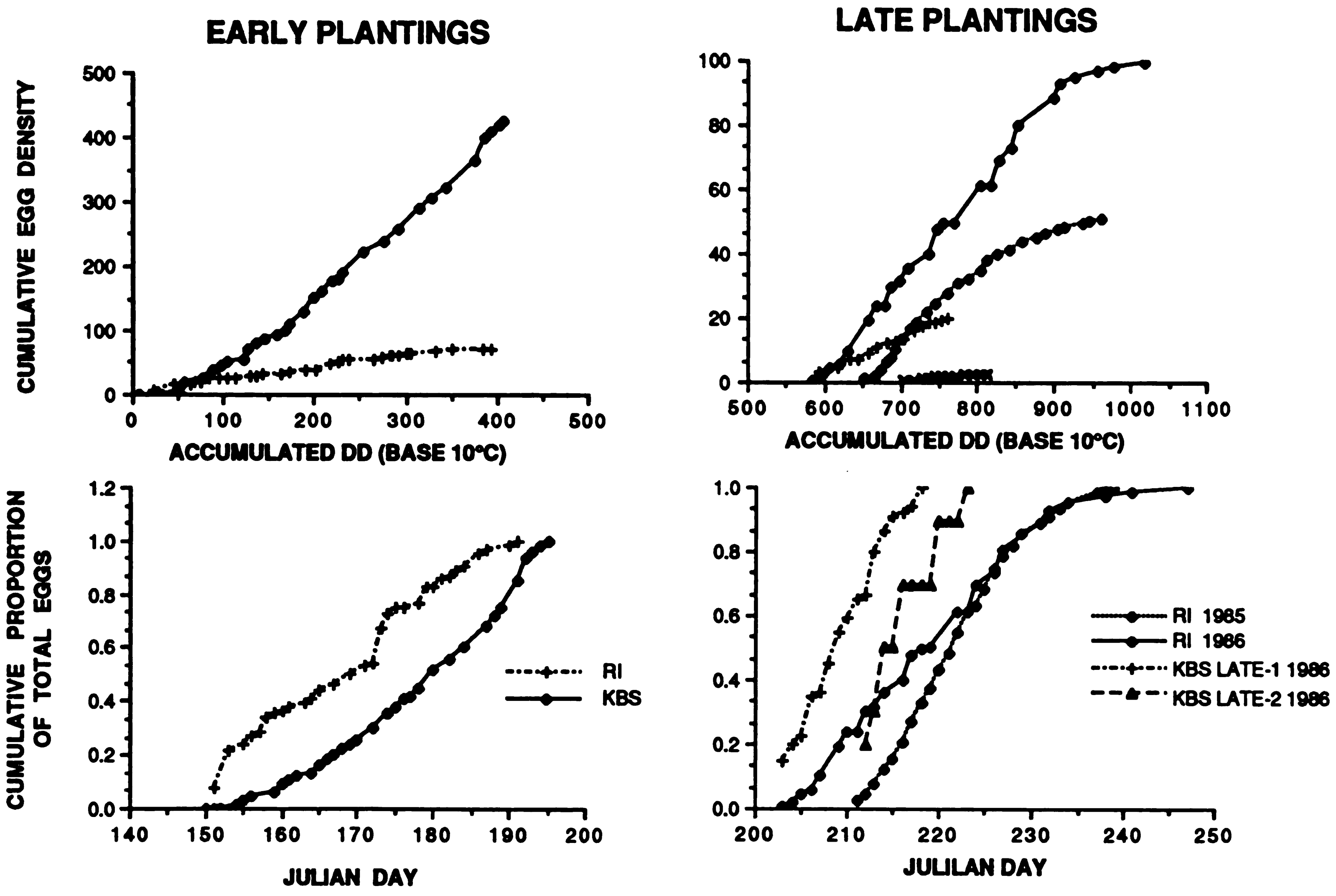

Figure 4. Daily oviposition of CPB eggs in potato plots in Rhode Island and Michigan, 1985 and 1986.

Table 2. Results of ANOVA's for CPB egg mass size observed in Rhode Island and Michigan potato research plantings in 1985 and 1986, and values of mean eggs/mass used for calculating egg densities from observed egg mass densities.

Site	Year	Planting	F value	p	Weeks	Observed eggs/mass[1]	Eggs/mass used for calculations[2]
Rhode Island	1985	early	$F_{(1,197)} = 8.12$	0.0049	1	27.54a	26.37[3]
					3	33.01b	34.70[3]
		late	$F_{(2,191)} = 2.06$	0.1297	1	23.93a	23.93
					2	28.51b	28.51
					3	25.44ab	25.44
	1986	early	$F_{(10,563)} = 7.33$	0.0001	1	24.11a	26.37
					2	26.57a	"
					3	34.70abc	34.70
					4	37.48bc	37.20
					5	35.88bc	"
					6	40.25bcd	"
					7	45.40d	45.40
					8	40.90cd	40.90
					9	27.29a	27.93
					10	32.43abcd	27.93
Rhode Island	1986	late	$F_{(6,198)} = 2.77$	0.0131	1	23.14a	23.14
					2	41.39b	36.52
					3	38.25b	"
					4	33.95b	"
					5	36.56b	"
					6	29.55ab	30.27

Table 2. (continued)

Site	Year	Planting	F value	p	Weeks	Observed eggs/mass[1]	Eggs/mass used for calculations[2]
KBS	1986	early	$F_{(6,106)} = 0.65$	0.6915	1 - 7	32.39	32.39
		late-1	$F_{(1,55)} = 0.05$	0.8289	1 - 2	30.72	30.72
		late-2	-----	----	1 - 2	28.90	28.90
Montcalm	1986	early	$F_{(5,170)} = 1.29$	0.2781	1 - 6	31.53	31.53
		late	$F_{(6,106)} = 0.65$	0.6915	1 - 6	32.43	32.43
	1987	early	$F_{(4,116)} = 2.44$	0.0505	1	25.85a	26.18
					2	26.35a	"
					3	37.18b	37.95
					4	40.50ab	"
					5	38.29b	"

---

[1] Means per week followed by same letter are not significantly different by ANOVA; Fisher's protected LSD procedure ($P > 0.05$). Where no significant differences were found within a planting, the mean eggs/mass over all weeks is presented.

[2] Based on significant differences observed in ANOVA.

[3] 1985 data showed similar trend to 1986, therefore, due to the small number of weeks sampled in 1985, means calculated from 1986 data were used in calculations of 1985 egg densities.

Observed egg mass densities were converted to egg densities by multiplying by the mean eggs per mass for the planting presented in Table 2. The values attained in 1986 were used in 1987.

The densities of CPB life stages and natural enemies estimated with visual counts at all the research sites from 1985-1987 are given in Appendix C. The composition of CPB predator complexes at each site is presented in Table 3. The coccinellid, *C. maculata* was the predominant predator in Rhode Island plantings, and *C. maculata* and the phalangid, *Phalangium opilio* were the prominent predators in Michigan plantings. Although *P. opilio* consume CPB eggs and small larvae, there is very little overlap between their populations in potato fields and that of their CPB prey (Drummond et al. 1988). Therefore, this species was not considered in any further analysis in this study. Pentatomids were more prominent in Michigan potato plantings than Rhode Island, and as expected from its reported distribution (McPherson 1982), *P. bioculatus* was not found in Rhode Island plantings.

Total Seasonal Production and Stage-Specific Survival.

Residence time of preyed egg masses. The residence time of haustellate-preyed egg masses observed in June and July 1988 was 157.77 ± 12.09 dd (mean ± S.E.). The residence time of mandibulate-preyed egg masses was 83.34 ± 16.95 dd (mean ± S.E.). Because of the small sample available for estimating the residence time of mandibulate-preyed egg masses (n=2), the mean was compared with that estimated by Mena (unpublished data), who observed the residence time of preyed CPB egg masses on native horsenettle, *Solanum carolinense* L. For 12 mandibulate-preyed egg masses, he calculated a mean residence time of 82.81 dd. Thus, for calculating the total seasonal density of preyed egg masses, the residence times of 158 and 83 dd were used for haustellate- and mandibulate-preyed egg masses, respectively.

Table 3. Composition of CPB predator complexes in potato research plots in Rhode Island and Michigan, 1985-1987.

Site	Planting	% of Total					
		Coelomegilla maculata	*Lebia grandis*	*Podisus maculiventris*	*Perillus bioculatus*	Phalangids	Others[1]
1985							
Rhode Island	early	56.18	23.29	9.40	0.00	6.71	0.00
	late	55.84	14.97	10.78	0.00	4.39	0.00
KBS	late	22.11	0.50	0.00	1.26	77.57	7.04
Montcalm	late	11.68	7.46	11.17	6.60	10.57	51.77
1986							
Rhode Island	early	56.15	7.80	1.04	0.00	11.96	19.24
	late	54.02	0.00	17.43	0.00	26.72	0.00
KBS	early	57.83	2.59	5.70	6.74	18.68	2.07
	late-1	31.25	0.92	7.35	15.63	35.85	8.28
	late-2	31.06	0.00	0.97	7.76	42.70	17.48
Montcalm	early	26.92	10.96	14.61	3.65	25.57	7.30
	late	28.93	0.00	26.30	2.63	21.04	21.04

Table 3 (continued)

		% of Total					
Site	Planting	*Coelomegilla maculata*	*Lebia grandis*	*Podisus maculiventris*	*Perillus bioculatus*	Phalangids	Others[1]
<u>1987</u>							
Rhode Island	early	47.73	20.81	0.00	0.00	17.80	2.44
	late	74.69	0.00	5.68	0.00	8.00	1.61
KBS	early	33.41	4.80	15.57	22.50	22.39	1.33
	late-1	27.41	0.00	6.30	17.04	49.42	0.00
	late-2	30.73	0.00	0.00	4.36	64.92	0.00
Montcalm	early	28.83	16.36	13.77	7.79	33.25	0.00
	late	26.78	13.56	23.73	27.63	8.31	0.00

[1] Includes Chrysopid species, *Coccinella novemnotata* and *C. transversoguttata* .

Error in estimates of first instar incidence. Using the data from those plantings in which first instar CPB densities could be estimated from egg survival and incidence and survival of large larvae, the errors in estimating first instar incidence ((first instars/plant) x dd) from observed field counts was examined. This error was found to be inversely related to density. As first instar incidence increased, the error decreased exponentially. The predicted model used to correct for the error in estimating first instar incidence is presented in Figure 5.

Total seasonal production and stage-specific survival. Estimates of total seasonal production and stage-specific survival are presented in Tables 4 and 5. It was not possible to calculate estimates of total season production and stage-specific survival in those late plantings where egg recruitment was not sampled directly or estimated from densities of preyed eggs or the oviposition model. Because the proportion of adults entering diapause was unknown, it was not possible to use the oviposition model to simulate egg recruitment in the late plantings.

Again, comparing all plantings, there was a dramatic difference in egg recruitment between early versus late planted potatoes. With the exception of the 1987 late planting in Montcalm, egg recruitment in the late planted potatoes was 71 to 92 percent less than that observed in the early plantings. The late planted potatoes in Montcalm in 1987 differed little from the early planting in recruitment of CPB eggs. This planting was established while overwintered CPB adults were still abundant, and it's close proximity to large plantings of early potatoes resulted in a large influx of both overwintered and summer adults. Boiteau (1986) also found no difference in colonization and egg and larval densities in delayed plantings of potatoes compared with adjacent early plantings in New Brunswick, due to the movement of overwintered adults from the early to the late plantings. In addition, more non-diapausing summer adults may have contributed to the large CPB population in the 1987 late planting in Montcalm. Warm temperatures experienced in Michigan in 1987 resulted in early emergence of summer adults and

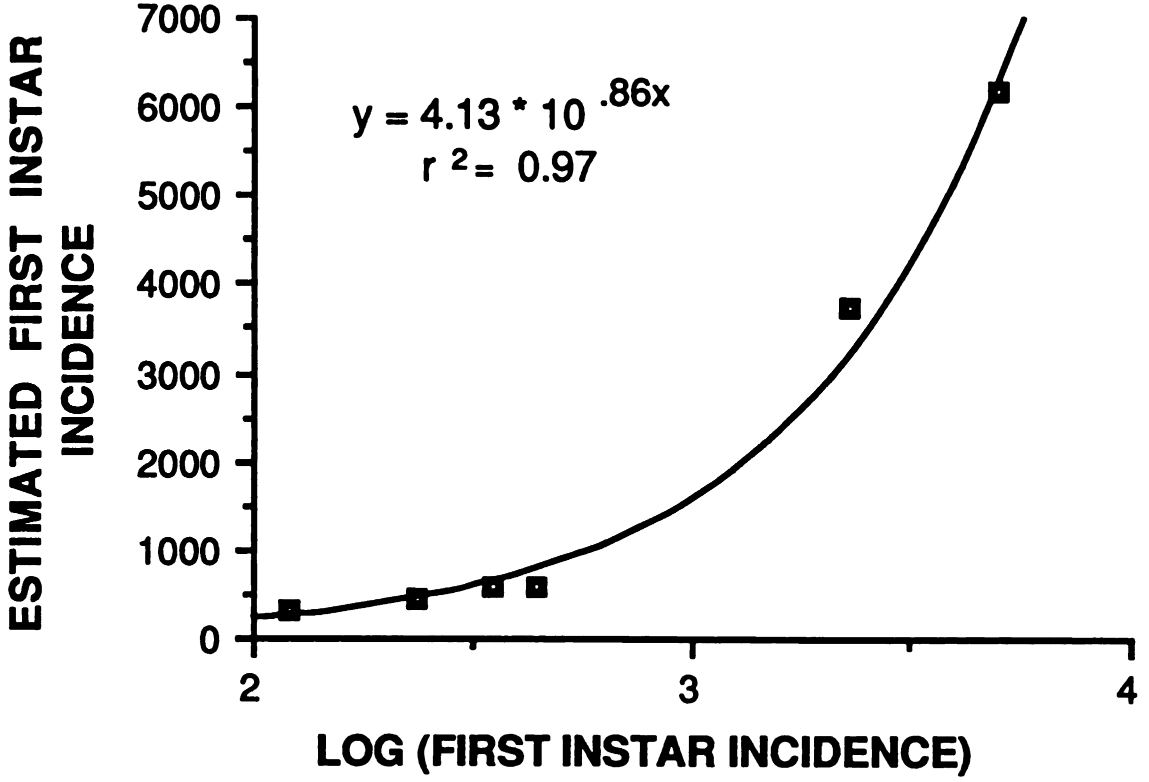

Figure 5. Error in sampling first instar CPB (incidence = mean per plant x dd).

Table 4. Seasonal production of CPB lifestages in potato plots in Rhode Island and Michigan in 1985-1987.

			Seasonal Production (mean per plant)				
Year	Site	Planting	Eggs	Small larvae	Large larvae	Pupae	Adults
1985	Rhode Island	early[1]	427.81	---	---	---	35.10
		late	50.69	17.13	12.19	10.88	5.22
1986	Rhode Island	early	362.83	283.46	43.68	45.02	24.70
		late	104.50	24.87	5.99	1.33	0.43
	KBS	early	68.72	33.88	3.31	3.80	2.63
		late-1	20.27	12.61	4.63	0.49	0.13
		late-2	2.89	2.89	0.56	0.19	0.00
	Montcalm	early	213.50	184.29	58.60	---	109.23
1987	Rhode Island	early	438.96	400.16	76.12	84.12	66.24
		late	34.19	32.33	3.63	1.60	0.27
	KBS	early	229.73	91.02	20.93	9.17	5.19
		late-1	25.11	10.81	1.61	0.00	0.00
		late-2	4.57	3.63	0.004	0.00	0.00
	Montcalm	early	435.84	339.96	30.09	---	---
		late	386.69	309.35	114.77	37.42	73.86

---

[1] Larval stages were not sampled.

Table 5. Stage-specific survival of CPB in potato research plots in Rhode Island and Michigan in 1985-1987.

			Stage-specific Survival[1]				
Year	Site	Planting	Eggs	Small larvae	Large larvae	Pupae	Total[2]
1985	Rhode Island	early	.72	---	---	---	.08
		late	.34	.71	.93	.48	.10
1986	Rhode Island	early	.78	.15	1.03	.55	.07
		late	.24	.24	.36	.33	.004
	KBS	early	.49	.11	1.04	.69	.04
		late-1	.62	.37	.11	.27	.006
		late-2	1.00	.20	.33	.00	---
	Montcalm	early	.86	.32	1.00	---	.51
1987	Rhode Island	early	.91	.21	1.10	.74	.15
		late	.95	.10	.58	.17	.008
	KBS	early	.40	.23	.44	.57	.02
		late-1	.43	.15	.00	---	---
		late-2	.80	.001	.00	---	---
	Montcalm	early	.78	---	---	---	---
		late	.80	.37	.33	1.97	.19

---

[1] Methods for calculating stage-specific survival are described in the text.

[2] Within generation survival: eggs to emerging adults.

hence, a larger portion of the population oviposited rather than entering reproductive diapause. First emergence of summer adults in Michigan in 1987 was 18 days earlier than that observed in 1986.

Although egg recruitment differed significantly between early and late plantings, there were not consistent differences in stage-specific survival. Key factor analysis (Morris 1963, Southwood 1966, 1978) was performed to identify significant trends and components in within-generation survival. It was necessary to eliminate from the key-factor analysis those data sets where estimates of stage-specific survival were incomplete either due to unsampled life-stages, or 100% mortality of the population before adult emergence. Also, total seasonal production of CPB large larvae and pupae, and larval and pupal survival estimates calculated for the 1986 and 1987 Montcalm planting were suspected of being inaccurate. All of these plantings experienced 100% defoliation prior to completion of the generation. As a result, the later part of the larval generations in these plots experience 100% mortality due to starvation. This pattern of mortality is not consistent with the mortality pattern assumed for this analysis and therefore it cannot be assumed to yield accurate results. Also, this extreme situation, although not unusual in uncontrolled CPB populations in regions with high regional densities, masks the contributions of other sources of biotic mortality of interest in this study. For these reasons, the Montcalm data sets were not used in the key-factor analysis.

Analysis of Within-Generation Survival of CPB

In this study, identifying mortality factors responsible for long-term trends in CPB population dynamics was not the objective. Instead, the objective was to identify those factors responsible for variations in within-generation population survival which result in varying degrees of plant damage in an agricultural system. For this reason, the following variation of Morris's model for population survival (Morris 1963), presented by Lampert and Haynes (1985) was used:

$$S_{WG} = S_E * S_{SL} * S_{LL} * S_P . \qquad [15]$$

To determine which of the components in this model contribute to most of the variation in S_{WG}, Pearson's bivariate correlation analysis was conducted with stage-specific survival data from the eight complete data sets available in this study. To obtain a linear model for examination, the above model was transformed by taking the natural logarithm of both side. Hence,

$$\ln S_{WG} = \ln S_E + \ln S_{SL} + \ln S_{LL} + \ln S_P . \qquad [16]$$

Graphical representation of each component of within-generation survival compared with total survival is presented in Figures 6a-d. The highest degree of curve similarity existed between total survival and large larval survival and total survival and pupal survival. The correlation analysis, concurs with this assessment. Correlation coefficients obtained between total within-generation survival and egg, small larval, large larval, and pupal survival were .271, .100, .864, and .785 respectively.

Density Dependence. The relationship between stage-specific survival and density was explored for each component of the model [16]. Density dependence was tested by plotting the number of individuals entering the stage against the number of individuals leaving the stage (or entering the successive stage). If the slope obtained from regression analysis of these data differed significantly from unity, this indicated that density-dependent mechanisms were operating (Morris 1963, Watt 1964). The only stage for which survival was density dependent was the pupal stage (Table 6). The slope of the regression line for pupal survival was significantly greater than unity, demonstrating that as the density of pupae increased, survival increased.

Pupal Survival. In this and previous studies, the factors responsible for pupal mortality included: parasitism by the tachinid, *M. doryphorae,* parasitism by the carabid larva, *L. grandis,* and infection by the entomopathogen, *B. bassiana.* Multiple

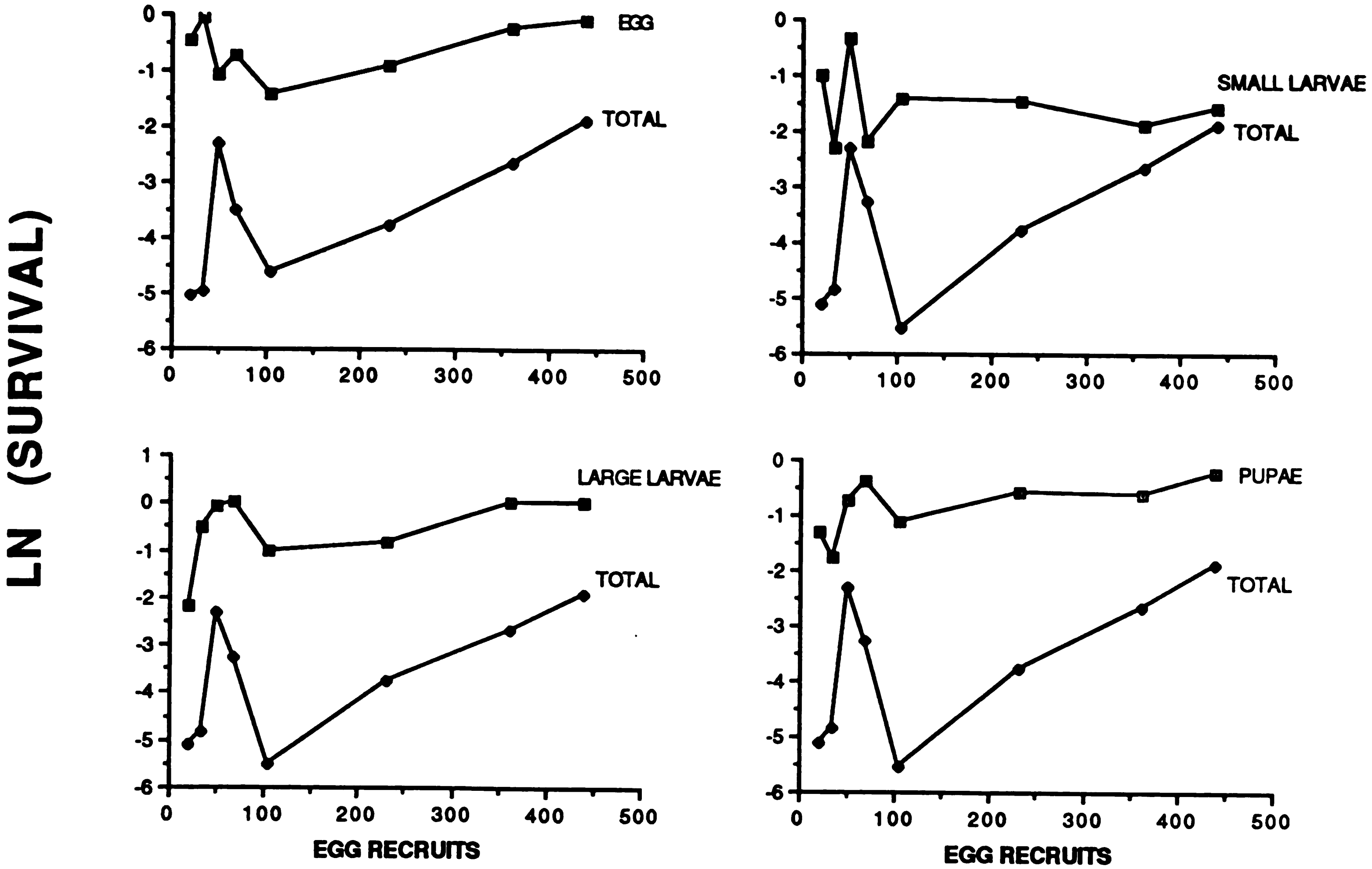

Figure 6. Graphical key-factor analysis of individual components of the CPB within-generation survival model

Table 6. Statistics from linear regression analysis testing for density dependence in survival of immature stages of the CPB. A slope that differs significantly from unity indicates density dependent mechanisms operating.

Stage	Slope[1]	95% C.I.	F value	p
Eggs	1.06	± 0.44	34.65	0.001
Small larvae	0.80	± 0.46	18.14	0.005
Large larvae	1.35	± 0.64	26.72	0.002
Pupae	1.22*	± 0.19	239.20	0.0001

[1] Values followed by * indicate significant difference from unity.

regression analysis was performed to detect significant correlations between CPB pupal survival and *M. doryphorae* parasitism and *B. bassiana* infection. Techniques for detecting parasitism of CPB pupae by the carabid *L. grandis* were not developed until the later part of this study, therefore, the significance of *L. grandis* parasitism could not be tested.

Parasitism of CPB pupae by *M. doryphorae* is presented in Table 7. *B. bassiana* infection of CPB pupae was not measured directly, however, it was assumed that mortality of CPB pupae by *B. bassiana* was directly proportional to that experienced by CPB adults. The percentage infection of CPB adults and larvae sampled at each research site are presented in Table 8. Only parasitism by *M. doryphorae* was significantly correlated with pupal survival ($p = 0.076$). The inverse relationship described by the equation: $y = 1.17 - 0.34x$, where $x =$ the ln (density of *M. doryphorae* parasitized pupae), and $y =$ the ln (density of emerging adults (surviving pupae)), explains 68% of the variation in surviving pupae ($F_{(1,5)} = 10.56$, $p = 0.023$; Figure 7).

M. doryphorae adults larviposit in the large larvae of the CPB, and the resulting CPB mortality is generally experienced in the ground-dwelling prepupal stage (Tamaki et al. 1983). Therefore, to explore the relationship between *M. doryphorae* parasitism and host density, the proportion parasitized (arcsin square root transformed) was regressed on the incidence of large larvae (large larvae x plant^{-1} x dd). This analysis revealed a significant inverse relationship between host incidence and parasitism ($F_{(1,9)}=7.14, p=0.03$; Figure 8), indicating an inability of *M. doryphorae* to respond to increases in host density. Harcourt (1971) reported the same relationship, and a relatively constant number of individuals parasitized independent of density. This resulted in a decline in the proportion parasitized as density increased.

Parasitism by *M. doryphorae* was higher in the late plantings or second CPB generation (Table 7). Kelleher (1966) observed the same pattern in Manitoba and suggested that overwintering mortality limited parasitism in the early season, but

Table 7. Parasitism of CPB pupae by *Myiopharius doryphorae* in potato reseach plots in Rhode Island and Michigan in 1985-1987.

	1985		1986		1987	
	early	late	early	late	early	late
Rhode Island	0.9[1] (588)[2]	41.0 (503)	0.5 (882)	30.5 (658)	0.0 (190)	54.2 (264)
KBS	---	66.7 (6)	3.9 (667)	30.4 (125)	13.7 (117)	---
Montcalm	0.0 (200)	15.5 (315)	0.0 (356)	22.2 (45)	---	10.0 (100)

[1] Percentage of pupae parasitized.

[2] Number sampled.

Table 8. *Beauveria bassiana* infection of CPB adults and larvae in potato research plots in Rhode Island and Michigan, 1985-1987.

		Larvae		Adults	
Site	Planting	n	% infected	n	%infected
<u>1985</u>					
Rhode Island	early	500	5.00	350	22.57
	late	400	6.00	300	6.67
KBS	early	---	---	---	---
	late	6	0.00	7	0.00
Montcalm	early	188	0.00	184	0.00
	late	250	0.40	301	0.33
<u>1986</u>					
Rhode Island	early	550	1.64	400	9.25
	late	412	1.27	200	10.50
KBS	early	300	0.00	312	0.32
	late	175	4.00	---	---
Montcalm	early	218	2.29	415	0.24
	late	47	0.00	363	0.00
<u>1987</u>					
Rhode Island	early	100	0.00	300	5.67
	late	264	0.00	49	2.00
KBS	early	117	0.00	205	0.00
	late	---	---	---	---
Montcalm	early	---	---	110	0.00
	late	100	0.00	98	0.00

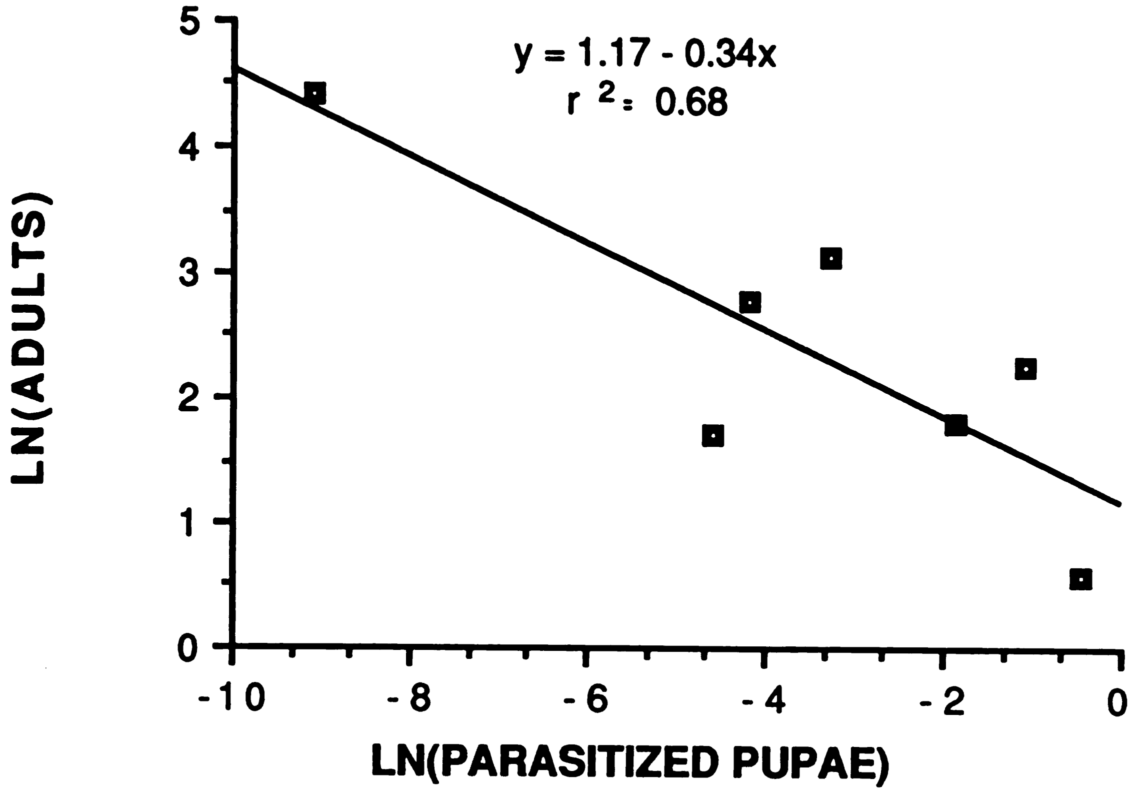

Figure 7. The density of emerging CPB adults per plant in relation to the number of *Myiopharius doryphorae* parasitized pupae per plant.

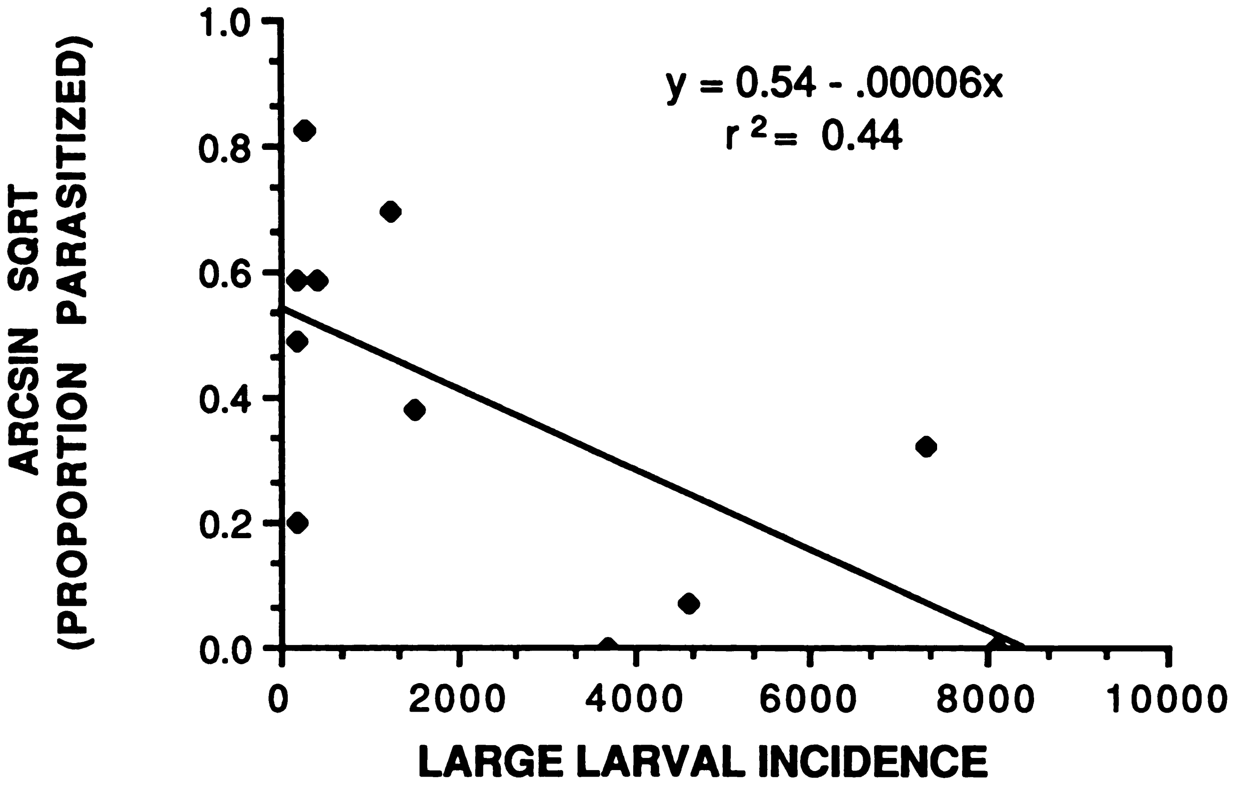

Figure 8. The relationship between the incidence of large CPB larvae (mean per plant x dd) and the proportion parasitized by *Myiopharius doryphorae*.

adults arising from this early generation attacked CPB larvae in the late season. He suggested that this second generation of parasitoids were often poorly synchronized with the host population, emerging in early August when the host population was rapidly declining. The relationship between *M. doryphorae* parasitism and the timing of host populations in this study was examined in the early and late plantings independently. Degree-day accumulation prior to the first occurrence of CPB large larvae was significantly correlated with parasitism in the late plantings ($F_{(1,4)} = 27.61$, $p = 0.006$, Figure 9). This relationship was not significant in the early planting ($F_{(1,3)}$=8.61, p=.06. However, a plot of degree-day accumulations at the mid-point in the large larval generation and *M. doryphorae* parasitism (Figure 10) indicates that parasitism increased sharply as hosts were available later in physiological time. Harcourt (1971) suggests that *M. doryphorae* parasitism of CPB in Ontario is a late season phenomena because the parasitoid overwinters in areas south of the province, and hence is a late arrival each year. These data suggest that *M. doryphorae* is not well synchronized with first generation CPB in Rhode Island or Michigan. Parasitism was related to degree-day accumulations suggesting that a temperature dependent process, such as spring emergence or arrival from southern overwintering sites determines the timing of *M. doryphorae* activity in potato fields. In most years in Rhode Island and Michigan, this lags behind the phenology of the CPB populations for both first and second generations.

From a pest management perspective, pupal mortality by *M. doryphorae* has been of little consequence in managing CPB populations with current production practices. However, these data suggest that the synchrony between the parasitoid and its host, and hence its impact on CPB mortality, may be enhanced by manipulating the timing of CPB host through delayed planting of potatoes. Studies of *M. doryphorae* 's overwintering mechanisms and survival are necessary to determine if potential exists for manipulating the timing of the parasitoid.

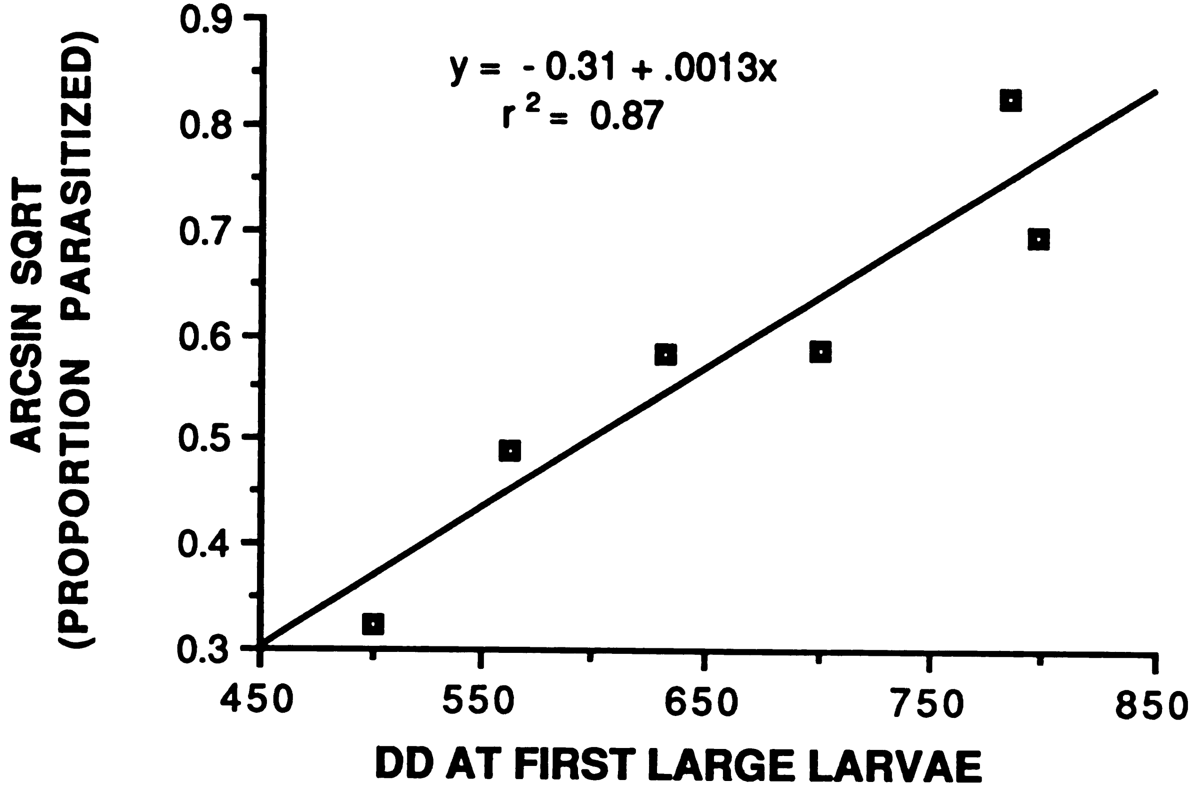

Figure 9. The relationship between parasitism by Myiopharius doryphorae and the occurrence of large CPB larvae in late plantings of potatoes in Rhode Island and Michigan.

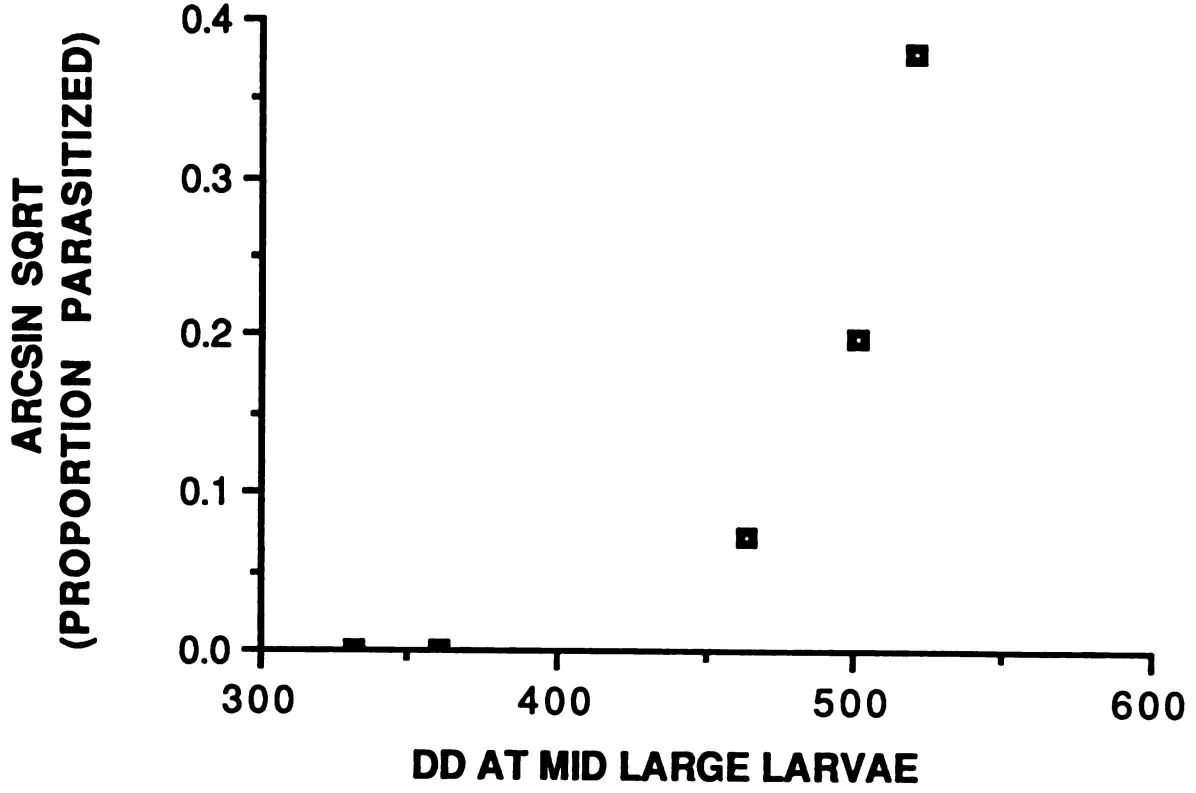

Figure 10. The relationship between parasitism by *Myiopharius doryphorae* and the occurrence of large CPB larvae in early plantings of potatoes in Rhode Island and Michigan.

Large larval survival. Factors responsible for mortality of CPB large larvae included predation by *L. grandis* adults and pentatomids, *P. bioculatus* and *P. maculiventris* , infection by *B. bassiana* , and starvation. Starvation was not a factor in the data used for this analysis. Methods for sampling *L. grandis* adults were not determined until the later part of this study and the influence of this predator was not evaluated in this analysis.

Percent *B. bassiana* infection of CPB larvae was difficult to determine from field samples, as many infected individuals held in the laboratory died of secondary infections. It was impossible to ascertain that the causal agent was *B. bassiana* as the fungus did not sporulate in these cases. Therefore, values for percent infection of CPB larvae given in Table 8, are conservative. For this analysis, both percentage of larvae infected and percentage of adults infected with *B. bassiana* were used as a relative measure of the impact of the disease on survival of large larvae. These plus the incidence of pentatomid predators, and parasitism by *M. doryphorae* were compared with survival of large larvae with stepwise regression analysis. There was a significant positive correlation between the incidence of pentatomid predators and large larval survival. However, when one of the eleven data points used in this analysis was removed, this relationship was not significant, and the trend in the relationship was negative. Thus, it is concluded that none of the factors monitored were responsible for significant variations in survival of large larvae.

Early versus late plantings. To examine difference in patterns of CPB survival between early and late planted potatoes, key factor analysis was repeated on the early and late plantings separately. Pearson's bivariate correlation analysis was used to identify significant correlations between components in model [16]. For the early plantings, correlation coefficients of .968, .025, .759, and .616 were obtained between total within-generation survival and egg, small larval, large larval, and pupal survival respectively. For the late plantings, the corresponding correlation coefficients were

.167, .705, .792, and .657. Thus, in the early plantings, egg survival rather than large larval and pupal survival was most highly associated total survival. For the late plantings, large larval survival was most highly correlated with total within-generation survival.

Egg survival. Factors responsible for CPB egg mortality included cannibalism by CPB adults, and predation by the carabid, *L. grandis,* the coccinellid, *C. maculata,* and the pentatomids, *P. maculiventris* and *P. bioculatus* . Stepwise regression analysis was performed to examine the relationships between the incidence of each of these mortality factors, (except *L. grandis* , and egg survival) for 14 plantings in this study. The pentatomid species were combined for analysis. No significant correlations were observed over all plantings, and no significant correlations were observed when early and late plantings were analyzed independently.

Egg mortality was measured directly in 1987 with observations of the density of preyed egg masses and the type of feeding damage. In Rhode Island, all detectable egg predation was caused by mandibulate predators (Table 9). In the Michigan plantings, more eggs were consumed by mandibulate predators in the early plantings, but the haustellate predators consumed more eggs in the late plantings. Over all plantings, the proportion of eggs consumed by predators ranged from .05 to .57.

Haustellate-preyed eggs were consumed by pentatomids, the only haustellate feeders found consistently in potatoes throughout this study. Stepwise regression analysis was used to identify any significant correlations between the incidence of two mandibulate feeders, CPB adults and *C. maculata* , and mandibulate-preyed eggs. A weakly defined positive correlation was found between CPB adult-dd/plant and the arcsin square root proportion of mandibulate-preyed eggs ($F_{(1,5)} = 6.85$ $p = 0.05$). Removing one of the seven data points used in this analysis resulted in a slope not significantly different from zero.

Table 9. Predation of CPB egg masses by haustellate and mandibulate predators in potato research plantings in 1987.

			Proportion of eggs preyed	
Site	Planting	Egg density	Mandibulate	Haustellate
Rhode Island	early	438.96	8.84	0.00
	late	34.19	5.42	0.00
KBS	early	229.73	39.38	17.10
	late-1	25.11	14.27	42.68
	late-2	4.57	0.00	20.41
Montcalm	early	435.84	22.02	0.00
	late	386.69	16.23	3.75

To determine if mandibulate egg predation was density dependent or density independent, the natural logarithm of 1 minus the number of mandibulate-preyed eggs was regressed with the natural logarithm of egg density As the slope of the regression did not differ significantly from 1.0 (slope ± 95% C.I. = 0.951 ± 0.088), it was concluded to be density independent.

Methods for estimating densities of *L. grandis* adults were developed in the last year of this study (see manuscript 2). Weekly density estimates from the 1987 early plantings in Rhode Island and KBS were used to examine the influence of this predator on CPB egg survival, as well as to gain additional insight into the influence of *C. maculata* and CPB adults. Weekly estimates of CPB adult densities, *C. maculata* densities, and *L. grandis* densities, were each regressed independently with weekly estimates of mandibulate-preyed eggs. Adult CPB densities were expressed as the ratio of adults to eggs when regressed with the density of mandibulate-preyed eggs to avoid a bias due to the obvious relationship between adult densities and egg densities. No significant correlations were found between adult densities and mandibulate-preyed eggs ($F_{(1,9)}$ = 1.68, p = .23).

Because *L. grandis* and *C. maculata* feed on other stages of CPB, to examine the relationship between the densities of these predators and mandibulate-preyed eggs, the proportion mandibulate-preyed eggs was weighted by the total prey available for each predator (multiplied by the density of eggs and small larvae for *C. maculata,* multiplied by the density of eggs and total larvae for *L. grandis*). This weighting assumes that the predators do not preferentially feed on one stage over another. This is the case for *L. grandis* (see manuscript 2), and is unknown for *C. maculata* . *C. maculata* densities were not significantly correlated with the weighted proportion of mandibulate-preyed eggs, either over both sites ($F_{(1,9)}$ = 0.23, p = .64) or in the Rhode Island and KBS sites independently. The relationship between *L. grandis* densities and the weighted proportion of mandibulate-preyed eggs were examined independently for the Rhode

Island and KBS site, as *L. grandis* densities were estimated with different methods. In both cases, there was a significant relationship between *L. grandis* densities and the weighted proportion of mandibulate-preyed eggs ($F_{(1,3)} = 21.13$, $p = 0.019$, and $F_{(1,4)} = 14.63$, $p = 0.019$, for Rhode Island and KBS respectively; Figure 11).

Harcourt (1971) found egg cannibalism by CPB adults to be the largest source of mortality of oviposited CPB eggs. In this study, no correlation was found between the incidence of CPB adults and total CPB egg survival. The significant correlation between the incidence of CPB adults and the proportion of mandibulate-preyed eggs in 1987 may indicate that adult cannibalism was a significant source of egg mortality during this year. This was a weakly defined relationship, however, and analysis of the data by week revealed no significant relationship. Harcourt identified cannibalized eggs by the remains of the egg mass on the leaf. As stated previously, it is difficult to distinguish signs of egg predation by the different mandibulate feeders. The remains of an egg mass preyed upon by *L. grandis* are identical to those which Harcourt describes for CPB adults. Harcourt does not mention predation by *L. grandis* in his life tables. Given the nocturnal habits of this predator (see manuscript 2), it may have been overlooked, and values reported for cannibalism by CPB adults may include *L. grandis* predation.

As *L. grandis* densities were not evaluated throughout most of this study, it is difficult to conclude on its impact on CPB egg survival. Analysis of 1987 data from the KBS and Rhode Island early plantings in which *L. grandis* densities were monitored, revealed this predator to be the only factor correlated with mandibulate-preyed eggs. It is possible that *L. grandis* was responsible for the unexplained sources of variation in egg and larval mortality over all study sites. That *C. maculata* densities were not correlated with densities of mandibulate eggs indicates that this predator was not a significant source of CPB egg mortality in 1987. However, as the feeding preference of this predator is unknown, this could reflect a preference of this predator for CPB larvae over eggs. That mandibulate predation of eggs was density independent, suggests that

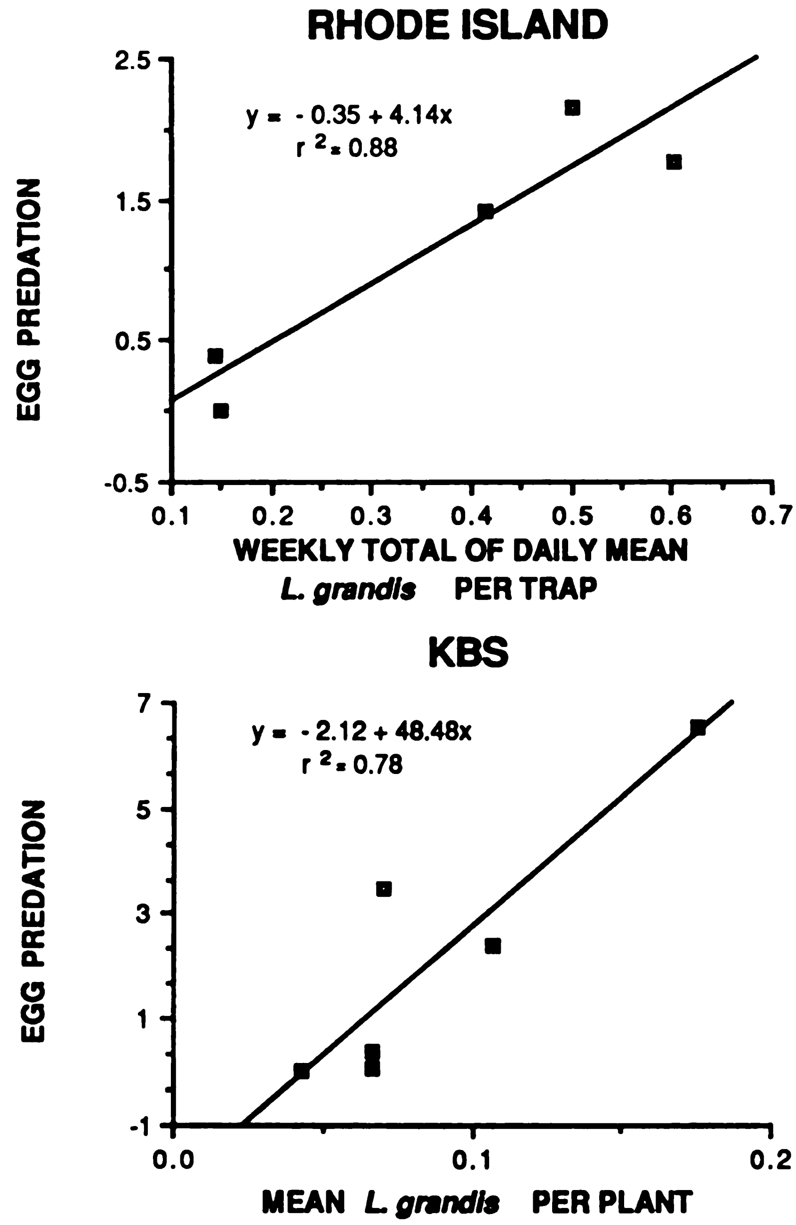

Figure 11. The relationship between weekly estimates of *Lebia grandis* densities and egg predation by mandibulate predators (weighted by the density of total available prey) in early planted potatoes at the KBS, Michigan and Rhode Island sites in 1987.

mandibulate feeders consume a constant proportion of the eggs, irrespective of egg density.

Survival of total prey. The relationship between the survival of total suitable prey and the incidence of the predators was examined for *C. maculata* and the pentatomid predators. The incidence of *C. maculata* was compared with CPB survival through the small larval stage ($S_E{}^*S_{SL}$). The incidence of pentatomid predators, which feed on all immature stages of the CPB, was compared with CPB survival through the large larval stage ($S_E{}^*S_{SL}{}^*S_{LL}$). Linear regression analyses for *C. maculata* and the pentatomid predators revealed no significant correlations between total prey survival and the incidence of these predators when tested over all sites and plantings. However, when Rhode Island and Michigan plantings were analyzed independently, a significant inverse relationship between the incidence of *C. maculata* and survival of its prey was identified in Rhode Island ($F_{(1,3)}$=41.56, p=0.008; Figure 12). *C. maculata* incidence accounted for 90% of the variability of CPB egg and small larval survival in Rhode Island. As reported in manuscript 3, this predator was well synchronized with both first and second CPB generations in Rhode Island, but only the first CPB generation in Michigan.

A measure of effectiveness of a predator is its ability to respond to changes in prey density. The responses of *C. maculata* and the pentatomid predators to changes in their prey densities were analyzed by regressing the incidence of each predator with the incidence of their total prey. *C. maculata* incidence increased significantly with increases in their prey ($F_{(1,9)}$ = 25.36, p = 0.0007; Figure 13). There was no significant correlation between the incidence of pentatomid predators and their prey ($F_{(1,9)}$ = 2.94, p =0.12; Figure 14a) when compared over all plantings. Due to the presence of *P. bioculatus* , which is not found in Rhode Island, pentatomids were more abundant in Michigan potatoes. When the incidence of pentatomid predators and their prey were compared in the Michigan plantings only there was a weakly defined, but significant correlation ($F_{(1,4)}$ = 47.36, p = 0.002, Figure 14b). For the 1986 and

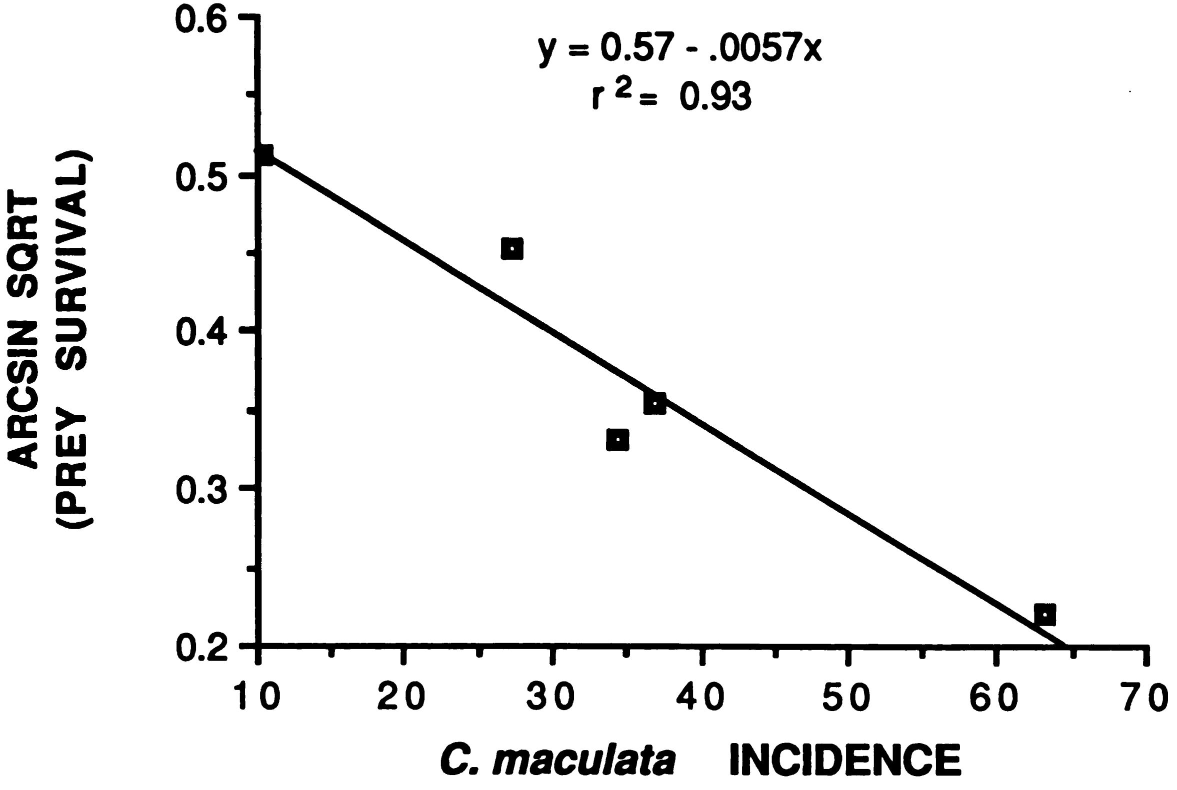

Figure 12. The relationship between Coelomegilla maculata incidence (mean per plant x dd) and survival of CPB eggs and small larvae in potato research plantings in Rhode Island, 1985-1987.

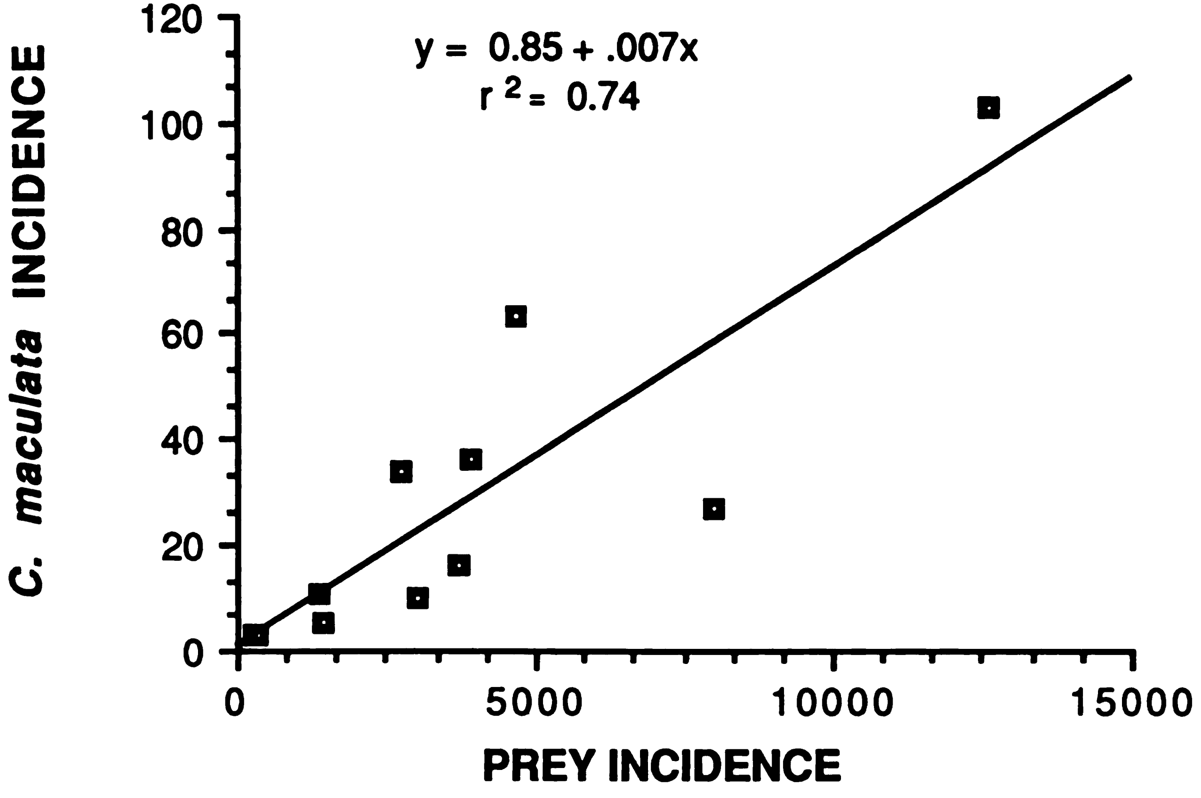

Figure 13. The relationship between the incidence (mean per plant x dd) of Coelomegilla maculata and its CPB prey (eggs and small larvae) in potato plantings in Rhode Island and Michigan, 1985-1987.

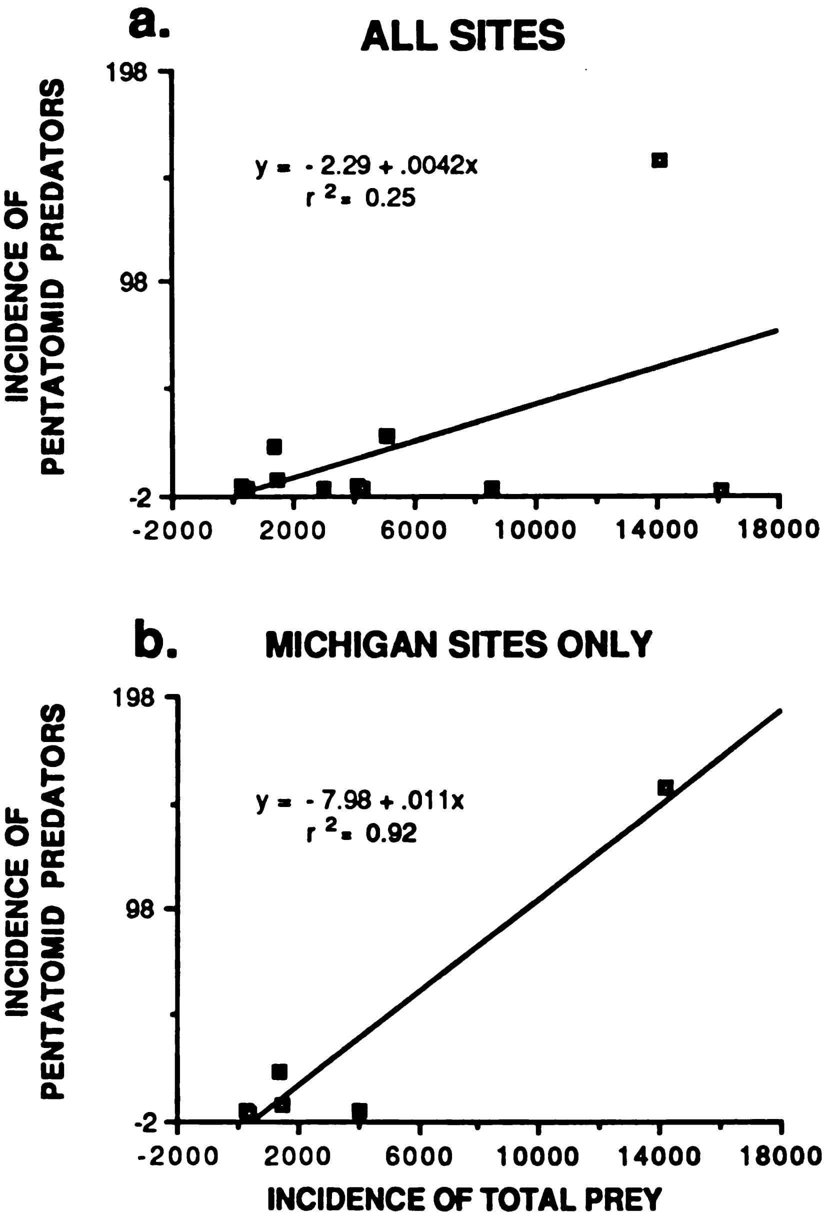

Figure 14. The relationship between the incidence (mean per plant x dd) of pentatomid predators and total CPB prey (eggs, small and large larvae) in a.) all potato plantings, 1985-1987, and b.) in Michigan potato plantings, 1985-1987.

1987 early potato plantings at KBS, *P. bioculatus* appear to have tracked their prey densities at about the same proportion of predator to prey (Figure 15a and b). The sporadic nature of *P. bioculatus* populations has been noted by several early observers and has been attributed to variation in overwintering survival by Knight (1922) who suggests that not more than 5 percent of the overwintering population usually survives in New York and Minnesota. Jermy (1980) also attributed the failure to establish this predator in Europe to mortality experienced by the overwintering population due to cool spring temperature. Thus, it seems evident that this predator responds to CPB prey densities within a season, but between season the ability of the predator to respond is limited by abiotic factors determining its density.

This study has demonstrated the importance of two previously unstudied CPB predators in the within-generation survival of the CPB. The carabid, *L. grandis* appears to be responsible for variation in mandibulate-preyed eggs, and densities of the coccinellid, *C. maculata* were positively correlated with mortality of CPB eggs and small larvae in Rhode Island. The analysis of key-factors in CPB survival has lead to insights into the dynamics of these and other CPB natural enemies. However, the fact that the pentatomids and *M. doryphorae* do not appear to regulate CPB populations should not be interpreted that they are insignificant to CPB survival. In 1987 at the KBS site, *P. bioculatus* adults were consuming > 110 CPB eggs per day, and reached densities of .34 predators per plant in late June. Tamaki and Butt (1978) determined that extremely high populations of this predator were necessary to reduce small populations of CPB below economic thresholds. However, the combined impact of predators was not assessed. At the same time that *P. bioculatus* densities peaked, *L. grandis* and *C. maculata* adults were consuming up to 100 and 22 eggs per predator per day, respectively, with densities of .18 *L. grandis* , and .21 *C. maculata* per plant. The CPB population in this planting had a seasonal recruitment of 230 eggs per plant and experienced 96% mortality before the prepupae left the plants to pupate. The combined

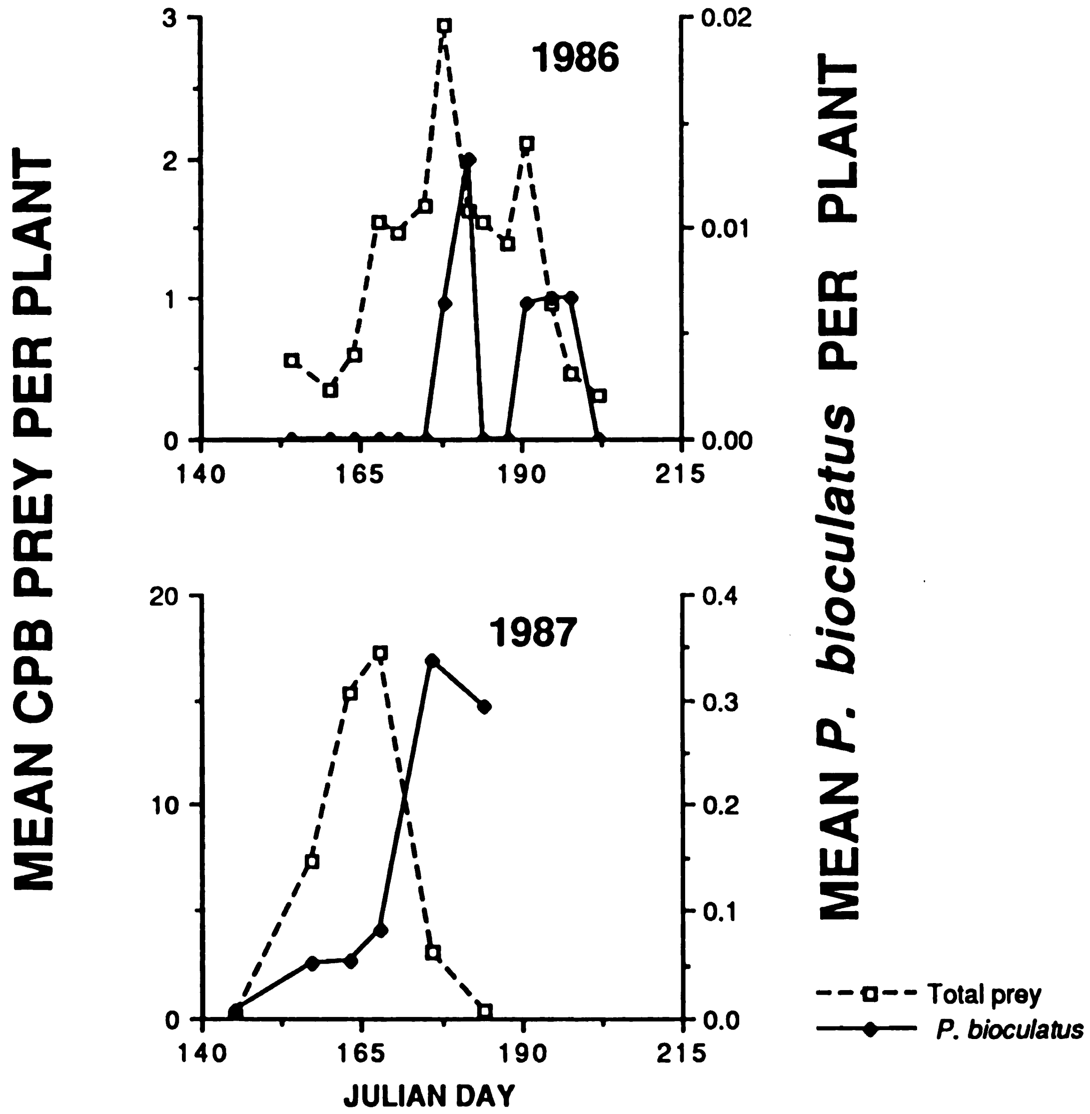

Figure 15. Perillus bioculatus and their CPB prey (egg masses + total larvae) densities in early planted potatoes at the KBS site in Michigan, 1986 and 1987.

impact of these natural enemies limited the CPB population and plant defoliation below economic thresholds. It can be speculated that the consecutively mild winters of 1986 and 1987 and the unusually warm spring temperatures in 1987 reduced the overwintering mortality of CPB predators and enhanced the early season build-up of predator populations. However, this situation does demonstrate that natural enemies can control CPB populations. Further studies on factors responsible for regulating natural enemy populations may identify potential options for manipulating and enhancing predator densities.

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MANUSCRIPT 2.

Biology and Seasonal Dynamics of *Lebia grandis* Hentz (Coleoptera: Carabidae), Predator and Parasitoid of the Colorado Potato Beetle, (Coleoptera: Chrysomelidae)

ABSTRACT - The biology and seasonal dynamics of the carabid beetle *Lebia grandis* Hentz were investigated in Rhode Island and Michigan, and its potential impact on Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say) populations was evaluated. *L. grandis* fed on all immature stages of the CPB, and was found to feed over a wide range of temperatures. This predator appeared to be quite specific to the CPB, only feeding on aphids when CPB prey were absent. *L. grandis* consumed more CPB per day than the five other endemic natural enemies studied to date. Field cage studies demonstrated the potential for *L. grandis* adults to reduce CPB populations and showed a strong density dependent response by this predator. *L. grandis* was found to be primarily nocturnal, with peak activity between 9 pm and 2 am. A burlap trap was designed which increased detection of this predator during daylight hours. Seasonal activity patterns were determined in the field, and in combination with laboratory development studies, indicated that this species completes one generation per year in R.I. and Mich.

L. grandis larvae are ectoparasitoids of CPB prepupae and a sampling technique of tethering hosts was developed which revealed the pupation site of the host without dislodging the parasitoids. In 1986 13.5% (n = 200) of tethered hosts released at the Mich. research site were parasitized. In 1987 weekly parasitism levels were determined at this site, and parasitism reached >50%. In R.I. in 1987, parasitism of tethered CPB was barely detectable, although production of summer adult *L. grandis* was evident from trap catches.

INTRODUCTION

The foliar searching carabid, *Lebia grandis* Hentz, was first reported as a predator of the Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say) by Riley (1871). In 1936 French entomologists collected *L. grandis* along with other CPB natural enemies in New York to study their potential for controlling the CPB in Europe (Bruneteau 1937). Chamboussou (1938, 1939) described the biology of *L. grandis* and succeeded in mass rearing the predator on the CPB. The life cycle of the genus *Lebia* is unusual. The adults are predaceous on eggs and larvae of chrysomelids, and the larvae are solitary ectoparasitoids killing pupae of the same hosts (Madge 1967).

No reports of field releases of *L. grandis* have been published, although Chamboussou (1938, 1939) suggested that it had tremendous potential for biological control of the CPB. We have found *L. grandis* to be one of the more common egg predators in potato research fields in R.I.. Madge (1967) reported it widely distributed throughout the Eastern half of the U.S. north of Mexico. No research concerning *L. grandis* has been published since Chamboussou (1939), making this species the least studied of the common CPB endemic natural enemies. In this study we investigated the life history and seasonal dynamics of *L. grandis* in potatoes in R.I. and Mich. as part of a larger study evaluating natural mortality of the CPB in the northeast and northcentral states.

MATERIALS AND METHODS

Research was conducted at the University of Rhode Island and Michigan State University. Field studies in R.I. were conducted in 0.1 ha potato plots at the University of Rhode Island Research Farm, Kingston, R.I. In Mich., field studies were conducted in 0.1 ha potato plots at the Michigan State University Kellogg Biological Station (KBS) in Hickory Corners, Mich. The incidence of *L. grandis* was also monitored at the MSU Potato Research Farm in Stanton, Mich.

Consumption rates and prey specificity. In August 1985 and 1986, *L. grandis* adults were collected in potato plots in R.I. and Mich. to determine their daily consumption of immature CPB. Predators were sexed and held individually in petri dishes with moist paper toweling and prey in excess of their daily consumption. Predators were given CPB eggs, first, second, third, or fourth instars, and held for 7 days in growth chambers set at 25°C and 16:8 (L:D) photoperiod. Five adult *L. grandis* were tested per prey type. Consumption was determined and new prey were added at 24 h intervals. To determine how temperature influenced *L. grandis* feeding, CPB egg consumption was monitored in growth chambers at constant temperatures of 15, 20, 25, and 30°C (±1°C) for five days (10 predators were tested at each temperature). Predators were handled as described above and consumption checked daily. Analysis of variance (SAS Institute 1985) was conducted to determine if predation varied significantly with temperature. An analysis of covariance (SAS Institute 1985) with temperature as the covariate was conducted to determine if daily consumption rates varied significantly over the duration of the study. The class variable was day.

A choice test was performed, to determine if *L. grandis* adults preferentially feed on CPB eggs or larvae. Five predators were held individually in petri dishes with moist paper toweling and fed 10-50 CPB eggs plus 5-10 first and 5-10 second instars every day. Consumption was recorded and new prey were added every 24 h for a period of five days. The difference between the starting and finishing proportions of each prey type was calculated, and it was assumed to be significant if the 95% confidence intervals about the difference did not overlap with zero.

To determine *L. grandis* prey specificity, adults were provided with three alternate prey commonly found in the Mich. study area. The prey tested included the eggs and larvae of both the coccinellid, *Epilachna varivestis* Mulsant, collected from bush beans and the chrysomelid, *Lema trilineata* (Oliv.), collected from wild solanaceous plants. We also tested the potato aphid, *Macrosiphum euphorbiae* (Thomas), collected from greenhouse grown potatoes. Adult predators were held individually in petri dishes with moist paper toweling and one type of prey for 2 or 3 days. In the *E. varivestis* test, eight predators were set up with either 30 to 55 eggs or four small larvae per dish. In the *L. trilineata* test, 13 predators were set up with 10 to 35 eggs or 6 to 34 small larvae. After three days the *L. trilineata* were replaced with three third instar CPB. For the aphid test, each of five predators was provided with 25 aphids per day, and five control dishes were set up without predators to monitor the survival or reproduction of the 25 aphids placed in each dish. On the fourth day, the aphids were replaced with a combination of 25 aphids and seven CPB second and third instars. All tests were examined daily and missing prey were replaced at initial densities.`

Cage studies. To determine the impact of *L. grandis* adults on CPB mortality, field cage studies were conducted in R.I. in August, 1986. Six screen walk-in cages (3.6 x 1.8 x 1.8 m) were erected in a newly tilled field. Into each cage two rows of 10 greenhouse grown potato plants were transplanted. Potato stems infested with CPB egg masses were collected from nearby plots, and placed in 6-inch pyrex test tubes with water. The tops of the tubes were sealed with parafilm, and the bouquets were set within the cages. Test tubes were sunk into the soil and the CPB-infested stems stood within the stems of the transplanted plants where they were secured with wire to existing stems. CPB egg densities in the cages were set at 500 eggs per cage in 3 cages, and 250 eggs per cage in 3 cages. At each of these prey densities, *L. grandis* adults were introduced at densities of 0, 10 and 15 predators per cage. All CPB eggs and larvae within each cage were counted every 3 to 4 days over a three week period. The data were pooled for all predator cages to examine the relationship between prey density and consumption rates. Consumption per predator per day over the interval was regressed on available prey at the beginning of each sampling interval.

Temperature-dependent development. *L. grandis* eggs adhere to soil particles and adult females proved reluctant to oviposit on other substrates. Thus to determine egg development rates, mating pairs of *L. grandis* adults were held in 10 cm petri dishes with moist sand and vermiculite in growth chambers held at constant temperatures of 20, 20.5, 23, 25, 26, and 30°C (± 1°C) with a photoperiod of 16:8 (L:D). The adults were removed daily and transferred to identical dishes. After the adults were removed, the dishes were incubated at the same temperatures and monitored daily for newly-hatched *L. grandis* larvae.

The development rate for the parasitic and pupal stage of *L. grandis* was determined using CPB prepupae harvested from laboratory cultures or collected from field plots as they began to burrow into the soil. The prepupae were introduced individually into 2 oz. plastic Solo ® cups with moist sand and vermiculite and allowed to burrow. Within 30 min. of introducing the prepupa, one *L. grandis* first instar was added to each cup. The cups were sealed to retain moisture and placed in growth chambers at constant temperatures of 17, 20, 23, 26, and 29°C (± 1°C). The dishes were checked regularly for emergence of CPB or *L. grandis* adults. The minimum standard error method (Casagrande 1971) was used to determine the best predictive thresholds for egg and larval and pupal development. Percent development per day was regressed on temperature to determine the appropriateness of a linear model over the range of temperatures tested.

Thirty-five CPB prepupae were parasitized by *L. grandis* first instars and held at variable ambient temperatures in a field laboratory at KBS. Emergence of adult CPB and *L. grandis* was monitored daily. Temperatures were recorded continuously throughout the development period and the degree-day accumulation at emergence was compared with that predicted from the model developed from the constant temperature studies.

Daily activity patterns of *L. grandis* adults. Chamboussou (1939) reported *L. grandis* to be primarily nocturnal. In order to optimize sampling periods, the daily activity patterns of adult *L. grandis* were determined in potato plots at the KBS research site in 1986. On three separate occasions in June and July, 100 CPB infested plants were sampled visually every 30 min. over a 24 h period. During the night, flashlights were used to illuminate plants. Care was taken to avoid illuminating plants except for the moments during which a plant was sampled. In 1987, the 24 h study was repeated at the KBS site on June 22. One hundred and fifty plants were randomly sampled once every two hours between 9 pm and 3 am, and once every three hours between 3 am and 9 pm. In 1987, similar observations were made in potato plots in R.I. On July 1, 150 randomly selected plants were sampled at 1 am, 6 am, 10 am, 3 pm, 7 pm, and 10 pm. On this date, after a plant was sampled visually, soil in ca. a 15 cm radius surrounding the plant was examined to a depth of ca. 4 cm to uncover any *L. grandis* in the soil.

Seasonal variation in prey consumption and oviposition. In 1987, 3 to 40 (ave. 11) *L. grandis* adults were collected weekly from potato plots in R.I. and Mich. to determine seasonal variation in prey consumption and oviposition. Predators were sexed and held in petri dishes with moist sand and vermiculite and 1-3 CPB egg masses (ca. 80-100 eggs). After 24 h predators were removed and released, and the number of eggs consumed was recorded. Dishes which had contained female predators were then incubated at 23 to 25°C until *L. grandis* eggs hatched and first instar *L. grandis* were counted, allowing calculation of the proportion of females ovipositing on the day of capture. A two-way analysis of variance was performed to determine if consumption rates varied by sex and month. Data were pooled by month for June, July, and August with n = 36, 13, and 65 for males, and n = 28 , 20, and 66 for females. Ninety-five % C.I. about the means were compared to detect significant differences between treatment combinations.

Seasonal incidence. In 1985, 1986, and 1987, densities of *L. grandis* adults and CPB eggs and larvae were monitored in potato plots in R.I. and Mich. Plots in R.I. included both an early and isolated late planting of potatoes in all three years. plots in Michigan included early and late plantings at the MSU potato research farm in Montcalm

Co., Mich. (a commercial potato growing region) in 1986 and 1987, and a late planting in 1985. Also, both early and late planted potato plots were monitored at the KBS site in Mich. At this site, plots included a late planting in 1985, and an early and an adjacent late planting in 1986 and 1987. Early plots were planted in late April and early May at all sites, and late plots were planted in late June in Mich., and early July in R.I. The fast maturing variety, Caribe', was used in all plots in this study, and with the exception of the Montcalm Co. site, no pesticides were applied to any plots. In Montcalm, herbicides and fungicides were used, as well as an insecticide (Imidan) for CPB in the early planting in 1987.

Visual counts of *L. grandis* adults and CPB life stages on plants were conducted two to three times per week in 1985 and 1986, and once per week in 1987. One hundred to 150 whole plants were sampled per sample date.

In 1986, it was observed that *L. grandis* adults aggregated during the day in rolls of burlap laid on the top of 1 m^3 field cages in potato plots. In 1987 a trap was designed using a 20 by 45 cm strip of burlap loosely wrapped and tied around a 40 cm wooden stake. Traps were set within the foliage of 12 to 50 potato plants in plots in R.I. and Mich. in 1987 (Figure 1).

In 1987, night observations were also made in potato plots at the KBS site in Mich.. to determine the seasonal incidence of *L. grandis* . Once per week, 100 potato plants were sampled with flashlights between midnight and 1 am, and *L. grandis* adults on the plants or on the surrounding soil (within a 15 cm radius around the plant) were counted. Adults were collected and held to determine whether they oviposited (as previously described).

***L. grandis* first instar longevity.** To determine the potential searching time for parasitic *L. grandis* larvae, their longevity was determined in the absence of hosts. Groups of ten newly hatched first instar *L. grandis* were placed in petri dishes with moist soil and held at 25°C in growth chambers. Surviving *L. grandis* larvae were

Figure 1. Burlap trap used for sampling *Lebia grandis.*

counted daily. Survival was compared in two soil types: a 50:50 sterilized sand and fine vermiculite mix (10 replicates) and a nonsterilized sandy loam from the Montcalm potato research field (6 replicates). Linear regression (SAS Institute 1985) was used to compare differences in mortality between soil types. The arc sine of cumulative mortality was regressed on days raised to the 2^{nd} power.

***L. grandis* parasitism.** Sifting soil for *L. grandis* parasitized CPB prepupae proved ineffective since it dislodged the ectoparasitoids from their host, making recovery difficult. In 1986, CPB prepupae were successfully tethered with standard polyester sewing thread. A noose made on a 20 cm long thread was slipped around a CPB prepupa behind the prothoracic shield and legs. Tethered prepupae were attached to a marker and released in potato plots where they burrowed into the soil and pupated (Figure 2a,b). Five to seven days following release, the thread was carefully uncovered revealing the pupation site of the CPB and if parasitized, the *L. grandis* larva lying adjacent to its host (Figure 2c).

In 1986, a total of 281 field collected CPB prepupae were tethered and released at the KBS site, July 5 - August 21. On July 15, the mortality of tethered prepupae was compared with that of nontethered prepupae. Forty nontethered prepupae were released into the research field and covered with a 6 oz. paper cup to restrict their area for burrowing. At the same time, 40 tethered CPB prepupae were released. Four hours later, the prepupae were checked to assure successful burrowing, and the paper cups were removed and the burrowing site of the nontethered prepupae was marked. The CPB prepupae were recovered eight days later and the depth of pupation was measured.

In 1987, at the KBS site 60 to 100 prepupae were collected, tethered, and released per week from mid June to late August. In 1987 in R.I., 108 tethered prepupae were released in the early planting on June 30, and 100 were released in the late planting on July 19. Both releases coincided with peak CPB pupation at the sites. In addition, two releases of tethered prepupae were made in a small plot of nonrotated

Figure 2a. Tethered CPB prepupa, b. Tethered prepupa burrowing into the soil, and c. Parasitized CPB prepupa with adjacent *Lebia grandis* larva.


a


b


c

potatoes in R.I. during peak pupation of first generation CPB. Twenty tethered prepupae were released on June 30, and 80 were released on July 7.

All released prepupae were recovered 5 to 7 days after release, and *L. grandis* parasitism and pupal mortality was recorded. Those unrecovered tethered CPB, and those parasitized as larvae by tachinids were deleted from the total when calculating percent mortality and *L. grandis* parasitism. The density of CPB prepupae in the soil was not sampled directly in the potato plots, thus fourth instar larval densities were used to examine the synchrony of *L. grandis* parasitism with CPB prepupal densities. The CPB fourth instar incidence curves were advanced 76 DD representing the development time for CPB fourth instars.

RESULTS

Consumption rates and prey specificity. *L. grandis* adults fed on all immature stages of the CPB (Table 1). Daily consumption of CPB eggs followed a significant quadratic trend between 15° and 30°C ($F_{1,197} = 114.39$, $P = 0.0001$), with consumption rates doubling between 15° to 20°C. Egg consumption per individual over all temperatures was significantly less on day 1 of the study, apparently due to the disturbance of collecting and setting up the experiment. Egg consumption during the remaining 4 days of the experiment did not change significantly. *L. grandis* did not demonstrate any preference for prey type when fed a combination of CPB eggs and first and second instar larvae. There was no significant difference in the initial and finishing proportions of each prey type (mean ± S.E. difference for eggs, first and second instars was -0.03 ± 0.03, -0.02 ± 0.02, and 0.05 ± 0.03, respectively).

Only two of the eight predators fed *E. varivestis* eggs and small larvae over two days consumed any prey (mean ± SE eggs consumed = 0.38 ± 0.26; mean larvae consumed = 0.0). Only four of the 13 individuals provided with *L. trilineata* eggs and first instars consumed any prey (mean ± SE, eggs consumed = 0.04 ± 0.04; mean ± SE

Table 1. *Lebia grandis* consumption of immature stages of the CPB.

CPB stage	N	Temperature	Consumed per day (mean ± S.E)
Eggs	10	25	47.38 ± 2.07[1]
1st instars	5	25	17.76 ± 1.14
2nd instars	5	25	6.75 ± 0.59
3rd instars	5	25	2.52 ± 0.27
4th instars	5	25	1.32 ± 0.13
Eggs	10	15	20.90 ± 1.45
Eggs	10	20	44.00 ± 1.50
Eggs	10	25	47.38 ± 2.07[1]
Eggs	10	30	41.92 ± 2.35

[1] Data from the same experiment.

larvae consumed = 2.11 ± 1.24). All 13 predators consumed prey when fed three CPB third instars on the fourth day (mean ± SE = 2.31 ± 0.71).

In the aphid consumption test, dishes with predators had fewer aphids than the controls on day two when *L. grandis* consumed 7.6 ± 1.50 aphids and on day three when they consumed 12.2 ± 4.12 (mean ± SE) aphids. *L. grandis* did not consume aphids on the first day they were given this prey, or on the fourth day when they were given aphids in combination with CPB larvae. With the combination of prey types, they did consume 5.6 ± 0.68 (mean ± SE) CPB larvae.

Cages studies. Field cage studies demonstrated the ability of *L. grandis* to control low to moderate CPB populations (0.4 to 0.75 egg masses per plant) with predator densities of 0.5 to 0.75 per plant (Figure 3). In three of the four predator cages, *L. grandis* consumed all available prey within 10 days (prior to the prey cohorts completing the third stadium). CPB survival in the control cages averaged 38% through the larval stages. In this study, the consumption rate per predator per day increased with the number of available prey (Figure 4), demonstrating a strong positive density dependent response.

Temperature-dependent development. The best predictive threshold for *L. grandis* egg development was 10.5°C (Figure 5a). Eggs required 129 DD, base 10.5°C, to complete development, or 8.82 ± 0.56 days at 25°C. Egg development was highly correlated with temperature over the range of temperatures tested (Figure 5b).

The best predictive threshold for *L. grandis* larval and pupal development was 11.25°C (Figure 6a). The parasitoids required 368 DD base 11.25°C to complete development or 24.89 ± 1.35 days at 26°C. Again, parasitoid development was highly correlated with temperature over the range tested (Figure 6b).

L. grandis parasitoids developing at variable ambient temperatures in the field laboratory required 384 ± 5.2 DD base 11.25°C to complete development, or 28 ± 0.2

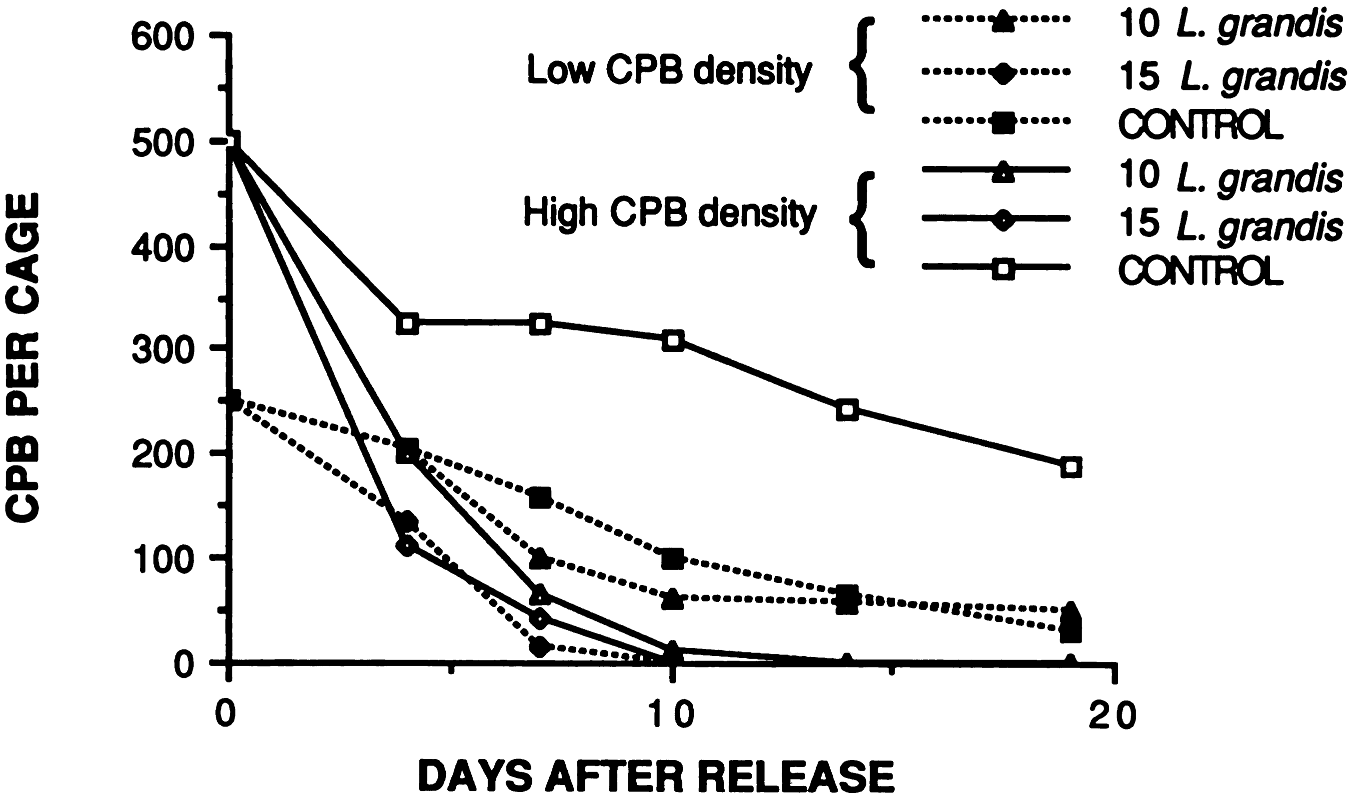

Figure 3. CPB survival in field cages with Lebia grandis released on August 15.

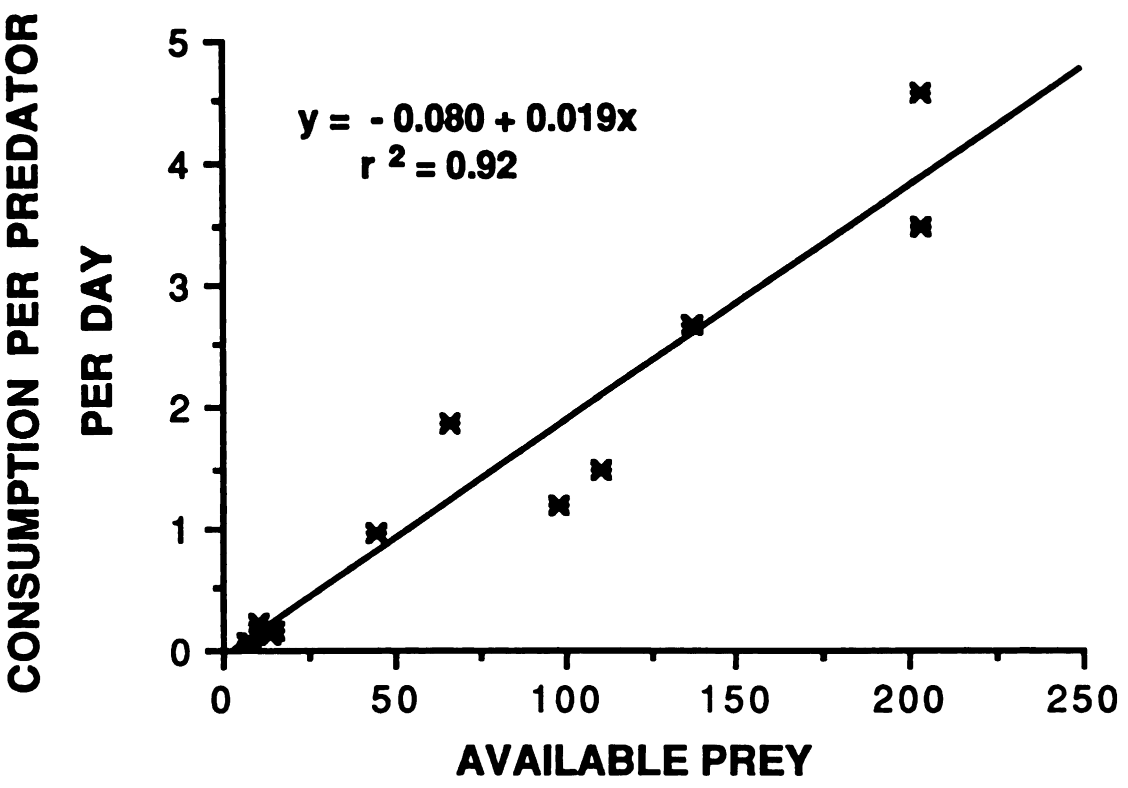

Figure 4. Lebia grandis consumption of CPB cohorts as a function of prey density.

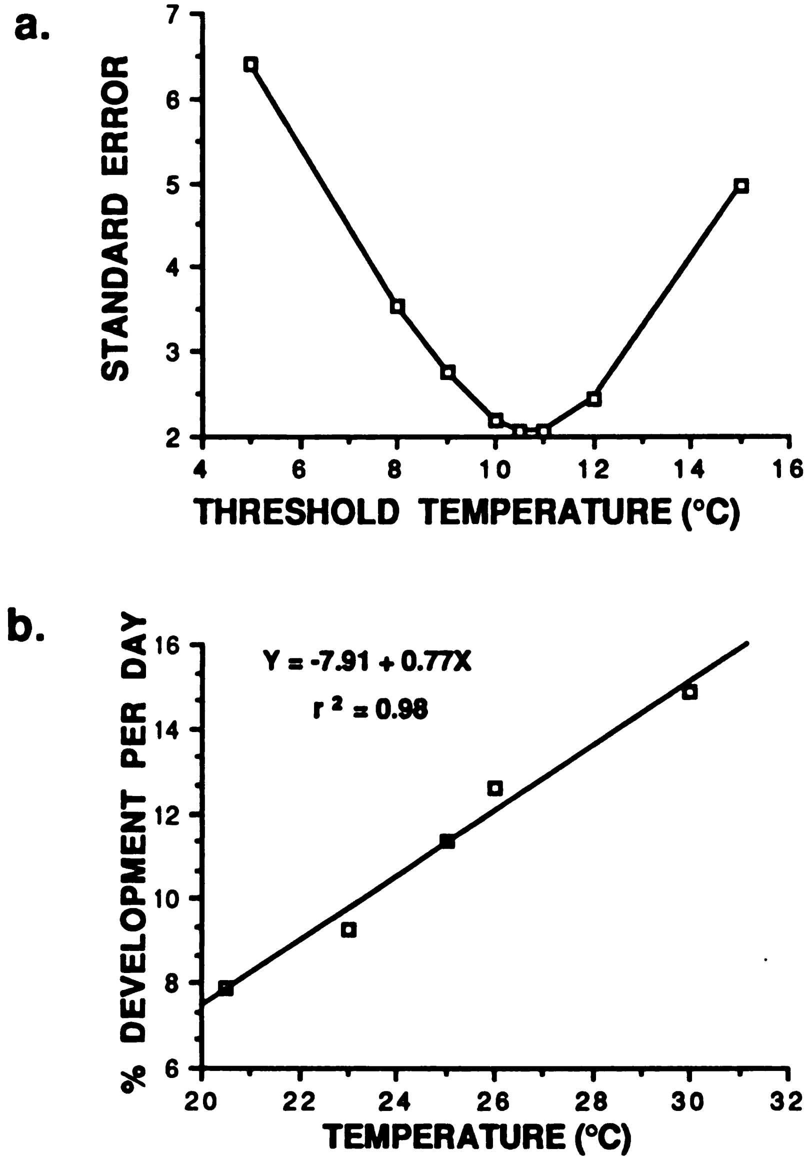

Figure 5. a.) Results of substituting different thresholds for Lebia grandis egg development data, and b.) Lebia grandis egg development as a function of temperature.

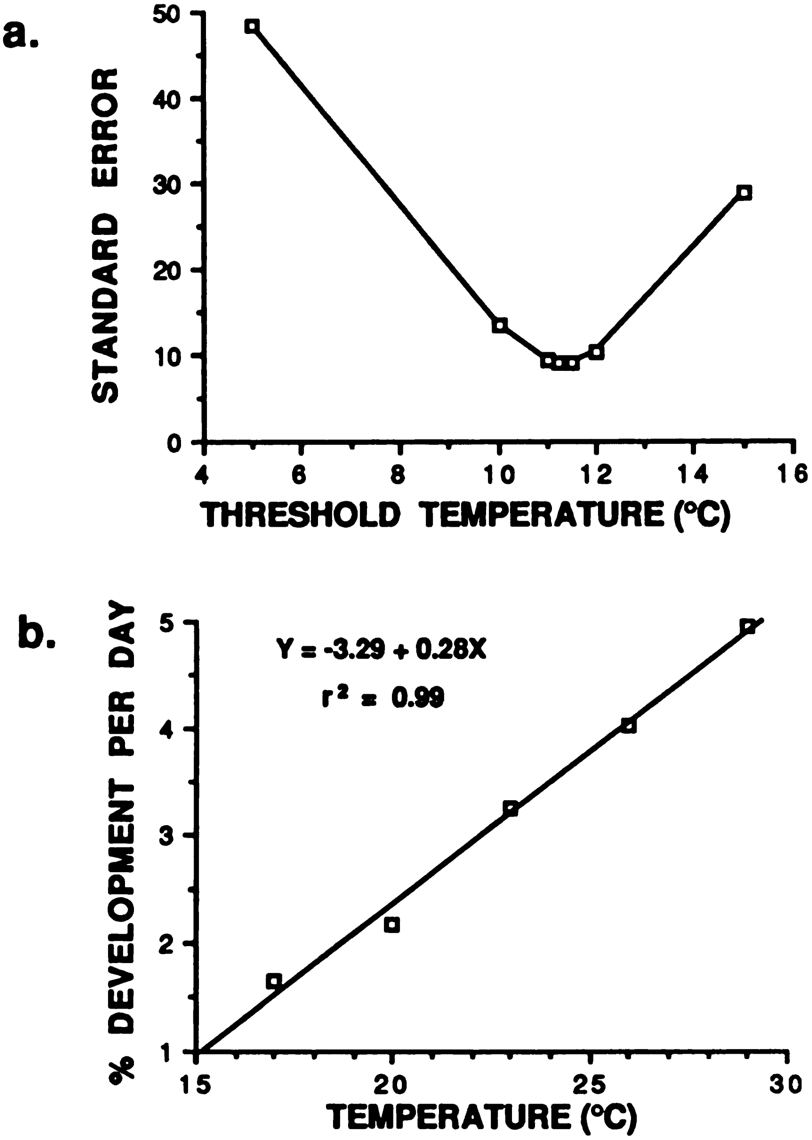

Figure 6. a.) Results of substituting different thresholds for Lebia grandis larval and pupal development data, and b.) Lebia grandis larval and pupal development as a function of temperature.

days. The mean observed emergence occurred within one day of the predicted 27 days or 368 DD base 11.25°C.

Daily activity patterns of *L. grandis* adults. In 1986 a total of 18 *L. grandis* adults were observed between 6 pm and 10 am on the three sample dates, and 12 of these individuals (67%) were observed between 11:30 pm and 2 am. In 1987 110 *L. grandis* adults were observed over the 24 h study period. Peak adult activity (mean=0.10 per plant) occurred between 9 pm and 2 am, with 37 percent of all sightings occurring within this period. At this higher density, adults were observed during each sampling interval with the lowest densities (mean= 0.04 per plant) at 3 pm.

In R.I. in 1987, seven *L. grandis* adults were observed on the plant foliage during the 24 h study period. Five of these seven were observed at 10 pm. An additional 35 *L. grandis* were found on or in the soil at the base of the plants. At 10 pm 63 percent of the observed *L. grandis* were on the foliage, however at all other sample times, 0-20 percent were on the foliage.

Seasonal variation in prey consumption and oviposition. Analysis of variance of prey consumption revealed a significant difference in consumption by month ($F_{1,224} = 28.49$, $P = 0.0001$) and sex ($F_{1,224} = 11.60$, $P = 0.001$), and a significant interaction between these variables ($F_{1,224} = 7.80$, $P = 0.006$). Prey consumption by females did not change significantly through time, averaging 43.68 ± 1.25 (mean ± SE) eggs per day. Males consumed significantly fewer eggs per day (mean ± SE = 23.97 ± 2.20) than females in June. However, their consumption increased throughout the summer (Figure 7), and by August was not significantly different from females.

Two female *L. grandis* were collected on May 31 (328 DD base 10°C from April 1) in Mich., and one oviposited within one day after collection. Oviposition peaked in mid June, with 88% of the 15 females collected between June 12 and 19 ovipositing. A second peak in oviposition was observed between July 14 and 22 with 4 of the 5

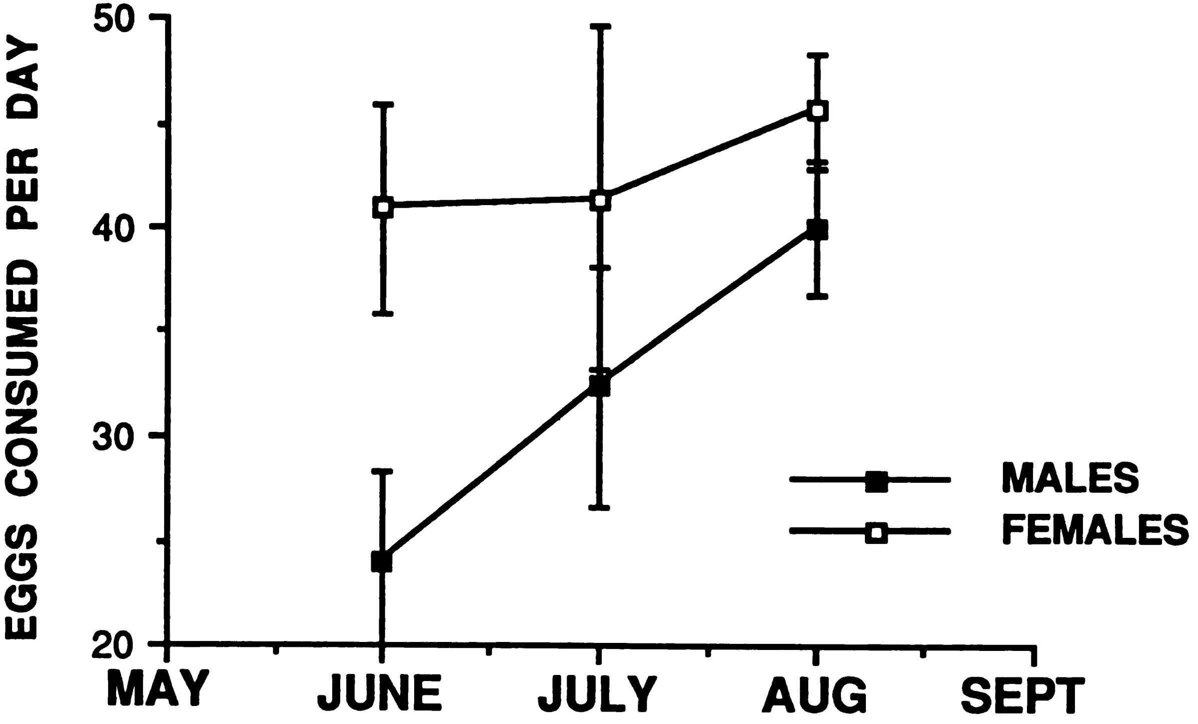

Figure 7. Seasonal variation in Lebia grandis consumption of CPB eggs.

individuals collected ovipositing. Of the 11 females collected in July 27, only three (27%) were ovipositing, and no ovipositing females were collected after this date.

In R.I. the first female *L. grandis* were collected on June 2, but oviposition was not observed until June 16 (327 DD base 10°C from April 1). Oviposition in R.I. peaked between July 1 and July 16, with 73% of the 15 females collected over this time period ovipositing. None of the 83 females collected between July 17 and August 19 oviposited. There was no difference in fecundity between R.I. and Mich. *L. grandis* . Females laid 15.47 ± 1.85 (mean ± SE) eggs per day.

Seasonal incidence. *L. grandis* was observed at all sites sampled in all years (Table 2 and 3). The adult predators were observed more frequently in early potato plantings than in the late plantings, although they were sighted as late as September. There was generally no correlation between the seasonal density of CPB eggs and the *L. grandis* densities in the sampled plots.

The 1987 trap catches from the MI-KBS site are plotted with the *L. grandis* densities observed during both the midnight and daytime predator counts at this site in Figure 8. The burlap trap catches gave a fairly good representation of the changes in predator densities observed at night. Daytime counts of this predator were generally considerably less than night counts, and did not indicate the seasonal change in density that the other sample methods showed.

The midnight observations of *L. grandis* and the densities of the immature stages of the CPB are plotted in Figure 9 a,b. The first predators were observed on May 29, coinciding with the initiation of CPB oviposition. *L. grandis* densities peaked in mid June, coinciding with the peak in CPB larval densities. Based upon soil temperatures and the first observance of *L. grandis* oviposition, the predicted first emergence of new adults of *L. grandis* at the KBS site was on July 19, and the predicted peak emergence was on July 30. No adult *L. grandis* were trapped or sampled at this site after August 10.

Table 2. CPB egg and *Lebia grandis* densities in early potato plantings in Rhode Island and Michigan, 1985-1987.

			Mean *Lebia grandis* per 10 plants per week									
		Seasonal CPB	May	June				July				
Site	Year	Egg Density	1	2	3	4	5	6	7	8	9	10
RI	1985	427.81	0.00	0.11	0.05	0.52	1.20	0.65	0.20	0.02	---	---
	1986	362.83	0.00	0.00	0.07	0.14	0.05	0.15	0.10	0.05	0.15	0.00
	1987	438.96	0.00	0.00	0.00	0.00	0.15	0.20	0.20	---	---	---
MI-KBS	1986	68.72	0.00	0.00	0.00	0.05	0.03	0.03	0.00	0.03	0.00	0.00
	1987	229.73	0.00	0.00	0.20	0.16	0.00	0.00	0.10	0.44	0.00	0.55
MI-M C	1986	213.50	0.00	0.06	0.00	0.06	0.13	0.00	0.00	0.00	---	---
	1987	435.84	0.00	0.00	0.00	0.20	---	---	---	---	---	---

Table 3. CPB egg and *Lebia grandis* densities in late potato plantings in Rhode Island and Michigan, 1985-1987.

			Mean *Lebia grandis* per 10 plants per week								
			July				August				Sept
Site	Year	Seasonal CPB Egg Density	7	8	9	10	11	12	13	14	15
RI	1985	50.69	---	---	0.00	0.00	0.00	0.00	0.15	0.05	0.05
	1986	104.50	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	1987	34.19	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MI-KBS	1985	5.73	---	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
	1986	20.27	---	---	0.00	0.00	0.00	0.00	0.00	0.00	0.07
	1987	25.11	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MI-M C	1985	---	0.00	0.06	0.00	0.00	0.00	0.00	0.22	0.00	0.00
	1986	---	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	1987	386.69	0.00	0.00	0.20	0.00	---	---	---	---	---

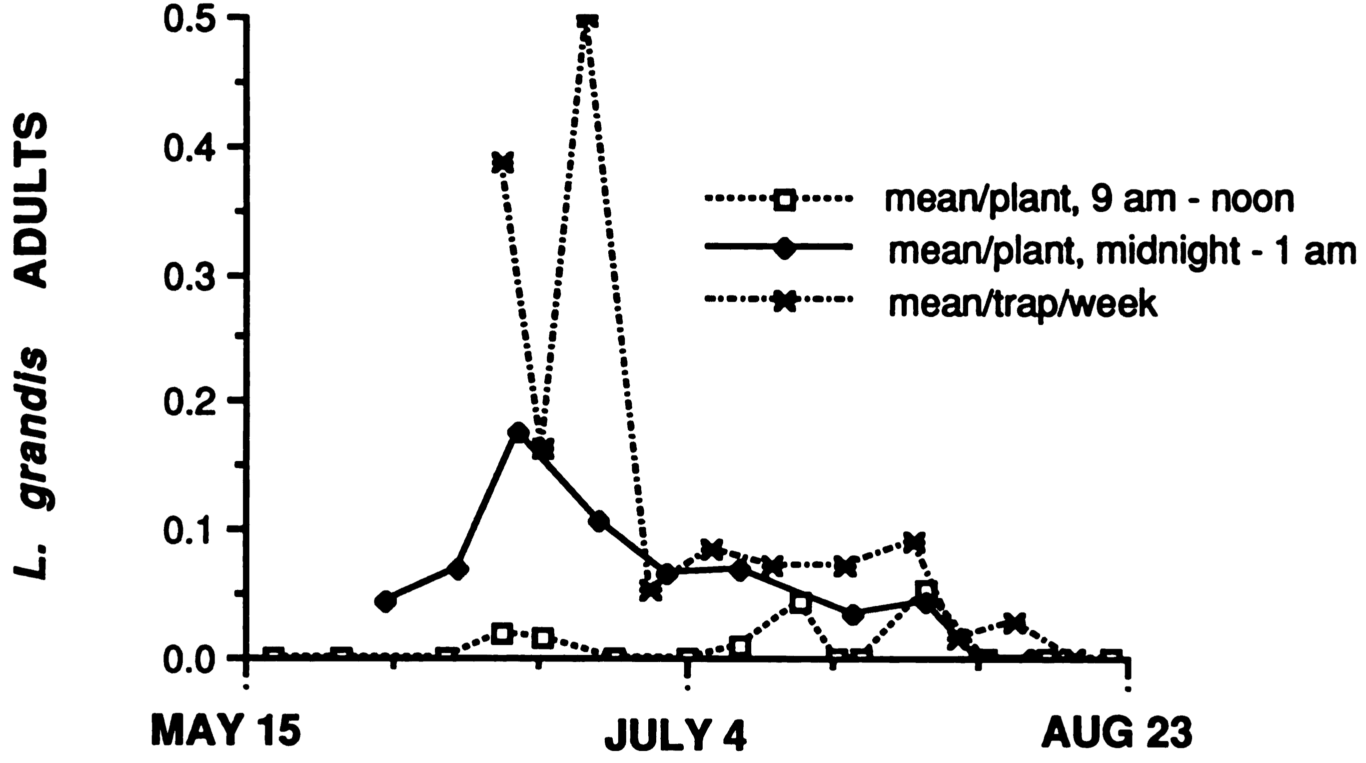

Figure 8. Comparison of sampling methods for Lebia grandis adults.

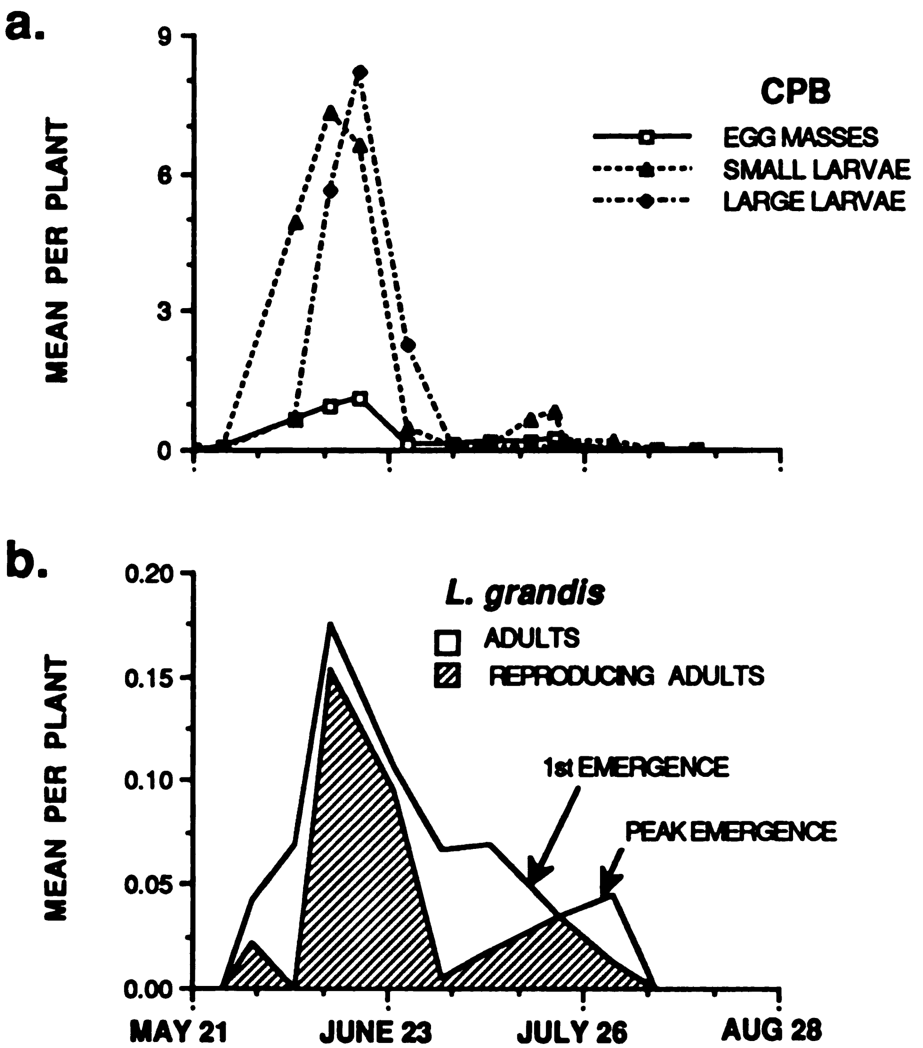

Figure 9. a.) Densities of CPB stages in Michigan potato plots in 1987, and b.) densities of *Lebia grandis* adults in Michigan potato plots in 1987 (from midnight observations).

The 1987 burlap trap catches of predators and densities of the immature stages of the CPB at the R.I. site are plotted in Figure 10 a,b. In R.I., the first predator was trapped on June 1, coinciding with the first occurrence of CPB eggs. Trap catches peaked in late June, coinciding with the peak in CPB larval densities. A large second peak in *L. grandis* trap catches was observed in early July, but none of these later individuals oviposited. No adult *L. grandis* were trapped after August 18 at this site.

***L. grandis* first instar longevity.** There was no difference in mortality rate of *L. grandis* first instars in the two soil types tested (95% confidence intervals for the slopes and y-intercepts completely overlapped). The mean longevity of first instar *L. grandis* at 25°C without hosts was 4.07 ± 0.14 days.

***L. grandis* parasitism.** Of the 200 tethered prepupae recovered at the KBS research site in Mich. in 1986, 13.5% were parasitized by *L. grandis* larvae. Parasitism peaked between July 9 and 20, with 29% of the tethered prepupae released on July 9 parasitized over this time period (Figure 11). This peak in parasitism coincided with peak CPB prepupal densities in the research plot . Mortality due to predation and other factors was fairly constant throughout the summer. There was no difference in mortality or *L. grandis* parasitism between tethered and nontethered CPB prepupae. Total mortality for nontethered CPB was 35.5% ($n=31$) versus 34.4% ($n=32$) for tethered CPB. In both cases, only two individuals were parasitized by *L. grandis.* There was no significant difference in the depth of pupation between tethered and nontethered CPB (mean ± SE = 2.96 ± 0.19 cm and 3.09 ± 0.30 cm, respectively).

In 1987, *L. grandis* parasitism of tethered prepupae was detected from June 15 through August 20 (Figure 12). During peak CPB prepupal densities in the research field, parasitism exceeded 50%. From observed soil temperatures and *L. grandis* oviposition, the predicted first hatch of *L. grandis* eggs occurred ca. three to five days prior to the presence of CPB prepupae, and continued through August. As indicated by the parasitism of the tethered prepupae, *L. grandis* larvae were present and active

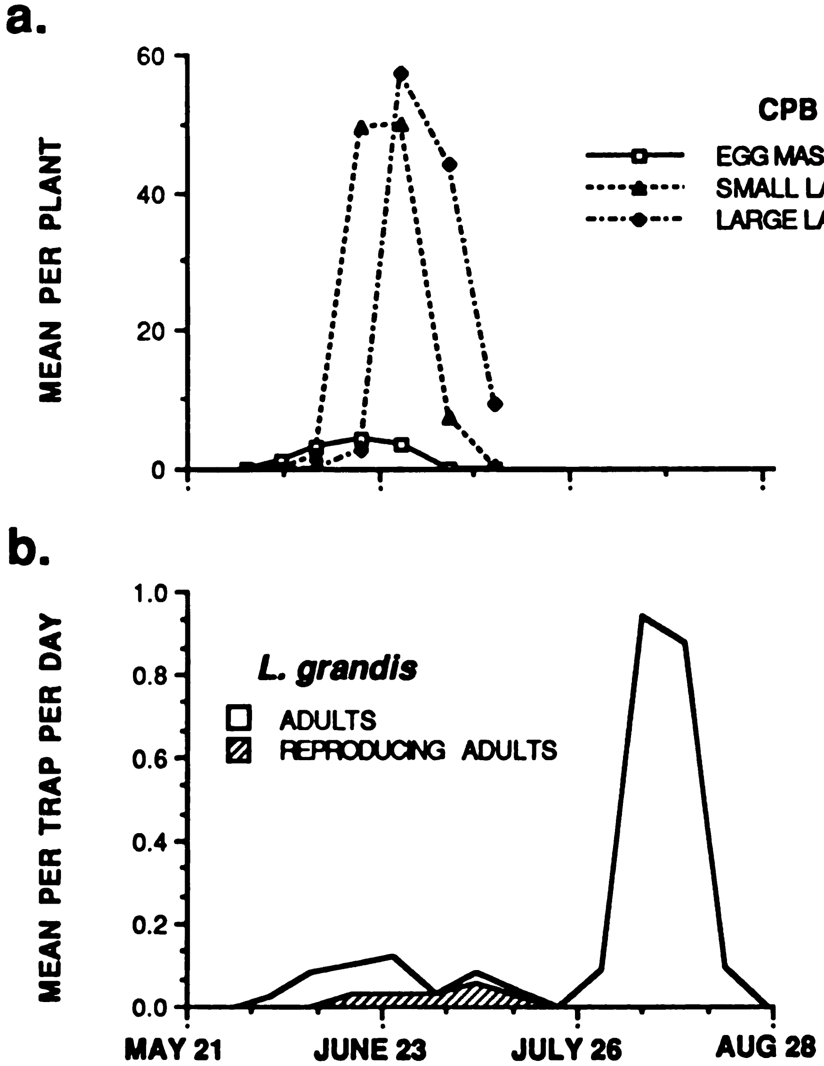

Figure 10. a.) Densities of CPB stages in Rhode Island potato plots in 1987, and b.) trap catches (mean per trap per day) of Lebia grandis adults in Rhode Island potato plots in 1987.

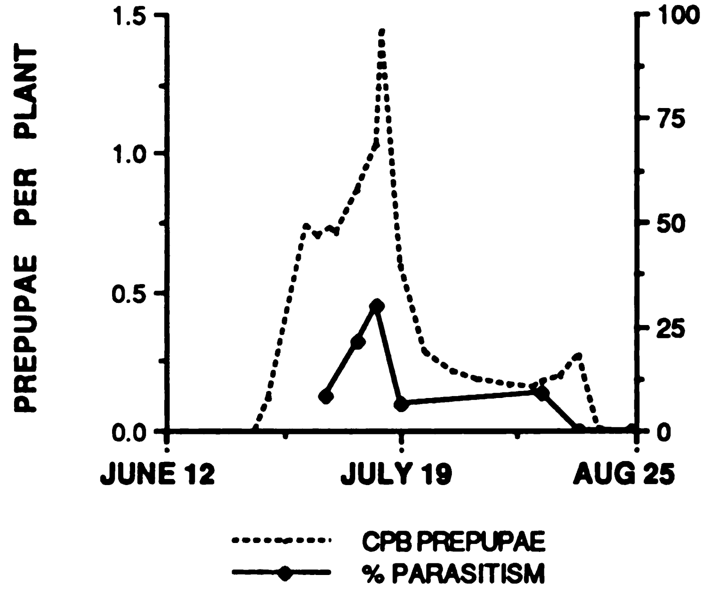

Figure 11. Parasitism rate of tethered CPB prepupae and density of CPB prepupae in Michigan plot in 1986

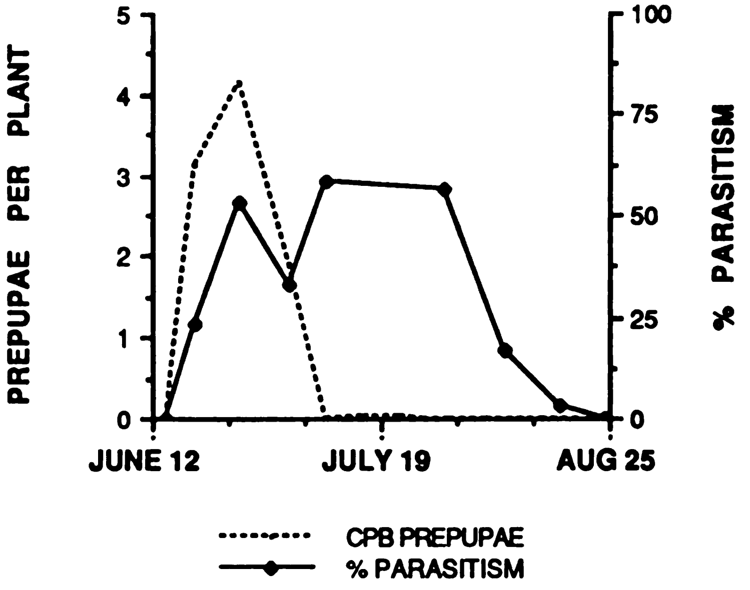

Figure 12. Parasitism rate of tethered CPB prepupae and density of CPB prepupae in Michigan plot in 1987.

throughout most of the growing season, even when hosts were at very low densities or absent. Again, percent mortality of prepupae due to factors other than *L. grandis* was fairly constant throughout the season.

Of the 102 tethered CPB recovered from the early planting in R.I. in 1987, 86% were healthy, 2.9% were infected with *Beauveria bassiana* , less than 1% were eaten, and 9.8% died due to unknown causes. No *L. grandis* parasitism was detected. Of the 100 tethered larvae released in the late planting at R.I., most (52.7%) were unsuccessful in burrowing, and no *L. grandis* parasitism was detected. Seventeen of the 108 tethered prepupae released in the nonrotated field in R.I. on June 30 were recovered, and 29.4% (5 individuals) were parasitized by *L. grandis* , 58.8% (10) were healthy, and the remainder (2) died due to unknown causes. Of the 74 tethered CPB recovered from the July 7 release of 80 tethered prepupae 6.8% were parasitized, 6.8% were infected with *B. bassiana* , 1.4% were eaten, 78.4% were healthy, and 9.5% died due to unknown causes.

DISCUSSION

Although *L. grandis* has been almost entirely overlooked for the past 50 years, it may be the most significant predator of the CPB in R.I. and Mich. This predator is primarily active at night and our sampling indicates that only a very small percentage of the *L. grandis* adults can be found during the day. Pitfall traps seldom catch these foliar-searching carabids which tend to move from one plant to another without contacting the soil. When disturbed, individuals drop to and crawl into the soil rather then run across it. Predation by *L. grandis* is difficult to distinguish from that of other mandibulate predators, particularly cannibalism by the CPB adults. The parasitic larval stage of *L. grandis* is easily dislodged from CPB pupae and is not readily apparent in the soil. All these behavioral features tend to mask the significance of *L. grandis* .

The burlap trap catches tracked the dynamics of *L. grandis* populations as observed with night observations. Population peaks indicated by the trap catches and the night observations were consistent with the peaks observed in the parasitism levels. Both burlap traps and nighttime counts appear superior to daytime counts, but these methods are also affected by weather conditions as both are positively influenced by high humidity and rainfall.

In laboratory studies, *L. grandis* consumed more CPB prey per day than any other predator studied to date (Table 4). Although it demonstrated no preference for any particular prey stage in choice tests, its largest impact is probably on the egg stage. *L. grandis* consumed more eggs than larvae before it was satiated, and when encountering an egg mass, it generally consumed all or most of the eggs in the mass. This is consistent with studies of CPB population dynamics which report that the highest mortality occurs in the egg stage (Harcourt 1971, Groden and Casagrande 1986). This was also evident in the cage studies with *L. grandis* where it continued impact on the larval populations was also evident.

The CPB emerges in late April and early May in R.I. and Mich. and oviposition is initiated in late May and early June. The CPB is well adapted for development at the cool temperatures experienced at this time of the year (Logan et al. 1985), however these cool temperatures have been a major limitation for endemic (Drummond et al. 1984) and imported (Obrycki et al. 1985, Drummond et al. 1987) natural enemies. *L. grandis'* predation activity at relatively low temperatures (less than 20°C) enhances its potential for control of this early season pest.

Thus far, *L. grandis* appears to be very specific to the CPB, not even feeding on other solanaceous feeding Chrysomelids. Although in the absence of CPB prey, *L. grandis* did consume aphids, it did not eat aphids in the presence of CPB. This specificity is advantageous with a life cycle so closely linked to that of its prey. From a management perspective, the fact that *L. grandis* will consume aphids in the absence of its preferred

Table 4. Consumption of CPB by endemic predators.

Predator	Eggs per day (mean ± SE)	Large larvae per day (mean ± SE)
Lebia grandis adults	47.38 ± 2.07	1.91 ± 0.55
Coleomegilla maculata adults	7.95 ± 0.74	0.33 ± 0.10
Perillus bioculatus 5th instars	39.00[1] ----	0.21[1] - - - -
Podisus maculaventris 5th instars	---- ----	1.00[2] - - - -
Phalangium opillio adults	9.63 ± 3.25[3]	0.00 - - - -

[1] Tamaki and Butt 1978.
[2] Drummond et al. 1984.
[3] Drummond et al. 1988.

host, is desirable. Predator populations may be maintained in the field at low CPB densities if alternate prey are available.

L. grandis populations are well synchronized with the CPB in both R.I. and Mich. Predator activity was first detected with the first occurrence of CPB eggs and it peaked along with peak CPB eggs and larvae. *L. grandis* oviposition began at 377-378 DD (base 10°C) from April 1, in both regions. The predicted first hatch of *L. grandis* eggs occurred 3-4 days prior to the first observed CPB prepupae in Mich. Since these parasitic larvae survive an average of 4 days in the absence of a host, it appears that the parasitic stage of *L. grandis* is also well synchronized with its host.

Based on their relatively long development times (28 days at 25°C) and the single peaks observed in reproducing *L. grandis,* it is likely that these predators complete one generation per year in both regions. A small second peak in reproducing females observed in late July in Mich. was likely due to overwintered first generation adults since the predicted first emergence of summer adult *L. grandis* was on July 19 and in the laboratory (at 26°C), they appear to have a minimum preoviposition period of 3-4 weeks. Although *L. grandis* summer adults do not oviposit until the following summer, they still may cause significant mortality to the second CPB generation since prediapausing adults consume a large number of prey. A large peak in prediapausing *L. grandis* adults was observed in 1987 in the plot in R.I., where CPB populations were high. This peak was not observed in Mich., where there were very few second generation CPB, and the predators probably dispersed on emergence.

Tethering CPB prepupae proved an effective means of evaluating the impact of the parasitic stage of *L. grandis.* Although some mortality was experienced due to tethering, it generally did not occur until the individual attempted to molt to the adult, hence it did not interfere with the evaluation of parasitism. Parasitism of tethered CPB indicated that *L. grandis* larvae were present and active at the KBS site throughout most of the growing season, irrespective of host density. *L. grandis* parasitism was higher in Mich.

in 1987 than in 1986, and higher than at the R.I. site in 1987. As this was the second consecutive year for potatoes at the Mich. site, the higher parasitism levels may reflect a build up of *L. grandis* . In R.I. a large CPB population produced at the primary research site in 1986 necessitated moving to a site a few miles away in 1987. There appeared to be fewer *L. grandis* in the new site, but *L. grandis* parasitism was detected in R.I. in 1987 in a small plot adjacent to the 1986 site. *L. grandis* activity may be hampered by long-distance rotations.

L. grandis adults were observed at every site we investigated in R.I. and Mich., including commercial potato growing areas. This study indicates that this species may be the most important endemic predator of the CPB, and further studies of the behavior and survival of *L. grandis* are necessary to fully assess its potential for managing CPB populations.

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MANUSCRIPT 3.

Coleomegilla maculata DeGeer (Coleoptera: Coccinellidae): Its Predation Upon the Colorado Potato Beetle (Coeoptera: Chrysomelidae), and Its Incidence in Potatoes and Surrounding Crops

ABSTRACT - The polyphagous coccinellid, *Coleomegilla maculata* DeGeer, was found to feed on the eggs and small larvae of the Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say). Prey consumption rates were highly correlated with temperature. In choice tests this predator did not prefer aphids over CPB larvae, but as aphid densities increased, consumption of CPB larvae decreased. Field cage studies demonstrated that *C. maculata* adults have the potential to significantly reduce populations of CPB eggs and small larvae.

The incidence of *C. maculata* adults was monitored in early and late planted potatoes in R.I. and Mich. This predator was well synchronized with first generation CPB prey in early planted potatoes in both states, and with second generation CPB prey in late planted potatoes in R.I. *C. maculata* adult densities were monitored in crops surrounding potatoes at one Mich. site. These included cole crops, snap beans, cucurbits, and sweet corn in 1986, and alfalfa and sweet corn in 1987. The predator was found in all crops, with highest densities observed in sweet corn during pollen production. Using observed temperatures and phenological models from the literature, we determined that *C. maculata* has the potential to complete 2-3 generations per year in R.I., and 3-4 generations per year in Mich.

INTRODUCTION

Much biological control research has focused on the interactions between coccinellids and aphids in potato fields (Shands and Simpson 1972; Mack and Smilowitz 1978, 1980, 1982a, b; Mack et al. 1981, Shands et al. 1972 a,b; Tamaki 1981), but little attention has been given to the impact of these species on the Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say). Riley (1869, 1871, 1872, 1873) observed six coccinellid species feeding on CPB eggs and larvae. Of these, we have found the spotted ladybird, *Coleomegilla maculata* DeGeer to be the most abundant species in potatoes in R.I. and Mich. We also observed this species feeding on the CPB on wild host plants in Mexico and Mich.

C. maculata is a polyphagous predator which Gordon (1985) reports to be primarily aphidaphagous. It has been commonly reported feeding on aphids in potatoes (Mack and Smilowitz 1980), corn (Ewert and Chiang 1966), and alfalfa (Hodek 1973). Wright and Laing (1978) suggest that it is found on most crops supporting aphid populations. *C. maculata* has also been reported to be an important egg predator of the European corn borer, *Ostrinia nubilalis* (Hbr.) (Bartholomai 1954, Conrad 1959) and the bollworm, *Heliothus zea* (Boddie) (Whitcomb and Bell 1964). Smith (1961) found that this predator can also complete development when reared solely on pollen. Consumption rates have been determined for this predator feeding on aphids (Mack et al. 1981), but its potential impact on the CPB is unknown.

The objectives of this study were to determine the impact of adult *C. maculata* on the CPB in the laboratory and in field cage studies, and to investigate its occurrence in potato fields in R.I. and Mich. This study was part of a larger project investigating natural mortality of the CPB.

MATERIALS AND METHODS

Consumption rates. In August 1986 and 1987, *C. maculata* adults were collected from potato research fields in Mich. and R.I. to determine their daily consumption of immature CPB stages. Predators were sexed and held individually in petri dishes with moist paper toweling and prey in excess of their daily consumption. Forty predators were given either 20-33 eggs, or first, second, third, or fourth instar CPB larvae (densities = 25, 7, 4 and 2 respectively) and held for five days at 22-23°C. Prey consumption was monitored and new prey added daily. To determine the influence of temperature, *C. maculata* consumption of CPB eggs was monitored at constant temperatures of 15, 20, 25, and 30°C ($n = 25$ per temperature). Predators were handled as described above and prey consumption checked daily for 8-13 days. An analysis of covariance (SAS Institute 1985) was performed to determine if consumption varied with the sex of the predator (with temperature as the covariate, SAS Institute 1985).

Another laboratory study was conducted to determine if *C. maculata* consumption of first instar CPB larvae was influenced by the presence of aphid prey. In the second week in May, 1987 ca. 500 *C. maculata* adults were collected in alfalfa fields near East Lansing, Mich. The adults were held at 22°C in ventilated 1 liter plastic cups for 24 h (25 *C. maculata* per cup), after which sluggish individuals or those parasitized by *Perilitus coccinellae* (Shrank) were eliminated from the study. The healthy *C. maculata* adults were held individually in 30.5 cm capped glass lantern globes. The globes were set over 1 liter plastic cups of sand, each with a single *Solanum dulcamara* L. leaf (trimmed to a standard 20 cm^2) held in a water-filled floral stem holder embedded in the sand. *S. dulcamara* was chosen as a host because all prey fed on this host, and unlike *S. tuberosum* , the stems remained turgid over the 24 h duration of the experiment. Ten first instar CPB larvae were transfered to each leaf, and non-alate aphids were added at densities of 0, 10, 15, 20, 25, 30, or 35 per leaf. Two aphid species were tested. Eleven replicates of each density were established with the green peach aphid, *Myzus persicae* (Sulzer), and 5 replicates of each density were established with the potato aphid, *Macrosiphum euphorbiae* (Thomas). Into each globe, a single *C. maculata* adult was released. The globes were held at 28°C with a photoperiod of 15 L:9 D for 24 h., after which the CPB larval and aphid densities were recorded. Linear regression analysis (SAS Institute 1985) was used to determine the effect of aphid prey density on consumption of CPB larvae by *C. maculata* adults.

Cage studies. The impact of *C. maculata* on CPB mortality, was investigated in R.I. in August, 1986 using six screen walk-in cages (3.6 x 1.8 x 1.8 m). These cages were erected in a newly tilled area and into each cage two rows of 10 greenhouse-grown potato plants were transplanted. Potato stems infested with CPB egg masses were collected from nearby research plots, and bouquets of stems were placed in 6-inch pyrex test tubes with water, and the tops of the tubes were sealed with parafilm. These bouquets were set within the cages with the test tubes sunk into the soil so that the CPB infested stems stood within the stems of the transplanted plants. Bouquet stems were secured to existing stems to assure that they did not droop away from the plant. Resulting CPB egg densities in the cages were set at 500 eggs per cage in 3 cages, and 250 eggs per cage in 3 cages.

At each of these prey densities, *C. maculata* adults were introduced at densities of 0, 10 and 20 predators per cage. CPB eggs and larvae within each cage were censused every 3 to 4 days for three weeks. A two-way analysis of variance (SAS Institute 1985) was performed for each weekly interval to determine effects of intial egg and predator densities on prey survival. The data were pooled for the first two sample dates (representing the egg and first instar stages of the prey) and all predator cages to examine the relationship between prey density and consumption rates. Available prey at the beginning of each sampling interval was regressed with consumption per predator over the interval.

Field Incidence. The densities of *C. maculata* and the CPB were sampled in early and late planted potatoes at two sites in Mich. and two sites in R.I. from 1985-1987. In Mich. these included a late planting in 1985, and an early and adjacent late planting in 1986 and 1987 at the Michigan State University Kellogg Biological Station (KBS) in Hickory Corners, Mich., and at the Michigan State University Potato Research Station in Stanton, Mich. An additional isolated third site with late planted potatoes at KBS was sampled in 1986 and 1987. In R.I. early and isolated late plantings were established at different sections (separated by 1 km) of the University of Rhode Island research farm in Kingston, R.I. The fast maturing potato cultivar Caribe´ was used at all sites. Seventy to 150 whole plant samples were taken at each site per sample date using nondestructive visual counts of all predators and CPB lifestages on a plant.

Given the mobility and polyphagous feeding habits of this predator, we felt that to understand the seasonal dynamics of *C. maculata* in potatoes, it was necessary to follow its populations in surrounding crops. In 1986 *C. maculata* densities and their prey were monitored in plots of alternate crops surrounding the potato research fields at the KBS sites including cole crops (broccoli and cabbage), snap beans, sweet corn, and curcubits (squash and cucumber). Nondestructive whole plant counts of *C. maculata* and possible prey were taken in each plot once per week throughout the growing season with samples of 50 plants for cole crops, 30 for beans, 75 for sweet corn, and 60 for cucurbits. In 1987, at these same sites, *C. maculata* and their prey were monitored in two alfalfa fields and two sweet corn plots. Ten samples consisting of 10 consective sweeps with a 36 cm diameter sweepnet were collected in the alfalfa once per week, and 25 visual whole-plant samples in each of three varieties of sweet corn were taken once per week from the pre-tassel stage through harvest.

Pesticides were not used in any plots at the KBS site in Mich. or any site in R.I., during the study. Weeds were controlled by mechanical cultivation. At the Montcalm research site in Mich., a pre-emergence herbicide and regular fungicide treatments were applied, as is standard for potato production in this area.

Daily maximum and minimum temperatures were recorded in a Stevenson screen located at each of the three research sites starting April 1 each year. From these temperature data, degree-day accumulations were calculated for the following *C. maculata* physiological events using published degree-day models: first oviposition by overwintered *C. maculata* females (82.2°D > 15.4°C, Wright and Laing 1978), total development for immature stages (198.8°D > 13.8°C, , Wright and Laing 1978, and 236°D > 11.3°C, Obrycki and Tauber 1978), and preoviposition by summer adults (22°D > 13.8°C, Mack and Smilowitz 1982b). Degree-day accumulations were calculated by $[(Tmax + Tmin)/2]-t$ when $Tmin > t$ and $[Tmax + t)/2]-t$ when $Tmin < t$ (Baskerville and Emin 1969). Predictions were made for first emergence of each *C. maculata* generation by accumulating degree-days for development and preoviposition from the predicted first oviposition by overwintered adults.

RESULTS

Consumption Studies. *C. maculata* adults consistently consumed the eggs and small larvae of the CPB (Table 1). Most individuals which were fed only third instar CPB larvae consumed a minimum of one larva throughout the study. Only two of the individuals which were fed only fourth instar larvae successfully consumed these prey . An adult *C. macualata* was also observed attacking a fourth instar CPB larva in the field. There was a significant difference in egg consumption between sexes in adult *C. maculata*

Table 1. Consumption of immature stages of the CPB by *Coleomegilla maculata* De Geer adults.

CPB Stage	Sample Size	Daily consumption per predator (mean ± SE)
Eggs	10	7.95 ± 0.74
1st instars	10	11.20 ± 0.78
2nd instars	10	3.07 ± 0.31
3rd instars	5	0.60 ± 0.16
4th instars	5	0.13 ± 0.09

($F_{(1,600)} = 49.2$, $p = 0.001$). Over all temperatures, females consumed 9.10 ± 0.24 eggs per day (mean ± SE), whereas, males consumed 6.64 ± 0.30 eggs per day (mean ± SE). Consumptions rates of *C. maculata* adults were linearly correlated with temperature over the range of temperatures tested (Figure 1).

The presence of both aphid species had an effect upon consumption of first instar CPB larvae by *C. maculata* adults ($F_{(1,6)} = 21.35$, $p = 0.004$ for *Myzuz persicae* ; and $F_{(1,6)} = 3.61$, $p = 0.106$ for *Macrosiphum euphorbiae*). Consumption of first instar CPB larvae decreased in a linear manner as aphid density increased (Figure 2, $y = 7.514 - 0.078\ x$, $r^2 = 0.78$ for *Myzuz persicae*; and $y = 7.218 - 0.061x$, $r^2 = 0.38$ for *Macrosiphum euphorbiae*). *C. maculata* adults consumed a fairly constant proportion of the both aphid species, 78.5 ± 1.5 % (mean ± SE) for *Myzus persicae* and 71.3 ± 2.8 % (mean ± SE) for *Macrosiphum euphorbiae* .

Cage studies. *C. maculata* adults significantly reduced the survival of CPB cohorts in the cage study over the first week of the study (Figure 3). A significant predator density effect ($F_{(2,2)} = 19.24$, $p = 0.049$), and a significant egg density effect ($F_{(1,2)} = 19.4$, $p = 0.048$) on CPB survival was observed over this period. There was, however, no significant difference in CPB survival between cages in the later two weeks of the study ($F_{(2,2)} = 0.48$, $p = 0.67$). This predator impacted the egg and first instar larval survival only. The relationship between prey density and predator consumption rates as shown in Figure 4, may be described by the function: $y = -1.31 + 0.69(\log\ x)$, $r^2 = 0.82$.

Field Incidence. In R.I. in all three years studied, *C. maculata* incidence in potatoes was well synchronized with CPB prey (eggs and first and second instar larvae) in both early and late planted potatoes (Figure 5). Adult *C. maculata* colonized early potatoes between June 3 and June 9. Their population densities peaked 7-14 days after the peak in prey density. In the late plantings, *C. maculata* adults were detected prior to

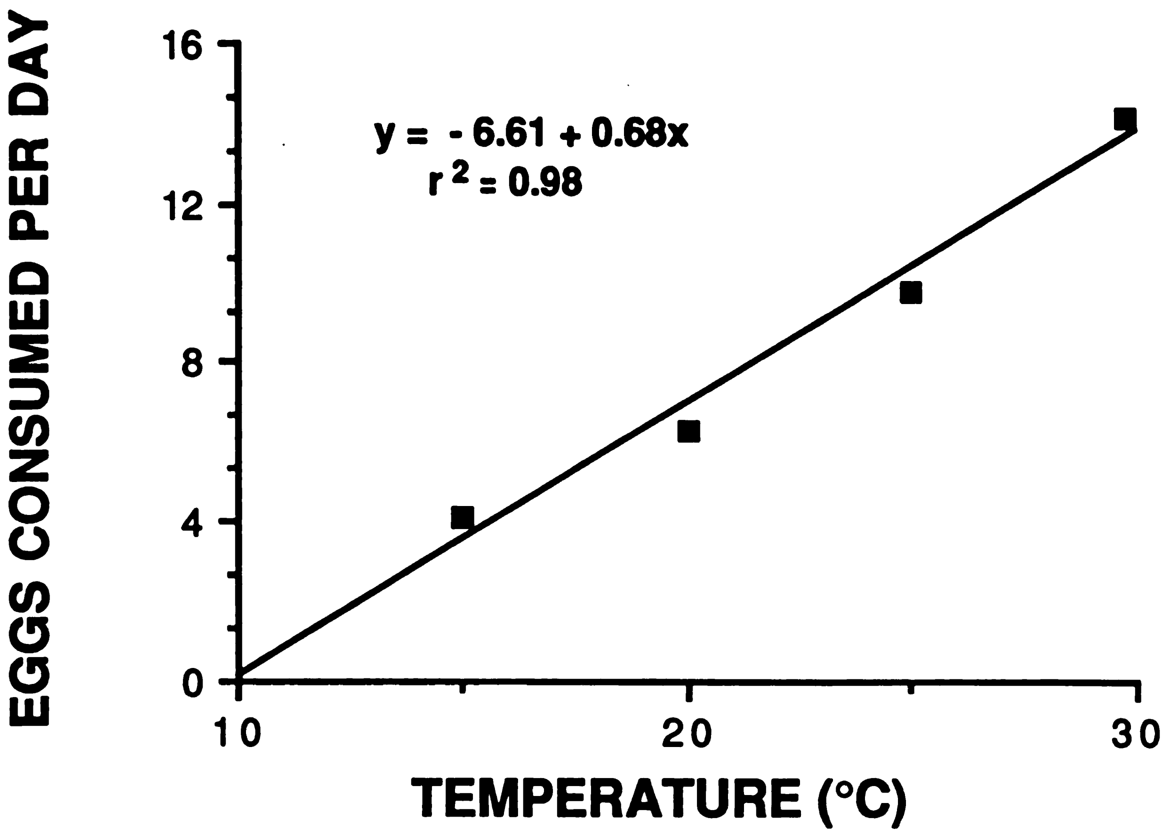

Figure 1. *Coleomegilla maculata* adults daily consumption of CPB eggs as a function of temperature.

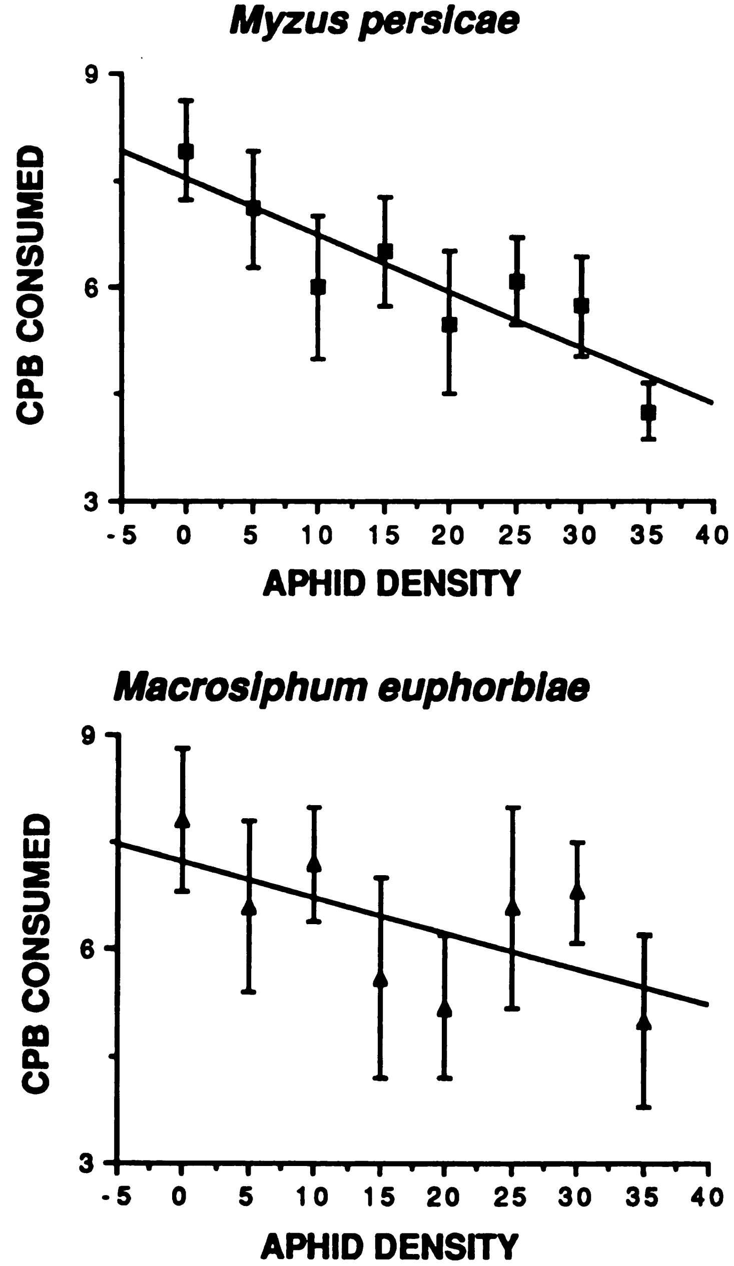

Figure 2. Coleomegilla maculata adult consumption of CPB first instar larvae in the presence of aphids (vertical bars are 95% confidence intervals).

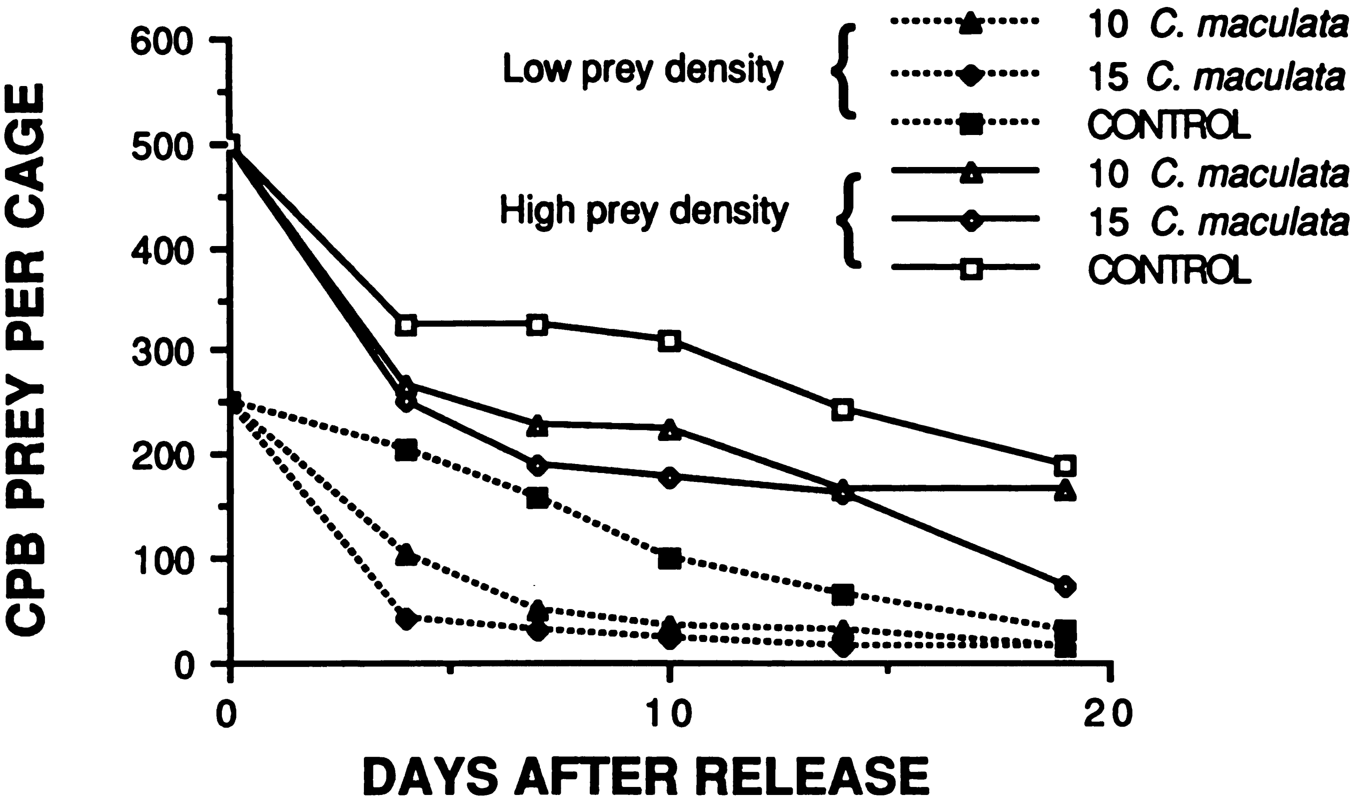

Figure 3. Predation on cohorts of CPB eggs by Coleomegilla maculata adults in field cages.

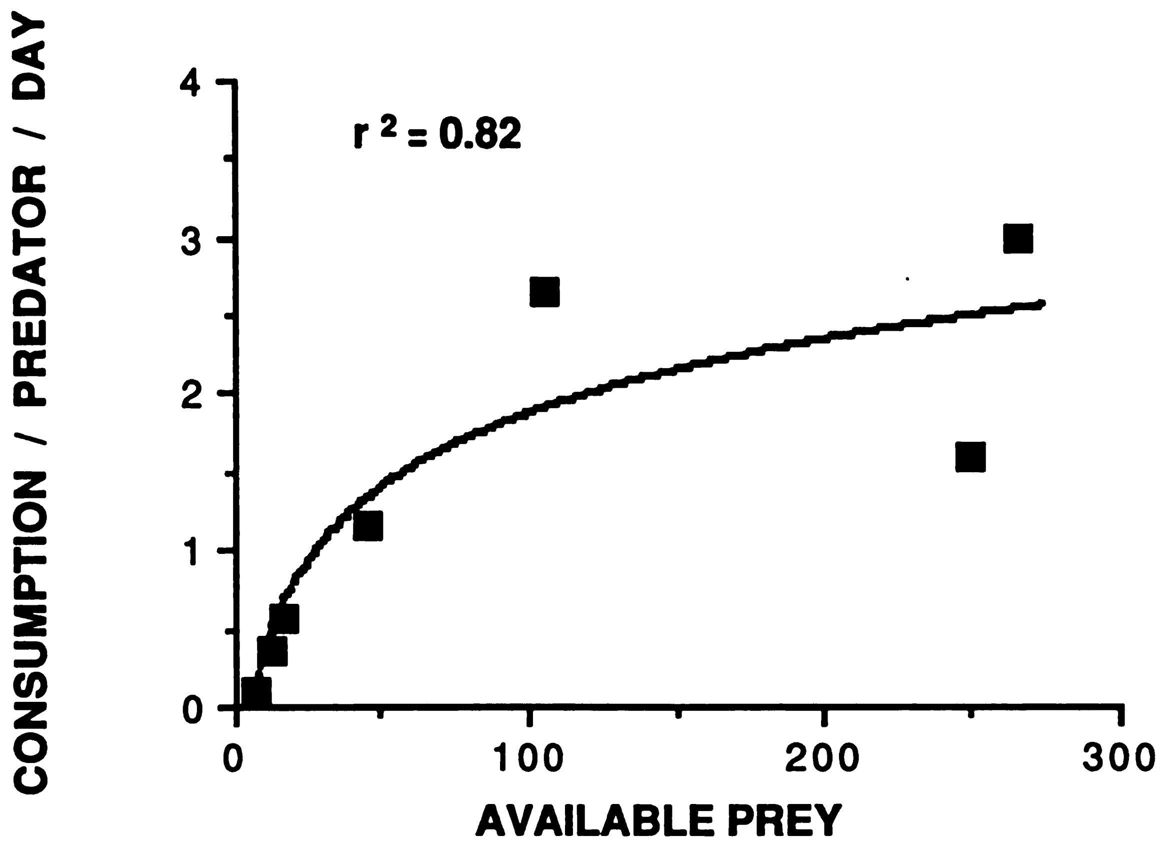

Figure 4. Daily consumption rate of Coleomegilla maculata adults as a function of prey (CPB egg masses plus small larvae) density in field cages.

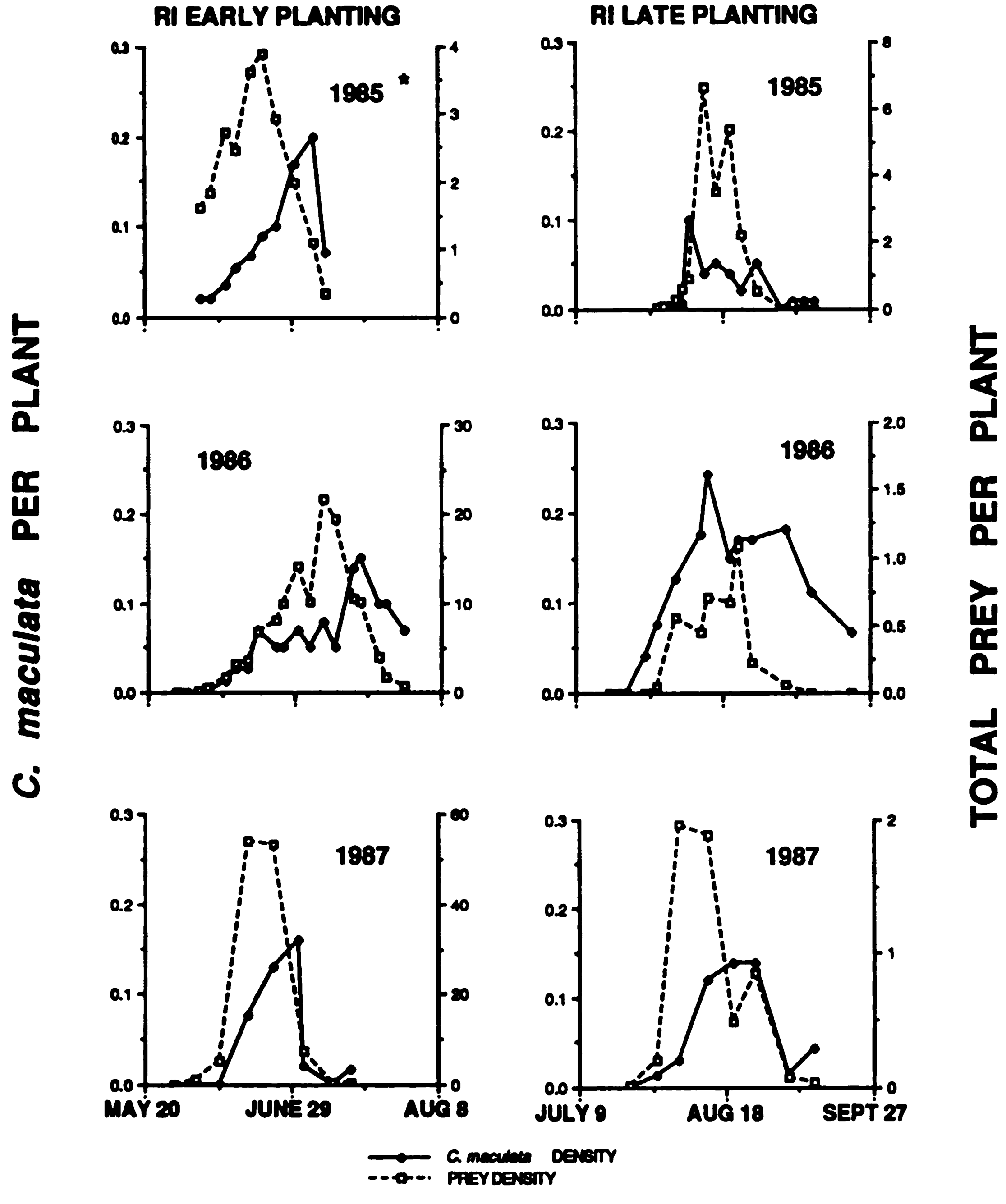

Figure 5. Densities of Coleomegilla maculata adults and CPB prey per plant in early and late planted potatoes in Rhode Island, 1985-1986.

or with the first available CPB prey. In 1986 and 1987, predator densities were similar in the early and late plantings, however the predator:prey ratio was 10- to 30-fold greater in the late plantings.

In Mich., adult *C. maculata* populations in potatoes responded to CPB prey in early plantings in 1986 and 1987, but not in the late plantings (Figure 6 and 7). Population trends were similar at all Mich. sites. *C. maculata* adults colonized early planted potatoes at the KBS site on June 9 in 1986, and June 7 in 1987. At the Montcalm site *C. maculata* adults were first observed in potatoes on June 19 in 1986, and June 3 in 1987. The later first occurrence of *C. maculata* at this site in 1986 coincided with a later build-up of CPB prey. *C. maculata* densities in potatoes in Mich. varied considerably between years and sites irrespective of CPB prey densities.

Of the different crops surveyed at KBS in 1986 and 1987, *C. maculata* adults were found in all plots at some point during the season. In 1986, potatoes were the earliest crop colonized by *C. maculata* adults (Figure 8), and these adults were consistently found at low densities in this crop throughout the field season. The cole crops and beans at site 1 were also colonized early in early June. The predator was found only once in broccoli and cabbage plots at site 2. Predator populations did not appear to coincide with aphids on these crop plants. Aphids were present intermittently and at very low densities in these crops at both sites. *C. maculata* incidence in cole crops at site 1 roughly coincided with *Pieris rapae* (L.) egg populations. Immature Mexican bean beetles, *Epilachna varivestris* Mulsant, were also an apparent prey for *C. maculata* on snap beans. (The predators readily consumed both *E. varivestris* eggs and small larvae in the laboratory.) *C. maculata* adults colonized the cucurbits in early July. No aphids were observed on these crops, however they were heavily infested with cucumber beetles, *Diabrotica undecimpuctata howardi* Barber, and *Acalymma vittata* (Fabricius), and squash bugs, *Anasa tristics* (De Geer). In 1986, the sweet corn at both sites was

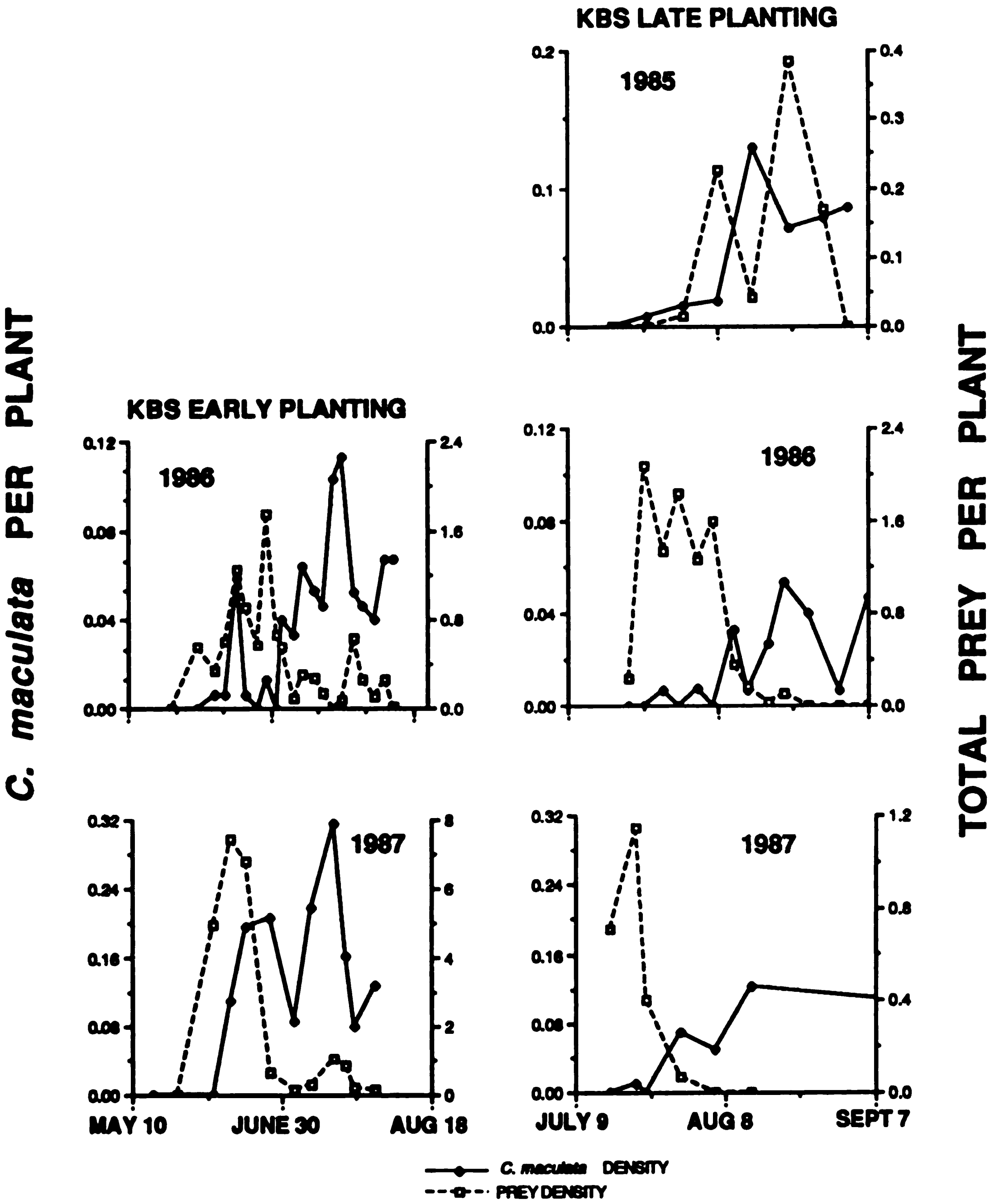

Figure 6. Densities of *Coleomegilla maculata* adults and CPB prey per plant in early and late planted potatoes at the KBS site in Michigan, 1985-1986.

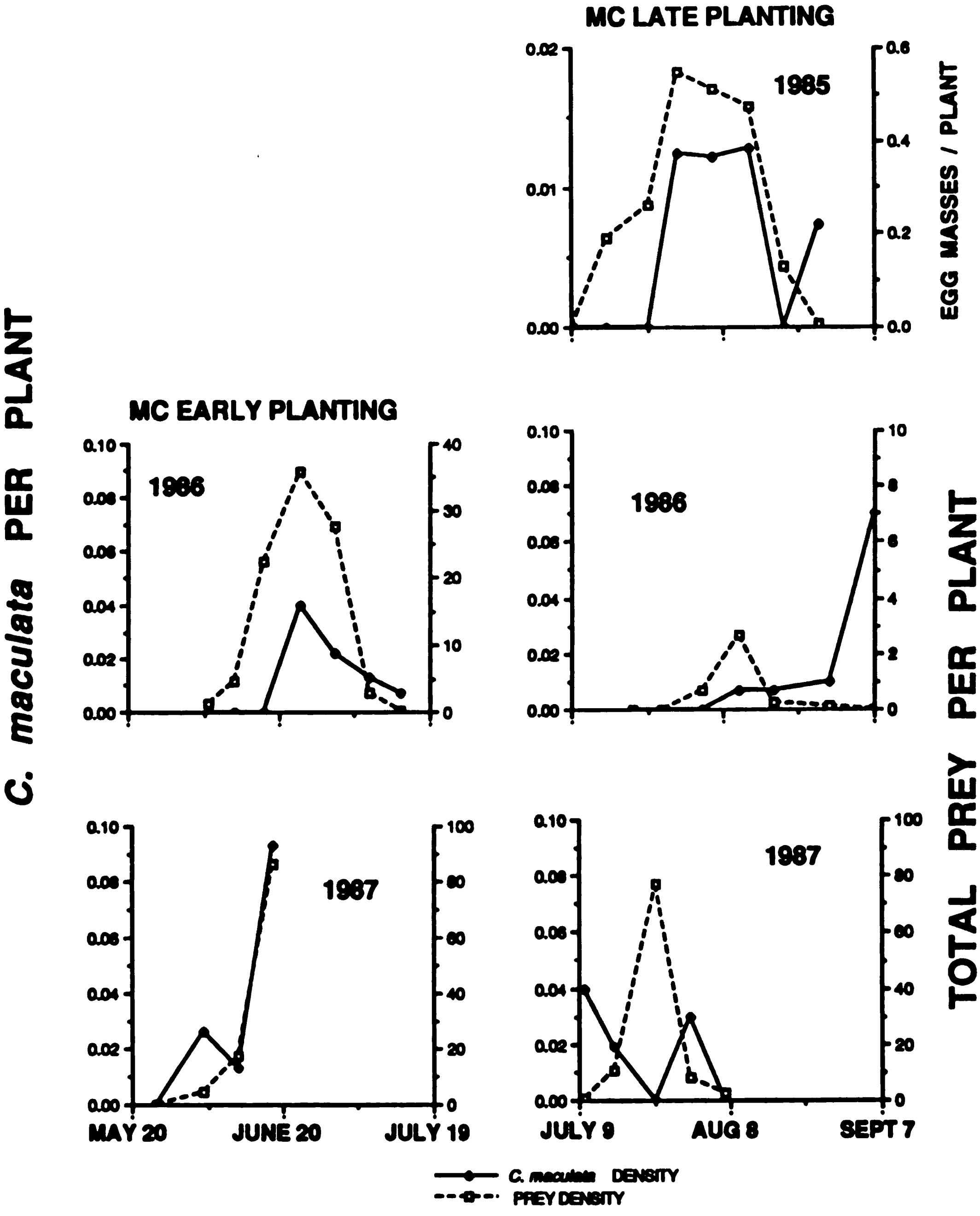

Figure 7. Densities of Coleomegilla maculata adults and CPB prey per plant in early and late planted potatoes at the Montcalm site in Michigan, 1985-1986.

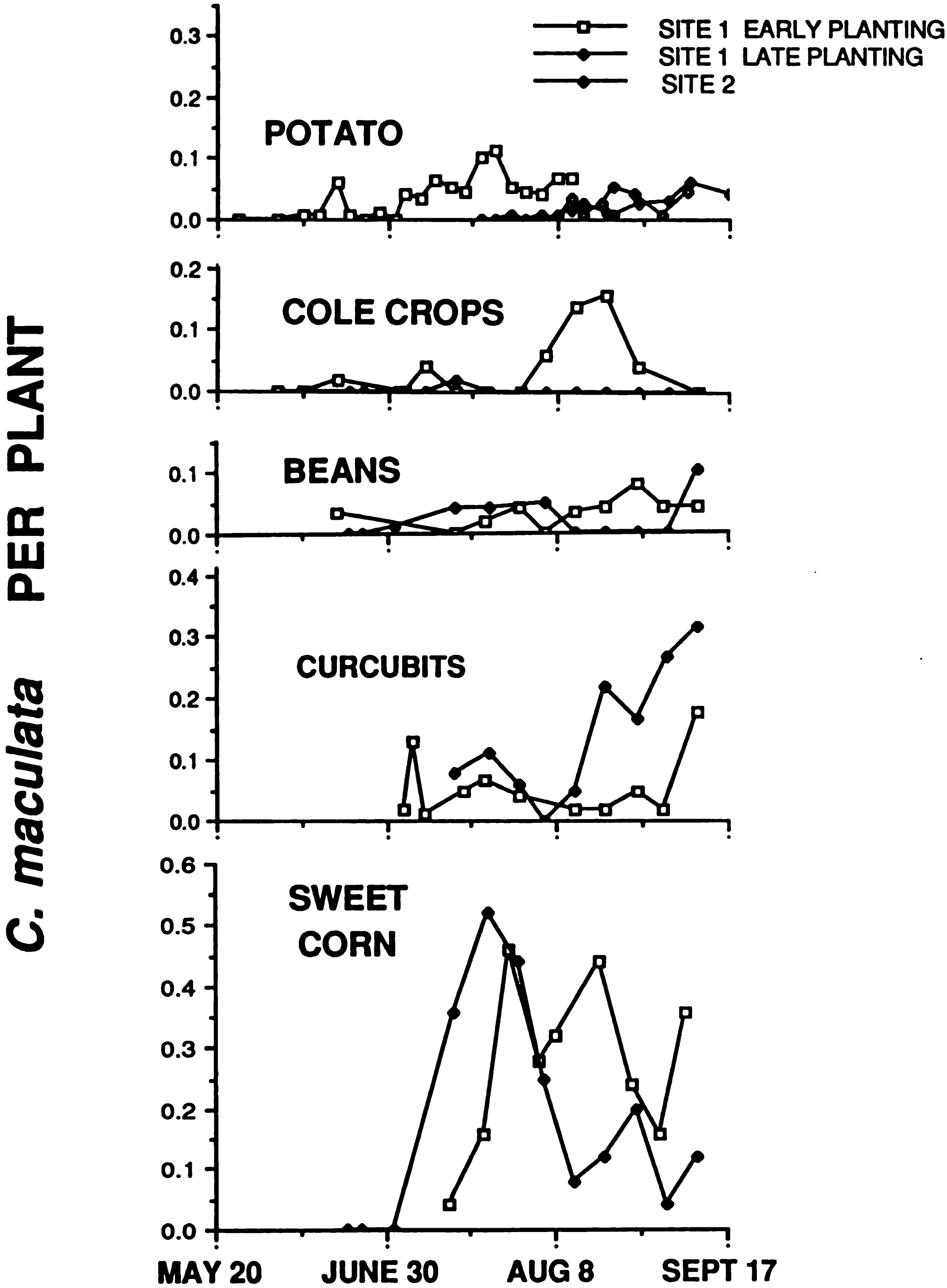

Figure 8. Densities of Coleomegilla maculata adults in potatoes and surrounding crops at the KBS site in Michigan, 1986.

colonized in July at the onset of tasseling when the tassels at both sites were heavily infested with aphids. Between the two peaks (Figure 8) in adult *C. maculata* populations in corn, *C. maculata* larvae were abundant. This crop supported the highest densities of this predator.

In 1987, *C. maculata* adults were sampled in alfalfa on April 24 (Figure 9). The populations declined in field 1 following the first cutting in mid May, and declined in field 2 prior to the first cutting in late May. This decline in field 2 coincided with a drop in aphid populations in this field (Groden 1988). *C. maculata* adults colonized potatoes in early June, and sweet corn again in early July. *C. maculata* densities were low in alfalfa throughout the month of June, but increased again in late July and August. Three peaks in adult densities are evident in potatoes, and two in sweet corn (Figure 9). *C. maculata* populations in potatoes were greater in 1987 than 1986, but about the same between years in corn.

The predicted *C. maculata* physiological events differed between Mich. and R.I. by as much as 25 days by the end of the season(Table 2). Due to the cooler spring temperatures in R.I., the predicted first oviposition by overwintered adults was 12 to 14 days later than in Mich. in 1986, and 9 to 17 days later in 1987. In R.I. *C. maculata* had the potential to complete 2 or 3 generation in 1986, and 3 generations in 1987. In Mich., it had the potential to complete 3 generations in 1986, and a possible fourth in 1987.

DISCUSSION

C. maculata is an important natural enemy of the CPB. It fed readily on CPB eggs and small larvae in the laboratory, and it has frequently been observed feeding on these prey in the field. Although some individuals fed on large larvae when confined in a petri dish, it is doubtful that *C. maculata* would handle such large prey in the field. The field

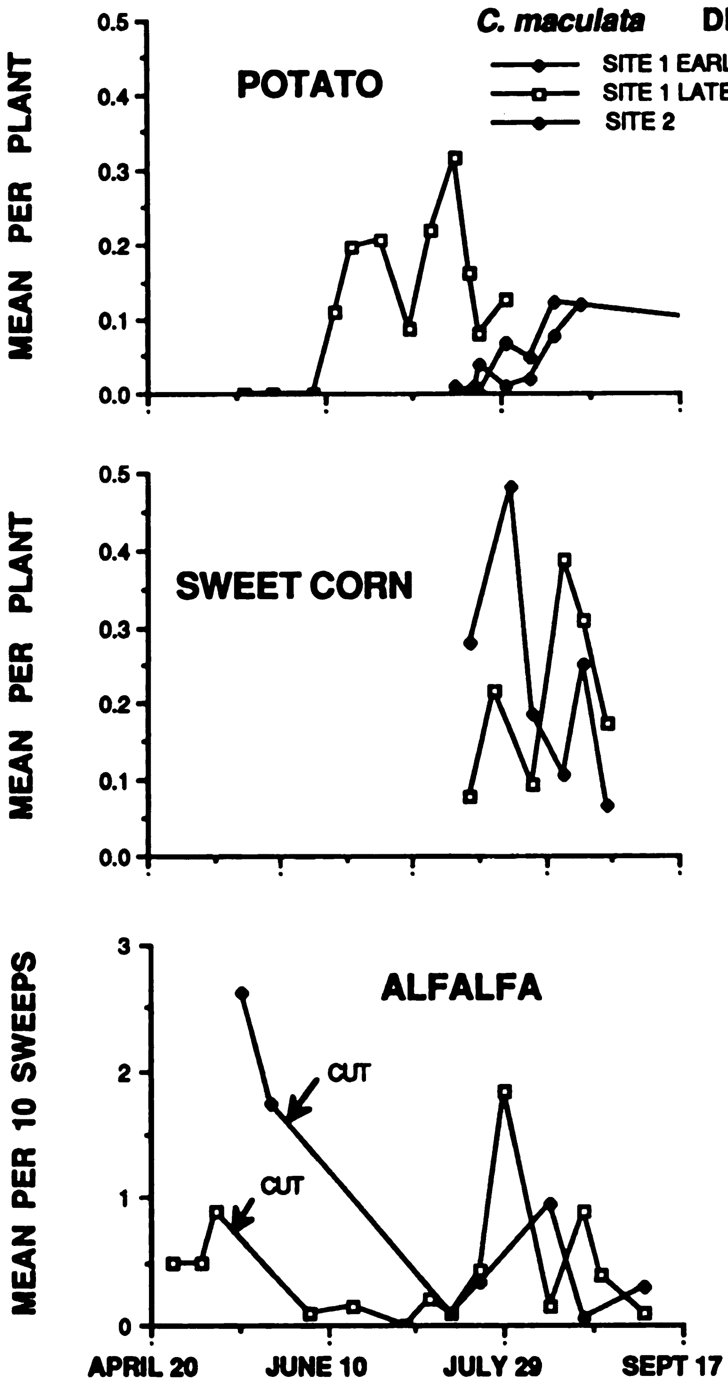

Figure 9. Densities of Coleomegilla maculata adults in potatoes and surrounding crops at the KBS site in Michigan, 1987.

Table 2. Predicted *C. maculata* physiological events at research sites in RI and MI in 1986 and 1987, based on temperatures and degree day models developed by Wright and Laing (1978), Obrycki and Tauber (1978), and Mack and Smilowitz (1982).

		Potential Generations	First	First Emergence^2 Generation 1		First Emergence^2 Generation 2		First Emergence^2 Generation 3		First Emergence^2 Generation 4	
Site	Year	per year	Oviposition^1	Model 1^3	Model 2^4	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
MI KBS	1986	3	May 13	June 19	June 24	July 18	July 22	Aug 15	Aug 21	- - -	- - -
	1987	4	May 14	June 9	June 11	July 3	July 6	July 24	July 27	Aug 15	Aug 20
MI ML	1986	3	May 11	June 19	June 22	July 19	July 22	Aug 16	Aug 23	- - -	- - -
	1987	4	May 6	June 3	June 5	June 30	July 2	July 22	July 24	Aug 13	Aug 16
RI	1986	2 - 3	May 25	June 26	June 28	July 24	July 28	Aug 22	Aug 30	- - -	- - -
	1987	3	May 23	June 21	June 22	July 20	July 22	Aug 15	Aug 18	- - -	- - -

[1] Degree-days accumulated from April 1.

[2] Degree-days accumulated from predicted first oviposition.

[3] From Obrycki and Tauber (1978); preoviposition model from Mack and Smilowitz (1982).

[4] From Wright and Laing (1978); preoviposition model from Mack and Smilowitz (1982).

cage study also demonstrated that this predator can significantly reduce populations of CPB eggs and small larvae, but it has no impact on large larvae. *C. maculata* adult predation increased with increased prey densities.

The predators's CPB consumption was reduced in the presence of alternate prey. Given the linear reduction in CPB consumtion as aphid density increased, and the constant proportion of aphids preyed upon, we conclude that *C. maculata* adults do not preferentially feed on aphids, but feed on whichever prey type they encounter. Therefore, high aphid densities in potatoes will decrease the effectiveness of *C. maculata* as a CPB predator. In evaluating the polyphagous behavior of *C. maculata,* Smith (1965b) demonstrated that previous feeding experience did not affect its food preference, and he also reported preferential feeding on corn pollen by *C. maculata* adults in choice tests with aphids. We are not able to determine from this study the impact of alternate food sources in adjacent crops on the densities of *C. maculata* in potatoes. With the higher densities in sweet corn in the July and August, and *C. maculata'* s known preference for corn pollen, it may be possible that this crop in close proximity can draw these predators out of crops with less prefered food.

In the early season, *C. maculata* adults colonized potatoes when suitable CPB prey became available. Other suitable prey were not available on potatoes at this time. Although potato aphids can be found on potatoes in Mich. in early June, their populations do not build up until mid-July and August. Green peach aphids are also a late season pest on potatoes. Aphid densities from the Montcalm research site in 1986 and 1987 (Grafius, unpublished data) confirm that in both years *C. maculata* colonized the plots prior to aphids.

In the late season, the diversity of prey types available on potatoes and surrounding crops increases. *C. maculata* populations are likely responding to total suitable prey densities. Generally, Mich. has a much smaller second CPB generation than R.I. The synchrony of *C. maculata* adults with the second CPB generation in R.I. may reflect the fact that the CPB constitutes a larger proportion of the predator's total available prey. Aphid build-ups in potatoes and other surrounding crops in conjunction with smaller CPB populations may be responsible for the lack of synchrony with CPB in the late season in Mich.

At the KBS site, *C. maculata* was first observed in late April in 1986 and 1987, feeding on pollen of dandelions, *Taraxacum officinale* Weger, surrounding alfalfa. In 1986, these predators had colonized alfalfa by May 10, and in 1987 they were abundant in this crop on April 26, more than one month prior to the first observance in potatoes. The predicted first *C. maculata* oviposition at the KBS site was on May 13 in 1986, and May 14 in 1987. *C. maculata* females collected at this site on May 10 in 1986, were ovipositing, as were females collected on May 24 in 1987. Obrycki and Tauber (1979) reported that photoperiodic control of diapause in this species ends in March in New York, and suggest that after this point the availability of food sources as well as temperature could be influencing factors. There is abundant supply of aphids in alfalfa in Mich. in early May, and with suitable temperatures, over-wintered *C. maculata* females may begin ovipositing in this crop before potatoes break ground.

The predicted first emergence of first generation adults in Mich. was between June 19 and June 24 in 1986, and between June 9 and June 11 in 1987. This predicted emergence in 1987 coincided with the initial colonization of potatoes by *C. maculata* adults, indicating that in some years in Mich., this predator may have the potential to go through one complete generation before colonizing potatoes. *C. maculata* had the potential to complete 3 generations in 1986, and 4 in 1987. In 1986, one generation was likely completed before the predators colonized cucurbits or sweet corn. In 1987, they apparently completed two generations before colonizing sweet corn.

The predicted physiological events do not coincide with the observed dynamics of adult *C. maculata* populations sampled at KBS in 1986, although they do in 1987. Many factors not accounted for in these predictions can influence the observed changes in this predator's populations. Mortality can shift the population curves if it is not constant throughout the generation. Different prey types and the consistancy of the prey supply has also been shown to influence development rates of this species (Putman 1957, Smith 1960, 1961, 1965a,c). And crop management practices, such as cutting alfalfa, can strongly influence *C. maculata* mortality and dispersal to different crop plants. Therefore, these predictions reflect the potential generations of *C. maculata* at each of the study sites given optimal conditions. A better understanding of the consequences of these factors on the behavior, mortality, and movement of these predators in the field is necessary before they can be effectively managed to maximize their impact upon the CPB.

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MANUSCRIPT 4.

Effects of Soil Fungistasis on *Beauveria bassiana* (Bals) Vuill. and its Relationship to Disease Incidence in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) in Michigan and Rhode Island Soils

ABSTRACT - The fungistatic effects on *Beauveria bassiana* were measured in soils collected from two potato fields each in Rhode Island and Michigan for two years. Michigan soils were more fungistatic than Rhode Island soils in 1986, but fungistasis levels varied between years, and in 1987 one Michigan soil was significantly more fungistatic than the Rhode Island soils. Fungistasis levels were found to increase exponentially with increases in soil pH. Pupae of the Colorado potato beetle, *Leptinotarsa decemlineata* (CPB) were inoculated with *B. bassiana* conidia and immediately incubated in the Michigan and Rhode Island soils to determine if a relationship exists between fungistasis and disease incidence. There was no significant soil effect on CPB mortality, but log-probit regressions of dose-mortality against fungistasis levels revealed a significant trend of increasing LD_{50} values with increasing fungistasis. There also were significant soil and dosage effects on *B. bassiana* sporulation in pupae previously inoculated with *B. bassiana.* More sporulation was found on individuals in Rhode Island soils than in Michigan soils.

INTRODUCTION

Beauveria bassiana (Balsamo) Vuillemin is a soil-borne pathogen of many insect pests, and its potential development as a microbial insecticide has heightened interest in its ecology in soils. Several authors have reported the inhibition of germination of *B. bassiana* conidia in natural (non-sterile) soils (Wartenburg and Freud 1962, Clerk 1969, Walstad et al. 1970, Lingg and Donaldson 1981, and Sharapov and Kalvish 1984). This inhibition was overcome by autoclaving the soils, by filtering soil extracts (Clerk 1969), or by the addition of organic amendments to soils. Walstad et al. (1970) demonstrated the fungistatic versus fungitoxic nature of this phenomenon, and it has been suggested that the inhibitory effects of soil are counteracted by the presence of insect hosts (Wartenberg and Freud 1961, Clerk 1969). As the level of fungistasis against *B. bassiana* has been shown to differ in different soils (Sharapov and Kalvish 1984), knowledge of the relationship between soil fungistasis and *B. bassiana* infection is necessary for determining effective inoculum dosages for adequate pest control under different soil conditions.

The purpose of this study was to quantify *B. bassiana* fungistasis in soils from potato fields in Rhode Island and Michigan, and to determine whether a relationship exists between fungistasis and mortality of Colorado potato beetle (*Leptinotarsa decemlineata* (Say) pupae inoculated with *B. bassiana* .

MATERIALS AND METHODS

Fungal Culture. A pure culture of *Beauveria bassiana* strain RS252 was obtained by inoculating plates of Sabouraud's maltose agar (SMA) plus 650 p.p.m. dodine (Beilharz and Parbery 1982) with a technical grade, foliar formulation of the fungus obtained from Abbott Laboratories, N. Chicago, IL. *B. bassiana* was maintained on SMA, and conidia for use in experiments were harvested from two- to three-week-old cultures on the same medium. Conidia were collected directly from plates with a sterile transfer loop and added to distilled water. The resulting concentration of conidia was determined by counting the conidia in a 1 ml droplet with a hemocytometer. The concentration was adjusted as needed by making dilutions in distilled water.

Soils. Soil samples were collected from two potato research sites at the University of Rhode Island Research Farm in Kingston, Rhode Island, and two potato research sites in Michigan. The Rhode Island soil samples included an Enfield silt loam from the Agronomy farm site, and a Merimack sandy loam from the Peckham Farm site. The Michigan soils included a McBride sandy loam from the Michigan State University Potato Research Farm in Montcalm Co., Michigan, and a Kalamazoo sandy loam from the Michigan State University Kellogg Biological Station (KBS) in Kalamazoo Co., Michigan. Of these sites, all except the KBS site are within commercial potato growing areas with high regional populations of the CPB. In 1986, soil samples were collected in August (R.I.) and September (Mich), and in 1987, all samples were collected in August. In all cases, soil was collected from an area currently planted to potatoes, *Solanum tuberosum* L. At the Montcalm site, herbicides were the only pesticides used during the two years sampled, and at all other sites, no pesticides were used. Vertical movement of commercially formulated *B. bassiana* conidia has been found to be restricted primarily to the top 15 cm of soil (Storey et al. 1987). For this study, only soil within 10 cm of the soil surface was used. Soils were seived (2 mm mesh) and stored moist in air-tight containers at 4.4°C for 3-6 months prior to use.

Characterization of the soils collected in 1987 included textural analyses, cation exchange capacity and organic matter content determined by the Soil Testing Laboratory, Michigan State University. In addition, organic carbon content was determined by the method described by Allison (1965), and pH was determined with an electronic pH meter. Moisture characteristic curves for the soils were determined using a pressure-plate apparatus (Richards 1965). Second order polynomial equations were fit to each of the curves for predicting the appropriate percentage of moisture for a given water potential. Soil pH was also determined for the samples collected in 1986.

Fungistasis Assay. A quantitative determination of fungistasis in the different soils was made by assessing the germination of *B. bassiana* conidia on 10-mm-diameter membrane filters (Gelman, IGA-8, pore size 0.2 microns) placed on soil supplemented with increasing concentrations of a 5:1 (w:w) solution of glucose and peptone. Ten g (dry weight) samples of the soils were measured and tamped to a smooth surface in 6-cm-diameter glass petri dishes. One ml glucose-peptone solution was added to each dish. Concentrations of glucose:peptone previously determined to yield an appropriate range of *B. bassiana* germination in soil were 10,000:2000, 5000:1000, 2500:500, 1250:250, 625:125, and 0:0 µg/g soil. After the addition of the nutrient solution, the soil was wet to saturation and the soil surface smoothed. Sterilized membrane filters bearing *B. bassiana* conidia were placed on the soil surface. *B. bassiana* conidia were aseptically transfered to the filters by pipetting 4 ul of a conidial suspension (100-200 conidia/µl) on each filter with a repeating micropipette. The dishes were then incubated at 22°C for 22 hours in moisture chambers to maintain high relative humidity. After incubation, the filters were removed and the bottoms were carefully pulled over moist filter paper to remove adhering soil particles before staining with phenolic rose bengal. Stained filters were then placed on glass slides and dried. Dried filters were cleared with mineral oil and viewed with transmitted light at 300x magnification to determine the percentage of germinated conidia. Two replicate dishes of each soil with three filters per dish were used per glucose concentration for the 1986 soil samples.

Using soil samples collected from the same sites in 1987, this experiment was repeated once with the above range of glucose:peptone concentrations and again with a glucose:peptone concentration of 312.5:12.5 µg/g soil. Two dishes of each soil were used with four inoculated filters per dish. In the 1987 test, due to a change in the polymer used in the manufacture of the membrane filters (GA-8S), it was necessary to use cinnamon oil to clear the filters for viewing the conidia. In both years, 100-200 conidia per filter were counted.

Probit transformations of germination percentages were regressed on the log concentrations of glucose for each soil, and the glucose concentration necessary for 50% germination was determined. An analysis of covariance (SAS Institute 1985) with glucose as the covariate was performed to detect significant difference between fungistasis levels (% germination) in the different soils. Data from fungistasis assays for both years were pooled, and regression analyses were used to explore the functional relationships between fungistasis levels (represented by the estimated glucose concentration necessary for 50% *B. bassiana* germination) and soil pH, and fungistasis levels and soil texture (represented by % sand and % silt). Data from the 1987 fungistasis assay were used to regress fungistasis levels on % organic matter, and fungistasis levels on % carbon.

As *B. bassiana* is an insect pathogen, and conidial germination has been shown to be stimulated by insect cuticles (Walstad et al. 1970),we were interested in determining if chitin, a major component of the insect cuticle, was a more appropriate amendment with which to assay fungistatic effects of soils on *B. bassiana.* First, the germination of *B. bassiana* on colloidal chitin was compared with that on ground elytra from CPB adults.

Colloidal chitin was prepared from unbleached chitin flakes as described by Hsu and Lockwood (1975), was autoclaved and stored in suspension. The final suspension contained 0.042 g chitin/ml. For the assays, this concentrated suspension was diluted by adding 1 ml to 9 ml of distilled water, and autoclaved. Elytra removed from two adult CPB were ground with a mortar and pestle and sterilized in aqueous suspension. Both the chitin and elytra particles were deposited aseptically onto 25-mm-diameter Gelman membrane filters (pore size 5 µm). These filters were transferred to sterilized 6-cm-diameter petri dishes containing two water-saturated filter papers. Ten-mm-diameter membrane filters bearing *B. bassiana* conidia (as described above) were placed over each substrate, and dishes were held in moisture chambers for 22 hours. After incubtion, the filters were stained and prepared for examination of *B. bassiana* conidial germination. Three dishes each containing one inoculated filter were used; these were compared with controls of inoculated filters on saturated filter paper. A one-way analysis of variance (SAS Institute 1985) was performed to compare the germination data.

A second experiment was conducted to determine the influence of colloidal chitin on the germination of *B. bassiana* conidia in the presence of soil, and to determine the effects of different concentrations of chitin on conidial germination on soil. The colloidal chitin suspension was sterilized and deposited onto membrane filters as described above, with resulting concentrations of chitin per filter equaling 4.2 mg, 2.1 mg, 1.05 mg, 0.525 mg, and 0 mg. Two filters per chitin concentration were transferred to 6-cm-diameter petri dishes containing 10 g saturated, tamped soil collected from the KBS site in Michigan in 1987 (a single dish for each filter). Controls consisted of two filters per chitin concentration placed on two saturated filter papers in sterile petri dishes. Filters bearing *B. bassiana* conidia were placed on the chitin and the dishes were incubated in a moisture chamber for 25 hours, before filters were stained and prepared for observation. Membrane filters with *B. bassiana* conidia were also incubated on SMA for 25 hours as a check on conidial viability. A two-way analysis of variance was applied to the data (SAS Institute 1985).

A third experiment was conducted comparing the germination of *B. bassiana* conidia on 4.2 mg chitin using the 1987 soil samples from Rhode Island and Michigan. Soil treatments were prepared as described for the previous experiment. Two *B. bassiana* membrane filters per soil type were incubated for 24 hours, and two filters per soil type were incubated for 48 hours. Controls included two filters incubated on chitin on saturated filter papers and two on SMA, both incubated 24 hours. After incubation, filters were stained and prepared for observation.

Dose-mortality Study. The mortality of CPB pupae inoculated with *B. bassiana* was determined in the different soils collected in 1987 and without soil. Diapausing CPB adults were collected in August, 1987, at the KBS site, and held in cold storage at 4°C for 3 months before rearing was initiated. After removal from cold storage, beetles were maintained on greenhouse grown potato plants in a rearing room with a 16:8 light:dark cycle, and temperatures ranging between 24-26°C. Egg masses were transferred daily to larval cages, where upon hatch, they fed on potato foliage until completion of the fourth stadium when the prepupae were collected. Prepupae were held at 26°C until pupation, after which they were transfered to 15°C until used for this study.

Sixteen 50-g (dry weight) samples of each of the four different soils were measured into 1 pint plastic containers. In each sample the percentage moisture was increased to the level necessary to equilibrate the soils at a water potential of -0.33 bars. Ten CPB pupae were individually placed ventral side down in each of eight of the containers per soil type. In addition to the soil treatments, 10 pupae were placed ventral side down on 3 layers of saturated filter paper in a 10-cm-diameter glass petri dish. The physiological age of the pupae ranged from 5 to 35 degree-days (base 10°C; total pupal development time = 76 degree-days). Pupae were distributed such that the age structure of the 10 pupae was equal across all containers. Once placed on the soil or filter paper, each pupa received two 3-ul drops of a *B. bassiana* conidial suspension on its dorsal surface. Each pupa received 1.3×10^7, 1.3×10^6, and 1.3×10^5 conidia. For each soil type and the no soil treatment, two dishes with 10 pupae per dish were treated with each concentration of inoculum. Pupae in two additional dishes per soil type were treated with two 3-ul drops of distilled water, as a control.

After inoculation, the pupae were immediately covered with 50 g of the same soil type. The pupae in petri dishes without soil were left uncovered. Containers were covered with an air-tight lid and held at 22-23°C, and checked daily for 7 days for emergence of CPB adults. When adult beetles emerged, they were surface-sterilized in a 0.1% solution of Zephran Chloride®, and transferred individually to 10-cm-diameter petri dishes with water-saturated filter paper and greenhouse-grown potato foliage. After 7 days the soil in the dishes was sifted to determine the fate of unemerged individuals. Those individual found alive were transferred to petri dishes with food, and all remaining beetles were monitored for an additional three days. Adult beetles were fed and their dishes cleaned as necessary. Dead individuals were kept moist for a minimum of two days to check for signs of *B. bassiana* sporulation.

This experiment was repeated with one container of each soil type per *B. bassiana* concentration and10 pupae per container. The dosages applied were 4.2 x10^5, 4.2 x 10^4, 4.2 x 10^3, and 0 conidia per pupa.

Pupal mortality data were corrected for control mortality using Abbott's formula (Busvine 1971). A two-way analysis of variance (SAS Institute 1985) was performed to detect significant differences in corrected percentage mortality between soil types and concentrations. Also, a two-way analysis of variance was performed to detect significant differences in *B. bassiana* sporulation on dead pupae between soil types and conidial concentrations. Log-probit regressions of dose-mortality were calculated for each soil type (SAS Institute 1985), and the resulting estimated LD_{50} values were regressed on the fungistasis levels (glucose concentration necessary for 50% germination) to determine the functional relationship between these two variables.

RESULTS

Soil Characteristics. The characteristics of the four soils collected in 1987 are given in Table 1. The texture of the two Rhode Island soils was very similar, but

Table 1. Characteristics of soils used in *Beauveria bassiana* fungistasis and dose-mortality assays.

Soil	Classification	% sand-silt-clay	pH 1986	pH 1987	% OM[1]	%C[2]
Rhode Island:						
Peckham Farm	Silt Loam	32-51-17	6.1	5.1	3.4	2.3
Agronomy Farm	Silt Loam	29-57-15	6.7	5.8	2.7	1.9
Michigan:						
Kellogg Biological Station	Loam	43-31-26	7.0	6.6	1.7	1.3
Montcalm Research Farm	Sandy Loam	74-15-11	6.9	5.9	1.6	0.9

[1] percentage organic matter

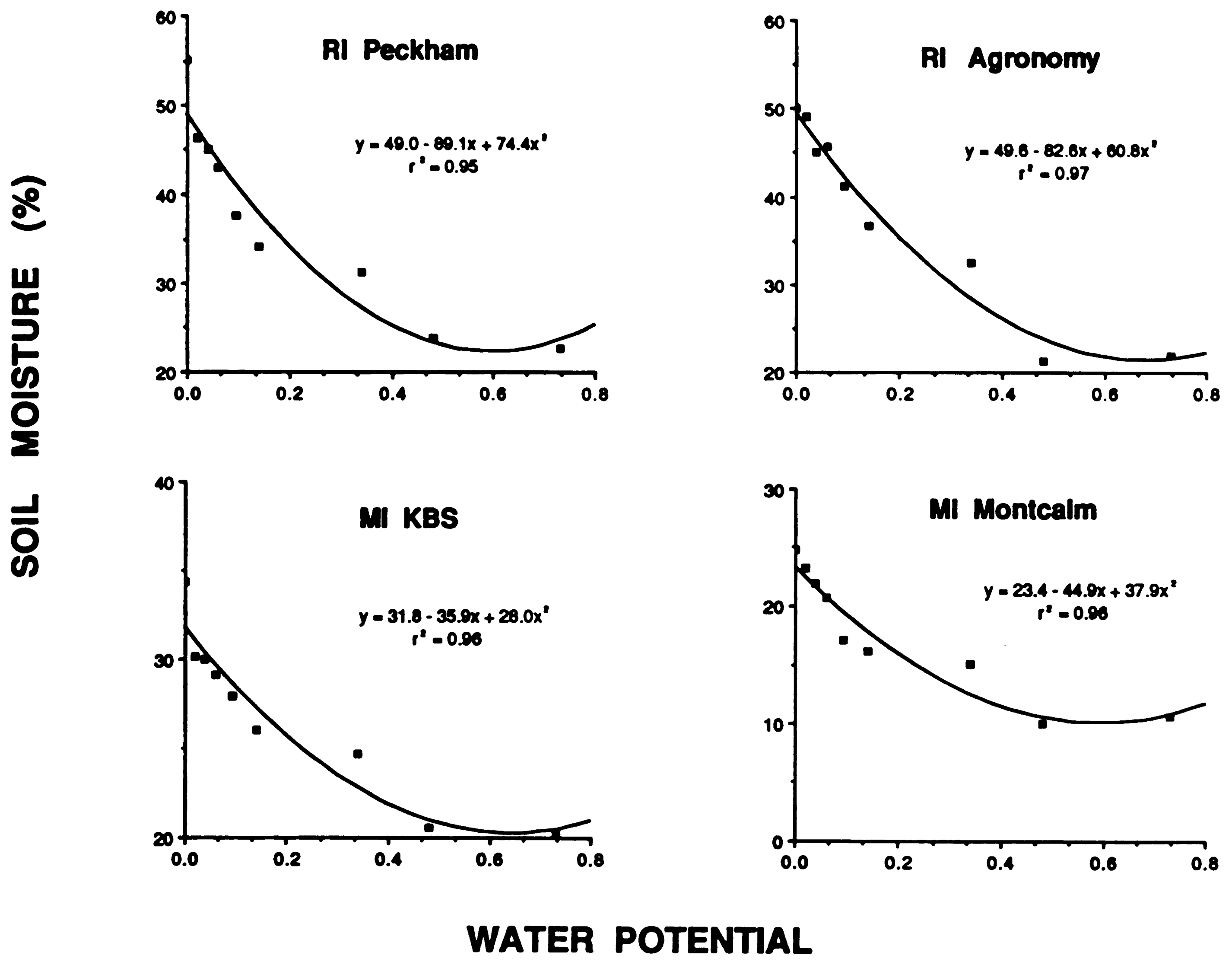
[2] percentage organic carbon

they differed in pH, organic matter and organic carbon contents. The texture of the Michigan soils differed considerably from each other and from the Rhode Island soils. The Montcalm soil was much sandier than the other soils, and the KBS soil had a higher clay content. Organic matter content and pH of the Michigan soils were similar, but differed from the Rhode Island soils. Organic matter content was higher in the Rhode Island soils, and the soil pH was lowest in one of the Rhode Island soils. The moisture characteristic curves for the different soils are given in Figure 1. These curves were used to standardize the water potential in the soils for the dose-mortality study.

Fungistasis Assay. The log-probit regressions of *B. bassiana* germination percentages in the fungistasis experiments are presented in Figure 2a,b. The equation coefficients, mean percentage germination across all concentrations, and the glucose concentration necessary for 50% germination for each soil type are given in Table 2. There was a significant difference in fungistasis levels between soils collected in 1986 ($F_{(3,129)} = 27.43$, $P = 0.0001$). Mean conidial germination was significantly less in both Michigan soils than in the Rhode Island soils. Germination also differed significantly between the Rhode Island soils in 1986, with the highest germination levels in the Peckham Farm sample. There were no significant differences in germination levels between the two Michigan soils.

In 1987 there was also a significant soil effect on germination of *B. bassiana* conidia ($F_{(3,175)} = 13.66$, $P = 0.0001$). Mean conidial germination was significantly less in the KBS sample than in all other soils tested (Table 2). There was greater variability in the germination response in the Montcalm soil in 1987 than when previously tested. Though the glucose concentration necessary for 50% germination in this soil was higher than that of the RI soils, germination was not significantly different when compared across all glucose concentrations. A repeated test with a glucose concentration of 312.5 μg / g soil revealed a significant soil effect on germination

Figure 1. Moisture characteristics curves for soils used in 1987 fungistasis assays and *Beauveria bassiana* dose-mortality study.


RI Peckham
$y = 49.0 - 89.1x + 74.4x^2$
$r^2 = 0.95$
RI Agronomy
$y = 49.6 - 82.6x + 60.8x^2$
$r^2 = 0.97$
MI KBS
$y = 31.8 - 35.9x + 28.0x^2$
$r^2 = 0.96$
MI Montcalm
$y = 23.4 - 44.9x + 37.9x^2$
$r^2 = 0.96$
60
50
40
30
20
10
0
0.0
0.2
0.4
0.6
0.8
SOIL MOISTURE (%)
WATER POTENTIAL

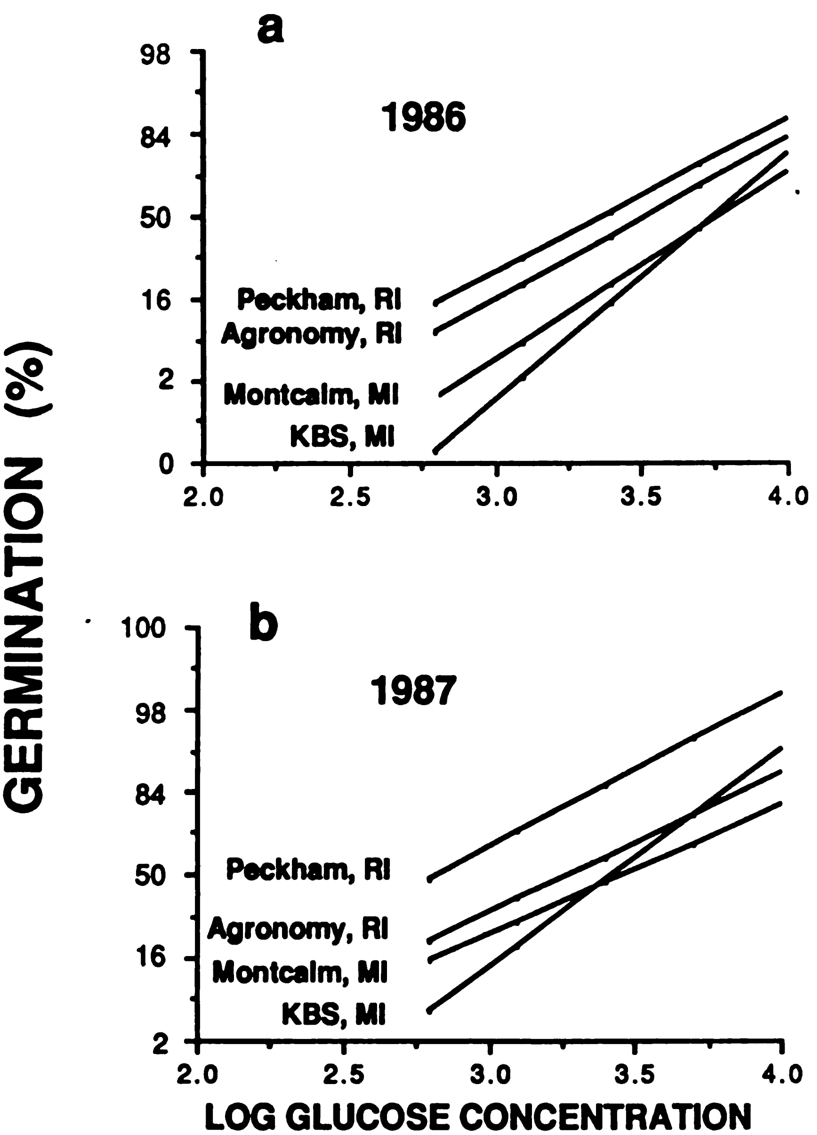


Figure 2. Log-probit regressions of germination of Beauveria bassiana in Rhode Island and Michigan soils in 1986 and 1987 as a function of added glucose-peptone (µg glucose/g soil).

Table 2. Germination and log-probit regression results from *Beauveria bassiana* fungistasis assay conducted for soils collected in 1986 and 1987 from potato fields in R.I. and Mich.

Soil	Germination[1] (%)	Log - probit[2] Regression Coefficients a	Log - probit[2] Regression Coefficients b	Estimated Glucose Concentration for 50% Germination (µg/g soil)
1986				
R.I. - Peckham Farm	43.5	-1.28	1.86	2371
R.I. - Agronomy Farm	35.4	-1.87	1.95	3348
Mich. - Kellogg Biological Station	24.3	-6.28	3.01	5624
Mich. - Montcalm Research Farm	23.1	-3.59	2.28	5916
1987				
R.I. - Peckham Farm	66.0	-0.27	1.87	665
R.I. - Agronomy Farm	69.5	0.50	1.68	480
Mich. - Kellogg Biological Station	41.0	-3.96	2.62	2654
Mich. - Montcalm Research Farm	59.4	0.40	1.56	877

[1] Mean over all glucose-peptone concentrations.

[2] Probit percent germination regressed on log concentration of glucose (µg/g soil).

between all soils, with germination in the Rhode Island soils greater than in the Michigan soils (Table 3).

There was no significant relationship between fungistasis levels and soil texture, percentage organic matter, or percentage carbon. However, using data from both years, there was a significant relationship between soil pH and fungistasis levels ($F_{(1,6)}$ = 23.32, P = 0.003). Fungistasis increased exponentially as pH increased (Figure 3).

Colloidal chitin stimulated germination of *B. bassiana* conidia in the absence of soil, but germination was significantly less than that observed on ground CPB elytra. In this first experiment, he percentage conidial germination (mean ± S.E.) was 26.6 ± 4.5 on colloidal chitin, 53.9 ± 2.4 on CPB elytra, and 5.1 ± 1.8 on the control. There was no chitin concentration effect on conidial germination ($F_{(3,7)}$ = 0.31, P = 0.82) in the second chitin experiment; however, there was a significant soil effect ($F_{(1,7)}$ = 145.70, P = 0.0001). Mean (± S.E.) percentage conidial germination on chitin was 44.6 ± 0.03 without soil, but only 1.3 ± 0.005 on soil. Ninety-nine percent of the *B. bassiana* conidia germinated on the SMA control. In the third experiment, in which conidial germination was compared on colloidal chitin in the presence of four different soils, no conidia germinated in any of the soil treatments. In the absence of soil, mean (± S.E.) conidial germination on colloidal chitin was 40.6 ± 14.8, and on SMA was 99.0.

Dose-mortality Study. Mortalities of CPB pupae incubated in the different soils, resulting from inoculation with differing concentrations of *B. bassiana,* are given in Table 4. There was a significant dosage effect on CPB pupal mortality ($F_{(4,20)}$ = 15.95, P = 0.0001), but no significant soil effect, and no significant soil X dosage interaction effect in the dose-mortality study with the four soils. There were significant dosage and soil effects on *B. bassiana* sporulation in dead pupae (for dosage: $F_{(5,30)}$ = 63.78, P = 0.0001; for soil: $F_{(4,30)}$ = 3.43, P = 0.02, and for dosage X soil: $F_{(20,30)}$ = 1.94, P = 0.049) (Tables 5 and 6). Over all dosages, fewer individuals sporulated in the Michigan soils than those in the Rhode Island soils. Regressing the

Table 3. Germination of *Beauveria bassiana* conidia in Rhode Island and Michigan soils with 312.5 µg glucose per g of soil, 1987.

Soil	% Germination (mean ± S.E.)
R.I. - Peckham Farm	61.7 ± 2.05
R.I. - Agronomy Farm	49.2 ± 5.44
Mich. - Kellogg Biological Station	3.3 ± 1.25
Mich. - Montcalm Research Farm	19.6 ± 3.62

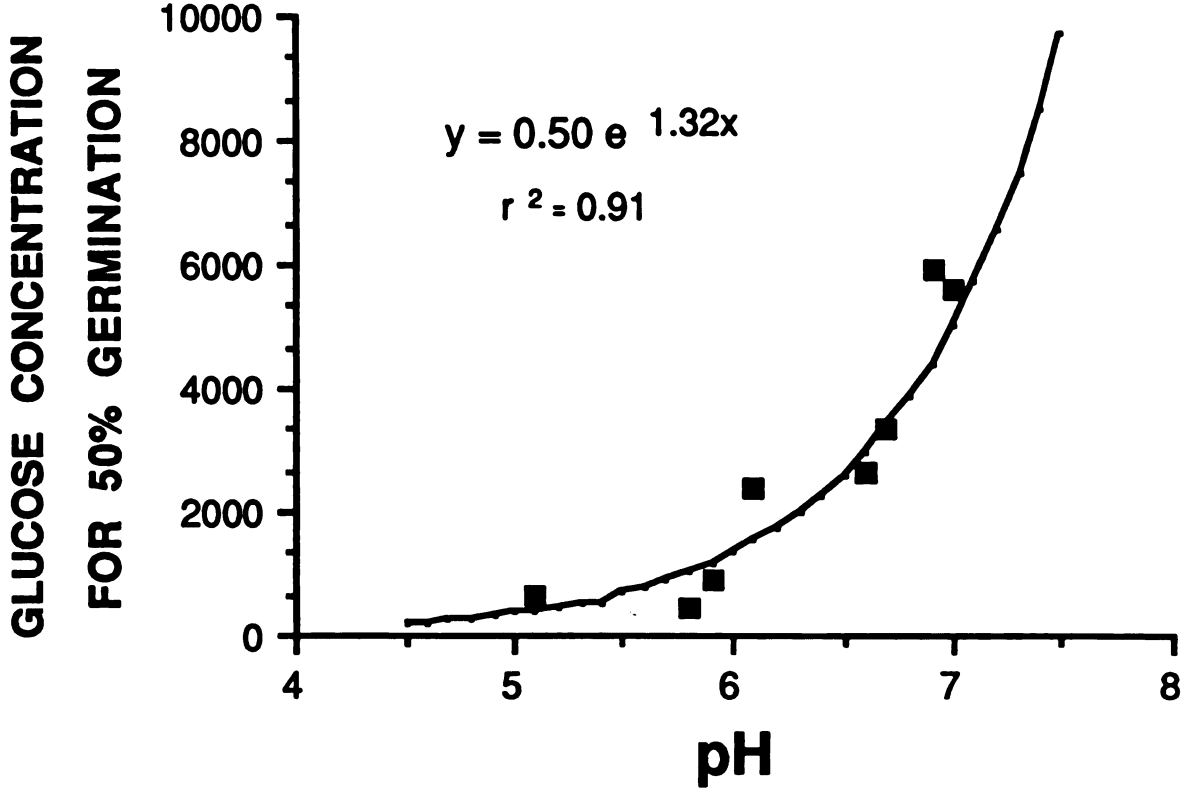


Figure 3. Relationship between fungistasis (expressed as glucose concentration required for 50% germination of *Beauveria bassiana* conidia) and soil pH.

Table 4. Mortality of CPB pupae inoculated with *Beauveria bassiana* and incubated in different soils from Rhode Island and Michigan, 1987.

	Mortality (%)[1]				
No. of conidia applied per pupa	Peckham Farm	Agronomy Farm	Kellogg Biological Station	Montcalm Research Farm	No Soil
Test 1:					
10^7	100.0	100.0	100.0	100.0	100.0
10^6	75.0	95.0	80.8	63.3	83.9
10^5	50.0	75.0	50.0	50.0	45.0
0	35.0	30.0	20.6	25.0	24.8
Test 2:					
10^5	90.0	66.7	60.0	55.6	70.0
10^4	60.0	60.0	22.2	30.0	40.0
10^3	40.0	20.0	20.0	50.0	33.3
0	0.0	10.0	30.0	20.0	20.0

[1] Mean of two replicates with 10 pupae per replicate in test 1, and single replicate with 10 individuals in test 2.

Table 5. Sporulation of ***Beauveria bassiana*** on CPB prepupae inoculated with different concentrations of conidia averaged over all soils and replications (n = 10 individuals per replication).

Conidia per pupa	Mean number of pupae sporulating
10^7	8.1
10^6	6.1
10^5	1.2
10^4	0.8
10^3	0.6
0	0.3

Table 6. Sporulation of *Beauveria bassiana* in inoculated CPB pupae in Rhode Island and Michigan soils averaged over all dosages and replications (n = 10 individuals / replication).

Soil	No. of pupae with spores
R.I. - Peckham Farm	3.1
R.I. - Agronomy Farm	4.1
Mich. - Kellogg Biological Station	2.3
Mich. - Montcalm Research Farm	2.3

estimated LD_{50} values for *B. bassiana* mortality in each of the soils with the fungistasis levels revealed a significant relationship ($F_{(1,2)} = 11.55$, $P = 0.077$). As the fungistasis levels increased, the LD_{50} values increased at a decreasing rate (Figure 4).

DISCUSSION

B. bassiana fungistasis levels were lower in the soils from Rhode Island than in those from Michigan in both years tested, and fungistasis was higher in the Montcalm, Michigan soil in 1986 than 1987. The differences in fungistasis were correlated with differences in soil pH between sites and years, but not with other soil characteristics measured, which included soil texture, percentage organic matter, and percentage carbon. Sharapov and Kalvish (1984) found fungistasis levels for *B. bassiana* to vary between soils, with increasing fungistasis corresponding to increased organic matter content. They also found fungistasis to vary with the seasons, with the greatest inhibition of *B. bassiana* germination in soils collected in the summer, and the least in soils collected in the winter. However, they did not report the pH of the soils. Other researches have shown increases in fungistasis of *B. bassiana* conidia in soils higher in organic matter, either from soils collected from different depths (Clerk 1969), or with the addition of organic amendments (Lingg and Donaldson 1981). Fungistatic effects on soil-borne plant pathogens are expressed most strongly in neutral or slightly acid soils (Lockwood 1977), possibly due to reduced competition from soil bacteria and actinomycetes which generally grow best at neutral pH, and are less tolerant of acid conditions than fungi (Gray and Williams 1971). Wartenberg and Freund (1962) implicated actinomycetes and possibly other bacteria as inhibitory agents to *B. bassiana* germination in soil. *B. bassiana* conidia are extremely small (2.4 µm), and Woods and Grula (1984) and Hunt et al. (1984) have both demonstrated the importance of exogenous nutrients on the surface of insect hosts in the stimulation of conidial germination. Natural soils are energy poor environments for the abundance of microbes

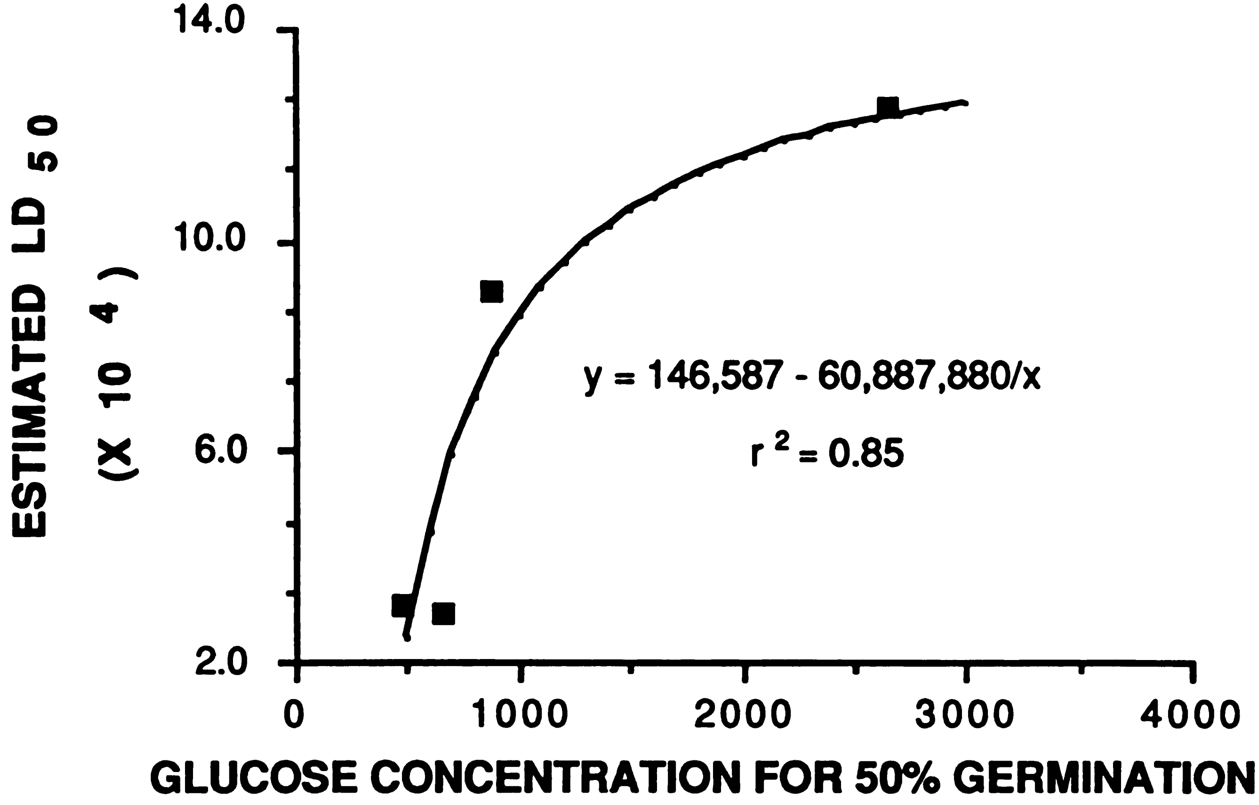


Figure 4. Relationship between fungistasis (expressed as glucose concentration required for 50% germination of *Beauveria bassiana* conidia) and estimated LD50 values (conidial concentrations/pupa necessary to kill 50% of the population).

inhabiting them (Lockwood and Filonow 1981). In this study, as in others, the ability to counter fungistatic effects with the addition of nutrients would suggest that nutrient deprivation due to intense competition for limited resources in the soil environment (Lockwood 1977) limits *B. bassiana* conidial germination. Lingg and Donaldson (1981) found that the common soil fungus *Pencillium urticae* grown in culture produced a water soluble inhibitor to *B. bassiana,* but they provided no direct evidence for the production or action of this inhibitor on germination of conidia in soil.

It is unknown whether pH may have a direct effect on germination of *B. bassiana* conidia. Although the fungus is routinely cultured in media at neutral pH, Saminakova et al. (1981) report maximum sporulation of the fungus at a pH of 5. It is not ruled out that differences in fungistasis levels between soils are due to the direct effect of pH on *B. bassiana* germination.

Colloidal chitin did not prove to be an effective amendment for quantifying fungistatis against *B. bassiana* in soils. In the absence of soil, colloidal chitin did not stimulate germination of *B. bassiana* conidia as readily as ground CPB elytra. Smith and Grula (1983) examined the response of *B. bassiana* conidia to different forms of chitin, and found that crude forms of powdered commercial chitin contain large amounts of protein which is removed in the preparation of colloidal chitin. These proteins stimulate germination of *B. bassiana* conidia, inducing the synthesis of chitinase. Woods and Grula (1983) reported that nutrients present on the surface of *Heliothus zea* larvae are sufficient for the germination and limited growth of infecting conidia, suggesting that in the natural process of infection, other exogenous energy sources would be more readily available to the fungus than the purified chitin macromolecule. That colloidal chitin was not stimulatory to conidial germination in the presence of soil suggests that other organisms in the soil may out-compete the fungus for this energy source, and may produce substances, such as ammonium, that could build up within the petri dish and inhibit the fungus.

Researchers have suggested that the fungistatic effects of soil on *B. bassiana* conidia are overcome by the introduction of insect hosts in the soil (Wartenburg and Freud 1961, Clerk 1969). Although we could not detect significant differences in CPB pupal mortality between soils over the range of *B. bassiana* inoculum tested, a significant trend of higher LD_{50} values with increased fungistasis levels in the soils was seen. This would suggest that more highly fungistatic soils would require higher concentrations of *B. bassiana* inoculum for a level of control equivalent to that in soils with lower fungistasis. Isakeit and Lockwood (1986) compared fungistasis levels with disease incidence for two plant pathogens, *Fusarium oxysporum* f. sp. *lycopersici* and *F. oxysporum* f. sp. *conglutinans*, and found an inverse relationship between disease incidence and fungistasis for *F. oxysporum* f. sp. *lycopersici*, but did not show a direct relationship with the other pathogen. However, our study demonstrated a significant relationship between fungistasis and disease by *B. bassiana*. This relationship warrants further investigation if pest management practices incorporating *B. bassiana* treatments are to be developed.

The decreased number of sporulating pupae in the Michigan soils compared with the Rhode Island soils may represent greater activity by secondary invading organisms in the Michigan soils suppressing *B. bassiana* development in infected individuals. Although *B. bassiana* is known to produce antibiotics that can suppress the growth of common saprophytes (Walstad et al. 1970), some inoculated individuals appeared to succumb to bacterial infection rather than to *B. bassiana*. The proportion of sporulating individuals among those that died was least at the lower inoculum concentrations and greatest at inoculum concentrations of 10^6 and 10^7 conidia per CPB. Regardless of the mechanism responsible for the decreased sporulation in the Michigan soils, it would result in lower populations of *B. bassiana* conidia in these soils. After monitoring the natural mortality of the CPB in these soils in Rhode Island and Michigan for three years, Groden (1988) found no mortality due to *B. bassiana* in Michigan CPB populations, whereas it was a major source of mortality in Rhode Island populations. Although differences in endemic disease levels in Michigan and Rhode Island soils are usually attributed to climatic conditions, this study suggests that differences between the fungistatic capacities of the soils may also influence the ecology of *B. bassiana* in the two regions.

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SUMMARY and CONCLUSIONS

These studies of the natural mortality of the Colorado potato beetle represent the first steps in the process of exploring the potential and developing and integrating biological control of the CPB into future potato production systems. The comparative approach of this study enabled us to explore the sources and impact of natural mortality under a variety of conditions, which has lead to insights that may have been obscured by solely examining mortality in the current conventional potato cropping system. Contrasting CPB populations in early and late planted potatoes it was observed that in isolated late plantings, the colonizing summer adult population was only a fraction of that observed in early planted potatoes. The timing of emergence of summer adults and their subsequent colonization of late plantings determined the proportion of the population that was reproductively active, the length of the oviposition period, and hence, the egg recruitment into late plantings. Manipulating planting date to reduce the number of reproductively active colonizing adults may be the most direct way to reduce CPB populations.

Evaluating seasonal densities and stage-specific survival for CPB populations was not possible with methodologies presented to date. Methods were developed in this study that required estimates of recruitment into the egg stage and adult emergence. It was found that estimating densities and survival of small larvae was further complicated by sampling errors and an increasing survival rate throughout the stage. The sampling errors were found to be related to density, and predictable, and a exponentially increasing survival function was applied for estimating density of small larvae. Because recruitment was not measured directly or could not be estimated for some of the potato research sites in this study, analysis of key factors in within generation survival was limited to those sites in which complete estimates of stage-specific survival were attainable. These did include plantings from both early and late planted potatoes in both regions with a range of regional population pressures.

Analysis of key factors in within generation survival of CPB revealed large larval and pupal survival to be most highly correlated with total survival in all plantings. When early and late plantings were analyzed independently, egg survival was found to be the key factor in early planted potatoes. Although pupal survival was found to be density dependent, survival increased with increases in density. (Mortality was inverse density-dependent.) Parasitism by the tachinid *Myiopharius doryphorae* appeared was responsible for the significant variations in pupal survival, but this parasitoid did not respond to changes in host density. *M. doryphorae* was most abundant in the late season, and was poorly synchronized with its host populations. Parasitism levels were highest when hosts became available later in physiological time. Again, manipulating planting date to manage the phenology of host populations could result in improving the synchrony of this parasitoid with its host, and its impact on pest suppression.

None of the mortality factors measured in this study explained the variations in survival of large larvae. It can be speculated that mortality by the fungal pathogen, *B. bassiana* , the impact of which is difficult to quantify in larvae, or that by the predator, *L. grandis* , whose densities were not adequately monitored throughout most of this study, may be responsible. There is no evidence of significant abiotic sources of mortality of large CPB larvae.

Although none of the mortality factors measured throughout this study explained the variations in egg survival over all plantings, analysis of the mandibulate preyed eggs in the Rhode Island and Michigan plantings in 1987 indicate that predation by *L. grandis* was the key factor. *C. maculata* densities were not correlated with egg survival, but they were significantly correlated with survival of their total CPB prey (eggs plus small larvae) in Rhode Island plantings. Further specific studies of these predators concurred with these results.

L. grandis which fed on all immature stages of the CPB over a wide range of temperatures, consumed more CPB prey than per individual than any other natural enemy studied to date. The contributions of this predator to the natural mortality of CPB may have been overlooked in previous studies due to its primarily nocturnal habits, and because the signs of egg predation by *L. grandis* are indistinguishable from that of cannibalizing CPB adults. The use of burlap traps if sampled early in the day proved to be an effective means of sampling for this predator. *L. grandis* adults were well synchronized with both first and second generation prey in the Northeast and Northcentral regions, with summer adults emerging as second generation CPB eggs are laid.

L. grandis is a particularly interesting natural enemy of the CPB, because not only do the adults appear to be specific predators of this pest, but the larvae of *L. grandis* live as ectoparasitoids on the pupae of the same host. Tethering CPB prepupae proved to be an effective method of sampling for *L. grandis* parasitism, and showed that *L. grandis* parasitism can account for greater than 50% mortality in first generation CPB pupae.

There are many aspects of the biology of this predator that remain to be explored. Adults appeared to be long-lived in the field, and though they appear to highly prefer CPB prey, they will switch to aphids when the former host is not available. Little is known of factors influencing *L. grandis* survival. It was observed that *L. grandis* adults do become infected with *B. bassiana*. The relationship between *B. bassiana* strains infecting CPB and those infecting the predator should be examined before integration of these two CPB biocontrol agents is encouraged.

C. maculata is a polyphagous predator and was found to feed on the eggs and small larvae of the CPB. This predator was well synchronized with its CPB prey in both early and late potatoes if Rhode Island, but only early potatoes in Michigan. When studying the dynamics of this predator, it is necessarily to consider all available prey. It does not appear to preferentially feed on aphids, but as aphids become more abundant on potatoes, their impact on CPB prey declines. *C. maculata* feeds on many food sources in many cropping systems. A better understanding of its regional population dynamics and its movement between crops is necessary before the potential for managing this predator can be evaluated. A multi-cropping system may be advantageous in providing continuous food sources for *C. maculata,* but highly preferred food sources such as corn pollen could function to draw the predator away from target pests. These relationships need to be examined if this predator is to be managed.

B. bassiana has been identified as a prominent source of CPB mortality in Rhode Island in previous studies. It was evident in the first year of the study that *B. bassiana* infections were much lower in Michigan than Rhode Island. As this fungus is primarily a soil borne pathogen, aspects of *B. bassiana* ecology in the Rhode Island and Michigan soils were compared. The comparisons of fungistasis in soils from the two regions revealed greater suppression of conidial germination in Michigan soils. This was found to be related to the pH of the soil, and may directly effect the incidence of the disease. That *B. bassiana* inoculated pupae were less likely to sporulate in Michigan than Rhode Island soils would further add to the lower incidence of the disease in Michigan CPB populations.

Soil formulations of *B. bassiana* are being developed commercially for control of several insect pests, including the CPB and the corn rootworm. The relationships between soil characteristics and the ecology of this pathogen should be further explored to maximize the effectiveness of this pest control measure.

Although no single natural enemy appears to regulate CPB populations in commercial potato production, this study has demonstrated that in some situations, natural mortality can suppress CPB populations in potatoes below economically damaging levels. Perhaps the more important question from the perspective of CPB pest management is: what regulates populations of CPB natural enemies? The dynamics of the specific predators and parasitoid, *L. grandis, P. bioculatus,* and *M. doryphorae* may be influenced by abiotic factors, and natural enemies of their own. That of the general predators, *C. maculata* and *P. maculiventris* , is also likely influenced by the distribution and abundance of alternate hosts. This next level of interactions must be examined to in order to identify mechanisms for enhancing natural enemy populations and biological control of the CPB.

APPENDICES

APPENDIX A

Modeling CPB Recruitment

APPENDIX A

Modeling CPB Recruitment

Attempts were made to develop a predictive model for CPB egg recruitment using multiple regression analysis with X-variables of adult incidence in physiological time (adult-dd), adult incidence in chronological time (adult-days), and accumulated degree-days (base 10°C). Recruitment, density, and temperature data collected from Rhode Island and KBS potato plantings in 1985 and 1986, were used for the development and validation of the model. Although models based on individual plantings were successful in explaining much of the variation in egg recruitment within a planting (r^2 values were generally very high), when compared between plantings and years, the models were poor predictors of egg recruitment either by day, week, or generation.

A second approach was taken which involved developing a computer simulation model of CPB oviposition to predict egg recruitment over a generation. The model-building software package, STELLA®, was used for this purpose. STELLA® was developed by High Performance System, Inc. for use on Apple Computer, Inc.'s Macintosh computers. STELLA® allows one to build models of dynamic systems by diagraming the conceptual framework of a model. This involves identifying the necessary components of the model, and defining the direction of flows between these components. Once this is complete, one can add the quantitative relationships that determine the rate of flows between components, either with equations, graphs, or tables. The STELLA® program converts these into differential equations which it solves numerically. The user sets the step-size (dt) of the model. When running the model, one can choose either graphical or tabular forms for the model output. As with most of the Macintosh software, STELLA® is a menu driven program, and the feedback for errors both in the conceptual model construction and the quantifying of relationships is very precise.

The STELLA® diagram of the CPB oviposition model is presented in Figure A1. The daily rate of CPB oviposition is defined as a function of adult density and daily degree-day accumulations (dd):

$$\text{oviposition} = \text{adults}/2 * ((2.21 * \text{dd}) - 4.434).$$

This linear function was developed from temperature dependent fecundity data presented by Grison (1950; Figure A2). The dt of the model equaled one day, and eggs are accumulated throughout the generation. The adult densities observed in the research plantings were inputted graphically as a function of accumulated degree-days, and degree-day accumulations were inputted by day. The models for each planting were run with colonizing adult densities only, to avoid the complications of a preoviposition period. Therefore, models were run to simulate oviposition of a single generation, and were ended before emergence of the next adult generation. The sex ratio of observed adults was assumed to be 50:50.

The model was run for plantings in which CPB egg recruitment was measured directly, or estimated from the density of preyed eggs. These included: the late planting in 1985 in Rhode Island and both early and late plantings in Rhode Island in 1986 and 1987, early plantings at KBS in 1986 and 1987, and early and late plantings at Montcalm in 1987. The predicted egg recruitment and the observed or estimated egg recruitment for each of these plantings are presented in Table A1. The variability in the accuracy of the oviposition model's predictions (underestimating recruitment in some instances and overestimating it in others) reveals that there are essential aspects of CPB dynamics that influence oviposition rates that are not accounted for in this simplistic model. However, some similarities in the predictions and observations of oviposition in the field are worth noting.

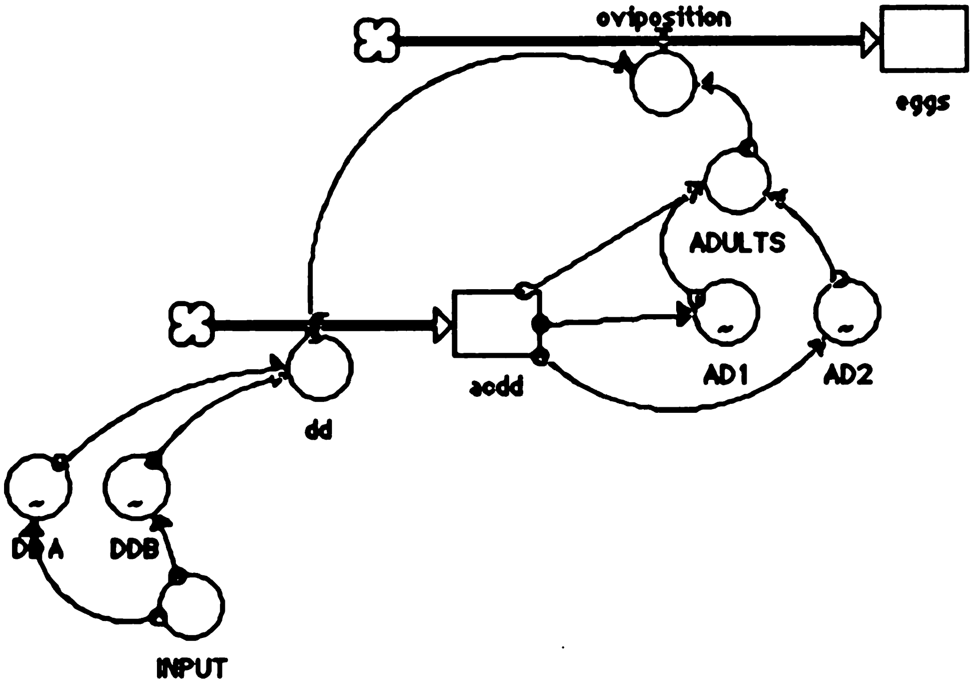

Figure A1. Diagram of Stella® model of CPB oviposition

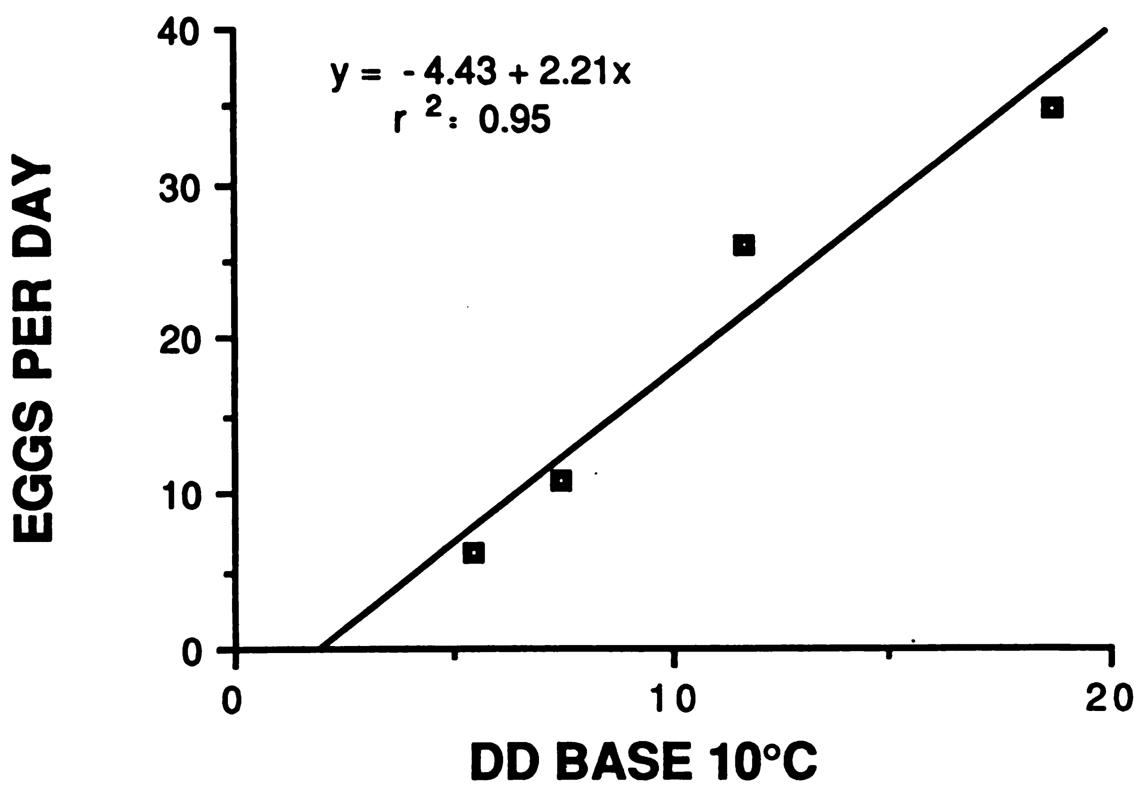

Figure A2. CPB daily oviposition rate as a function of degree-day accumulations (data from Grison 1950).

Table A1. Predicted and observed egg recruitment in Rhode Island and Michigan potato research plantings, 1985-1986.

			Egg Recruitment		
Planting	Site	Year	Observed	Predicted	Ratio[1]
Early	Rhode Island	1986	362.8	162.7	0.45
		1987	443.0	203.8	0.46
	KBS	1986	59.8	68.7	1.02
		1987	234.0	270.2	1.15
	Montcalm	1987	434.8	200.0	0.46
Late	Rhode Island	1985	50.7	89.1	1.76
		1986	104.5	46.8	0.45
		1987	34.2	25.2	0.74
	Montcalm	1987	386.7	422.6	1.09

[1] Predicted/Observed.

Late plantings

As discussed in Manuscript 1, egg recruitment in late planted potatoes is related to the time the plot is colonized by CPB adults, because of the relationship between the timing of emergence of summer adults and the proportion of the population entering reproductive diapause. If the plot is colonized later by emerging adults, a smaller proportion of the population is reproductively active and ovipositing. Therefore, to predict recruitment in the late plantings, the proportion of the CPB adult population that is reproductively active must be known. Voss et al. (1988) determined the date after which emerging adults would be in reproductive diapause for Massachusetts, but suggests that this date would likely vary between populations in different geographic regions throughout the CPB's range. This would appear to be the case for Rhode Island and Michigan, because although first generation beetles generally emerged later in Rhode Island than Michigan, a larger portion of the Michigan population appeared to enter reproductive diapause. Because this was not monitored directly in this study, it was not possible to incorporate this relationship into the oviposition model and predict recruitments for late plantings.

Early plantings

It is interesting to note that the ratio of predicted to observed egg recruitment in early planted potatoes is consistent within the Rhode Island and Montcalm plantings, but varies between these and the KBS plantings. Field observations of CPB oviposition revealed that female beetles lay a considerable number of eggs on weeds in the potato field. Weed densities, although not sampled directly, were observed to be noticably higher at the KBS site than the Rhode Island or Montcalm sites. A study of oviposition on weeds at the KBS site (see Appendix C) revealed that about 60% of the egg masses oviposited at this site may have been on weeds in the potato field. These eggs were not taken into account when estimating egg recruitment in this plot. If the 60% eggs on weeds is added, the observed egg recruitment in 1986 and 1987 at the KBS site was 149.5 and 585.0 eggs, respectively. With these estimates, the ratio of predicted to observed in these plantings was 0.46 and 0.46 respectively, consistent with that observed in the early plantings at the Rhode Island and Montcalm sites.

The consistency of the error in the model predictions indicates that whatever factor or factors influencing the number of eggs oviposited is in direct proportion to temperature and adult densities which drive the model. The laboratory fecundity study from which this model was based, may under represent oviposition in the field at a constant proportion. This study was based on the avg. fecundity per day over the life of the beetle, with an average longevity of 118 days. Differences in the rate of oviposition over the life of the females were not reported. Kowalska (1969) did find that the oviposition rate of overwintered females declined dramatically after 30 to 40 days, although they continued to oviposit for 110 days. In Kowalska's study, the avg. oviposition rate estimated over 110 days was 55% of the avg. estimated over the first 40 days. Egg recruitment observed in the early plantings in this study represent those eggs oviposited by female beetles within the first 40 days of spring emergence, thus, the oviposition rate would be expected to be higher than that observed over a longer period. As the rates used in the model are based on those observed over the life of the beetle, this could account for the error in the model's predictions.

This model assumes a constant 50:50 sex ratio throughout the generation. There is some indication that the mortality rate of males may be greater than that of females, which would change the sex ratio of the field population over time. This would also result in underestimating recruitment with the model.

The consistency of the error in predicted versus observed recruitment over a range of densities and sites, allows us to incorporate a scaling factor into the model to correct for this error regardless of its cause. Therefore, the oviposition model with the scaling factor was used to predict egg recruitment in the 1985 early planting in Rhode Island, and the 1986 early planting in Montcalm.

APPENDIX B

CPB Oviposition on Weeds

APPENDIX B.

CPB Oviposition on Weeds

In 1987 at the KBS site, it was observed that a number of CPB egg masses were oviposited on weeds in the potato field. This was thought to represent a considerable source of mortality, because first instar larvae emerging from hatching egg masses cannot feed on these weeds, and are not very efficient at locating their host plant (Harcourt 1971). Thus a study was initiated to determine what proportion of the CPB eggs oviposited in the potato field were oviposited on non-host plants.

MATERIALS AND METHODS

In 1987, two potato research plots at the KBS site were sampled to determine the proportion of CPB eggs oviposited on weeds in these two plots. The first plot consisted of 30 x 30 m of Caribe´ potatoes planted during the first week of May. The second plot consisted of 30 x 15 m of Russett Burbank potatoes planted in mid May. Potato seed pieces were hand planted ca. 30 cm apart in a row and ca. 90 cm between rows. In both plots a range of weed densities were maintained with hand weeding and mechanical cultivation, and no pesticides were applied. The sample unit for this study consisted of a 100 x 90 cm quadrat centered a row of potatoes. Within each quadrat the densities of potatoes and weeds were recorded and all plants were examined for healthy and preyed CPB egg masses. The densities of weeds were recorded by the following predominant weed types: grasses, lambs quarter (*Chenopodium album*), red root pigweed (*Amaranthus retroflexus*), and others. Others were those weeds found sporadically at very low densities and included: purslane (*Portulaca oleracea*), velvet leaf (*Abutilon theophrasti*), milkweed (*Asclepias syriaca*) and yarrow (*Achillea millefolium*). In the Caribe´ plot, 20 randomly selected samples were taken on May 30, June 6, and June

17, and in the Russet burbank plot, 25 and 14 samples were taken on June 7 and June 18, respectively.

Analyses of covariance (SAS Institute 1985) were conducted for each week to test for differences in egg densities by plant type. Plot and plant type density were covariates. Analyses of covariance were similarly conducted to test for differences in the arcsin proportion of preyed egg masses.

RESULTS AND DISCUSSION

CPB adults did lay significantly more egg masses on potatoes than any individual weed type in the samples (Table B1). However, over all weed types, 63 ± 0.04 percent of the egg masses were oviposited on weeds. The arcsin proportion of eggs on weeds was regressed with weed density, and though a significant regression resulted, weed density explained only 3.3% of the variation in the proportion of eggs on weeds (Figure B1). The proportion of eggs preyed upon varied from 0 to 0.75. The natural logarithm of egg masses per plant was regressed with the natural logarithm of preyed egg masses per plant to determine if differences in predation levels were density dependent. The slope of the regression was significantly less than unity (slope ± S.E. = 0.65 ± 0.05), indicating that egg predation rates were density dependent. Therefore, the significantly higher predation levels on potatoes over grasses in the week 1 sample, and pigweed over grasses in the week 3 sample can be explained by predators response to increased in egg densities on these plant types. Otherwise, there were no differences in egg predation between weed hosts and potato.

Visser and Ave (1978) reported that CPB adults respond to "green-leaf" volitales in long range host finding. As CPB females have frequently been observed ovipositing, not only on nonhost plants in potatoes, but wooden stakes left in the field, it appears that their short range host recognition is very poor. It is assumed that egg masses oviposited on nonhost plants result in 100% mortality of hatching first instars unless the leaves of

Table B1. Comparison of CPB egg densities and the proportion of eggs preyed upon on potato plants and weeds in potatoes at KBS research plots, 1987.

Week	Weed type	Weeds per sample[1]	Eggs per plant[2]	Proportion of eggs preyed[2]
1	grasses	9.70 ± 3.52	0.90a	0.06a
	lambs quarter	17.30 ± 2.91	1.45a	0.19ab
	redroot pigweed	9.20 ± 1.23	1.75a	0.32ab
	other[3]	0.15 ± 0.08	0.20a	0.00ab
	potato	2.90 ± 0.07	5.65b	0.45b
2	grasses	9.09 ± 1.45	2.09a	0.37a
	lambs quarter	26.35 ± 5.12	1.50ab	0.34a
	redroot pigweed	3.57 ± 0.94	1.35ab	0.36a
	other[3]	1.48 ± 0.41	0.30b	0.41a
	potato	3.04 ± 0.08	3.70c	0.60a
3	grasses	6.45 ± 1.14	0.45a	0.41a
	lambs quarter	18.42 ± 2.90	2.21ab	0.63a
	redroot pigweed	5.15 ± 1.19	2.45b	0.75b
	other[3]	1.21 ± 0.23	0.30a	0.42a
	potato	2.94 ± 0.16	3.94bc	0.50a

[1] Mean ± S.E. per 100 x 90 cm quadrat centered over a row of potatoes.

[2] Values followed by the same letter are not significantly different with LS means test (SAS Institute 1985) at p=0.05 corrected for the number of comparisons (Jones 1985).

[3] Other includes purslane, velvet leaf, milkweed, and yarrow.

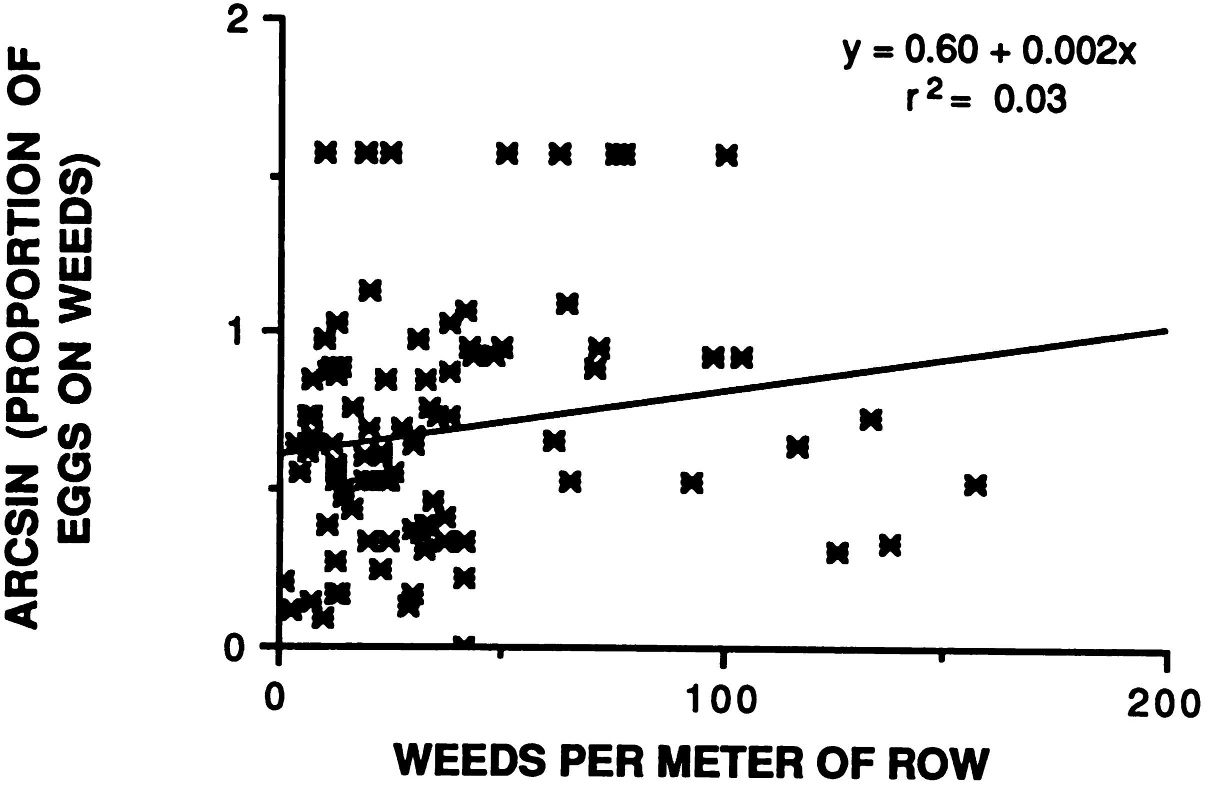

Figure B1. The proportion of CPB eggs oviposited on weeds in relation to weed density.

the nonhost plant touch those of potatoes. (Harcourt (1971) reported that small larvae are unsuccessful at reestablishing themselves on their host plant once they are knocked off.) The evidence indicates that CPB egg predators are just as likely to search nonhost plants as potatoes for prey, so predation is not avoided by oviposition on weeds. This seemly maladaptive behavior may provide potential for managing early season weeds or ground cover in potatoes to increase CPB mortality.

APPENDIX C

Densities of CBP Lifestages and Predators at Research Sites in Rhode Island and Michigan, 1985-1987

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Densities of CPB Lifestages and Predators at Research Sites in Rhode Island and Michigan, 1985-1987

Table C1. CPB densities at potato researh sites in Rhode Island (RI), and Michigan, 1985-1987. (JD=Julian Day, DD= Accumulated degree-days base 10°C from May 1)

		ADULTS		EGG MASSES		L1		L2		L3		L4	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
1985													
RI EARLY PLANTING:													
143	96	0.176	0.016	0.000	0.000								
148	127	0.582	0.047	0.669	0.051								
151	140	0.469	0.749	0.893	0.045								
155	171	0.825	0.049	1.615	0.060								
158	190	0.743	0.070	1.827	0.086								
162	218	1.056	0.080	2.728	0.127								
165	244	0.607	0.082	2.453	0.145								
169	274	0.827	0.104	3.620	0.218								
172	302	1.090	0.136	3.890	0.282								
176	341	0.670	0.100	2.920	0.432								
181	364	0.380	0.070	2.000	0.191								
186	427	0.210	0.054	1.100	0.134								
189	454	0.140	0.045	0.360	0.077								
192	489	0.320	0.066	0.280	0.057								
198	575	6.020	0.654	0.090	0.032								

Table C1. (continued)

		ADULTS		EGG MASSES.		L1		L2		L3		L4	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
RI LATE PLANTING:													
210	711	0.191	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
212	731	0.187	0.038	0.053	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
214	747	0.553	0.119	0.087	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
217	769	0.374	0.06 5	0.277	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
219	791	0.399	0.065	0.385	0.056	0.203	0.151	0.000	0.000	0.000	0.000	0.000	0.000
221	819	0.320	0.066	0.400	0.064	0.500	0.357	0.010	0.010	0.000	0.000	0.000	0.000
225	870	0.420	0.115	0.460	0.106	2.630	0.626	3.540	1.062	0.740	0.313	0.000	0.000
228	916	0.470	0.085	0.250	0.058	0.820	0.274	2.460	0.565	2.340	0.652	1.290	0.367
232	962	0.130	0.037	0.140	0.047	3.370	1.247	1.860	0.624	3.820	0.697	5.490	0.856
325	987	0.130	0.044	0.230	0.063	0.680	0.313	1.300	0.528	3.480	0.760	3.780	0.638
239	1035	0.060	0.034	0.060	0.034	0.140	0.140	0.330	0.174	1.810	0.369	4.760	0.685
246	1091	0.110	0.042	0.010	O.010	0.010	O.010	0.000	0.000	0.240	0.082	1.080	0.186
249	1134	0.691	0.095	0.009	0.009	0.000	0.000	0.118	0.068	0.100	0.043	0.445	0.104
252	1168	1.810	0.245	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.210	0.057
255	1183	1.340	0.180	O.000	0.000	0.000	0.000	0.010	0.010	0.010	0.010	0.080	0.034
KBS LATE PLANTING:													
199	217*	0.006	0.006	0.000	0.000								
206	298	0.030	0.015	0.000	0.000								
213	389	0.485	0.388	0.015	0.011								
220	464	0.182	0.049	0.227	0.183								
227	549	0.186	0.062	0.043	0.032								
234	617	0.000	0.000	0.000	0.000								
241	687	0.026	0.018	0.000	0.000								
246	736	0.714	0.714	0.000	0.000								

*FROM JULY 1

Table C1. (continued)

JD	DD	ADULTS MEAN	ADULTS S.E.	EGG MASSES MEAN	EGG MASSES S.E.	L1 MEAN	L1 S.E.	L2 MEAN	L2 S.E.	L3 MEAN	L3 S.E.	L4 MEAN	L4 S.E.
MONTCALM LATE PLANTING:													
190	178*	0.036	0.025	0.000	0.000								
197	253	0.078	0.022	0.190	0.042								
205	334	0.636	0.176	0.259	0.048								
211	397	0.422	0.069	0.547	0.078								
218	445	1.012	0.137	0.512	0.085								
225	516	0.449	0.083	0.474	0.091								
232	568	0.338	0.066	0.130	0.043								
239	613	0.279	0.047	0.007	0.007								
1986													
RI EARLY PLANTING:													
148	126	0.053	0.010	0.010	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
150	146	0.227	0.041	0.033	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
154	179	0.188	0.043	0.242	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
156	191	0.333	0.060	0.480	0.069	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
161	230	0.369	0.063	1.195	0.112	0.396	0.208	0.114	0.075	0.000	0.000	0.000	0.000
164	254	0.463	0.062	1.242	0.101	1.852	0.480	0.094	0.074	0.000	0.000	0.000	0.000
167	284	0.357	0.067	1.157	0.116	1.609	0.392	0.791	0.159	0.052	0.037	0.000	0.000
170	305	0.450	0.081	1.470	0.145	3.570	0.814	1.730	0.347	0.660	0.178	0.070	0.043
175	345	0.770	0.100	1.770	0.162	3.930	0.843	2.400	0.368	1.930	0.271	1.340	0.238
177	357	0.620	0.101	2.430	0.252	5.210	1.103	3.460	0.508	2.650	0.404	1.750	0.233
181	403	0.350	0.712	1.530	0.161	8.150	1.715	4.390	0.743	3.550	0.383	5.100	0.691
184	425	0.450	0.093	1.550	0.188	7.129	2.332	1.452	0.409	2.323	0.465	3.000	0.626
188	471	0.520	0.077	1.730	0.208	11.235	3.086	8.157	1.290	6.373	0.775	5.706	0.679
191	514	0.340	0.068	1.060	0.129	8.680	2.074	9.780	1.081	8.960	1.040	9.820	1.053
196	556	0.300	0.070	0.920	0.135	5.320	1.190	4.280	0.702	7.280	1.229	14.560	1.430
198	576	0.350	0.066	1.110	0.148	4.392	1.168	4.667	0.916	7.373	0.836	15.137	1.435

*FROM JULY 15

Table C1. (continued)

		ADULTS		EGG MASSES		L1		L2		L3		L4	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
203	633	2.390	0.197	0.470	0.081	1.961	0.845	1.510	0.403	3.510	0.436	12.627	1.333
205	656	3.290	0.073	0.360	0.073	0.547	0.213	0.717	0.312	1.302	0.286	6.887	0.797
210	715	8.765	0.971	0.196	0.063	0.471	0.413	0.059	0.033	0.255	0.068	1.706	0.251
RI LATE PLANTING:													
199	587	0.013	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
202	622	0.018	0.011	0.024	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
204	643	0.047	0.019	0.063	0.031	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
209	705	0.114	0.035	0.336	0.068	0.000	0.000	0.040	0.040	0.000	0.000	0.000	0.000
212	735	0.090	0.028	0.224	0.044	0.096	0.053	0.135	0.095	0.032	0.021	0.000	0.000
217	793	0.160	0.035	0.220	0.042	1.273	0.535	1.287	0.606	0.393	0.141	0.193	0.088
224	875	0.228	0.047	0.503	0.077	0.557	0.252	0.329	0.118	0.423	0.099	0.671	0.120
226	889	0.132	0.029	0.428	0.080	1.283	0.454	0.375	0.141	0.559	0.136	0.809	0.146
232	934	0.139	0.037	0.248	0.062	2.327	0.809	0.366	0.105	0.624	0.168	0.515	0.153
234	970	0.160	0.049	0.270	0.069	2.630	0.921	1.380	0.363	0.350	0.077	0.580	0.114
238	1005	0.099	0.033	0.119	0.038	1.208	0.508	0.683	0.159	0.911	0.171	0.554	0.125
247	1062	0.264	0.068	0.055	0.029	0.945	0.585	0.242	0.074	0.615	0.143	0.824	0.157
254	1115	0.178	0.049	0.033	0.019	0.089	0.056	0.044	0.027	0.111	0.043	0.411	0.097
265	1168	0.200	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.011	0.056	0.024
272	1227	0.242	0.093	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
KBS EARLY PLANTING:													
154	183	0.194	0.050	0.561	0.082	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
160	235	0.111	0.030	0.346	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
164	267	0.135	0.035	0.256	0.040	0.340	0.150	0.013	0.009	0.000	0.000	0.000	0.000
168	297	0.203	0.056	0.163	0.064	0.739	0.284	0.346	0.091	0.307	0.083	0.000	0.000
171	323	0.259	0.050	0.204	0.080	0.506	0.244	0.198	0.049	0.451	0.104	0.117	0.030
175	360	0.147	0.035	0.140	0.031	0.240	0.221	0.187	0.075	0.353	0.061	0.740	0.119

Table C1. (continued)

JD	DD	ADULTS MEAN	ADULTS S.E.	EGG MASSES MEAN	EGG MASSES S.E.	L1 MEAN	L1 S.E.	L2 MEAN	L2 S.E.	L3 MEAN	L3 S.E.	L4 MEAN	L4 S.E.
178	393	0.141	0.035	0.372	0.110	1.250	0.428	0.135	0.044	0.227	0.074	0.733	0.102
182	420	0.067	0.020	0.027	0.013	0.520	0.180	0.120	0.043	0.227	0.074	0.733	0.102
184	434	0.153	0.043	0.080	0.080	0.320	0.193	0.160	0.057	0.267	0.062	0.713	0.117
188	491	0.140	0.034	0.047	0.017	0.007	0.007	0.040	0.016	0.273	0.084	1.027	0.134
191	521	0.179	0.040	0.077	0.030	0.128	0.067	0.103	0.041	0.359	0.070	1.442	0.205
195	564	0.153	0.035	0.240	0.173	0.007	0.007	0.027	0.016	0.107	0.027	0.593	0.113
198	617	0.280	0.040	0.127	0.101	0.000	0.000	0.007	0.007	0.047	0.020	0.280	0.058
202	678	0.288	0.045	0.006	0.006	0.000	0.000	0.000	0.000	0.026	0.026	0.269	0.059
205	719	0.523	0.064	0.067	0.026	0.000	0.000	0.007	0.007	0.040	0.028	0.087	0.033
209	768	0.645	0.117	0.461	0.303	0.105	0.105	0.066	0.066	0.092	0.038	0.184	0.097
212	804	0.629	0.010	0.126	0.057	0.093	0.080	0.046	0.046	0.086	0.030	0.166	0.034
216	839	0.193	0.037	0.073	0.038	0.000	0.000	0.033	0.017	0.060	0.019	0.293	0.066
220	879	0.253	0.044	0.007	0.007	0.147	0.080	0.107	0.046	0.160	0.035	0.500	0.079
223	906	0.060	0.019	0.000	0.000	0.000	0.000	0.013	0.009	0.020	0.011	0.391	0.064
KBS LATE PLANTING-1													
202	678	0.106	0.012	0.160	0.016	0.060	0.030	0.020	0.015	0.000	0.000	0.001	0.001
205	719	0.193	0.036	0.280	0.041	1.153	0.500	0.020	0.011	0.027	0.021	0.287	0.198
209	768	0.408	0.053	0.159	0.036	0.643	0.224	0.535	0.206	0.236	0.082	0.153	0.086
212	804	0.574	0.076	0.142	0.046	0.878	0.225	0.811	0.176	0.264	0.063	0.068	0.027
216	839	0.216	0.049	0.094	0.032	0.727	0.292	0.453	0.112	0.554	0.080	0.381	0.069
219	869	0.274	0.049	0.051	0.018	1.134	0.417	0.414	0.096	0.306	0.057	1.497	0.162
223	906	0.195	0.047	0.013	0.009	0.182	0.115	0.156	0.059	0.117	0.034	0.662	0.086
226	931	0.054	0.023	0.000	0.000	0.061	0.061	0.101	0.030	0.203	0.050	0.459	0.075
230	980	0.060	0.019	0.013	0.009	0.000	0.000	0.013	0.009	0.013	0.009	0.173	0.040
233	1009	0.027	0.013	0.000	0.000	0.000	0.000	0.100	0.063	0.020	0.011	0.100	0.025
238	1049	0.161	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.016	0.042	0.017
244	1074	0.073	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007

Table C1. (continued)

		ADULTS		EGG MASSES		L1		L2		L3		L4	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
250	1112	0.027	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007
KBS LATE PLANTING-2													
202	678	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
205	719	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
209	768	0.051	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
212	804	0.113	0.027	0.099	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	839	0.131	0.034	0.131	0.065	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
220	869	0.080	0.024	0.080	0.024	0.340	0.166	0.393	0.225	0.000	0.000	0.000	0.000
223	906	0.053	0.016	0.029	0.014	0.112	0.093	0.015	0.011	0.005	0.005	0.000	0.000
226	931	0.034	0.015	0.007	0.007	0.000	0.000	0.013	0.009	0.040	0.016	0.007	0.007
231	980	0.013	0.009	0.000	0.000	0.060	0.054	0.268	0.110	0.074	0.029	0.289	0.063
233	1009	0.006	0.006	0.000	0.000	0.000	0.000	0.038	0.027	0.058	0.029	0.391	0.079
239	1051	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007	0.127	0.038
246	1092	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.010
250	1112	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007
MONTCALM EARLY PLANTING													
156	207	0.950	0.101	1.381	0.125	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
161	245	0.844	0.096	3.525	0.174	1.194	0.578	0.000	0.000	0.000	0.000	0.000	0.000
167	295	0.456	0.068	2.444	0.174	18.125	1.621	2.781	0.416	0.231	0.165	0.000	0.000
174	357	0.147	0.049	1.200	0.165	16.973	2.130	17.627	1.788	15.467	1.806	4.307	0.674
181	411	0.022	0.022	0.370	0.095	9.435	2.086	17.696	2.094	34.500	3.605	33.348	3.268
188	482	0.013	0.009	0.031	0.013	0.525	0.136	2.213	0.268	7.350	0.556	18.025	0.949
194	540	4.807	0.414	0.000	0.000	0.000	0.000	0.233	0.056	0.927	0.111	7.220	0.647
MONTCALM LATE PLANTING													
202	648	3.073	0.240	0.027	0.013	0.000	0.000	0.000	0.000	0.007	0.007	0.020	0.011

Table C1. (continued)

JD	DD	ADULTS MEAN	ADULTS S.E.	EGG MASSES MEAN	EGG MASSES S.E.	L1 MEAN	L1 S.E.	L2 MEAN	L2 S.E.	L3 MEAN	L3 S.E.	L4 MEAN	L4 S.E.
208	720	1.422	0.118	0.022	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	807	1.444	0.152	0.093	0.026	0.320	0.145	0.247	0.090	0.180	0.079	0.027	0.013
223	874	0.133	0.031	0.053	0.020	0.973	0.268	1.627	0.359	0.887	0.181	0.207	0.071
230	940	0.113	0.029	0.047	0.017	0.160	0.111	0.027	0.013	0.333	0.079	0.420	0.084
241	1021	0.105	0.033	0.038	0.023	0.057	0.057	0.019	0.019	0.181	0.063	0.276	0.067
251	1077	0.158	0.039	0.008	0.008	0.000	0.000	0.008	0.008	0.025	0.019	0.092	0.037
1987													
RI EARLY PLANTING:													
154	170	1.127	0.093	1.217	0.083	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
160	208	0.884	0.089	3.123	0.146	1.923	0.498	0.000	0.000	0.000	0.000	0.000	0.000
168	278	0.952	0.105	4.357	0.282	37.143	3.291	12.352	1.001	2.410	0.420	0.343	0.130
175	359	0.520	0.086	3.405	0.325	27.000	5.670	23.050	3.500	33.100	4.566	24.250	4.476
183	431	0.097	0.051	0.183	0.051	1.630	0.355	5.609	0.805	13.261	1.346	31.022	2.513
191	612	0.677	0.142	0.152	0.052	0.091	0.032	0.313	0.110	1.242	0.187	8.697	1.116
RI LATE PLANTING:													
204	675	0.020	0.015	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
211	767	0.053	0.023	0.147	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
217	826	0.120	0.033	0.350	0.064	1.520	0.514	0.090	0.081	0.060	0.060	0.000	0.000
225	921	0.070	0.029	0.160	0.075	0.700	0.244	0.920	0.396	1.100	0.368	0.570	0.181
232	1006	0.080	0.030	0.099	0.054	0.337	0.317	0.069	0.032	0.297	0.121	0.782	0.138
238	1058	0.030	0.017	0.070	0.038	0.470	0.201	0.310	0.112	0.240	0.073	0.660	0.157
247	1114	0.014	0.010	0.014	0.010	0.029	0.020	0.029	0.020	0.057	0.028	0.214	0.061
254	1175	0.211	0.056	0.000	0.000	0.000	0.000	0.014	0.014	0.000	0.000	0.014	0.014
259	1219	0.257	0.066	0.014	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.014

Table C1. (continued)

JD	DD	ADULTS		EGG MASSES		L1		L2		L3		L4	
		MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
KBS EARLY PLANTING:													
145	147	0.474	0.073	0.052	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
157	292	0.731	0.123	0.647	0.111	3.308	0.790	1.628	0.364	0.615	0.256	0.000	0.000
163	359	0.980	0.127	0.940	0.141	5.050	0.944	2.270	0.403	2.510	0.455	3.130	0.466
168	433	0.492	0.098	1.107	0.165	4.262	1.189	2.361	0.500	4.049	0.626	4.148	0.634
176	553	0.402	0.074	0.103	0.036	0.326	0.227	0.120	0.034	0.326	0.064	1.924	0.274
184	642	1.424	0.150	0.141	0.048	0.043	0.026	0.000	0.000	0.022	0.015	0.011	0.011
190	722	2.545	0.201	0.163	0.046	0.000	0.000	0.059	0.034	0.000	0.000	0.040	0.040
197	817	1.693	0.168	0.218	0.057	0.703	0.290	0.030	0.017	0.030	0.017	0.050	0.029
201	871	0.352	0.065	0.229	0.047	0.676	0.482	0.019	0.013	0.010	0.010	0.029	0.021
204	918	0.050	0.026	0.045	0.019	0.110	0.078	0.010	0.010	0.010	0.010	0.010	0.010
KBS LATE PLANTING-1													
195	817	0.159	0.037	0.186	0.040	0.522	0.306	0.000	0.000	0.027	0.027	0.000	0.000
202	886	0.090	0.035	0.215	0.048	0.880	0.421	0.050	0.033	0.020	0.020	0.000	0.000
204	918	0.086	0.033	0.156	0.042	0.151	0.106	0.097	0.077	0.086	0.036	0.000	0.000
211	1020	0.039	0.024	0.010	0.010	0.000	0.000	0.059	0.027	0.029	0.022	0.010	0.010
218	1129	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.014
225	1214	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
234	1311	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
KBS LATE PLANTING-2:													
198	827	0.040	0.028	0.015	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
202	886	0.014	0.014	0.029	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
204	919	0.010	0.010	0.040	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
211	1021	0.020	0.014	0.040	0.024	0.000	0.000	0.020	0.014	0.000	0.000	0.000	0.000
218	1130	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.010	0.010
225	1215	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table C1. (continued)

JD	DD	ADULTS MEAN	ADULTS S.E.	EGG MASSES MEAN	EGG MASSES S.E.	L1 MEAN	L1 S.E.	L2 MEAN	L2 S.E.	L3 MEAN	L3 S.E.	L4 MEAN	L4 S.E.
232	1312	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.014
MONTCALM EARLY PLANTING:													
154	267	1.714	0.182	2.104	0.171	2.364	0.685	0.000	0.000	0.000	0.000	0.000	0.000
161	331	1.973	0.194	4.713	0.322	8.773	1.555	3.933	0.771	3.000	0.528	0.240	0.153
168	416	2.068	0.311	6.761	0.850	48.159	5.168	29.841	4.102	17.796	3.599	0.527	0.161
MONTCALM LATE PLANTING:													
191	671	0.920	0.108	0.845	0.098	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
198	774	1.606	0.143	4.418	0.250	6.106	1.306	0.875	0.375	0.000	0.000	0.010	0.010
205	887	1.290	0.179	2.705	0.254	31.952	4.611	41.000	5.133	12.714	2.253	5.524	1.103
212	1002	0.574	0.115	0.669	0.128	4.296	1.728	3.482	0.487	6.778	0.988	38.750	3.483
219	1101	2.431	0.268	0.304	0.108	1.765	0.967	0.177	0.061	0.412	0.109	3.804	0.535

Table C2. CPB predator densities at potato researh sites in Rhode Island (RI), and Michigan, 1985-1987. (JD=Julian Day, DD= Accumulated degree-days base 10°C from May 1, CMAC= *Coleomegilla maculata*, LEBIA=*Lebia grandis*, PODISUS=*Podisus maculiventris*, PERILLUS=*Perillus bioculatus*, DLL=phalangids).

		CMAC		LEBIA		PODISUS		PERILLUS		DLL	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
1985											
RI EARLY PLANTING:											
155	171	0.021	0.006	0.022	0.006	0.000	0.000			0.006	0.003
158	190	0.020	0.009	0.000	0.000	0.000	0.000			0.000	0.000
162	218	0.036	0.080	0.004	0.004	0.000	0.000			0.016	0.080
165	244	0.053	0.018	0.007	0.007	0.000	0.000			0.000	0.000
169	274	0.067	0.024	0.073	0.021	0.000	0.000			0.013	0.009
172	302	0.090	0.029	0.030	0.017	0.000	0.000			0.010	0.010
176	341	0.100	0.036	0.120	0.033	0.000	0.000			0.010	0.010
181	364	0.170	0.043	0.080	0.031	0.020	0.014			0.060	0.024
186	427	0.200	0.045	0.050	0.022	0.040	0.027			0.060	0.060
189	454	0.070	0.026	0.030	0.017	0.030	0.024			0.000	0.000
192	489	0.070	0.026	0.010	0.010	0.030	0.024			0.020	0.009
198	575	0.180	0.043	0.020	0.009	0.060	0.060			0.000	0.000
RI LATE PLANTING:											
210	711	0.0.00	0.000	0.000	0.000	0.000	0.000			0.000	0.000
212	731	0.000	0.000	0.000	0.000	0.000	0.000			0.000	0.000
214	747	0.000	0.000	0.000	0.000	0.000	0.000			0.000	0.000
217	769	0.006	0.006	0.000	0.000	0.000	0.000			0.000	0.000
219	791	0.007	0.007	0.000	0.000	0.000	0.000			0.000	0.000
221	819	0.010	0.010	0.000	0.000	0.000	0.000			0.000	0.000
225	870	0.040	0.020	0.000	0.000	0.000	0.000			0.000	0.000
228	916	0.050	0.026	0.000	0.000	0.000	0.000			0.000	0.000
232	962	0.040	0.020	0.010	0.010	0.000	0.000			0.000	0.000
335	987	0.040	0.014	0.020	0.014	0.000	0.000			0.000	0.000

Table C2. (continued)

		CMAC		LEBIA		PODISUS		PERILLUS		DLL	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
239	1035	0.050	0.022	0.010	0.010	0.010	0.010			0.000	0.000
246	1091	0.000	0.000	0.010	0.010	0.010	0.010			0.000	0.000
249	1134	0.010	0.010	0.000	0.000	0.010	0.010			0.040	0.020
252	1168	0.010	0.010	0.000	0.000	0.020	0.020			0.000	0.000
255	1183	0.010	0.010	0.000	0.000	0.000	0.000			0.020	0.014
<u>KBS LATE PLANTING:</u>							*FROM JULY 1				
199	217*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.008
206	298	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.052	0.022
213	389	0.015	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.123	0.029
220	464	0.018	0.013	0.009	0.009	0.000	0.000	0.009	0.009	0.136	0.035
227	549	0.129	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.414	0.094
234	617	0.071	0.037	0.000	0.000	0.000	0.000	0.014	0.014	0.257	0.070
241	687	0.078	0.031	0.000	0.000	0.000	0.000	0.000	0.000	0.156	0.042
246	736	0.086	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.271	0.061
<u>MONTCALM LATE PLANTING:</u>							*FROM JULY 15				
190	178*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
197	253	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000
205	334	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.012	0.000	0.000
211	397	0.012	0.009	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000
218	445	0.012	0.012	0.000	0.000	0.037	0.021	0.000	0.000	0.000	0.000
225	516	0.013	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.013
232	568	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.013	0.013	0.013
239	613	0.007	0.007	0.022	0.016	0.000	0.000	0.000	0.000	0.015	0.010

Table C2. (continued)

		CMAC		LEBIA		PODISUS		PERILLUS		DLL	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
1986											
RI EARLY PLANTING:											
148	126	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007
150	146	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
154	179	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
156	191	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
161	230	0.013	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
164	254	0.027	0.016	0.013	0.009	0.000	0.000	0.000	0.000	0.000	0.000
167	284	0.026	0.019	0.017	0.012	0.000	0.000	0.000	0.000	0.026	0.015
170	305	0.070	0.029	0.010	0.010	0.000	0.000	0.000	0.000	0.030	0.017
175	345	0.050	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.010
177	357	0.050	0.026	0.010	0.010	0.000	0.000	0.000	0.000	0.030	0.017
181	403	0.070	0.041	0.010	0.010	0.010	0.010	0.000	0.000	0.010	0.010
184	425	0.083	0.043	0.033	0.023	0.000	0.000	0.000	0.000	0.017	0.017
188	471	0.080	0.027	0.020	0.014	0.000	0.000	0.000	0.000	0.010	0.010
191	514	0.050	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.020
196	556	0.140	0.040	0.010	0.010	0.000	0.000	0.000	0.000	0.010	0.010
198	576	0.150	0.041	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.010
203	633	0.100	0.033	0.010	0.010	0.010	0.010	0.000	0.000	0.000	0.000
205	656	0.100	0.033	0.020	0.014	0.010	0.010	0.000	0.000	0.010	0.010
210	715	0.070	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.014
RI LATE PLANTING:											
199	587	0.000	0.000	0.000	0.000	0.000	0.000			0.000	0.000
202	622	0.000	0.000	0.000	0.000	0.000	0.000			0.000	0.000
204	643	0.000	0.000	0.000	0.000	0.000	0.000			0.016	0.011
209	705	0.041	0.023	0.000	0.000	0.000	0.000			0.047	0.017
212	735	0.077	0.023	0.000	0.000	0.000	0.000			0.038	0.015

Table C2. (continued)

		CMAC		LEBIA		PODISUS		PERILLUS		DLL	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
217	793	0.126	0.034	0.000	0.000	0.013	0.009			0.179	0.034
224	875	0.180	0.033	0.000	0.000	0.013	0.009			0.107	0.027
226	889	0.250	0.045	0.000	0.000	0.013	0.009			0.020	0.011
232	934	0.158	0.042	0.000	0.000	0.040	0.020			0.149	0.047
234	970	0.170	0.040	0.000	0.000	0.080	0.031			0.070	0.026
238	1005	0.180	0.041	0.000	0.000	0.170	0.150			0.040	0.020
247	1062	0.209	0.046	0.000	0.000	0.110	0.035			0.066	0.026
254	1115	0.110	0.036	0.000	0.000	0.044	0.027			0.011	0.011
265	1168	0.067	0.026	0.000	0.000	0.033	0.019			0.000	0.000
KBS EARLY PLANTING:											
154	183	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.020	0.014
160	235	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.019
164	267	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.017
168	297	0.059	0.017	0.010	0.010	0.000	0.000	0.000	0.000	0.064	0.017
171	323	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
175	360	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
178	393	0.013	0.009	0.006	0.006	0.006	0.006	0.000	0.000	0.000	0.000
182	420	0.000	0.000	0.000	0.000	0.013	0.009	0.013	0.009	0.000	0.000
184	434	0.040	0.019	0.007	0.007	0.000	0.000	0.007	0.007	0.013	0.009
188	491	0.033	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
191	521	0.069	0.022	0.000	0.000	0.006	0.006	0.019	0.011	0.000	0.000
195	564	0.053	0.021	0.000	0.000	0.007	0.007	0.000	0.000	0.000	0.000
198	617	0.047	0.020	0.007	0.007	0.007	0.007	0.000	0.000	0.000	0.000
202	678	0.103	0.106	0.000	0.000	0.000	0.000	0.006	0.006	0.000	0.000
205	719	0.113	0.141	0.000	0.000	0.007	0.007	0.007	0.007	0.000	0.000
209	768	0.053	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
212	804	0.047	0.017	0.000	0.000	0.000	0.000	0.007	0.007	0.007	0.007

Table C2. (continued)

		CMAC		LEBIA		PODISUS		PERILLUS		DLL	
JD	DD	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
216	839	0.040	0.019	0.000	0.000	0.000	0.000	0.013	0.009	0.000	0.000
220	879	0.067	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.009
223	906	0.060	0.020	0.000	0.000	0.000	0.000	0.007	0.007	0.007	0.007
KBS LATE PLANTING-1											
202	678	0.106	0.012	0.160	0.016	0.060	0.030	0.020	0.015	0.000	0.000
205	719	0.000	0.000	0.000	0.000	0.000	0 000	0.019	0.005	0.000	0.000
209	768	0.007	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.006
212	804	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	839	0.007	0.007	0.000	0.000	0.000	0.000	0.014	0.010	0.000	0.000
219	869	0.000	0.000	0.000	0.000	0.032	0.014	0.019	0.011	0.032	0.014
223	906	0.033	0.014	0.000	0.000	0.007	0.007	0.000	0.000	0.026	0.020
226	931	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.012
230	980	0.027	0.013	0.000	0.000	0.000	0.000	0.020	0.012	0.007	0.007
233	1009	0.053	0.018	0.000	0.000	0.013	0.009	0.013	0.009	0.020	0.012
238	1049	0.040	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.016
244	1074	0.007	0.007	0.007	0.007	0.000	0.000	0.000	0.000	0.007	0.007
250	1112	0.047	0.020	0.000	0.000	0.000	0.000	0.020	0.012	0.100	0.038
KBS LATE PLANTING-2											
202	678	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
205	719	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
209	768	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
212	804	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	839	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
220	869	0.007	0.007	0.000	0.000	0.000	0.000	0.007	0.007	0.000	0.000
223	906	0.015	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.067
226	931	0.027	0.013	0.000	0.000	0.000	0.000	0.007	0.007	0.013	0.010
231	980	0.013	0.010	0.000	0.000	0.000	0.000	0.040	0.016	0.000	0.000

Table C2. (continued)

JD	DD	CMAC MEAN	CMAC S.E.	LEBIA MEAN	LEBIA S.E.	PODISUS MEAN	PODISUS S.E.	PERILLUS MEAN	PERILLUS S.E.	DLL MEAN	DLL S.E.
216	839	0.040	0.019	0.000	0.000	0.000	0.000	0.013	0.009	0.000	0.000
220	879	0.067	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.009
223	906	0.060	0.020	0.000	0.000	0.000	0.000	0.007	0.007	0.007	0.007
KBS LATE PLANTING-1											
202	678	0.106	0.012	0.160	0.016	0.060	0.030	0.020	0.015	0.000	0.000
205	719	0.000	0.000	0.000	0.000	0.000	0 000	0.019	0.005	0.000	0.000
209	768	0.007	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.006
212	804	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	839	0.007	0.007	0.000	0.000	0.000	0.000	0.014	0.010	0.000	0.000
219	869	0.000	0.000	0.000	0.000	0.032	0.014	0.019	0.011	0.032	0.014
223	906	0.033	0.014	0.000	0.000	0.007	0.007	0.000	0.000	0.026	0.020
226	931	0.007	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.012
230	980	0.027	0.013	0.000	0.000	0.000	0.000	0.020	0.012	0.007	0.007
233	1009	0.053	0.018	0.000	0.000	0.013	0.009	0.013	0.009	0.020	0.012
238	1049	0.040	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.016
244	1074	0.007	0.007	0.007	0.007	0.000	0.000	0.000	0.000	0.007	0.007
250	1112	0.047	0.020	0.000	0.000	0.000	0.000	0.020	0.012	0.100	0.038
KBS LATE PLANTING-2											
202	678	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
205	719	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
209	768	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
212	804	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	839	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
220	869	0.007	0.007	0.000	0.000	0.000	0.000	0.007	0.007	0.000	0.000
223	906	0.015	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.067
226	931	0.027	0.013	0.000	0.000	0.000	0.000	0.007	0.007	0.013	0.010
231	980	0.013	0.010	0.000	0.000	0.000	0.000	0.040	0.016	0.000	0.000

Table C2. (continued)

JD	DD	CMAC		LEBIA		PODISUS		PERILLUS		DLL	
		MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
233	1009	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
239	1051	0.027	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.060	0.020
246	1092	0.029	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.093	0.027
250	1112	0.067	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.025
260		0.041	0.023	0.000	0.000	0.014	0.014	0.000	0.000	0.041	0.023
MONTCALM EARLY PLANTING											
156	207	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000	0.006	0.006
161	245	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.016
167	295	0.000	0.000	0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000
174	357	0.040	0.023	0.013	0.013	0.013	0.013	0.000	0.000	0.013	0.013
181	411	0.022	0.022	0.000	0.000	0.022	0.022	0.000	0.000	0.000	0.000
188	482	0.013	0.009	0.000	0.000	0.013	0.009	0.006	0.006	0.000	0.000
194	540	0.007	0.007	0.000	0.000	0.013	0.009	0.000	0.000	0.000	0.000
MONTCALM LATE PLANTING											
202	648	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
208	720	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
216	807	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
223	874	0.007	0.007	0.000	0.000	0.013	0.009	0.000	0.000	0.000	0.000
230	940	0.007	0.007	0.000	0.000	0.020	0.012	0.000	0.000	0.020	0.012
241	1021	0.010	0.010	0.000	0.000	0.000	0.000	0.010	0.010	0.048	0.021
251	1077	0.067	0.026	0.000	0.000	0.042	0.018	0.000	0.000	0.000	0.000
1987											
RI EARLY PLANTING:											
154	170	0.000	0.000	0.000	0.000	0.000	0.000			0.000	0.000
160	208	0.000	0.000	0.000	0.000	0.006	0.006			0.000	0.000

Table C2. (continued)

JD	DD	CMAC MEAN	CMAC S.E.	LEBIA MEAN	LEBIA S.E.	PODISUS MEAN	PODISUS S.E.	PERILLUS MEAN	PERILLUS S.E.	DLL MEAN	DLL S.E.
168	278	0.076	0.029	0.000	0.000	0.000	0.000			0.019	0.013
175	359	0.130	0.039	0.010	0.010	0.000	0.000			0.020	0.014
182		0.160	0.039	0.100	0.030	0.020	0.014			0.070	0.026
183	431	0.020	0.014	0.050	0.022	0.010	0.010			0.010	0.010
191	612	0.000	0.000	0.020	0.020	0.000	0.000			0.020	0.014
RI LATE PLANTING:											
204	675	0.000	0.000	0.000	0.000	0.000	0.000			0.000	0.000
211	767	0.020	0.014	0.000	0.000	0.000	0.000			0.000	0.000
217	826	0.030	0.017	0.000	0.000	0.000	0.000			0.000	0.000
225	921	0.120	0.033	0.000	0.000	0.000	0.000			0.020	0.014
232	1006	0.140	0.049	0.000	0.000	0.000	0.000			0.000	0.000
238	1058	0.140	0.045	0.000	0.000	0.010	0.010			0.020	0.014
247	1114	0.014	0.014	0.000	0.000	0.014	0.014			0.000	0.000
254	1175	0.043	0.024	0.000	0.000	0.000	0.000			0.014	0.014
259	1219	0.000	0.000	0.000	0.000	0.014	0.014			0.000	0.000
KBS EARLY PLANTING:											
145	147	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.007	0.022	0.013
157	292	0.000	0.000	0.000	0.000	0.192	0.192	0.128	0.080	0.051	0.025
163	359	0.110	0.037	0.020	0.014	0.020	0.014	0.050	0.022	0.030	0.017
168	433	0.197	0.040	0.016	0.016	0.164	0.048	0.082	0.035	0.033	0.023
176	553	0.207	0.056	0.011	0.011	0.076	0.028	0.337	0.058	0.043	0.021
184	642	0.087	0.027	0.000	0.000	0.098	0.031	0.239	0.059	0.054	0.024
190	722	0.219	0.052	0.010	0.010	0.069	0.025	0.059	0.024	0.020	0.014
197	817	0.317	0.056	0.040	0.020	0.059	0.024	0.099	0.033	0.089	0.032
201	871	0.162	0.041	0.010	0.010	0.086	0.059	0.010	0.010	0.152	0.038
204	918	0.080	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.140	0.040

Table C2. (continued)

JD	DD	CMAC MEAN	CMAC S.E.	LEBIA MEAN	LEBIA S.E.	PODISUS MEAN	PODISUS S.E.	PERILLUS MEAN	PERILLUS S.E.	DLL MEAN	DLL S.E.
211		0.127	0.052	0.091	0.002	0.000	0.000	0.018	0.018	0.327	0.090
KBS LATE PLANTING-1											
195	817	0.000	0.000	0.000	0.000	0.000	0.000	0.044	0.019	0.009	0.009
202	886	0.000	0.000	0.000	0.000	0.010	0.010	0.108	0.032	0.075	0.028
204	918	0.010	0.010	0.000	0.000	0.010	0.010	0.050	0.022	0.090	0.029
211	1020	0.069	0.029	0.000	0.000	0.098	0.098	0.059	0.023	0.206	0.047
218	1129	0.049	0.021	0.000	0.000	0.000	0.000	0.059	0.017	0.128	0.027
225	1214	0.123	0.035	0.000	0.000	0.000	0.000	0.019	0.013	0.208	0.002
234	1311	0.060	0.031	0.000	0.000	0.000	0.000	0.010	0.010	0.140	0.035
KBS LATE PLANTING-2:											
198	827	0.010	0.010	0.000	0.000	0.000	0.000	0.010	0.010	0.020	0.014
202	886	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.015	0.030	0.017
204	919	0.032	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.021
211	1021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.160	0.039
218	1130	0.019	0.013	0.000	0.000	0.000	0.000	0.009	0.009	0.132	0.036
225	1215	0.078	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.097	0.029
232	1312	0.140	0.035	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.030
MONTCALM EARLY PLANTING:											
154	267	0.039	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.039	0.022
161	331	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.027	0.162
168	416	0.063	0.043	0.063	0.043	0.000	0.000	0.031	0.031	0.063	0.043
MONTCALM LATE PLANTING:											
191	671	0.063	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
198	774	0.019	0.013	0.000	0.000	0.047	0.021	0.038	0.019	0.000	0.000

Table C2. (continued)

JD	DD	CMAC		LEBIA		PODISUS		PERILLUS		DLL	
		MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
205	887	0.030	0.017	0.000	0.000	0.110	0.031	0.010	0.010	0.010	0.010
212	1002	0.040	0.020	0.000	0.000	0.070	0.026	0.090	0.029	0.000	0.000
219	1101	0.026	0.018	0.000	0.000	0.013	0.013	0.026	0.018	0.030	0.017

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