Ecology of the bean leaf beetle Cerotoma trifurcata (Forster): improving preventive and curative insect management

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Ecology of the bean leaf beetle, *Cerotoma trifurcata* (Forster):
Improving preventive and curative insect management

by

Michael Ralph Zeiss

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
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DOCTOR OF PHILOSOPHY

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1. INTRODUCTION

This dissertation addresses several different aspects of the ecology of the bean leaf beetle, *Cerotoma trifurcata*, within the context of soybean production in Iowa. The diverse research topics are united by a common goal: decreasing the environmental impact of soybean production while maintaining grower profits. Specifically, the goal is to reduce insecticide use by providing alternative tools for managing the bean leaf beetle. Information about bean leaf beetle ecology is the foundation for the alternative management tools. In short, this dissertation is an attempt to substitute information for insecticide use.

The futurists Naisbitt & Aburdene (1990) state that the world economy is transforming from an energy-intensive to an information-intensive model. Clearly, many industries could reduce their environmental impact by substituting information for consumption of physical inputs (energy, synthetic chemicals, etc.) This is certainly true for agricultural production. For example, reducing the use of nitrogen fertilizers in agriculture can reduce environmental impact (i.e., reduce consumption of petroleum and contamination of surface water). However, information must be substituted for the inputs. Specifically, to reduce fertilizer inputs, growers must increase the amount of time spent gathering and managing information about soil nitrogen levels (Hallberg et al. 1991).

The same is true for managing agricultural insect pests. Growers can reduce environmental impact by substituting information for pesticides (Feder 1979, Mumford & Norton 1984). Specifically, information on pest abundance and impact can be substituted
for prophylactic insecticide applications (Pedigo et al. 1986). In addition, preventive insect-management tactics (which are based on information about pest biology and ecology) can be substituted for curative insecticide applications (Pimentel et al. 1991, Pedigo 1992, Entomological Society of America 1994).

Unfortunately, there are several barriers to the substitution of information for insecticide use. First, in the current economy, information is often expensive relative to physical inputs. Especially for a low-value crop such as soybean, growers often lack the cash-flow needed to hire personnel to gather and manage pest information. Further, growers often lack time to gather and manage pest information themselves. Another barrier is growers' need to avoid risk and uncertainty. The research described herein was intended to help overcome these barriers for bean leaf beetle management.

1.1 Dissertation organization

This dissertation is organized around the concept of prevention and cure. The Literature Review (dissertation section 2), immediately following this Introduction, outlines the preventive and curative components of bean leaf beetle management. Next, original research on overcoming barriers to bean leaf beetle management is presented in three separate papers (dissertation sections 3, 4, and 5). Because there are different barriers to preventive and curative management, these papers are grouped into Part I (Improving Preventive Management) and Part II (Improving Curative Management). Criteria for these groupings are discussed below.
Improving Preventive Management (Part I of dissertation)


Barrier to adoption by growers: uncertainty about efficacy if adopted throughout a large region (e.g., several square kilometers).

Research objective for overcoming barrier: determine the effect of large-scale adoption of delayed soybean planting on bean leaf beetle population dynamics (dissertation section 3).

Improving Curative Management (Part II of dissertation)

Existing management tactic: economic thresholds, in units of beetle abundance, for determining whether insecticide application is justified (Smelser & Pedigo 1992b).

Barrier to adoption by growers: growers have limited time and money to dedicate to monitoring beetle abundance and impact.

Research objective for overcoming barrier: make monitoring more efficient by restricting sampling only to the times when beetles are most likely to be injuring soybean pods.

This objective had two components:

1) predict emergence of F2-generation beetles via a degree-day model (dissertation section 4);

2) predict whether soybean pods that coincided with beetle emergence would be susceptible to injury (dissertation section 5).

Results of the three papers and their implications for bean leaf beetle management
are summarized in the Conclusions (dissertation section 6). This is followed by a comprehensive References Cited section, which includes references from the Literature Review as well as from the three papers. Finally, seven appendices tabulate additional data and materials relevant to preventive or curative management of the bean leaf beetle.
2. LITERATURE REVIEW: REDUCING INSECTICIDE USE VIA PREVENTIVE AND CURATIVE MANAGEMENT

The purpose of this literature review is to provide the reader with the background necessary to understand how the dissertation is organized and why the research was needed. In other words, it introduces the bean leaf beetle and the concepts of preventive and curative management. Readers wishing a comprehensive review of literature on the bean leaf beetle should consult Kogan et al. (1980), Kogan et al. (1988), and Smelser (1990). Detailed reviews of the literature on selected aspects of bean leaf beetle ecology are found in dissertation sections 3, 4, and 5.

2.1 Bean leaf beetle in the North Central region

When defined in terms of soybean production (i.e., soil, climate, and cultural practices), the North Central region comprises Illinois, Indiana, Iowa, Kansas, Kentucky, Michigan, Minnesota, central and northern Missouri, Nebraska, Ohio, and Wisconsin (Suguiyama & Carlson 1985, Jordan et al. 1987). In the past 10 years, the bean leaf beetle, Cerotoma trifurcata (Forster), has become one of the most damaging soybean insects in the North Central region (Edwards et al. 1991, Smelser & Pedigo 1991, Rice & Pedigo 1994). Adult C. trifurcata feed on soybean leaves, stems, pods, and peduncles (Kogan & Kuhlman 1982, Smelser & Pedigo 1992a). Larvae feed on soybean roots and nodules (McConnell 1915, Layton 1983). Most economic damage is caused by adults feeding on pod surfaces (Turnipseed & Kogan 1987), which reduces seed yield and
The need to reduce insecticide use

For all arthropods and crops, there are four principal incentives for reducing insecticide use (Stem et al. 1959, Higley et al. 1992).

1) Insecticides pose health risks to humans, including poisoning of applicators and other agricultural workers before harvest, consumption of residues on food after harvest, and exposure via contaminated water sources (Schuman 1993).

2) Insecticides are toxic to other nontarget organisms including beneficial insects (pollinators and natural enemies), livestock, and wildlife (Jepson 1989, Pimentel et al. 1992).

3) Insecticide use imposes selective pressure on pest populations, encouraging evolution of insecticide-resistant pests (Georghiou 1986, Rousch & McKenzie 1987). Resistance directly reduces the number of tools for managing the pest, and indirectly forces the agrichemical industry to dedicate substantial capital and labor to the continuous pursuit of novel toxicants (Knight & Norton 1989, Higley et al. 1992).

4) Regardless of the true magnitudes of risks, insecticide use is perceived as hazardous by the public. The U.S. Environmental Protection Agency considers pesticides a "medium-risk" problem, less serious than (for example) the human-health risks of indoor pollution (Loehr 1991). In contrast, surveys show that the public perceives pesticides as a serious risk (Slovic 1987, Krauss et al. 1992). By pursuing practical strategies for reducing insecticide use, scientists reduce the chance that public pressure will force the
adoption of impractical strategies (Higley et al. 1992).

Until recently, insecticide application was the preeminent tool for managing bean leaf beetle in the North Central region (e.g., Holscher et al. 1990, Witkowski et al. 1990, Edwards et al. 1991). In most years, insecticide use on soybean in the North Central region is relatively light. For example, in 1980 growers used insecticides on less than 2% of the soybean hectarage in the North Central region, while more than 40% of the Southeast hectarage was sprayed (Suguiyama & Carlson 1985). Similarly, in 1982, only 76,200 kg of insecticide active ingredient were applied to North Central region soybean, while over 3.2 million kg were applied in the Southeast (Osteen & Szmedra 1989). However, in response to a bean leaf beetle outbreak in 1988, over 250,000 soybean hectares were sprayed in Illinois and Indiana alone (Paul 1989). Thus, there is enough insecticide use to justify research on alternatives. In other words, bean leaf beetle on North Central region soybean is a suitable model system for studying the incentives and barriers to reducing insecticide use for other arthropods and crops.

2.3 Strategies for reducing insecticide use: preventive and curative management

To reduce insecticide use, entomologists have long advocated using non-chemical tactics as complements to insecticide applications. For example, Isely & Baerg (1924) recognized that heavy insecticide use against the cotton boll weevil killed the natural enemies of the cotton aphid, leading to aphid outbreaks. Therefore, Isely & Baerg (1924) recommended area-wide destruction of boll weevil hibernation sites to reduce insecticide use. More generally, Stern et al. (1959) outlined a strategy for integrating biological
control (i.e., the action of parasitoids, predators, and pathogens) with chemical control.

Geier & Clark (1961) encouraged the use of multiple tactics, emphasizing that pest population management, "does not imply the adoption or rejection of any mode of defence against undesirable populations, for it is not concerned primarily with means but with the way in which means are employed". This basic philosophy underlies the current concept of integrated pest management (Pedigo 1989, Cate & Hinkle 1994, Luckmann & Metcalf 1994).

Definitions of integrated pest management (IPM) usually stress the need to "integrate", "combine", or "consolidate" multiple tactics to create a "unified program" or "comprehensive approach" for pest management (NAS 1969, Pedigo 1989, Luckmann & Metcalf 1994). The goal of the resulting IPM program is to reduce the status of pests to tolerable levels while maintaining a quality environment (Geier & Clark 1961, Pedigo 1989) and maintaining adequate profits for growers (Pedigo 1995). This concept of integrated pest management is invaluable as a goal towards which pest managers should strive. However, it is too vague to serve as a roadmap for reaching the goal. In particular, it offers no specific guidance on how to integrate multiple tactics into a harmonious stable system that is greater than the sum of its parts. Instead, most discussions of IPM merely recommend that pest managers use as many different tactics as possible, to increase the likelihood that at least one tactic will work (e.g., NAS 1969, Pedigo 1989, Hoy 1990, Luckmann & Metcalf 1994).

A more useful concept for combining multiple tactics comes from the field of disease management. For example, doctors have long managed human disease via a two-pronged
approach of prevention and cure. Similarly, in plant disease management, “almost all control methods are aimed at protecting plants from becoming diseased rather than at curing them after they have become diseased” (Agrios 1969, p. 174). Pedigo (1992) has recommended transferring the “prevention and cure” paradigm to insect pest management.

As part of pest management, prevention:

- involves preemptive actions before pest injury has occurred. Such actions are taken . . . without specific knowledge of pest presence or status at a particular time. Preventive tactics are employed because the pest or pest complex has caused losses in the past and is likely to do so in the future. To be effective, preventives must persist, at least for the growing season, or be applied regularly. . . . Ecologically, preventive tactics aim to prohibit establishment, limit growth, and/or reduce injuriousness of a given pest population. . . . The most common tactics include most biological controls; crop rotation; sanitation and tillage; planting date; trap cropping; plant spatial arrangements; nutrient inputs; and cultivar selection. Although pesticides have been used for prevention . . . this has resulted in pest resurgence and resistance to pesticides . . . and is not recommended (Pedigo 1992).

To transform current crop production practices into sustainable systems, curative insecticide use should be replaced by non-chemical preventive tactics whenever possible (Entomological Society of America 1994). Opportunities exist in many cropping systems. For example, an entire issue of the journal “Environmental Management” was devoted to preventive management of insect pests (Means & Komarek 1983). Further, Pimentel et al. (1991) estimated that yields would not decline and food prices would rise less than one percent if half the pesticides (including herbicides) now applied to crops were replaced by
non-chemical tactics.

However, in even the best-managed systems, prevention will sometimes fail to hold
the status of pests to tolerable levels. This potential for failure must be addressed,
because American agriculture depends on stable predictable harvests. Unpredictable yield
reductions from insect outbreaks would cause untenable economic hardships for many
growers (Higley et al. 1992). Therefore, to function as a truly integrated whole, an IPM
system must include tactics to cure pest outbreaks that exceed tolerable levels.

The curative component of IPM:

is applied only after pest assessment indicates that injury has occurred
and/or economic damage is imminent; it is used at any time in the crop
production cycle when a favorable cost/benefit ratio exists. This
strategy relies on both well developed sampling programs and sound
economic thresholds. IPM therapy seeks to interrupt ongoing pest
population growth and injury and it serves to dampen damage peaks.
The beneficial action of therapeutics is temporary. The most
important therapeutic tactic is the selective use of conventional
pesticides. Other tactics used in IPM therapy include fast-acting,
non-persistent biological controls (e.g., microbial pesticides); early
harvest; replanting; and mechanical removal of pests (e.g., cultivation,
roguing, and pruning) (Pedigo 1992).

Thus, an "integrated" pest management system is one that includes both preventive
and curative tactics. This prevention-and-cure concept of integration, "is not concerned
primarily with means but with the way in which means are employed" (Geier & Clark
1961). In other words, it directly addresses the question of how to construct an
integrated system from multiple tactics. In addition, the concept is inherently easy to
understand. Further, the public is already familiar with the concept because of its use in human medicine. For all of these reasons, this dissertation is organized around the concept of an IPM system that comprises both prevention and cure.

In the context of prevention and cure, there are three ways for pest managers to reduce insecticide use:

1) Use preventive tactics to prevent pest damage from reaching levels that require curative insecticide use. This can be accomplished either by reducing pest abundance, or by reducing the amount of damage per pest without changing pest abundance (Pedigo 1992, Pedigo & Higley 1992).

2) Use non-chemical curative tactics. Promising tactics include use of entomopathogens that have been genetically engineered for greater virulence (Kirschbaum 1985), and inundative releases of natural enemies including parasitoids or predators (Parrella et al. 1992) and entomopathogenic nematodes (Kaya & Gaugler 1993).

3) Eliminate all unnecessary use of curative insecticides. In other words, insecticides should be used only when pest numbers exceed an economic threshold. "This strategy relies on both well developed sampling programs and sound economic thresholds" (Pedigo 1992).

2.4 Barriers to reducing insecticide use, and research needed to overcome them

As discussed above, it is easy to identify approaches for reducing insecticide use. However, it is far harder to put these into practice. Several authors have reviewed the impediments to IPM implementation (OTA 1979, Stoner et al. 1986, Pedigo 1995). A
complete discussion is beyond the scope of this dissertation. Instead, the discussion will be limited to those barriers that can be overcome (at least partially) via biological research.

2.4.1 Lack of tools for reducing insecticide use

In some cropping systems, researchers have not yet developed tools for reducing insecticide use (i.e., accurate economic thresholds, preventive tactics, or non-chemical curative tactics) (OTA 1979, Stoner et al. 1986). Obviously, biological research can overcome this barrier by developing such tools. For the bean leaf beetle, researchers have developed both economic thresholds (Smelser & Pedigo 1992b) and preventive tactics (Pedigo 1992). Therefore, lack of tools is not a major constraint to bean leaf beetle IPM, and will not be discussed further.

2.4.2 Growers' need to minimize uncertainty

As was discussed previously, unpredictable yield reductions would cause untenable economic hardships for many growers (Higley et al. 1992). This is particularly true for soybean production, where the low average profit margin does not provide much of a cushion against unprofitable years. Based on national average market values during the past decade (Anon. 1990), estimates of average profit per hectare of soybean range from $49 to $138 (Hatcher et al. 1974, Zavaleta & Dixon 1982, Boggess et al. 1986, McPherson et al. 1987, Szmedra et al. 1988, Szmedra et al. 1990, Duffy & Judd 1992). Thus, many soybean producers must adopt strategies that reduce the risk of unprofitable years. Specifically, growers use pesticides not only to maximize yields, but to stabilize them (Norgaard 1976, Luckmann & Metcalf 1994). Indeed, the single tactic of insecticide
use often provides simple and predictable pest management. Therefore, growers are reluctant to take risks on more complicated multiple-tactic programs (Pedigo 1995).

Biological research can help overcome this barrier in two ways. First, by improving knowledge about pest biology and ecology, researchers should develop non-chemical management tactics that are as risk-free as possible. However, any tactic (including insecticide use) will sometimes fail. Therefore, the second way that research can help overcome this barrier is to quantify the risk of failure as precisely as possible. For example, computer simulation can provide information on the costs and benefits of non-chemical tactics under a wide range of conditions (Szmedra et al. 1988, 1990). Growers can then incorporate accurate information about risk into their decisions (Moffitt et al. 1983, Mumford & Norton 1984, Hutchins et al. 1986).

It should be noted that there are other ways to address risk. Most notably, the risk of yield losses from pests can be addressed directly, via insurance programs to indemnify growers against losses (Turpin 1977, Carlson 1979, Higley et al. 1992) or financial incentives to reward growers for accepting the risks associated with certain non-chemical tactics (Higley et al. 1992).

2.4.3 Monitoring pests requires scarce labor or money

The key to environmentally-sound use of insecticides is monitoring insect abundance. Insecticides should be used only when insect abundance exceeds the economic threshold. However, surveys indicate that less than half of U.S. soybean growers monitor insect abundance in their fields (Hatcher et al. 1984, McPherson et al. 1987, Pike et al. 1990, Szmedra et al. 1990, Herbert 1992). One reason is lack of time and money. In surveys
of producers of multiple crops (including soybean), the two most common reasons given for not scouting fields were that commercial scouting services were too expensive, and that survey respondents did not have enough time to scout themselves (Rajotte et al. 1987, Wintersteen et al. 1995). Similarly, Mumford & Norton (1984) state that farmers have so many managerial responsibilities that they may adopt “standard operating procedures” (e.g., prophylactic insecticide applications) simply to reduce decision-making effort. Biological research can help overcome this barrier by making sampling as efficient as possible. This includes reducing the number of dates on which a field must be sampled, as well as reducing the effort required to sample the field on a given date (Zeiss & Klubertanz 1994).

It should be noted that sampling efficiency is only one of many factors that determine whether growers will sample fields. For example, the exact costs and benefits of pest monitoring change with crop and year (Hatcher et al. 1984, Greene 1985, Adkisson et al. 1986, Rajotte et al. 1987). In addition, future government policy could increase the costs of physical inputs (e.g., insecticides) relative to the cost of information (Higley et al. 1992). Further, many agricultural producers consider long-term environmental effects, not just short-term profits, when making decisions about pest management (Higley & Wintersteen 1992). Despite these complexities, making sampling as efficient as possible will increase the likelihood of growers sampling fields, and will thereby decrease unnecessary insecticide use.
PART I.

IMPROVING PREVENTIVE MANAGEMENT
3 TIMING OF FOOD PLANT AVAILABILITY: EFFECT ON SURVIVAL AND OVIPOSITION OF THE BEAN LEAF BEETLE (COLEOPTERA: CHRYSOMELIDAE)

A paper submitted to
Environmental Entomology
Section "Community and Ecosystem Ecology"

M.R. Zeiss and L.P. Pedigo

3.1 Abstract

The objective of these experiments was to estimate the effects of large-scale adoption of delayed soybean planting on population dynamics of the bean leaf beetle, *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae), in the Midwest. If growers throughout a region (e.g., thousands of contiguous hectares) planted soybean at the end of the optimal planting period (i.e., late May), beetles would be forced to remain on alternate food plants until soybean emerged. To simulate this consequence of delayed soybean planting, overwintered adult *C. trifurcata* were caged on foliage of selected plant species for 5 to 28 d. Plants tested were alfalfa ('Blazer' and 'Vernal'), oats ('Starter'), wheat ('Guard'), maize ('Garst 8532' and 'Renze 6338'), and soybean ('Corsoy 79') as a control. Beetles that survived were transferred to soybean ('Corsoy 79') foliage for the remainder of their lives.

In all treatments, female lifespans and oviposition rates were reduced significantly relative to the soybean control. Females caged on grasses had significantly shorter lifespans and lower oviposition rates than those caged on alfalfa. Lifespan and oviposition
declined in proportion to number of days without soybean. Survivors from alfalfa regained relatively high oviposition rates once transferred to soybean. In contrast, beetles caged on grasses for 14 d or longer never oviposited even after being transferred to soybean. Results suggest that large-scale adoption of delayed soybean planting would reduce beetle survival and reproduction, with the magnitude of reductions being greatest in regions without alfalfa.

3.2 Introduction

Patterns in time of resource availability can have strong effects on arthropod population dynamics (Price 1984, Hunter et al. 1992). In particular, altering the planting date of a crop that is fed upon by an oligophagous arthropod can reduce the survival or reproduction of the arthropod (Teetes 1991). Even if it does not affect arthropod abundance, changing the planting date can reduce arthropod damage by disrupting the synchrony between the injurious stage of the arthropod and the susceptible stage of the crop plant. "By changing or carefully selecting the time when a crop is planted, we may avoid the egg-laying period of a particular pest, get young plants well established [thereby increasing tolerance to injury] before the attack comes, allow a shorter period of susceptibility . . . or even get a crop matured before a certain pest becomes abundant” (Metcalf & Metcalf 1993, p. 7.68).

This study focuses on how changing the planting date of soybean, *Glycine max* (L.) Merrill, would affect population dynamics of the bean leaf beetle, *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae), in the Midwest. *C. trifurcata* overwinters as adult beetles, predominantly in woodlands but sometimes in clumps of grass, under rocks, in soybean fields of the previous season, or in alfalfa fields (Eddy & Nettles 1930, Boiteau et al. 1980, Mueller & Haddox 1980, Jeffords et al. 1983; M.R.Z. & L.P.P., unpublished

For agronomic reasons, soybean normally yields best in Iowa when planted during the first three weeks of May (Buhr 1971, Benson 1984). Six years of Iowa field experiments have demonstrated that delaying soybean planting until the end of this optimal planting period significantly reduces bean leaf beetle damage to pods (Pedigo 1992; L.P.P. & M.R.Z., unpublished data). Indeed, delayed planting was so effective in field experiments that it seemed appropriate to recommend it to soybean producers throughout Iowa.

However, the effectiveness of delayed planting might have been an experimental artifact. Specifically, to reduce experimental error (variability within experimental blocks), the field experiments had been conducted using relatively small treatment units (each about 0.1 ha). It is often impossible to extrapolate results from one spatial scale into a larger scale (Levin 1992). In particular, in the field experiments, part of the reason that late-planted soybean had lower bean leaf beetle damage was that plots of early-planted soybean were nearby. Beetles concentrated in early-planted plots, thereby reducing beetle density in late-planted plots. In contrast, if nearly all soybean producers planted in late May, most beetles would not have access to early-planted soybean. Instead, beetles would be forced to remain on alternate food plants until late-planted...
soybean emerged. Therefore, the effect of region-wide delayed soybean planting might depend on the alternate food plants that were available in a region.

Bean leaf beetles are oligophagous, feeding primarily on legumes (Turner 1979, Kogan et al. 1980, Helm 1989) but capable of some feeding on certain plants in the families Urticaceae and Celastraceae (Helm et al. 1983). A previous study showed that wild legumes in the genera *Amphicarpaea*, *Desmodium*, and *Strophostyles* are better alternate foods (i.e., produce greater bean leaf beetle longevity and fecundity) than the cultivated forage legumes red clover (*Trifolium pratense* (L.)) or alfalfa (Turner 1979). However, in the Midwest, wild food plants of *C. trifurcata* (both legumes and non-legumes) are much more scarce than forage legumes (Helm et al. 1983, Eilers & Roosa 1994). In particular, in the Midwest alfalfa is by far the most abundant alternate food plant available before soybean emerges. Thus, as part of sustainable *C. trifurcata* management, it might be practical for growers who produce both alfalfa and soybean to manage the abundance and dispersion of alfalfa fields in the agricultural landscape.

Maize, *Zea mays* L., is also a major component of the Midwestern landscape. Despite questions about their accuracy (Herzog 1973, Kogan et al. 1980), reports of bean leaf beetle feeding on maize continue to be published (Metcalf & Metcalf 1993). In mid-May 1992, we observed rounded feeding holes on seedlings of maize ('Garst 8532' and 'Renze 6338') planted in fields. Bean leaf beetles were present in the whorls of some seedlings, though we did not observe beetles feeding. Data on the suitability of maize as an alternate food plant would help in rating the quality of different landscapes as habitat for overwintered *C. trifurcata*.

The ultimate objective of this experiment was to estimate the effects on *C. trifurcata* population dynamics if growers throughout a region (e.g., thousands of contiguous hectares) delayed soybean planting. In particular, would the effects be different in regions
where alfalfa or maize is, versus is not, available as a temporary alternate food plant?
The specific experimental objective was to quantify survival and oviposition of beetles
boxed for various periods on a preferred food plant (soybean), a non-preferred food plant
(alfalfa), a suspected food plant (maize), or a non-food plant (oats, *Avena sativa* L., or
wheat, *Triticum aestivum* L.). Oats and wheat were intended to serve as experimental
controls for the non-nutritional effects of a plant canopy (e.g., increased relative humidity
and shade).

3.3 Materials and Methods

Preliminary experiments in 1990 showed that mated *C. trifurcata* females, caged on
field plots of alfalfa ('Blazer') in May-June, fed on alfalfa foliage and laid some eggs in
soil below alfalfa plants. However, the difficulty of recovering eggs or living adults from
soil and plant debris precluded quantitative field experiments on beetle survival or
oviposition. Instead, delayed soybean planting was simulated via a greenhouse
experiment. Overwintered *C. trifurcata* beetles (about 500 each in 1991 and 1992, about
200 in 1993) were collected via sweepnet from alfalfa fields in mid-May (14 May 1991,
20 May 1992, and 21 May 1993), as soon as beetles became abundant and before soybean
had emerged in nearby fields. Beetles (both sexes) were evenly divided among screened
cages (80 by 80 by 150 cm) within a greenhouse. Each cage contained soil-filled flats
planted to one of the following plant species (three cages per plant species per year):
soybean ('Corsoy 79', a Group II indeterminate cultivar, in each year); alfalfa ('Blazer' in
1991, 'Vernal' in 1992 and 1993); oats ('Starter', in 1991); wheat ('Guard', in 1992); or
maize ('Garst 8532' in 1992, 'Renze 6338' in 1993). Except for 'Blazer', which is highly
resistant to aphids (Potter & Carlson 1992), none of the cultivars had any known marked
resistance to arthropods.
To promote mating, beetles were held in cages 5 or 7 d. Then, subsamples of beetles were removed from each cage and placed in cardboard rearing cups (600 ml) with screen tops (in 1991, three females per cup; in 1992, three females and one male per cup; in 1993, two females and one male per cup). Female beetles not needed for rearing cups were removed from screen cages, frozen, then later thawed and dissected to remove spermathecae. Each spermatheca was placed in a drop of 0.75% sodium chloride on a microscope slide, gently crushed beneath a cover slip, then examined via phase contrast microscopy for the presence of spermatozoa. Males not needed for rearing cups were discarded in 1991, but in 1991 and 1992 were caged on soybean foliage for possible use as replacements for dead males in rearing cups.

The bottom of each rearing cup was lined with moistened paper toweling, and was pierced by a hole that accommodated a water-filled bottle. Bouquets of field-grown plant foliage were placed in each water-filled bottle. The plant used for foliage depended on the treatment (summarized in Table 3.1). Each year, the treatment design included a control in which beetles were continuously held on soybean foliage. In addition, we tested a factorial set of treatments comprising two factors: 1) the plant on which beetles were held (alfalfa, wheat, oats, or maize), and 2) the number of days beetles were held on that plant before being transferred to soybean. Levels of the second factor ranged from 5 to 28 days. Assuming that soybean emerged 10 days after planting, and based on the average date on which beetles were collected (18 May), these levels corresponded to soybean planting dates of about 13 May through 5 June, versus about 8 May for the control.

In each treatment, beetles spent the first 5 or 7 d in screened cages, and spent subsequent days in rearing cups. Low beetle survival in maize cages, and very low field populations in 1993, precluded a balanced treatment design. Instead, maize was tested at
Table 3.1. Treatment design: years in which each factorial treatment was tested

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Cultivar</th>
<th>FACTOR 2: Time (d) that beetles spent on the plant before being transferred to soybean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>'Vernal'</td>
<td>1993</td>
</tr>
<tr>
<td>Maize</td>
<td>'Garst 8532'</td>
<td>1992</td>
</tr>
<tr>
<td></td>
<td>'Renze 6338'</td>
<td>1993</td>
</tr>
</tbody>
</table>

*a* In addition to these treatments, a control was tested each year. In the control, beetles were held continuously on foliage of soybean (‘Corsoy 79’).

Fewer levels of time than other plants, and neither oats nor wheat was tested in 1993. Rearing cups were held in a greenhouse under conditions approximating those of agricultural fields (temperature range 18 to 34°C, ambient solar illumination). Each year, the experimental design was a randomized complete block, with seven blocks. Thus in each year, each treatment was tested in seven rearing cups (21 females per treatment in 1991 and 1992, 14 females per treatment in 1993). Blocking controlled for the cage from which beetles were taken and the position of the rearing cup on the greenhouse bench.
All beetles in a given rearing cup had been taken from the same cage.

Every one to two days, foliage bouquets and paper toweling were replaced, rearing cups and old foliage and paper toweling were inspected for eggs, and number of surviving females were counted. Any dead males (1992 and 1993) were replaced from the colony on soybean foliage. Dead females were not replaced. Each year, the experiment was continued until all females had died.

Data were used to calculate three response variables: mean female lifespan, mean oviposition rate (eggs per day) of females that survived long enough to be transferred to soybean, and mean lifetime egg production per female. Lifespan was measured beginning from the date beetles were collected, and therefore does not include the months before emergence from the overwintering site. Oviposition rate was calculated only for females that had been transferred to soybean because females only began ovipositing several days after being transferred. In other words, none of the females that died before being transferred to soybean oviposited. Preliminary analyses showed that the magnitude of residuals (positive and negative) increased in proportion to the mean. Therefore, data were transformed via \( \log(y + 1) \) before analysis (Draper & Smith 1981).

A separate analysis of variance was conducted for each transformed response variable, with treatment effects partitioned into orthogonal contrasts that tested the effect of plant and holding time. In addition, because the three response variables were correlated with each other, multiple analysis of variance (MANOVA) was conducted to test treatment effects on the combined set of response variables. Several experimental parameters were confounded with year (e.g., plants and times tested, presence of males in rearing cups). Therefore, data were analyzed separately for each year. All analyses were conducted via the Statistical Application System (SAS 1989) using an \( \alpha \) level of 0.05.
3.4 Results and Discussion

Beetles’ daily consumption was greatest on soybean, though beetles were observed to feed on alfalfa foliage. No feeding was detected on maize, oats, or wheat. Because these three grass species span two subfamilies (Watson et al. 1985), it seems unlikely that they contain a common toxin. Thus, poor beetle performance on grasses (discussed below) was probably due to starvation rather than the effect of a toxin.

3.4.1 Response variable: female longevity. Longevity was always significantly lower in beetles held for a given time on grasses versus beetles held for the same time on alfalfa (Fig. 3.1). In the one year it was tested (1992), longevity on maize was significantly lower than on wheat. In 1991 and 1992, longevity declined significantly in proportion to the number of days beetles had spent without soybean (Table 3.2). In 1991, the quadratic relationship between longevity and time was the same for alfalfa and oats. In contrast, in 1992 the relationship was significantly different between alfalfa and wheat treatments (Table 3.2). Separate analyses by plant for 1992 (Table 3.3) showed significant linear declines in longevity for each plant. In 1993, when only alfalfa was tested at multiple times, the effect of time was not significant (Table 3.2).

3.4.2 Response variable: oviposition rate of surviving females. In all years, survivors from alfalfa treatments achieved relatively high oviposition rates once transferred to soybean, regardless of how long they had spent on alfalfa. In other words, the slope of the line for the alfalfa treatments was never significantly different from zero (Fig. 3.2). In contrast, oviposition rate declined to zero for beetles that spent 14 d or more on grasses. In 1991, oviposition rates were significantly lower for beetles held on oats than for beetles held on alfalfa (Table 3.2). However, because all 1991 treatments had low oviposition rates, neither time nor plant-by-time interaction was significant. In 1992, the plant-by-time interaction was significant. Separate analyses by plant (Table 3.3) showed a
### Table 3.2. *F* tests for selected contrasts, by response variable and year

<table>
<thead>
<tr>
<th>Year</th>
<th>Contrast</th>
<th>Response Variable</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Lifespan</td>
<td><em>F</em></td>
<td><em>P&gt;F</em></td>
<td>Oviposition Rate</td>
<td><em>F</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>F</em></td>
<td><em>P&gt;F</em></td>
<td></td>
<td><em>F</em></td>
</tr>
<tr>
<td>1991</td>
<td>Control vs. treatments</td>
<td></td>
<td>30.29</td>
<td>0.0001</td>
<td>14.11</td>
<td>0.0005</td>
</tr>
<tr>
<td></td>
<td>Alfalfa vs. oats</td>
<td></td>
<td>194.54</td>
<td>0.0001</td>
<td>11.15</td>
<td>0.0016</td>
</tr>
<tr>
<td></td>
<td>Time linear</td>
<td></td>
<td>6.97</td>
<td>0.0112</td>
<td>0.62</td>
<td>0.4351</td>
</tr>
<tr>
<td></td>
<td>Time quadratic</td>
<td></td>
<td>7.82</td>
<td>0.0074</td>
<td>1.35</td>
<td>0.2513</td>
</tr>
<tr>
<td>1992</td>
<td>Control vs. treatments</td>
<td></td>
<td>28.60</td>
<td>0.0001</td>
<td>7.09</td>
<td>0.0100</td>
</tr>
<tr>
<td></td>
<td>Alfalfa vs. grasses</td>
<td></td>
<td>20.68</td>
<td>0.0001</td>
<td>3.57</td>
<td>0.0638</td>
</tr>
<tr>
<td></td>
<td>Maize vs. wheat</td>
<td></td>
<td>9.34</td>
<td>0.0034</td>
<td>4.40</td>
<td>0.0401</td>
</tr>
<tr>
<td></td>
<td>Time linear</td>
<td></td>
<td>47.18</td>
<td>0.0001</td>
<td>11.88</td>
<td>0.0010</td>
</tr>
<tr>
<td></td>
<td>Time quadratic</td>
<td></td>
<td>18.91</td>
<td>0.0001</td>
<td>3.18</td>
<td>0.0797</td>
</tr>
<tr>
<td></td>
<td>Plant x Time-linear</td>
<td></td>
<td>16.90</td>
<td>0.0001</td>
<td>11.85</td>
<td>0.0011</td>
</tr>
<tr>
<td></td>
<td>Plant x Time-quad</td>
<td></td>
<td>3.40</td>
<td>0.0700</td>
<td>4.82</td>
<td>0.0321</td>
</tr>
<tr>
<td>1993</td>
<td>Control vs. treatments</td>
<td></td>
<td>3.88</td>
<td>0.0630</td>
<td>1.61</td>
<td>0.2196</td>
</tr>
<tr>
<td></td>
<td>Alfalfa vs. maize</td>
<td></td>
<td>21.28</td>
<td>0.0002</td>
<td>2.26</td>
<td>0.1484</td>
</tr>
<tr>
<td></td>
<td>Time linear</td>
<td></td>
<td>0.33</td>
<td>0.5693</td>
<td>0.14</td>
<td>0.7109</td>
</tr>
<tr>
<td></td>
<td>Time quadratic</td>
<td></td>
<td>0.13</td>
<td>0.7227</td>
<td>1.05</td>
<td>0.3175</td>
</tr>
</tbody>
</table>

*a* All tests used data transformed via log (*y* + 1). In 1991, d.f. 1, 48.
In 1992, d.f. 1, 60. In 1993, d.f. 1, 20.

*b* All the contrasts that were significant for at least one response variable, plus the Time contrasts in 1993 (which were not significant).

*c* For 7 and 14 d only, because maize was not tested at other levels of time.

*d* Alfalfa and wheat only; maize was not included because it was tested at only two levels of time (7 and 14 d).

*e* The contrast between 7 d on alfalfa vs. 7 d on maize.

*f* Only for beetles held on alfalfa.
Table 3.3. *F* tests for Time contrasts, by plant species and response variable, 1992 only

<table>
<thead>
<tr>
<th>Plant</th>
<th>Contrast</th>
<th>Response Variable</th>
<th>Lifespan</th>
<th>Oviposition Rate</th>
<th>Total Oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>F</em></td>
<td><em>P &gt; F</em></td>
<td><em>F</em></td>
</tr>
<tr>
<td>Alfalfa</td>
<td>Time linear</td>
<td>Lifespan</td>
<td>17.18</td>
<td>0.0004</td>
<td>1.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oviposition Rate</td>
<td>0.97</td>
<td>0.3335</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total Oviposition</td>
<td>314.80</td>
<td>0.0001</td>
<td>61.35</td>
</tr>
<tr>
<td>Wheat</td>
<td>Time quadratic</td>
<td>Lifespan</td>
<td>0.00</td>
<td>0.9543</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oviposition Rate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total Oviposition</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*a* Each test used data transformed via log (y + 1), and had d.f. 1, 24.

*b* A separate analysis was conducted for each plant species because Plant x Time interactions were significant in 1992 (see Table 3.2).

significant linear decline in oviposition over time for wheat treatments.

In 1992, the shape of the response curve for wheat treatments was distorted by an anomalistically high oviposition rate in the 7 d wheat treatment (Fig. 3.2). After being transferred to soybean, a single female in one block of the treatment oviposited at a rate greater than most females in the soybean control. It seems likely that this female had larger than average fat-body reserves. Alternatively, it is conceivable that *C. trifurcata* has considerable intra-species variation in ability to utilize wheat as food.

3.4.3 **Response variable: lifetime oviposition** (averaged over all females including those that did not survive long enough to be transferred to soybean). The previous two
Figure 3.1 Mean lifespan (d) for all females in a treatment (beginning on collection date)
Figure 3.2 Mean oviposition rate (eggs per d) of females transferred to soybean
Figure 3.3 Total oviposition (eggs per female) averaged over all females in a treatment
response variables (longevity, and oviposition rate of survivors) each influenced lifetime oviposition. In each year, oviposition averaged over all treatments was significantly less than oviposition in the soybean control (Table 3.2). Beetles held on grasses for a given time always had significantly lower lifetime oviposition than beetles held on alfalfa (Fig. 3.3). As for the previous response variable, mean oviposition was relatively high in all alfalfa treatments, but declined to zero for beetles that spent 14 d or more on grasses. This plant-by-time interaction was significant in 1992 but not 1991, although oviposition declined significantly with time in both years (Tables 3.2, 3.3).

Within a given treatment (including the soybean control), mean lifetime oviposition was substantially higher in the years when males were continuously present (1992 and 1993) versus the year when males were present only for the initial seven days in screen cages (1991). We hypothesize that this was caused by a higher mean number of matings per female in 1992 and 1993. In many insect species, including some chrysomelids, multiply-mated females are more fecund than females that have only mated once (Ridley 1988, Whittier & Shelly 1993). Oviposition rates of feral bean leaf beetles would probably range between these extremes, because males would be present for longer than 7 days (as in 1991) but would not be continuously present for all females (as in 1992 and 1993).

3.4.4 Multiple analyses of variance (MANOVAs). Two variables consistently showed high correlation: 1) oviposition rate (eggs per day) of females that survived long enough to be transferred to soybean, and 2) mean lifetime oviposition averaged over all females in a treatment (Table 3.4). Nonetheless, MANOVA results (Table 3.5) paralleled the results of univariate tests. The plant species on which beetles were held significantly affected the multivariate response in each year. Time that beetles spent without soybean had a significant effect in 1991 and 1992, but not in 1993. The plant-by-time interaction
Table 3.4. Partial correlation coefficients$^a$ among response variables, by year.

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Year</th>
<th>Lifespan</th>
<th>Oviposition rate of survivors</th>
<th>Total oviposition of all females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lifespan</td>
<td>1991</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oviposition rate</td>
<td>1991</td>
<td>-0.002</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>0.613</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>0.228</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>Total oviposition</td>
<td>1991</td>
<td>0.243</td>
<td>0.908</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>0.770</td>
<td>0.956</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>0.603</td>
<td>0.890</td>
<td>1.000</td>
</tr>
</tbody>
</table>

$^a$ From the MANOVA Error matrix (i.e., sum-of-squares and cross-products matrix).

Table 3.5. $F$ tests$^a$ for treatment effects in MANOVA (three response variables together)

<table>
<thead>
<tr>
<th>Year</th>
<th>Source</th>
<th>d.f.$^b$</th>
<th>$F$</th>
<th>$P &gt; F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1991</td>
<td>Plant on which beetles held</td>
<td>3, 40</td>
<td>75.24</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Time held without soybean</td>
<td>9, 98</td>
<td>2.05</td>
<td>0.0421</td>
</tr>
<tr>
<td></td>
<td>Plant x Time</td>
<td>9, 98</td>
<td>1.08</td>
<td>0.3860</td>
</tr>
<tr>
<td>1992</td>
<td>Plant on which beetles held</td>
<td>6, 104</td>
<td>7.62</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Time held without soybean</td>
<td>9, 127</td>
<td>8.79</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>Plant x Time</td>
<td>12, 138</td>
<td>2.84</td>
<td>0.0016</td>
</tr>
<tr>
<td>1993</td>
<td>Plant on which beetles held</td>
<td>3, 13</td>
<td>6.86</td>
<td>0.0052</td>
</tr>
<tr>
<td></td>
<td>Time held without soybean$^c$</td>
<td>6, 26</td>
<td>0.88</td>
<td>0.5245</td>
</tr>
</tbody>
</table>

$^a$ $F$ statistic was estimated from Wilks' Lambda (Rao 1973). All tests used data transformed via log ($y + 1$).

$^b$ Degrees of freedom for numerator and denominator. These differ among tests within a year because, for a MANOVA analysis, SAS excludes observations with missing independent or dependent variables (SAS 1989).

$^c$ Only for beetles held on alfalfa.
was significant only in 1992. Thus, the MANOVA results support the conclusions drawn from univariate tests (discussed above).

3.4.5 Dissections to confirm insemination. Regardless of the plant species in their cage, >78% of females had been inseminated by the end of 5 or 7 d in screened cages (Fig. 3.4). Thus, insemination occurred even in the absence of soybean. This finding increases the reliability of the experiment, because it indicates that the preceding results were not merely an artifact of the experimental procedures. In other words, treatments affected inseminated females rather than interfering with insemination per se.

![Figure 3.4. Percent of females inseminated after 5 to 7 days in screened cage](image-url)
3.4.6 Implications for pest management. These results suggest that, even if implemented by all soybean producers in a region, delaying soybean planting by 14 d would reduce the abundance and fecundity of beetles that colonize soybean. Approximately, this corresponds to delaying soybean planting from 8 May until 22 May. Longer delays seemingly would have little additional effect. The magnitude of the reductions in beetle abundance and fecundity would be far greater in regions that lacked alfalfa or other food plants of similar quality. As will be discussed below, additional research is needed to determine the size of a region from which alternate food plants must be excluded. Maize seemingly is of poor quality as a food plant for *C. trifurcata*. Therefore, producers probably do not need to consider *C. trifurcata* population dynamics when deciding where to plant maize. However, beetles might feed on maize cultivars other than the two tested.

When choosing a soybean planting date, producers must consider factors in addition to bean leaf beetles. In Iowa, soybean yields are not significantly reduced by delaying planting even until late May (Buhr 1971). However, planting after mid-June can substantially reduce yields (Benson 1984, Elmore & Flowerday 1984). The principal risk of delaying soybean planting until mid-May is that May rains will make fields too wet for planting, thereby delaying planting so long that yields decline. Therefore, the incentive to delay soybean planting will depend on factors including the forecast of May rain, the proximity of alfalfa fields, the *C. trifurcata* population density (mean and year-to-year variation) in a region, the cost of a curative insecticide application, and the financial benefits (if any) of producing insecticide-free soybean.

3.4.7 Research needs in landscape ecology. This research simulated the extremes of alfalfa dispersion. In the alfalfa treatments, all beetles that were transferred to soybean had access to alfalfa. This simulated a region in which all overwintered beetles have
access to alfalfa fields, and all beetles in alfalfa have access to soybean fields. In the
glass treatments, none of the beetles had access to alfalfa. This simulated a region where
beetles could not move from overwintering sites to alfalfa fields and then on to soybean
fields.

Additional research is needed on the ecology of landscapes in which alfalfa
availability is intermediate. How does beetle invasion of alfalfa fields from overwintering
sites, or invasion of soybean fields from alfalfa fields, decline with distance? Can the
suitability of a landscape for *C. trifurcata* be predicted solely from the abundance of
alfalfa, or will a given abundance of alfalfa affect beetles differently depending on how it
is arranged in space? Are all alfalfa cultivars equally good habitat for *C. trifurcata*? The
answers to these questions will determine the practicality of changing the abundance and
dispersion of alfalfa fields to manage *C. trifurcata*. The same set of questions also must
be answered for other widely-planted legumes such as crown vetch (*Coronilla varia*) and
birdsfoot trefoil (*Lotus corniculatus*). *C. trifurcata* is occasionally found in plantings of
crown vetch (Turner 1979), which is commonly planted along roadsides.

We believe this is a promising model system in which to investigate the importance
of landscape "composition" (e.g., abundance and habitat quality of forage legumes) and
landscape "physiognomy" (e.g., arrangement of forage legume patches in space) *sensu*
Dunning et al. (1992). To paraphrase Gould (1991), as young landscape ecologists ponder
what organism should be the subject of their research, we hope they will consider the
benefits that could accrue should they choose this intriguing agricultural insect pest.

3.5 Acknowledgments

We gratefully acknowledge B. Kusel for locating early-season beetle populations,
C.D. Lidtke and C.L. Carr for many exacting hours of technical assistance, Renze Hybrids
of Carroll IA for providing seed of their cultivar 'Renze 6338', E.S. Krafsur for guidance in dissections to determine insemination status, B. Danielson and K. Moloney for their stimulating discussions of landscape ecology, M.J. Wallendorf and C. Tsao for assistance with statistical analysis, D. Lewis for information about abundance of wild food plants, and E. Levine and anonymous reviewers for critiquing earlier drafts of this manuscript. Research supported in part by Grant 91-09 from the Leopold Center for Sustainable Agriculture, Ames, IA. This is Journal Paper Number J-16101 of the Iowa Agric. and Home Econ. Exp. Stn., Ames; Project Nos. 3183 and 3207.
PART II.

IMPROVING CURATIVE MANAGEMENT
INTRODUCTION: INCREASING SAMPLING EFFICIENCY

Increasing sampling efficiency (i.e., decreasing the amount of time and effort required to estimate insect abundance) will help increase grower acceptance of sampling. This includes reducing the number of dates on which a field must be sampled, as well as reducing the effort required to sample the field on a given date. For the bean leaf beetle, considerable progress has been made on reducing the effort required to sample a field. Specifically, sequential count plans have been developed for estimating, with a desired level of precision, the mean density of beetles (Boiteau et al. 1979b, Smelser & Pedigo 1992c) or of injured pods (Smelser & Pedigo 1992c). Further, sequential sampling plans for classifying the beetle population as above or below an economic threshold have been published (Boiteau et al. 1979b, Kogan et al. 1980). However, these sequential sampling plans are based on outdated economic thresholds (Smelser & Pedigo 1992b).

Little has been published on reducing the number of dates on which a field must be sampled for bean leaf beetle. Instead, most publications recommend sampling fields approximately weekly whenever beetles are present. In Illinois, the Extension Service previously advised growers to sample soybean fields at least 2 or 3 times between the middle of July and the end of August (Kogan & Kuhlman 1982). More recent recommendations (Steffey et al. 1992) state that Illinois soybean fields should be scouted weekly. In Nebraska, "growers are encouraged to survey their fields at least once a week during the known times of bean leaf beetle activity" (Witkowski et al. 1990). A recent Indiana publication recommends scouting for beetles, but gives no specific guidelines for
first or last sample dates (Edwards et al. 1991). In Iowa, Rice & Pedigo (1994) recommend scouting every 5 days beginning at soybean stage R4 and continuing until beetle counts begin to decline or until soybean stage R7, whichever comes first.

Reducing the number of sampling dates can greatly increase sampling efficiency (Zeiss & Klubertanz 1994). Therefore, the overall objective of this research was to develop guidelines for restricting sampling only to the times when beetles are most likely to be injuring soybean pods. This objective had two components:

1) predicting when F2-generation beetles were most likely to be present (dissertation section 4), and

2) predicting whether soybean pods were likely to be susceptible to injury at that time (dissertation section 5).
4 DEGREE-DAY REQUIREMENTS FOR DEVELOPMENT OF THE BEAN LEAF BEETLE (COLEOPTERA: CHRYSOMELIDAE): NEAR-OPTIMAL VS. NEAR-NATURAL REARING CONDITIONS

A paper submitted to
Journal of Economic Entomology
Section “Ecology and Behavior”

M.R. Zeiss, K.J. Koehler, and L.P. Pedigo

4.1 Abstract

Bean leaf beetles, *Cerotoma trifurcata* (Forster), were reared from egg to adult at temperatures from 18 to 32°C under two regimes. In near-optimal rearing, larvae fed on cotyledons of cowpea, *Vigna unguiculata* (L.). In near-natural rearing, larvae fed on nodulated roots of potted soybean plants, *Glycine max* (L.) Merrill. *C. trifurcata* required $491 \pm 8.1$ degree-days (developmental threshold 11.58°C) to complete development from egg to adult under near-optimal conditions. The relationship between developmental rate and temperature was significantly different under near-natural conditions, where *C. trifurcata* required $646 \pm 17.4$ degree-days (developmental threshold 7.61°C) to complete development.

Degree-day requirements under each rearing regime were not significantly different from requirements of field populations, as estimated from seven years of field sampling data (nine *C. trifurcata* populations total). To complete development, F1-generation field populations required $495 \pm 19.6$ degree-days (developmental threshold 11.58°C) or
40

674±28.7 degree-days (developmental threshold 7.61°C). F2-generation field populations required 542±42.5 degree-days (developmental threshold 11.58°C) or 740±58.2 degree-days (developmental threshold 7.61°C).

4.2 Introduction

Forecasts of pest phenology can help guide decisions about the need for pest sampling or control. Forecasts are particularly useful for systems in which the degree of synchrony between the damaging stage of the pest and the susceptible stage of the crop greatly influences pest impact. One such system is the bean leaf beetle, Cerotoma trifurcata (Forster) (Coleoptera: Chrysomelidae), on soybean, Glycine max (L.) Merrill.

The bean leaf beetle has long been an important pest of soybean in the southern U.S. (Kogan et al. 1980, Hammond et al. 1991) and, in the past 10 years, has become one of the most damaging soybean insect pests in the North Central region (Edwards et al. 1991, Smelser & Pedigo 1991). C. trifurcata adults chew holes in leaves, stem surfaces, peduncles, or pod surfaces (Kogan & Kuhlman 1982, Smelser & Pedigo 1992a). Larvae feed on roots and nodules (McConnell 1915).

Adult feeding on soybean leaves seldom causes economic loss directly (Turnipseed & Kogan 1987; Hammond 1987, 1989; Steffey et al. 1992; Hunt et al. 1995), although leaf feeding can transmit soybean viruses (Patel & Pitre 1976). In contrast, pod feeding directly reduces soybean seed yield and quality and promotes pod infection by Alternaria spp. (Shortt et al. 1982, Turnipseed & Kogan 1987, Smelser & Pedigo 1992b). Therefore, sampling and control efforts should focus on beetles that will be feeding while soybean pods are present. For this reason, forecasting C. trifurcata phenology could help reduce unnecessarily-early sampling.

Because temperature is the preeminent determinant of poikilotherm developmental
rate, degree-day models are used widely for forecasting insect phenology (Pruess 1983, Wagner et al. 1984a, Higley et al. 1986). Indeed, several researchers have studied the effect of temperature on bean leaf beetle developmental rate (Eddy & Nettles 1930, Isely 1930, Herzog et al. 1974, Turner 1979). However, these studies lack true replication (e.g., multiple incubators per temperature) or report data from only a few temperatures or life stages.

To maximize larval survivorship, most researchers have reared *C. trifurcata* larvae on cotyledons or radicles of germinated seeds of cowpea, *Vigna unguiculata* (L.) Walpers, or snap beans, *Phaseolus* spp. However, food quality can influence the rate of insect development (Appiah et al. 1990, Cooper & Schal 1992, Murugan & George 1992). Therefore, developmental rates of larvae reared on seeds might differ from those of larvae feeding on soybean roots and nodules. Marrone and Stinner (1984) reared *C. trifurcata* on intact root systems of potted soybean plants. To date, however, there have been no published comparisons of developmental rates for *C. trifurcata* reared on near-optimal food (e.g., cowpea cotyledons) versus near-natural food (i.e., soybean roots and nodules). Therefore, the objectives of this research were to develop a degree-day model for *C. trifurcata* based on near-optimal rearing conditions, and to quantify deviations from the model (if any) under near-natural and field conditions.

4.3 Materials and Methods

4.3.1 Eggs from feral females. From 1990 to 1993, overwintered female adults were collected each May via sweepnet from alfalfa fields to serve as sources of eggs. F1-generation females were collected from soybean fields each June or July to provide additional eggs. Females were collected from several counties within Iowa, and eggs were used without regard to county or generation (overwintered or F1) of females.
Females were divided among cardboard-carton rearing containers which were provisioned with bouquets of soybean foliage (cv. 'Corsoy 79') and lined with moistened paper toweling. Rearing containers were held at 30°C with a photoperiod of 16:8 (L:D) h. Each day, foliage and paper toweling were replaced and were inspected for eggs.

4.3.2 Near-optimal rearing. Methods were adapted from Tumer (1979). On the day they were oviposited, eggs were transferred in groups of about 20 to plastic cups lined with moistened paper toweling. Cups of eggs were divided among 3 incubators (Model I-30BLL, Percival Manufacturing Co., Boone IA), each maintained at a constant temperature. Nine temperatures were tested (15, 18, 20, 22, 25, 28, 30, 32, and 35°C), with three replicates (i.e., three separate incubators) per temperature. All incubators maintained a photoperiod of 16:8 (L:D) h, were monitored constantly with minimum/maximum thermometers, and were controlled within ±0.5°C of the target temperature. Eggs were inspected daily for hatching.

For larval rearing, seed coats and radicles were removed from cotyledons of recently sprouted cowpea seed (cv. 'Mississippi Silver'). Cotyledons were surface-sterilized in a 1% sodium hypochlorite solution, then thoroughly air-dried. On the day they eclosed, larvae were individually transferred via camel-hair brush to the concave surface of a prepared cotyledon. Infested cotyledons were placed, concave-side down, in individual plastic cups lined with moistened paper toweling. Cups then were held at the same temperature as the eggs from which they eclosed.

First and early-second instars fed by boring a tunnel into their cotyledons. Thus, to determine whether a larva had ecdysed, it would have been necessary to break apart the cotyledon to expose the larva. Initial experiments showed that this inspection procedure killed most first instars. Therefore, no attempt was made to determine the duration of the first larval stage. Instead, each cotyledon was broken open to expose the larva near the
end of the second larval stadium, as estimated from previous rearing results. Larvae thus exposed were transferred to a new cotyledon and returned to their incubator. These late-second instars fed by chewing broad shallow holes in the new cotyledon, and therefore were monitored daily for ecdysis.

On the day they ecdysed, third instars were individually transferred to plastic cups half-filled with moistened sand and provisioned with a cowpea cotyledon. These cups were monitored daily for formation of pupation cells in the sand and for subsequent emergence of adults. No attempt was made to determine the date of pupation per se, because this would have required breaking open the pupation cells and thereby killing many late-third instars (Eddy & Nettles 1930). Thus, durations of four life stages were measured: 1) egg stage (oviposition through egg hatch), 2) combined first and second larval stages (larval eclosion through the ecdysis at the end of the second larval stage), 3) feeding portion of the third larval stage (emergence of the third instar through formation of pupation cell), and 4) pupation cell stage (formation of pupal cell by late-third instar through adult emergence). In each replicate incubator, rearing was continued until at least 200 eggs had hatched and at least 40 larvae had reached the adult stage.

4.3.3 Near-natural rearing. In 1992 and 1993, soybean seeds (cv. 'Corsoy 79') were dusted with commercial Bradyrhizobium japonicum inoculum to promote nodulation, then planted into plastic pots (15 cm diam, 11 cm tall) filled with soil mix (1 part perlite, 1 part pasteurized field soil, 2 parts sphagnum moss). Pots were placed in a greenhouse, watered as needed, and thinned to 2 plants per pot. Additional inoculum was watered into each pot twice weekly. Because even moderate levels of soil nitrate can inhibit nodulation, plants were fertilized weekly with a low-nitrate nutrient solution (Imsande & Edwards 1988). To preclude adverse effects on C. trifurcata, fertilization was halted approximately 14 d before pots were infested with C. trifurcata.
When plants reached the 8-leaf stage, pots were placed in incubators used for near-optimal rearing at 22, 25, or 30°C for 48 hours. Preliminary experiments indicated that 48 hours was sufficient for soil temperature to equilibrate with ambient temperature. After 48 hours, surface soil was gently scraped away to expose roots and nodules. On the day they eclosed, neonate larvae were transferred to root surfaces via camel-hair brush (20 larvae per pot), and roots were lightly re-covered with soil. Infested pots were individually caged in mesh sleeves, then returned to their incubators (3-4 pots per incubator). Preliminary attempts to regulate soil moisture via rope wicks (Marrone 1982) were unsuccessful; soil became too dry. Instead, caged pots were lightly watered once or twice daily to keep soil moist and were monitored daily for beetle emergence.

4.3.4 Data analysis: near-optimal rearing. Data were not analyzed from the 15 and 35°C treatments, because *C. trifurcata* did not complete development at these temperatures. Data were analyzed for the remaining 21 replicate incubators (7 temperatures x 3 incubators per temperature). Within an incubator, larvae were included in analyses only if they completed development to the adult stage. A FORTRAN computer program (Koehler et al. 1995) was used to fit Weibull models (Wagner et al. 1984b) to the distribution of times required for individuals to complete a life stage. Separate Weibull distributions were fit for each of the four life stages (egg, combined first and second larval stage, feeding portion of third larval stage, and pupal cell stage) within each replicate incubator (4 stages x 21 incubators = 84 Weibull distributions). For each of these 84 Weibull distributions, the computer program estimated the median stadium, i.e., the number of days required for 50% of individuals to reach the stage. The program also estimated the median developmental rate (proportion of development per day) by taking the reciprocal of the median stadium, and estimated the standard error of each developmental rate via bootstrapping (Koehler et al. 1995). To verify the computer
program, each median developmental rate was also calculated manually, using linear interpolation to estimate the median stadium and then taking the reciprocal of the median stadium.

Degree-day calculation procedures are summarized in Table 4.1. For each of the four life stages, developmental rate was regressed against rearing temperature, with each developmental rate (one data point per replicate incubator) weighted in inverse proportion to its standard error (SAS Institute 1989). The bootstrap estimates of the standard errors (Koehler et al. 1995) accounted for possible correlation among stadia within cohorts (e.g., among hatch times for eggs in a single rearing cup). For a given life stage, standard errors tended to be larger at lower temperatures, where there was greater dispersion in stadia. Variation in standard errors also reflected differences in the numbers of individuals monitored in different replicate incubators. Two dummy variables were included in the regression model to test whether regression slopes or intercepts were significantly different between the two procedures used to estimate median developmental rate (Weibull computer program versus linear interpolation) (SAS Institute 1989).

The regression equations (one per life stage) were solved for the minimum developmental threshold (i.e., the x-intercept) (Arnold 1959). For each life stage in each replicate incubator, the minimum developmental threshold was used to convert the median stadium from units of days to units of degree-days, by subtracting the minimum developmental threshold from the incubator temperature and multiplying the difference by the median stadium. An overall mean (over all 21 replicate incubators) for median stadium (in units of degree-days) then was computed for each of the four life stages.

4.3.5 Data analysis: near-natural rearing. In near-natural rearing, too few beetles emerged per replicate incubator to permit estimation of a separate Weibull distribution for each replicate. Instead, combined larval/pupal developmental rates were
Table 4.1 Calculations of degree-day requirements for total development (egg to adult) under near-optimal rearing conditions

<table>
<thead>
<tr>
<th>&quot;A&quot;</th>
<th>&quot;B&quot;</th>
<th>&quot;C&quot;</th>
<th>&quot;D&quot;</th>
<th>&quot;E&quot;</th>
<th>&quot;F&quot;</th>
<th>&quot;G&quot;</th>
<th>&quot;H&quot;</th>
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<tr>
<td>Rearing Temperature (°C)</td>
<td>Replicate</td>
<td>Median stadium days for incubator</td>
<td>Median stadium (days) for egg stage</td>
<td>Median stadium (days) for combined larva and pupa stages</td>
<td>Median development rate (1/days)</td>
<td>Degrees above minimum cardinal temperature (A - 11.58°C)</td>
<td>Median degree-days required for total development (E x G)</td>
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<td>0.038</td>
<td>20.42</td>
<td>535.2</td>
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</table>

*a* C. *trifurcata* did not complete development at 15 or 35° C.

*b* Estimated from a Weibull distribution via the computer program (Koehler et al. 1995).

*c* 11.58° C is the minimum developmental threshold estimated from x-intercept of regression for total development (Fig. 4.1).
calculated for each beetle by taking the inverse of the number of days that elapsed between egg hatch and beetle emergence \((n=97\) beetles for near-natural rearing, \(n=1404\) beetles for near-optimal rearing). In addition, total (egg-to-adult) developmental rate was estimated for each beetle by adding the median egg stadium (from near-optimal rearing) to the duration of each beetle's combined larval/pupal development and taking the reciprocal of the sum. Developmental rates then were regressed against rearing temperature. Two dummy variables were included in the regression model to test whether regression slopes or intercepts were significantly different for near-natural versus near-optimal rearing (SAS Institute 1989). The minimum developmental threshold was estimated and was used to convert stadia to units of degree-days as described under near-optimal rearing.

4.3.6 Data analysis: field validation. Estimates of adult \(C.\) trifurcata density were available from twice-weekly sweepnet sampling of 9 soybean fields, all near Ames IA, including at least one field sampled in each year 1986 to 1992 inclusive (Smelser & Pedigo 1991; L.P.P., unpublished data). Density of mature adults and tenernals (i.e., recently-emerged adults) had been recorded separately, which made it easier to distinguish successive generations. For each field, data were inspected to determine dates of peak density for each \(C.\) trifurcata generation. Daily air-temperature maxima and minima from the corresponding years, recorded at a weather station approx. 15 km from the sampled fields, were converted to cumulative degree-days via the sine-wave method using the DEGDAY program (Higley et al. 1986). For each year, DEGDAY was run twice, to give separate degree-day calculations based on the minimal developmental threshold from near-natural or from near-optimal regression models. For each model, the number of degree-days required for development of each generation (F1 or F2) was estimated by calculating the difference between cumulative degree-days on the dates of peak densities.
of two successive generations.

Published studies had shown that *C. trifurcata* development is slower in dry soils (Marrone & Stinner 1983, 1984). Therefore, degree-day requirements for each generation were regressed against total rainfall in May, June, May plus June, July, and June plus July in the corresponding year. In addition, overall means (over all nine field populations) for degree-day requirements were computed for each generation. Because variances of field and experimental populations differed, each mean was tested against the mean from the corresponding degree-day model (near-optimal or near-natural rearing) using approximate *t* values computed with "effective" degrees of freedom (Searle 1971).

### 4.4 Results

#### 4.4.1 Near-optimal rearing.

Larvae eclosed from at least 37% of eggs at each rearing temperature (Table 4.2). However, no larvae survived to the third stage at either 15 or 35°C. In contrast, *C. trifurcata* completed development at 18 through 32°C. For these temperatures, regressions of developmental rate versus temperature are shown in Fig. 4.1. Regression equations are listed in Table 4.3. The method by which developmental rate was estimated (Weibull computer program versus linear interpolation) did not significantly affect any regression coefficients. Therefore, regressions of rates estimated via the computer program were used for all subsequent calculations, because the program also provided estimates of standard errors of developmental rates. Similarly, regression coefficients were not significantly different between males and females, thus data for both sexes were pooled. From the x-intercept for the egg-to-adult regression, the minimum developmental threshold was estimated as 11.58°C. Based on this estimate, *C. trifurcata* required 491 ± 8.1 degree-days (x ± SEM) to complete development from egg to adult under near-optimal rearing conditions (n = 21 replicate incubators). Degree-day
Table 4.2. Stage-specific survival under near-optimal and near-natural rearing, by rearing temperature.

<table>
<thead>
<tr>
<th>Rearing temperature (°C)</th>
<th>No. of eggs at beginning of rearing(^a)</th>
<th>Proportion of eggs that hatched</th>
<th>No. of larvae at beginning of rearing(^a)</th>
<th>Proportion of larvae that survived to adult stage</th>
<th>Cumulative survival from egg to adult stage</th>
</tr>
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<tbody>
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<td>NEAR-OPTIMAL REARING</td>
<td></td>
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<td></td>
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<td></td>
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<tr>
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<td>0.575</td>
<td>485</td>
<td>0.462</td>
<td>0.266</td>
</tr>
<tr>
<td>25</td>
<td>4118</td>
<td>0.613</td>
<td>653</td>
<td>0.371</td>
<td>0.227</td>
</tr>
<tr>
<td>28</td>
<td>1136</td>
<td>0.704</td>
<td>406</td>
<td>0.429</td>
<td>0.302</td>
</tr>
<tr>
<td>30</td>
<td>3387</td>
<td>0.752</td>
<td>710</td>
<td>0.358</td>
<td>0.269</td>
</tr>
<tr>
<td>32</td>
<td>1481</td>
<td>0.629</td>
<td>456</td>
<td>0.243</td>
<td>0.153</td>
</tr>
<tr>
<td>35</td>
<td>2377</td>
<td>0.379</td>
<td>145</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>NEAR-NATURAL REARING</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>NA</td>
<td>NA</td>
<td>700</td>
<td>0.126 (0.244)(^b)</td>
<td>NA</td>
</tr>
<tr>
<td>25</td>
<td>NA</td>
<td>NA</td>
<td>240</td>
<td>0.013 (0.150)(^b)</td>
<td>NA</td>
</tr>
<tr>
<td>30</td>
<td>NA</td>
<td>NA</td>
<td>920</td>
<td>0.007 (0.100)(^b)</td>
<td>NA</td>
</tr>
</tbody>
</table>

\(^a\) Total from all replicate incubators.

\(^b\) Numbers in parentheses are proportions of larvae that survived only in pots from which at least one adult emerged. Pots in which no adults emerged may have been too dry or wet to permit survival, and therefore may reduce unrealistically the estimate of survival.
Table 4.3. Regressions of median development rate (1/days) vs. rearing temperature for near-optimal and near-natural rearing.

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Equation</th>
<th>$R^2$</th>
<th>Standard error of intercept</th>
<th>Standard error of slope $^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>NEAR-OPTIMAL REARING</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Egg</td>
<td>$Y = -0.094 + 0.0082 X$</td>
<td>0.946</td>
<td>0.0111</td>
<td>0.0004</td>
</tr>
<tr>
<td>L I and L II</td>
<td>$Y = -0.076 + 0.0076 X$</td>
<td>0.806</td>
<td>0.0211</td>
<td>0.0008</td>
</tr>
<tr>
<td>Active L III</td>
<td>$Y = -0.111 + 0.0137 X$</td>
<td>0.659</td>
<td>0.0553</td>
<td>0.0022</td>
</tr>
<tr>
<td>Pupation cell</td>
<td>$Y = -0.079 + 0.0060 X$</td>
<td>0.946</td>
<td>0.0082</td>
<td>0.0003</td>
</tr>
<tr>
<td>Combined larvae and pupa stages</td>
<td>$Y = -0.030 + 0.0027 X$</td>
<td>0.926</td>
<td>0.0013</td>
<td>0.0001</td>
</tr>
<tr>
<td>Total (egg to adult)</td>
<td>$Y = -0.024 + 0.0021 X$</td>
<td>0.954</td>
<td>0.0026</td>
<td>0.0001</td>
</tr>
<tr>
<td><strong>NEAR-NATURAL REARING</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Combined larvae and pupa stages</td>
<td>$Y = -0.009 + 0.0018 X$</td>
<td>0.314</td>
<td>0.0098</td>
<td>0.0004</td>
</tr>
<tr>
<td>Total (egg to adult) $^d$</td>
<td>$Y = -0.012 + 0.0016 X$</td>
<td>0.515</td>
<td>0.0057</td>
<td>0.0003</td>
</tr>
</tbody>
</table>

$a$ Each slope was significantly different from zero ($\alpha = 0.001$).

$b$ For near-optimal rearing, "$Y$" is the inverse (1/days) of the median duration of the life stage in each incubator (n = 21 replicate incubators).

$c$ For near-natural rearing, "$Y$" is the inverse (1/days) of the duration of the life stage for each individual (n = 97 individual beetles).

$d$ Estimated by adding the near-optimal egg stadium for a given temperature to the near-natural stadium for combined larvae/pupa development.
Figure 4.1. Regressions of development rate versus rearing temperature
Table 4.4. Cumulative degree-day requirements for development from oviposition to selected developmental stages under near-optimal rearing

<table>
<thead>
<tr>
<th>Cumulative development from oviposition to this developmental stage:</th>
<th>Degree-days(^a) required for 50% of a cohort to reach the stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>EGG HATCH (first instar ecloses from egg)</td>
<td>121.2 ± 2.90</td>
</tr>
<tr>
<td>THIRD LARVAL STAGE (ecdysis that begins L III)</td>
<td>238.8 ± 4.81</td>
</tr>
<tr>
<td>PUPATION CELL (third instar ceases feeding,)</td>
<td>300.0 ± 5.93</td>
</tr>
<tr>
<td>ADULT (teneral adult emerges from soil)</td>
<td>491.3 ± 8.06</td>
</tr>
</tbody>
</table>

\(a\) Developmental threshold 11.58°C

\(b\) \(n = 21\) replicate incubators

Requirements for selected developmental stages are listed in Table 4.4. Results agreed closely with those of published studies (Table 4.5).

4.4.2 Near-natural rearing. Combined larval/pupal survival was substantially lower under near-natural versus near-optimal rearing (Table 4.2). For the regressions of larval/pupal developmental rate versus rearing temperature, the intercepts (but not the slopes) were significantly different between near-natural and near-optimal rearing (for intercepts, \(t = -2.046, 1\ \text{d.f., } P > t = 0.042\); for slopes, \(t = 1.833, 1\ \text{d.f., } P > t = 0.061\).
Table 4.5. Comparison of stadia (days) for near-optimal rearing:
previously published estimates vs. present results

<table>
<thead>
<tr>
<th>Mean rearing temperature (°C)</th>
<th>Source of estimate</th>
<th>Egg stage</th>
<th>Combined larvae and pupa stages</th>
<th>Total development (egg to adult)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21.0 to 21.2</td>
<td>1</td>
<td>14</td>
<td>34</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>NA</td>
<td>35</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>13</td>
<td>37</td>
<td>49</td>
</tr>
<tr>
<td>26.0 to 26.2</td>
<td>1</td>
<td>9</td>
<td>22</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>11</td>
<td>30</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>NA</td>
<td>20</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>NA</td>
<td>23</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>8</td>
<td>25</td>
<td>33</td>
</tr>
<tr>
<td>30.0</td>
<td>1</td>
<td>7</td>
<td>18</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>NA</td>
<td>19</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>7</td>
<td>20</td>
<td>26</td>
</tr>
</tbody>
</table>

\(^a\) Table modified from Turner (1979).

\(^b\) 1, Isely 1930; 2, Eddy & Nettles 1930; 3, Herzog et al. 1974; 4, Turner 1979; 5, present results.

NA Not available; researcher did not report data for this temperature or life stage.
Regression equations for actual larval/pupal development and for estimated egg-to-adult development under near-natural conditions are listed in Table 4.3. Larval/pupal developmental rates predicted by the regression agreed well with the near-natural rates measured by Marrone & Stinner (1984) at 30 and 25°C, but were about 16% lower than the rate measured by Marrone & Stinner (1984) at 20°C. From the x-intercept for the egg-to-adult regression, the minimum developmental threshold was estimated as 7.61°C. Based on this estimate, C. trifurcata required 646.4 ± 17.4 degree-days (x ± SEM) to complete development from egg to adult under near-natural rearing conditions (n = 97 individual beetles).

4.4.3 Field validation. Degree-day requirements for field populations were not significantly different from either near-optimal or near-natural experimental results (for each approximate t, P > 0.56). To complete development, F1-generation field populations required 495.1 ± 19.6 degree-days (developmental threshold 11.58°C) or 673.6 ± 28.7 degree-days (developmental threshold 7.61°C). F2-generation field populations required 541.6 ± 42.5 degree-days (developmental threshold 11.58°C) or 740.0 ± 58.2 degree-days (developmental threshold 7.61°C). Phenology of field populations relative to predictions from the near-optimal model (developmental threshold 11.58°C) or the near-natural model (developmental threshold 7.61°C) are shown in Figs. 4.2 and 4.3, respectively. None of the rainfall totals was significantly correlated with the duration of either C. trifurcata generation.

4.5 Discussion

The methods used in near-optimal rearing are labor-intensive and require careful attention to detail. In particular, cotyledons must be carefully disinfested to prevent mold from killing larvae. Equally important, surfaces of cotyledons must be completely dry,
Figure 4.2. Near-optimal model: degree-days at peak beetle densities, by generation.
Degree-days (base 7.61°C) of peak density relative to predicted mean (646 °d)

Figure 4.3. Near-natural model: degree-days at peak beetle densities, by generation
because neonate larvae can easily become entrapped and drown in even a thin film of water. However, the methods have the advantage of reliability; they produce predictable numbers of *C. trifurcata*. In contrast, survival was low and unpredictable under near-natural rearing. The principal difficulty was regulating soil moisture with sufficient precision to prevent larvae from drowning or desiccating. Rope wicks (Marrone 1982) did not transfer enough water to the soil to keep pace with evapotranspiration. For future efforts at near-natural *C. trifurcata* rearing, researchers may wish to consider using drip irrigation.

The near-natural degree-day model is based on less than a tenth as many individuals as the near-optimal model (97 versus 1404 beetles, respectively). Nonetheless, the two models predicted development of field populations with nearly identical precision. However, it seems likely that the minimal developmental threshold from the near-natural rearing is the better estimate of the true minimal developmental threshold of field populations. Therefore, the near-natural model probably should be used for future predictions of development of field populations.

Although mean degree-day requirements were very similar, variability was nearly twice as high for the F2 generation relative to the F1 generation (Figs. 4.2 and 4.3). Increased variability per se was expected, because successive generations of a multivoltine species often have progressively more variable population curves (e.g., Clark et al. 1967). Unexpectedly, however, the distribution of F2-generation peak abundances was positively skewed relative to the distribution of F1 peaks (Figs. 4.2 and 4.3). In other words, both degree-day models tended to predict peak F2-generation emergence earlier than it actually occurred. Although any bias in a model is undesirable, this bias towards early predictions is compatible with the research objective. If model predictions were used to time sampling, sampling would at worst begin too early, but would very seldom begin too late
(i.e., after peak F2 emergence). Nonetheless, additional research is needed to identify the causes for under-predicting F2-generation developmental times.

4.6 Acknowledgments

The authors gratefully acknowledge B. Kusel for locating early-season beetle populations, C. D. Lidtke and C. L. Carr for many hours of exemplary technical assistance, J. Imsande for guidance in developing the low-nitrate nutrient solution, P. G. Marrone for consultations on near-natural rearing procedures, and J. J. Obrycki and M. J. Wallendorf for assistance with data analysis. Research supported in part by Grant No. 91-09 from the Leopold Center for Sustainable Agriculture, Ames, IA. This is Journal Paper No. J-15985 of the Iowa Agric. and Home Econ. Exp. Stn., Ames; Project Nos. 3030, 3183, and 3207.
5 VARIABLE PLANTS AND HERBIVORES: SEASONAL CHANGES IN FEEDING BY BEAN LEAF BEETLE (COLEOPTERA: CHRYSTOMELIDAE)

A paper to be submitted to

*Environmental Entomology*

Section "Community and Ecosystem Ecology"

M.R. Zeiss, M.J. Wallendorf, and L.P. Pedigo

5.1 Abstract

Feeding rates of adult bean leaf beetles, *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae), on selected age classes of pods and leaves of soybean, *Glycine max* (L.) Merrill, were measured in free-choice feeding tests in the greenhouse. A series of five experiments, spanning soybean growth stages R3 to R7, tested progressively more mature pods against the youngest fully-developed trifoliate leaves.

The youngest pods, which had not yet reached full length, were less preferred than pods that had reached full length. Among age classes of pods that had reached full length, beetles consistently preferred the younger pod class present in an experiment. However, beetle consumption rates were seldom statistically significant among pod classes. Beetles in the three later experiments (during crop stages R5 to R7) consumed a greater proportion of their total diet from pods than did beetles in the two earlier experiments (during R3 and R4). However, in every experiment, beetle consumption rates
were at least 3-fold higher on leaves than on pods, regardless of whether consumption was measured in units of tissue volume or in units of nutrients (water, nitrogen, or dry matter). Increasing the pod/leaf ratio from 1:1 to 2:1 did not significantly increase pod feeding.

These results suggest that field populations of beetles do not switch abruptly from leaf feeding to pod feeding at a particular stage of soybean development. Rather, apparent differences over time in rates of pod injury by field populations might be due partly to greater F2-generation preference for pods, and partly to higher daily feeding rates of F1-generation beetles.

5.2 Introduction

As plant tissues develop, changes in their chemical or physical properties can affect the feeding preferences of phytophagous arthropods (Denno & McClure 1983). For example, several species of stink bugs (Heteroptera: Pentatomidae) that suck legume seeds feed preferentially on late pod development stages (Todd & Herzog 1980, Slansky & Panizzi 1987, Panizzi & Alves 1993). In contrast, larvae of Helicoverpa zea (Boddie) (Lepidoptera: Noctuidae) on soybean, Glycine max (L.) Merrill, feed preferentially on early pod stages (McWilliams 1983). The velvetbean caterpillar, Anticarsia gemmatalis Hübner (Lepidoptera: Noctuidae), feeds preferentially on leaves from pre-bloom stages of soybean development (Moscardi et al. 1981). In contrast, the Mexican bean beetle, Epilachna varivestis Mulsant (Coleoptera: Chrysomelidae), feeds preferentially on leaves from post-bloom stages (Stinner et al. 1982). For all these arthropod species, feeding preference on soybean is positively correlated with food quality. That is, these arthropods feed preferentially on the soybean tissues that allow them to develop most quickly or produce the most eggs (McWilliams & Beland 1977, Kitayama et al. 1979, Lockwood et
al 1979, Moscardi et al. 1981, Terry et al. 1987, Panizzi & Alves 1993). However, the
same soybean tissue can be high-quality food for one species but low-quality food for
another. In other words, food quality depends on both the plant and the herbivore.

Field observations suggest that adults of the bean leaf beetle, Cerotoma trifurcata
(Forster) (Coleoptera: Chrysomelidae), change their feeding preferences during soybean
development. Adult C. trifurcata chew holes in soybean leaves, stem surfaces, peduncles,
and pod surfaces (Kogan & Kuhlman 1982, Smelser & Pedigo 1992); larvae feed in the
soil on roots and root nodules (McConnell 1915). Several researchers have stated that C.
trifurcata adults prefer young plant tissues and begin feeding on pods when production of
new leaves ceases (Boiteau et al. 1980, Kogan & Herzog 1980, Kogan & Kuhlman 1982,
Smelser & Pedigo 1992). However, field measurements of pod injury at successive stages
of soybean development suggest that beetles feed less on the youngest and oldest pod
stages, and more on intermediate pod stages (Appendix 1).

The apparent seasonal changes in C. trifurcata feeding preference could be artifacts
of changes in the relative abundances of plant parts (leaves and pods) during soybean
development. As soybean pods develop and leaves abscise, the number of pods per plant
increases and the number of leaves per plant decreases (Ritchie et al. 1992). Thus, even if
beetles feed randomly, they would be expected to injure progressively more pods as
soybean plants matured. Further, as a food type (e.g., pods) increases in relative or
absolute abundance, herbivores sometimes alter their feeding choices to increase the
proportion of their total diet that is composed of that food type (Crawley 1983).

Therefore, one objective of our research was to measure C. trifurcata feeding rates on
soybean plant parts of various maturity stages, and to determine whether beetle feeding
rates changed in response to experimental changes in the relative abundance of plant parts.
In addition, we quantified the seasonal changes in abundance and food quality of plant
parts within soybean fields, with the objective of testing the correlation between food quality and *C. trifurcata* feeding rate.

5.3 Materials and Methods

5.3.1 Beetle feeding rates. Beetle consumption was measured via free-choice feeding tests in the greenhouse. Plastic food crispers (36 by 20 cm base, 20 cm deep) were converted to test arenas by replacing sides and lids with aluminum window screening. Twelve 3-cm holes, evenly spaced in a 3 by 4 grid, were bored through the base of each arena. A narrow-neck plastic bottle was inserted into each hole from the exterior of the arena and secured by screwing the bottle lid on from the interior of the arena. A small hole was drilled through the center of each bottle lid to allow a plant stem to be inserted. When completed, each arena rested on the bases of its 12 bottles with soybean stems (discussed below) protruding into the arena interior. Immediately before an experiment, all bottles were filled with water and each arena was filled with moist sand to a depth of about 3 cm.

On the morning of an experiment, about 150 field-grown soybean plants ('Corsoy 79', an indeterminate Group II cultivar) were clipped at the base, placed in water, and transported to the greenhouse. Plants were collected from a replicated planting date experiment (two planting dates, early and late May) planted at 76 cm row spacing using standard production practices near Ames, Iowa. In the greenhouse, clipped plants were pruned to provide 252 experimental stems (12 stems for each of 21 arenas). Each experimental stem consisted of about 18 cm of primary plant stem terminated by one or two nodes bearing the desired plant part (three pods in the same age class, or one trifoliate leaf). Plant parts (flowers, leaves, etc.) were removed from any lower nodes of an experimental stem. All experimental stems were free from insect injury before an
experiment.

On a given date, only a subset of all pod age classes were present on field-grown soybean plants (Appendix 1). Therefore, different pod age classes were tested at different times during the season. Nonetheless, there was sufficient overlap in pod development from one soybean growth stage to the next to permit most pod classes to be tested against a range of alternative plant parts. Soybean growth stages are described by Ritchie et al. (1992), based on the categories of Fehr et al. (1971). Each experiment tested three categories of plant parts:

**Experiment 1** (soybean growth stage R3): leaves; green pods that had not yet reached full length (i.e., in which seeds had not begun to fill) but which were at least 2.5 cm long ("green immature" pods, GIMM); and green pods longer than 3.5 cm whose largest seed filled less than 1/4 of the pod width ("green small seed early" pods, GSSE).

**Experiment 2** (soybean growth stages R4 or R5): leaves; GSSE pods; and green pods whose largest seed filled more than 1/4 but less than the entire pod width ("green small seed late" pods, GSSL).

**Experiment 3** (soybean growth stages R5 or R6): leaves; GSSL pods; and green pods whose largest seed completely filled the width of the pod ("green full seed" pods, GFS).

**Experiment 4** (soybean growth stages R6 or R7): leaves; GFS pods; and pods that were beginning to yellow but were still partly green ("green-yellow/yellow-green" pods, GYYG).

**Experiment 5** (soybean growth stage R7): leaves; GYYG pods; and pods that had started to turn brown but were still partly yellow ("yellow-brown/brown-yellow" pods, YBBY).

In Experiments 1 to 5, each leaf was the youngest fully developed trifoliate on the plant from which it was collected, i.e., the youngest leaf that had a leaf above it with
leaflet edges not touching (Ritchie et al. 1992). An additional experiment tested whether beetles distinguished between this leaf (the “first trifoliate”) and the leaf located two stem nodes below it on the plant (the “third trifoliate”):

**Leaf Preference Experiment** (soybean growth stage R4): “first trifoliate” leaves, “third trifoliate” leaves, and GSSE pods.

Experiment 1 was conducted in both 1992 and 1993, and the Leaf Preference experiment was conducted only in 1992. The other experiments were conducted in both 1991 and 1992. Low densities of *C. trifurcata* field populations in 1993 and 1994 precluded subsequent experimentation.

Experimental design was a randomized complete block with three replications (i.e., three arenas) per treatment. Each experiment tested seven treatments (summarized in Table 5.1). Treatments consisted of particular mixtures of experimental stems, to provide beetles with particular relative abundances of each plant part. The set of seven mixtures was chosen to include each of the three plant parts as 100%, 50%, and 33.3% of a mixture (Table 5.1). This treatment design was adapted from designs and analyses developed for mixture-optimization problems (e.g., optimizing proportions of bulk, protein, and high-calorie foodstuffs in animal diets) (Cornell 1990). Specifically, for three mixture components (e.g., three plant parts), this seven-mixture design represents the simplex-centroid treatment design for a mixture experiment (Cornell 1990). Arrangement of experimental stems in bottles was randomized separately for each arena.

Whenever a plant part was present in a treatment, it was present on at least four experimental stems (4 leaves or 12 pods total). This ensured that enough biomass of each plant part was present to permit beetles to feed exclusively on a single plant part throughout the experiment. In other words, feeding choice was not constrained by food availability. *C. trifurcata* consume about 0.3 to 1.0 cm² of soybean tissue per beetle per d
Table 5.1. Explanation of mixtures (i.e., treatments) within an experiment

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Number of bottles in arena occupied by stems of:</th>
<th>Overall ratio pods/leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Younger pods</td>
<td>Older pods</td>
</tr>
<tr>
<td>1</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>4</td>
</tr>
</tbody>
</table>

Experiments 1 to 5 only. In contrast, the Leaf Preference experiment comprised two categories of leaves and one category of pods in an analogous set of seven mixtures.

A total of 12 bottles per arena, each occupied by an experimental stem bearing either three pods in the same age class or one trifoliate leaf.

Specific pod age classes vary with experiment; see text.

Each leaf was the youngest fully developed trifoliate on the plant from which it was collected.

Data from the two mixtures with 1:1 ratio were pooled in Fig. 5.1.
(Waldbauer & Kogan 1976, Smelser & Pedigo 1992, Hunt et al. 1995), and injure pods at a rate of about 0.5 pods per beetle per d (Smelser & Pedigo 1992).

Once experimental stems had been placed in the arenas of a complete block, six female beetles were placed in each arena, and the arena lids were secured with metal clips. Females were used because they consume more per day than male C. trifurcata, thus a random mixture of sexes would have increased experimental error. Beetles were collected via sweepnet from soybean fields on the day of each experiment. The only exception was experiment 3 in 1991. Because field populations were declining rapidly, a large number of beetles were caged in the greenhouse on field-grown soybean plants for 28 d before being used in that experiment.

Phenology of C. trifurcata generations was determined by twice-weekly sampling of beetle densities in the experimental fields and calculations of cumulative degree-days (Zeiss et al. 1995; L.P.P. & M.R.Z., unpublished data). In all years, experiments 1 and 2 used F1-generation beetles, and Experiments 4 and 5 used F2-generation beetles. Experiment 3 used a mixture of F1- and F2-generation beetles in 1991 and used F2-generation beetles in 1992.

Beetle-infested arenas were arranged by block on benches in a greenhouse under conditions approximating those of an agricultural field (temperature range 18 to 34°C, ambient solar illumination). After 48 hours, arenas were opened and numbers of live and dead beetles were recorded. Beetle feeding days were calculated assuming that dead beetles had fed for 24 hours and live beetles had fed for 48 hours (97% of beetles were alive). Plant parts were removed from experimental stems and inspected for beetle feeding. Uninjured plant parts were weighed, oven dried to a constant weight, and re-weighed to determine percent moisture.

Injured plant parts were placed in labeled plastic bags and refrigerated. Surface area
consumed by beetles was quantified within 3 d of experiment completion, as follows. An image of each injured plant part was captured via a color video camera (Sony 3 CCD, Sony Electronics Inc., San Diego, CA) and digitized via an image processing system (IBAS version 2.00, Carl Zeiss Inc., Thomwood, NY). A separate image was evaluated for each side of an injured pod. Technicians measured the image to determine total surface area of the plant part, then interactively outlined and measured the areas that had been removed by beetle feeding.

For each arena, total surface area eaten in each category of plant part was divided by beetle feeding days to give consumption rates (mm² per beetle per d). Consumption rates were converted to units of volume (mm³ per beetle per d) by multiplying by the mean thickness (mm) of the plant tissue (discussed below). Because thickness of a given leaf category was not significantly different between years, data were pooled from 1992 and 1993, and the mean thickness for each leaf category was used in all years. In contrast, pod thickness was significantly different between 1992 and 1993. Therefore, within-year estimates of thickness were used for 1992 and 1993. Thickness was not measured in 1991, so the pooled means from 1992 and 1993 were used for 1991.

Rates of volume consumption (mm³ per beetle per d) then were multiplied by mean nitrogen, water, and dry matter content of the plant tissue (discussed below) to convert to rates of nitrogen, water, and dry matter consumption (g per beetle per d).

5.3.2 Quantity and food quality of soybean plant parts. In 1992 and 1993, the soybean fields from which experimental stems were collected were sampled during stages R2 through R7 (mid-July through mid-September). Each plot was sampled weekly (stratified random sample; 2 planting dates x 4 blocks = 8 sample units per week). For each sample unit, all soybean plants in 30.5 cm of row were clipped at soil level, then placed in a plastic bag in an insulated chest.
In the laboratory, all leaves and pods were removed from stems. Pods were classified into the age classes previously described. Leaves were classified according to position on the stem and color. "Unopened" leaves had leaflet edges still touching, and were found only at the uppermost stem nodes. The next-lowest stem node bore the "first open" leaf (leaflet edges not touching). Progressively-lower nodes bore the "first trifoliate" (the youngest fully developed trifoliate), "second trifoliate", and "third trifoliate". Leaves at all lower nodes that had not begun to yellow were pooled into the category "green leaves". Any yellowed or browned leaves were classified as "discolored". For each sample unit, the total surface area of each pod and leaf category was measured (LI-3100 Area Meter, LI-COR Corp., Lincoln, NE) and the number of leaves or pods was recorded.

From each category, subsamples of 15 leaves or 30 pods were weighed, dried to constant weight, then re-weighed to determine percent moisture. Additional subsamples of 30 pods were shelled, and percent moistures of the resulting seeds and empty pod walls (pericarps) were determined. Selected samples of dried leaves or pods were ground until maximum particle diameter was less than 2 mm, then analyzed for percent total nitrogen using a semimicro-Kjeldahl procedure (Bremner & Breitenbeck 1983). Individual samples of seeds, pod walls, and leaves did not contain enough mass for nitrogen analysis. Therefore, two samples from the same planting date and sample date were pooled for nitrogen analysis (seeds or pod walls from 60 pods, or 30 leaves) before grinding.

Thickness of selected pod walls and leaves were measured by sectioning the plant part with a razor blade then examining the section via a dissecting microscope equipped with an ocular micrometer. In both 1992 and 1993, thickness was measured on 30 pods per pod age class, selected randomly from at least two sample dates. Combined thickness of exocarp and mesocarp was recorded, because C. trifurcata feeding seldom extends into
the endocarp (Shortt et al. 1982, Rice & Pedigo 1994). For leaves, thickness was measured only for categories “first trifoliate” and “third trifoliate” in 1992, but for categories “first open” through “third trifoliate” in 1993 (15 leaves per category per crop stage from R2 to R7). In addition, in 1993, trichome density on pod surfaces was measured for 15 pods per category by using a dissecting microscope to count all trichomes within a wire-mesh quadrat (8 mm²) placed at the midpoints of the pod axes.

5.3.3 Statistical analysis. A separate analysis of variance (ANOVA) was conducted for each repetition (i.e., each year) of Experiments 1 to 5. In addition, results from the two repetitions (i.e., two years) of each experiment were pooled and analyzed. The only exception was Experiment 2, in which a damaged computer file of injury measurements allowed analysis of only the first repetition. Each ANOVA tested the overall effect of treatments on beetle consumption, and tested beetle preference for leaves by contrasting consumption in all treatments that contained leaves versus all treatments that did not. Additional ANOVAs for Experiments 1 to 5 (both single-year and pooled), using data from only the treatment comprising 50% younger pods and 50% older pods, contrasted beetle consumption on younger versus older pods. An ANOVA for the single repetition (1992) of the Leaf Preference experiment, using data from only the treatment comprising 50% “first trifoliate” and 50% “third trifoliate” leaves, contrasted beetle consumption of these two leaf categories. All ANOVAs were repeated for each of the response variables, namely, beetle consumption measured in units of tissue volume, water, dry matter, or nitrogen. All analyses were conducted via the Statistical Application System (SAS 1989) using an α level of 0.05.

5.4 Results

5.4.1 Beetle preference for leaves versus pods. Mean consumption on each plant
part category is tabulated in Appendix 4. Beetle consumption rates were significantly higher on leaves than on pods, regardless of whether consumption was measured in units of tissue volume or in units of nutrients (water, nitrogen, or dry matter) (Table 5.2). The only exception was the 1992 repetition of Experiment 5, in which the $F$ test for the dry-matter response variable narrowly missed significance ($F = 4.24; \text{d.f. } 1, 12; P > F = 0.0618$). When both repetitions (1991 and 1992) of Experiment 5 were pooled, the contrast was significant (Table 5.2). Within the range tested, the relative abundance of pods versus leaves had little effect on preference; beetles fed preferentially on leaves even when pods were twice as abundant (Fig. 5.1).

Beetle preference for leaves declined later in the season. On average, $C.~trifurcata$ consumption of both leaves and pods declined as soybean plants matured (Fig. 5.2). However, the changes in consumption from one experiment to the next (i.e., the shapes of the curves in Fig. 5.2) were significantly different for consumption of leaves versus pods. In other words, the plant part by experiment interaction was significant. In 1991, $F = 8.25; \text{d.f. } 3, 20; P > F = 0.0009$. In 1992, $F = 6.06; \text{d.f. } 4, 29; P > F = 0.0011$. In particular, beetles in Experiments 3 to 5 consumed a greater proportion of their total diet from pods than did beetles in Experiments 1 and 2 (Fig. 5.1).

5.4.2 Preferences among pod classes. In Experiment 1, mean beetle consumption was higher on GSSE than on GIMM pods. In all subsequent experiments, mean beetle consumption was higher on the younger pod class present in an experiment. These trends were consistent in both repetitions; the only exception was a single block in the 1992 repetition of Experiment 3. Nonetheless, consumption differences between pod classes were significant in only a few experiments, and were not significant in any analyses pooled across years (Table 5.3). In other words, no abrupt decline in pod feeding was detected between one pod age class and the pod age
Table 5.2. *F* tests to detect preference for leaves, by the units in which consumption was measured.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Volume consumed</th>
<th>Water consumed</th>
<th>Dry matter consumed</th>
<th>Nitrogen consumed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>F</em></td>
<td><em>P &gt; F</em></td>
<td><em>F</em></td>
<td><em>P &gt; F</em></td>
</tr>
<tr>
<td>1</td>
<td>68.52</td>
<td>0.0002</td>
<td>67.95</td>
<td>0.0002</td>
</tr>
<tr>
<td>2</td>
<td>89.91</td>
<td>0.0001</td>
<td>82.44</td>
<td>0.0001</td>
</tr>
<tr>
<td>3</td>
<td>26.60</td>
<td>0.0021</td>
<td>25.79</td>
<td>0.0023</td>
</tr>
<tr>
<td>4</td>
<td>38.49</td>
<td>0.0008</td>
<td>42.60</td>
<td>0.0006</td>
</tr>
<tr>
<td>5</td>
<td>26.65</td>
<td>0.0021</td>
<td>26.69</td>
<td>0.0021</td>
</tr>
</tbody>
</table>

*a* With the exception of Experiment 2, data were pooled from two repetitions of an experiment (i.e., two years). The error term was Experiment x Year; each test had d.f. 1, 6. For Experiment 2, only a single year of data available. Therefore, for Experiment 2, the error term was within-experiment error; the test had d.f. 1, 12. Similar single-year tests for Experiments 1, 3, 4, and 5 were likewise significant (*P* < 0.05) for each response variable, with the exception of the dry matter response variable in the 1992 repetition of Experiment 5.

*b* The contrast between all mixtures that contained leaves versus all mixtures that did not.
Figure 5.1. Pod consumption as a percentage of total consumption, by experiment.
Figure 5.2. Mean consumption rate in two treatments (100% older pods, or 100% leaves)
Table 5.3.  $F$ tests\(^a\) to detect preference among pod age classes\(^b\),
for total volume consumed\(^c\)

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Year</th>
<th>Mean daily consumption rate(^c) on:</th>
<th>$F$</th>
<th>$P &gt; F$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Younger pods</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1992</td>
<td>0.09</td>
<td>1.95</td>
<td>0.2571</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>1.07</td>
<td>37.40</td>
<td>0.0257</td>
</tr>
<tr>
<td></td>
<td>Pooled</td>
<td>0.51</td>
<td>13.81</td>
<td>0.1673</td>
</tr>
<tr>
<td>2</td>
<td>1991</td>
<td>3.55</td>
<td>1464.42</td>
<td>0.0007</td>
</tr>
<tr>
<td>3</td>
<td>1991</td>
<td>0.70</td>
<td>3.30</td>
<td>0.2111</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>1.30</td>
<td>0.21</td>
<td>0.6950</td>
</tr>
<tr>
<td></td>
<td>Pooled</td>
<td>1.00</td>
<td>0.11</td>
<td>0.7954</td>
</tr>
<tr>
<td>4</td>
<td>1991</td>
<td>2.91</td>
<td>3.70</td>
<td>0.1941</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>4.42</td>
<td>4.29</td>
<td>0.1740</td>
</tr>
<tr>
<td></td>
<td>Pooled</td>
<td>3.66</td>
<td>10.62</td>
<td>0.1896</td>
</tr>
<tr>
<td>5</td>
<td>1991</td>
<td>0.58</td>
<td>1.05</td>
<td>0.4131</td>
</tr>
<tr>
<td></td>
<td>1992</td>
<td>0.88</td>
<td>146.84</td>
<td>0.0067</td>
</tr>
<tr>
<td></td>
<td>Pooled</td>
<td>0.73</td>
<td>12.49</td>
<td>0.1756</td>
</tr>
</tbody>
</table>

\(^a\) Single-year analyses used within-experiment error, and had d.f. 1, 2.
Pooled analyses used year-by-treatment interaction as error term, and had d.f. 1, 1.

\(^b\) Analyses used data only from the treatment that comprised a 1:1 mixture of younger and older pods.

\(^c\) Rate of consumption measured in units of volume (mm\(^3\) per beetle per d).
Patterns of significance were very similar for consumption measured in other units.
class that immediately followed it.

5.4.3 Preferences among leaf classes. In the Leaf Preference experiment, analysis of the treatment that comprised a 1:1 mixture of “first trifoliate” / “third trifoliate” leaves did not detect a significant difference in beetle consumption ($P > 0.20$) between these leaf categories, regardless of the units in which consumption was measured (volume, dry matter, etc.).

5.4.4 Relative abundance of plant parts in soybean fields. Complete data on surface area of each plant part category are presented in Appendix 3. As stated previously, the Leaf Preference experiment suggested that beetles had equally high preference for the three youngest fully-developed trifoliate leaves. Therefore, the surface areas of these three leaves are summed in Fig. 5.3 to provide a minimum estimate of leaf tissue available as $C. trifurcata$ food. In the field samples, the summed leaf surface area remained fairly high through R6, then declined rapidly during R7 (Fig. 5.3A). To calculate approximate pod/leaf ratios in the field samples, the combined surface area of all pods was divided by the summed surface area of the three uppermost trifoliate leaves. The surface area ratio of pods/leaves increased linearly from R2 through R7, then increased exponentially during R7 (Fig. 5.3B). By stage R7, this ratio was greater than 2, which was the highest ratio tested in greenhouse experiments.

5.4.5 Food quality of plant parts. Leaf food quality (i.e., water and nitrogen content) declined as soybean plants matured (Table 5.4), a pattern that is common in many plants (Mattson 1980, Raupp & Denno 1983) including soybean (Hanway & Weber 1971, Matsumoto et al. 1977, Wittenbach et al. 1980). Similarly, pod walls declined in nitrogen concentration and water content as soybeans matured (Table 5.5). Nonetheless, at all reproductive growth stages, young leaves (Table 5.4) had higher concentrations of
In 1992, ratio at stage R7 was 17.7

Figure 5.3. Total surface areas (cm²) of plant parts in soybean fields per 30.5 cm of row

A) Combined areas of 3 uppermost fully-developed trifoliate leaves; these three leaves probably are equally preferred by beetles

B) Surface area ratio of all pods / 3 uppermost trifoliate leaves
Table 5.4. Characteristics of soybean ('Corsoy 79') pod age classes.
Mean and (SEM), data pooled from 1992 and 1993

<table>
<thead>
<tr>
<th>Age class</th>
<th>Percent moisture</th>
<th>Percent total nitrogen</th>
<th>Trichomes</th>
<th>Surface area, both sides, cm²</th>
<th>Thickness of exocarp plus mesocarp, µm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intact pod</td>
<td>Pod wall</td>
<td>Seed</td>
<td>Intact pod</td>
<td>Pod wall</td>
</tr>
<tr>
<td>GIMM</td>
<td>82</td>
<td>NM</td>
<td>NM</td>
<td>4.3</td>
<td>NM</td>
</tr>
<tr>
<td></td>
<td>(2.5)</td>
<td>(0.33)</td>
<td>NM</td>
<td>(0.33)</td>
<td>NM</td>
</tr>
<tr>
<td>GSSE</td>
<td>82</td>
<td>84</td>
<td>84</td>
<td>NM</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>(3.1)</td>
<td>(4.0)</td>
<td>(2.3)</td>
<td>(0.45)</td>
<td>(0.80)</td>
</tr>
<tr>
<td>GSSL</td>
<td>78</td>
<td>75</td>
<td>80</td>
<td>3.7</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>(2.7)</td>
<td>(2.4)</td>
<td>(6.1)</td>
<td>(0.15)</td>
<td>(0.27)</td>
</tr>
<tr>
<td>GFS</td>
<td>70</td>
<td>72</td>
<td>70</td>
<td>3.5</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>(3.0)</td>
<td>(2.1)</td>
<td>(5.2)</td>
<td>(0.45)</td>
<td>(0.34)</td>
</tr>
<tr>
<td>GYYG</td>
<td>65</td>
<td>69</td>
<td>61</td>
<td>4.6</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>(3.4)</td>
<td>(5.2)</td>
<td>(5.8)</td>
<td>(0.72)</td>
<td>(0.17)</td>
</tr>
<tr>
<td>YBBY</td>
<td>53</td>
<td>52</td>
<td>53</td>
<td>NM</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>(3.8)</td>
<td>(5.7)</td>
<td>(3.2)</td>
<td>(0.14)</td>
<td>(0.31)</td>
</tr>
<tr>
<td>B</td>
<td>28</td>
<td>22</td>
<td>26</td>
<td>NM</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>(8.2)</td>
<td>(5.9)</td>
<td>(6.9)</td>
<td>(0.10)</td>
<td>(0.43)</td>
</tr>
</tbody>
</table>
Trichome density data are from 1993 only (n = 15 pods per age class). Thickness data presented by year.

GIMM, green immature; GSSE, green small seed early; GSSL, green small seed late; GFS, green full seed; GYYG, green/yellow yellow/green; YBBY, yellow/brown brown/yellow; B, brown. See Materials & Methods for a complete description.

Sample units for percent moisture: for intact pods, each sample comprised 30 pods. For pod walls or seeds, each sample comprised the walls (entire pericarps) or seeds from 30 shelled pods.

Sample units for percent nitrogen: for intact pods, each sample comprised 30 pods. For pod walls or seeds, each sample comprised the walls (entire pericarps) or seeds from 60 shelled pods.

The distance from the pod exterior to the beginning of the membranous endocarp layer; *C. trifurcata* feeding seldom extends into the endocarp. This averaged 81% of the total pericarp (pod wall) thickness. Measured individually on 30 pods per pod age class per year.

NM  Not measured
Table 5.5. Characteristics of soybean ('Corsoy 79') leaves at two stem nodes, by crop development stage. Mean and (SEM), data pooled from 1992 and 1993.

<table>
<thead>
<tr>
<th>Crop stage</th>
<th>Percent total nitrogen</th>
<th>Percent moisture</th>
<th>Thickness (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1st trifol</td>
<td>3rd trifol</td>
<td>1st trifol</td>
</tr>
<tr>
<td>V7</td>
<td>5.6 (0.32)</td>
<td>4.3 (0.30)</td>
<td>81 (1.0)</td>
</tr>
<tr>
<td>R2</td>
<td>5.9 (0.14)</td>
<td>4.8 (0.32)</td>
<td>80 (2.3)</td>
</tr>
<tr>
<td>R3</td>
<td>5.7 (0.51)</td>
<td>5.5 (0.29)</td>
<td>80 (1.0)</td>
</tr>
<tr>
<td>R4</td>
<td>5.6 (0.50)</td>
<td>5.2 (0.39)</td>
<td>78 (1.8)</td>
</tr>
<tr>
<td>R5</td>
<td>5.3 (0.46)</td>
<td>5.0 (0.33)</td>
<td>74 (4.1)</td>
</tr>
<tr>
<td>R6</td>
<td>4.6 (0.79)</td>
<td>4.4 (0.74)</td>
<td>72 (2.9)</td>
</tr>
<tr>
<td>R7</td>
<td>4.0 (0.81)</td>
<td>4.0 (0.67)</td>
<td>72 (5.9)</td>
</tr>
<tr>
<td>R8</td>
<td>NM</td>
<td>NM</td>
<td>69 NM</td>
</tr>
</tbody>
</table>

a 1st trifol, youngest fully-expanded trifoliate leaf. 3rd trifol, trifoliate leaf at the position two nodes lower on the main stem than 1st trifol.

b As described by Ritchie et al. (1992), based on the categories of Fehr et al. (1971).

c Sampling unit for percent nitrogen: each sample comprised 30 trifoliate leaves.

d Sampling unit for percent moisture: each sample comprised 15 trifoliate leaves.

e Thickness was measured individually on 15 trifoliate leaves per crop stage per year.

NM Not measured.
water and nitrogen than pod walls (Table 5.5). Similar findings were reported by Hanway & Weber (1971).

Nitrogen and moisture levels were similar to published values for intact pods, seeds, and leaves (Hanway & Weber 1971, Rubel et al. 1972). We are not aware of published values for pod walls (pericarps) alone. Both leaves and pod walls were thicker in 1992 than in 1993; this difference was significant for pod walls ($F = 116.91$; d.f. 1, 6; $P > F = 0.0001$) but not for leaves. Leaf thickness agreed closely with published values (Dornhoff & Shibles 1976, Lugg & Sinclair 1980, Wittenbach et al. 1980). In contrast, combined thickness of pod exocarp and mesocarp layers was less than half the thickness of these layers reported for five Japanese cultivars (Nishijima 1954b).

After 2 d in arenas, leaves and intact (unshelled) pods had percent moistures that were not significantly different from field means for the corresponding plant part. No other food quality parameters were tested on plant parts from arenas.

5.5 Discussion

Results of these experiments suggest five conclusions.

1) **Beetles strongly prefer leaves to pods** at all crop stages tested (R3 through R7), regardless of *C. trifurcata* generation tested (F1 or F2 generation) (Table 5.2).

2) **Changes in the relative abundance of pods and leaves did not significantly affect beetle preference** within the range tested (ratios of pods/leaves of 1:1 and 2:1) (Fig. 5.1). Nonetheless, additional research using lower ratios might detect an effect of abundance. Field cage experiments with the same soybean cultivar ('Corsoy 79') showed that *C. trifurcata* will feed on pods at soybean stage R6 (Smelser & Pedigo 1992), when the pod/leaf ratio on field plants is usually less than 1:1 (Fig. 5.3). However, at younger stages (R2 to R5), this ratio is lower than 1:1 (Fig. 5.3). Perhaps future experiments that
included proportions lower than 1:1 would reveal an influence of abundance. However, to ensure that food supply does not constrain beetle feeding choice, experiments that tested lower ratios would need to use larger test grids (i.e., larger arenas) to maintain a minimum of four grid positions occupied by pods.

At the other extreme, future experiments that included very high pod/leaf ratios might reveal an effect of abundance. The highest ratio tested in greenhouse experiments was 2:1. However, by stage R7, pod/leaf ratios often exceed 2:1 even for indeterminate cultivars (Fig. 5.3). For determinate cultivars, pod/leaf ratios greater than 2:1 probably occur earlier in the season, when most pods are still green and relatively attractive to bean leaf beetles. When flowering begins, indeterminate cultivars typically have reached only half their final height (Kogan & Tumipseed 1980), and continue to grow new nodes on the main stem (i.e., new leaves) for several more weeks (Johnson 1987). In contrast, determinate cultivars have reached nearly their full height when flowering begins (Kogan & Tumipseed 1980) and cease main stem growth soon thereafter (Johnson 1987).

Alternatively, changes in relative abundance of plant parts in soybean fields may affect *C. trifurcata* in ways that our experimental design could not detect. Specifically, our measurements of changes in relative surface areas of pods versus leaves (Fig. 5.3) may have failed to capture important information about spatial patterns in food availability. Arthropod feeding behavior can be affected not only by food abundance but also by how the food is arranged in space (Stanton 1983, Ohgushi 1992). For example, if the ratio of pods/leaves increased 2-fold, *C. trifurcata* might perceive the resulting increase in pod availability as more than 2-fold or less than 2-fold, depending on how the change affected the spatial dispersion of pods. Additional research is needed on the effect of pod dispersion on *C. trifurcata* feeding preference. Again, this may differ with cultivar growth type. At maturity, indeterminate cultivars have roughly equal numbers of pods on
each pod-bearing branch, with number of pods diminishing towards the tips of stems. In contrast, determinate cultivars have a dense cluster of pods near the top of the plant (Carlson & Lersten 1987, Hammond et al. 1991).

3) **Beetle preference for leaves is lower later in the season.** In other words, beetles consume a higher portion of their total diet as pods later in the season (Figs. 5.1 and 5.2). Possible explanations are discussed below.

4) **Late-season increases in pod consumption as a percent of total consumption seemingly are not caused by changes in the relative nitrogen or moisture contents of pods and leaves.** Two results support this tentative conclusion. First, pod tissue had lower concentrations of water and nitrogen than leaves at all crop stages (Tables 5.4 and 5.5). Second, beetle consumption was significantly higher on leaves versus pods even when measured in units of water or nitrogen consumed (Table 5.2).

Many herbivores feed preferentially on plant parts that have high concentrations of available nitrogen (McNeil & Southwood 1978, Mattson 1980, Waldbauer et al. 1984). Total nitrogen content often provides a good estimate of the amount of nitrogen available for arthropod growth (Mattson 1980, Scriber 1984). Further, for many leaf-feeding arthropods, a combination of high nitrogen and high water contents is correlated strongly with overall food quality (Scriber 1984). Nonetheless, it is possible that our measurements of nitrogen and water content did not reflect food quality for *C. trifurcata*. For example, some forms of nitrogen in plants cannot be utilized by arthropods (Mattson 1980). Further, plant allelochemicals can reduce the availability of nitrogen to herbivores by forming complexes with proteins (Swain 1977).

Alternatively, beetles' feeding preferences may be a response to non-nutrient plant chemicals. Some arthropods can sense the relative concentrations of nutrients in foods (Waldbauer et al. 1984 and references therein). However, for other arthropods, feeding
preference is largely determined by non-nutrient feeding stimulants or deterrents. The absence of stimulants or presence of deterrents may cause arthropods to feed at suboptimal rates even on nutritionally adequate diets (Waldbauer 1968). Further, the absolute concentration of a single plant compound (whether nutrient or non-nutrient) may not allow prediction of arthropod preference; feeding preference can be a function of the ratio between two or more compounds (House 1969, Dethier 1982, Waldbauer et al. 1984, Bernays & Chapman 1994). Additional research is needed on how non-nutrient soybean chemicals affect *C. trifurcata* feeding. Recent publications (Miller & Miller 1986, Fischer et al. 1990) provide good models for experimental methodology.

In addition, plant chemistry is only one of the factors that affect arthropod feeding preference. Plant physical characteristics such as toughness and trichome density can affect arthropod feeding (Wolfenbarger & Sleesman 1963, Lambert et al. 1992, Bernays & Chapman 1994). Indeed, recent studies have shown that on pods, *C. trifurcata* beetles feed preferentially on regions with the lowest trichome densities (R.A. Cloyd, personal communication). Therefore, beetle feeding preference may be affected by differences in trichome density among plant parts or age classes. For example, beetle preference for GSSE pods versus GIMM pods (Table 5.3) may be a response to the 3-fold lower trichome density on GSSE pods (Table 5.4). In addition, trichomes may change qualitatively from one pod age class to the next; as pods mature, the clavate trichomes disappear but the setaceous trichomes persist and develop thick walls (Carlson & Lersten 1987).

We did not measure trichome densities on leaves. Other researchers have reported that a "normal" soybean cultivar had about 6 trichomes per mm² on adaxial (upper) leaf surfaces (Lambert & Kilen 1989), comparable to densities on fully-elongated green pods (Table 5.4). However, trichome densities can be higher on young leaves (Eckel et al. 1990).
Further, there are consistent differences among cultivars in trichome density, both on leaves (Wolfenbarger & Sleesman 1963) and on pods (Nishijima 1954). Clearly, additional research is needed on how trichomes affect C. trifurcata feeding.

The search for plant qualities that determine C. trifurcata feeding preference may be futile. For example, beetle preference for feeding in particular locations on the plant might have evolved to minimize the risk of attack from natural enemies (Schultz 1992). Further, random searching (presumably including random biting of potential foods such as pods) can be part of an efficient searching algorithm for herbivores (Morris & Kareiva 1991). Nonetheless, if such plant qualities can be discovered, they may allow sustainable management of C. trifurcata via host plant resistance. Some varietal differences in C. trifurcata pod feeding have been reported in free-choice field trials (Helm et al. 1990).

5) There seem to be differences between F1 and F2 generation beetles in total daily consumption and in preference for leaves versus pods. In these experiments, as in nature, soybean crop stage is confounded with C. trifurcata generation. Experiments 1 and 2 were conducted with F1-generation beetles at crop stages R3 to R5. Experiments 3 through 5 were conducted with mostly F2-generation beetles at crop stages R5 through R7. Therefore, it is not possible to separate the effects of crop stage from the effects of beetle generation. However, our measurements of food quality changed gradually, not abruptly, from one crop stage to the next (Tables 5.4 and 5.5). In contrast, consumption rates changed rather abruptly; they were high in Experiments 1 and 2 (with F1-generation beetles) and low in subsequent experiments (Fig. 5.2). This suggests that F2-generation beetles have lower total consumption rates than F1-generation beetles. Likewise, the relative consumption of pods increased rather abruptly in Experiments 3 to 5 (with F2-generation beetles) (Fig. 5.1). This suggests that F2-generation beetles have a greater preference for pods.
It seems plausible that the generations differ in nutrition requirements, and thus in feeding preferences. In the North Central region, *C. trifurcata* produces two annual generation (Smelser & Pedigo 1991 and references therein). Adults of the F1 generation are reproductively active and live about 30 to 40 d (Eddy & Nettles 1930, Herzog et al. 1974). In contrast, adults of the F2 generation are in reproductive diapause while feeding on soybean during late summer and autumn, are dormant through the winter, and do not reproduce until the following spring (Boiteau et al. 1979, Loughran & Ragsdale 1986). Perhaps F1-generation *C. trifurcata* females have greater requirements for nitrogen (i.e., leaves) than F2-generation females. Several insect species are known to increase total food consumption, and consumption of nitrogen in particular, in preparation for vitellogenesis (Bernays 1985).

Regarding total consumption, there is some tentative evidence for generational differences within *C. trifurcata*. Illinois researchers have reported consumption rates of about 1 cm$^2$ of leaf per beetle per d (Waldbauer & Kogan 1976). Because this report focused on leaf feeding by the F1 generation, it seems likely that the consumption estimate is for F1 generation adults. In contrast, Smelser & Pedigo (1992) reported mean consumption of only 0.38 cm$^2$ per beetle per d for F2-generation adults feeding in late summer. Similarly, Hunt et al. (1995) reported mean consumption of 0.31 cm$^2$ per beetle per d for overwintered F2-generation beetles feeding in the spring. Although the Illinois estimates are more than double the other estimates, perhaps all of these researchers are correct. In our Experiments 1 to 2, mean consumption was about 1.3 cm$^2$ per beetle per d [to calculate, divide volumes in Fig. 5.2 by tissue thicknesses in Tables 5.4 and 5.5]. In contrast, mean consumption in Experiments 3 to 5 was about 0.5 cm$^2$ per beetle per d. Generations of *C. trifurcata* may differ substantially in total consumption and in preference for pods. Additional research is needed to determine the roles of variable
herbivores and variable plants in this fascinating system.

5.6 Acknowledgments

The authors gratefully acknowledge P. N. Hinz for assistance with experimental design, C. D. Lidtke and C. L. Carr for assistance in conducting the experiments, M. Carter and the technicians of the Iowa State University Image Analysis Facility for measuring injury on soybean parts, D. Sundberg for coordinating Kjeldahl analyses of soybean parts, and R. Cao for translating a Japanese publication. Research supported in part by Grant No. 91-09 from the Leopold Center for Sustainable Agriculture, Ames, IA. The Image Analysis Facility is supported by the Iowa State University Biotechnology Council. This is Journal Paper No. J- of the Iowa Agric. and Home Econ. Exp. Stn., Ames; Project Nos. 3183 and 3207.
6. CONCLUSIONS

6.1 Preventive tactics

Even if adopted by all growers in a region, delayed soybean planting would reduce bean leaf beetle survival and reproduction. Magnitudes of reductions would be greatest in regions without alfalfa, because beetles can use alfalfa as an alternate food while waiting for late-planted soybean to emerge. However, even in regions with alfalfa fields, delayed planting would substantially reduce beetle survival and reproduction. Most Iowa counties that produce soybean also produce some alfalfa, but the proximity of alfalfa to soybean varies from region to region. Therefore, additional research is needed to determine how the arrangement of alfalfa and soybean fields in the agricultural landscape affects beetle movement and survival.

6.2 Curative tactics

The degree-day model gives reasonably precise predictions of the date of emergence of F2-generation beetles. The F2 generation is responsible for most of the economic damage caused by the bean leaf beetle. Thus, by using the degree-day model, soybean growers can reduce the number of weeks during which they need to sample their fields for bean leaf beetles. Because sampling for bean leaf beetle should now require less time, this may increase grower acceptance of sampling. However, additional research is needed to determine why the model tends to predict F2-generation emergence earlier than it actually occurs. If such research was successful, the increased precision of predictions
would make sampling even more efficient, and thus even more acceptable to growers.

In addition, considerable progress has been made on predicting the susceptibility of soybean to pod injury. On average, beetles preferred the younger of the two pod classes that were common at a given soybean crop stage. However, beetles would feed even on pods that had begun to turn brown. Thus, it is not yet possible to state that soybean is exempt from pod feeding after a certain stage of development. Additional research is needed to answer a key question: does a given amount of pod feeding reduce soybean yield by different amounts depending on pod maturity? Quantifying the effect of pod age class on the damage/injury ratio would greatly increase the utility of the research in dissertation section 5.

Observations on pod phenology in soybean fields (Appendices 1 and 3) are being incorporated into a model for predicting pod phenology (Batchelor et al. 1995). This model will be combined with the degree-day model to allow simultaneous predictions of F2-generation beetle emergence and pod phenology (Zeiss et al. 1995). This combined model should further increase sampling efficiency, and thus may further increase acceptance of sampling by soybean producers. However, the true value of the model will be as a building block. The modular structure of the model will make it easy to incorporate results of future research on predicting C. trifurcata pod injury. As stated above, a key question for future research is how damage/injury ratios change as pods mature. In addition, future research should focus on predicting the abundance of the F2 generation based on the density of F1 or even overwintered beetles (Appendix 6).
6.3 Integrating preventive and curative tactics

This research contributed to a truly integrated approach for managing the bean leaf beetle. Early in the season, growers should plant their soybean as late in the recommended planting period as their production schedule will allow to help prevent pest problems. In mid-season, Extension personnel or pest management advisors should use models of beetle and soybean development to predict the likelihood and the timing of pod damage. If pod damage is likely, growers or pest management advisors should monitor beetle abundance and make decisions about curative insecticide use based on economic thresholds. Certainly, additional research is needed to fine-tune this system. Nonetheless, the progress to date on preventive and curative tactics forms the backbone of practical and sustainable management of the bean leaf beetle.
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McWilliams, J.M. 1983. Relationship of soybean pod development to bollworm and tobacco budworm damage. J. Econ. Entomol. 76: 502-506.


APPENDIX 1

PERCENT OF SOYBEAN PODS ('CORSOY 79')

INJURED BY BEAN LEAF BEETLE
Sampling unit was all plants in 30.5 cm of row. Four sampling units were collected from a given field on each sampling date. Soybean fields and pod age classes are described in section 5.3 of this dissertation. For corresponding beetle densities, see Appendix 2. In summary, the number of injured pods was very low until crop stage R5, and peaked at stages R6 to R7. Similar results have been reported by Helm et al. (1990) and Smelser & Pedigo (1992a).

Table A1. 1991 EARLY-PLANTED FIELD (planted 10 May)

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<th>Date</th>
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Note: The table presents data on the number of pods injured per plant. The values are given with standard deviations (±) for each category.
APPENDIX 2
BEAN LEAF BEETLE MEAN DENSITY IN THE SOYBEAN FIELDS
FROM WHICH APPENDIX 1 DATA WERE TAKEN

Sampling unit was 50 pendulum sweeps with an insect net (38 cm diam). Sixteen sampling units were collected from a given field on each sampling date.

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APPENDIX 3

SURFACE AREAS OF SOYBEAN PLANT PARTS ('CORSOY 79'),
BY CROP STAGE
Mean of two fields (early and late planted) per year. For early-planted fields, the numbers of pods are tabulated in Appendix 1 (surface areas were not measured in 1991). Sampling unit was all plants in 30.5 cm of row. Four sampling units were collected from a given planting-date treatment on each sampling date. Most crop stages persisted over two successive sampling dates, thus each mean comprises about 16 sampling units (2 treatments x 4 sampling units/treatment x 2 dates/crop stage = 16 sampling units/crop stage). Leaf categories and pod age classes are described in section 5.3.

Table A3.

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<th>1st trifol</th>
<th>2nd trifol</th>
<th>3rd trifol</th>
<th>Green</th>
<th>Discolor</th>
<th>GIMM</th>
<th>GSSE</th>
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a For crop stages R2 and R3, "3rd trifoliate" leaves were included in the "Green" category.

b Includes addition of new leaves at top of plant and loss of old leaves at bottom.
| CATEGORIES | GSSL | GFS | GYYG | YBBY | BRN | Number of main-stem nodes bearing green leaves$^b$
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Table A3 (continued).

SURFACE AREAS (cm², ± S.D.) IN 1993 FIELDS  
(planted 21 May & 15 June)

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<td>± 0</td>
<td>± 63</td>
<td>± 155</td>
<td>± 141</td>
<td>± 137</td>
<td>± 202</td>
<td>± 573</td>
<td>± 8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>± 123</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\*a\* Includes addition of new leaves at top of plant and loss of old leaves at bottom.
<table>
<thead>
<tr>
<th>CATEGORIES</th>
<th>GSSL</th>
<th>GFS</th>
<th>GYYG</th>
<th>YBBY</th>
<th>BRN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of main-stem nodes bearing green leaves</td>
<td>6.1</td>
<td>7.4</td>
<td>7.6</td>
<td>8.2</td>
<td>7.3</td>
</tr>
<tr>
<td>188 ± 213</td>
<td>86 ± 41</td>
<td>261 ± 213</td>
<td>59 ± 49</td>
<td>14 ± 28</td>
<td></td>
</tr>
<tr>
<td>514 ± 327</td>
<td>251 ± 135</td>
<td>158 ± 93</td>
<td>41 ± 63</td>
<td>131 ± 142</td>
<td></td>
</tr>
<tr>
<td>627 ± 297</td>
<td>420 ± 142</td>
<td>567 ± 382</td>
<td>41</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

*Note: The values represent the average number of main-stem nodes bearing green leaves across different categories.*
APPENDIX 4

BEETLE CONSUMPTION RATES IN PREFERENCE EXPERIMENTS,

BY TREATMENT AND PLANT PART
Table A4. Beetle consumption rates in preference experiments (\( \pm \) S.E.M.)

<table>
<thead>
<tr>
<th>Exper</th>
<th>Treatment: no. bottles(^a) with</th>
<th>Surface area (mm(^2)/beetle/day) consumed on:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaf(^b)</td>
<td>Younger pod(^c)</td>
</tr>
<tr>
<td>1</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>0</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
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<td>6</td>
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<tr>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>0</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
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<td>6</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>4</td>
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<tr>
<td>6</td>
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<tr>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>0</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Treatments: 12 bottles. 
\(^b\) Younger leaves: 0. 
\(^c\) Older leaves: 12. 
\(^d\) Leaves: 100 pods. 

\(\pm\) indicates standard error of the mean.
GYYG
pods

YBBY
pods
Table A4 (continued).
Beetle consumption rates in preference experiments ($x \pm S.E.M.$)

<table>
<thead>
<tr>
<th>Exper</th>
<th>Treatment: no. bottles$^a$ with</th>
<th>Surface area (mm$^2$/beetle/day) consumed on:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaf$^b$</td>
<td>Younger pod$^c$</td>
</tr>
<tr>
<td>4</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>6</td>
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<tr>
<td>0</td>
<td>0</td>
<td>6</td>
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<tr>
<td>0</td>
<td>12</td>
<td>0</td>
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<tr>
<td>5</td>
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<td>6</td>
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<td>6</td>
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<tr>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
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<td>6</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>0</td>
<td>12</td>
<td>0</td>
</tr>
</tbody>
</table>

$^a$ A total of 12 bottles per arena, each bottle occupied by an experimental stem bearing either three pods in the same age class or one trifoliate leaf.

$^b$ In all experiments, leaves were "first trifoliate" (see section 5.3 of this dissertation).

$^c$ Specific pod age classes vary with experiment; see section 5.3 of this dissertation.
<table>
<thead>
<tr>
<th>GYYG pods</th>
<th>YBBY pods</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>± 0.8</td>
</tr>
<tr>
<td>9</td>
<td>± 2.9</td>
</tr>
<tr>
<td>3</td>
<td>± 0.7</td>
</tr>
<tr>
<td>2</td>
<td>± 0.8</td>
</tr>
<tr>
<td>0</td>
<td>± 0.1</td>
</tr>
<tr>
<td>1</td>
<td>± 0.2</td>
</tr>
<tr>
<td>2</td>
<td>± 0.9</td>
</tr>
<tr>
<td>1</td>
<td>± 0.7</td>
</tr>
<tr>
<td>5</td>
<td>± 2.7</td>
</tr>
<tr>
<td>3</td>
<td>± 1.0</td>
</tr>
<tr>
<td>12</td>
<td>± 0.2</td>
</tr>
<tr>
<td></td>
<td>± 2.4</td>
</tr>
</tbody>
</table>
APPENDIX 5
RELATIVE EFFICIENCIES OF 5 SOIL QUADRAT SIZES
FOR SAMPLING BEAN LEAF BEETLE EGGS

Objectives
Determine which of 5 quadrat sizes is most efficient for estimating absolute abundance of bean leaf beetle (BLB) eggs.
Quantify the correlation between within-field variation in soybean stand density and BLB egg abundance.

Procedures
Sampling was conducted in a 0.5 ha field located adjacent an established alfalfa stand (2 ha) at Johnson Research Farm (2 km S of Ames, IA). Soil type was Webster silty clay loam. On 3 May 1990, the field was planted to soybeans (cv. 'Corsoy 79') in rows oriented E-W with 76 cm (30 in) row spacing and mean planting density approx. 1.8 seeds per 30 cm (11 seeds/ft). To quantify BLB invasion from adjacent alfalfa, BLB adults in four, 5-m sections of soybean row were counted twice weekly beginning at seedling emergence (14 May 1990).

On 12 or 16 June 1990, when soybeans had attained growth stages V3 and V4 respectively, a total of 26 locations within the field were sampled for BLB eggs. Egg sampling consisted of pushing contiguous sets of hollow rectangular sheetmetal corers into the soil to a depth of 8 cm. Corer dimensions and positions relative to soybean rows are diagrammed in Fig. A5.1. At half of the 26 locations, samples were taken N of a soybean row; the remaining locations were sampled S of a row. At each sample location, number of soybean plants per 30 cm was counted. Each corer and the soil core it enclosed were dug out of the surrounding soil, scraped to remove soil adhering to exterior of corer,
NOTE: all quadrats 8 cm deep

Quadrat 1Q (5 cm of row by 14 cm): core "B"
Quadrat 2Q (10 cm of row by 14 cm): core "D"
Quadrat 4Q (20 cm of row by 14 cm): core "C" plus core "D"
Quadrat Q4 (10 cm of row by 28 cm): core "D" plus core "E"
Quadrat 6Q (30 cm of row by 14 cm): sum of cores "A", "B", "C", and "D"

Figure A5.1. Positions of soil corers at each sample location, and quadrat sizes which result from combining contiguous cores (not to exact scale).
placed in a labelled plastic bag, and transported to a freezer. Time required for each sampling step was recorded for each corer at each location.

Soil cores were stored at -15°C until technicians were available to extract eggs (up to 6 months storage). BLB eggs were extracted from each soil core by sieving, flotation, and settling (see Appendix 6 for details), then were counted using a dissecting microscope. Number of hatched and unhatched BLB eggs, and time requirements for extracting and counting eggs, were recorded for each core. Counts of unhatched eggs from contiguous cores were summed within each sample site to provide the total number of unhatched eggs in 5 quadrat sizes (Fig. A5.1): quadrat 1Q (5 cm of row by 14 cm), quadrat 2Q (10 cm of row by 14 cm), quadrat 4Q (20 cm of row by 14 cm), quadrat 4Q (10 cm of row by 28 cm), and quadrat 6Q (30 cm of row by 14 cm).

For each of these quadrat sizes, the mean density (and standard error) of unhatched eggs among all sample locations was computed. Similarly, the total sampling, processing, and counting time requirements for each quadrat size were computed by summing time requirements for contiguous cores. The relative net precision (R.N.P.) of each quadrat size was then computed from relative variability (R.V.) and total cost using the following formula:

\[
R.N.P. = \frac{100}{R.V. \times (\text{total cost for 26 locations})}, \quad \text{where} \quad R.V. = \frac{\text{S.E.M.}}{\text{mean}}
\]

Total cost was expressed in units of person-hours required to collect, extract, and count 26 units of a given quadrat.

For all locations, the numbers of unhatched eggs in each quadrat size (1Q, 2Q, 4Q, etc.) were regressed against the number of soybean plants per 30 cm of row. In each regression, both linear and quadratic models were tested. Effect of row side (N or S) on number of unhatched eggs was tested via analysis of variance for each quadrat size.
To quantify the precision and accuracy of the egg extraction and counting process, 18 control cores (10 by 14 by 8 cm) of soil (Webster silty clay loam) known to be free of BLB eggs were each amended with 10 unhatched BLB eggs obtained from a laboratory culture. Four of these control cores were further amended with various numbers of hatched BLB eggs (empty chorions). Eggs were extracted from each control core as described for experimental cores, with the exception that control cores were not frozen prior to extraction. Numbers of unhatched and hatched eggs extracted were recorded for each control core. Percent recoveries for unhatched and hatched eggs were computed for each control core as follows: % recovery = 100 x (# eggs recovered / # eggs added to core).

Results

Results from control cores indicated that the egg extraction and counting process was reasonably reliable for unhatched eggs, but not reliable for hatched eggs. Mean percent recovery (n = 18 control cores) for unhatched eggs was 90.6% (S.E.M. 2.66%, range 70.0-100.0%). In contrast, mean percent recovery (n = 4 control cores) was only 17.5% for hatched eggs (S.E.M. 7.4%, range 0.0-40.0%). Accordingly, only data for unhatched eggs were used in calculating correlations and relative net precisions for experimental quadrats.

Regardless of quadrat size, abundance of unhatched eggs was not significantly correlated with soybean stand density (P > 0.30 in all regressions). Nor did row side (N or S) have a significant effect on egg abundance (P > 0.50). Therefore, neither stand density nor row side was used in calculating quadrat efficiencies (i.e., neither was used as a covariate).

Precision (R.V.), cost, and efficiency (R.N.P.) for each of the 5 quadrats are summarized in Table A5. The 2 smallest quadrats (1Q and 2Q) were most efficient, i.e.,
Table A5. Precision (R.V.), cost, and efficiency (R.N.P.) of 5 quadrat sizes for sampling unhatched BLB eggs

<table>
<thead>
<tr>
<th>Quadrat dimensions*</th>
<th>&quot;A&quot; Mean # unhatched eggs</th>
<th>S.E.M.</th>
<th>&quot;B&quot; Relative variability 100 x (B/A)</th>
<th>&quot;D&quot; Hours to collect 26 samples</th>
<th>&quot;E&quot; Hours to extract 26 samples</th>
<th>&quot;F&quot; Hours to count 26 samples</th>
<th>&quot;G&quot; Total hours 26 samples (D + E + F)</th>
<th>&quot;H&quot; Relative Net Precision 100 / (C x G)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1Q (5 x 14 cm)</td>
<td>3.92</td>
<td>1.50</td>
<td>38.3</td>
<td>0.57</td>
<td>10.48</td>
<td>3.67</td>
<td>14.72</td>
<td>0.178</td>
</tr>
<tr>
<td>2Q (10 x 14 cm)</td>
<td>6.81</td>
<td>2.09</td>
<td>30.7</td>
<td>0.67</td>
<td>12.76</td>
<td>4.77</td>
<td>18.2</td>
<td>0.179</td>
</tr>
<tr>
<td>4Q (20 x 14 cm)</td>
<td>14.42</td>
<td>2.64</td>
<td>18.3</td>
<td>1.35</td>
<td>31.28</td>
<td>11.80</td>
<td>44.43</td>
<td>0.123</td>
</tr>
<tr>
<td>Q4 (10 x 28 cm)</td>
<td>7.88</td>
<td>2.19</td>
<td>27.8</td>
<td>1.09</td>
<td>23.63</td>
<td>9.37</td>
<td>34.09</td>
<td>0.105</td>
</tr>
<tr>
<td>6Q (30 x 14 cm)</td>
<td>20.15</td>
<td>3.89</td>
<td>19.3</td>
<td>1.83</td>
<td>42.71</td>
<td>16.62</td>
<td>61.16</td>
<td>0.085</td>
</tr>
</tbody>
</table>

* All quadrats 8 cm deep
had the highest R.N.P.'s. For the remaining 3 quadrats, efficiency decreased as
quadrat size increased.

Mean egg density in core E was 2.20 eggs (S.E.M. = 1.65), corresponding to
28% of all eggs found in quadrat Q4. In other words, 28% of the eggs in quadrat
Q4 were located more than 14 cm from the nearest soybean plant.

Discussion

Mean egg density at the time the field was sampled was approx. 7.9 eggs per 10
cm of row. At that mean density, the 3 largest quadrats were more precise (had
lower R.V.'s) than either 1Q or 2Q. However, this increase in precision was
accompanied by a disproportionate increase in sampling cost. Extrapolation from a
study such as this is unreliable, because either organism abundance or sampling costs
may change abruptly (rather than continuously) as quadrat size changes.
Nonetheless, it seems likely that sampling at mean egg densities close to 7.9 eggs/10
cm would be most efficient if conducted using quadrats that enclosed no more than
10 row-cm. With n = 26 samples per field, both 1Q and 2Q gave R.V.'s considerably
greater than the 10% usually considered desirable for population dynamics studies.
To increase precision (decrease R.V.), sampling effort should apparently be invested
in increasing the number of samples "n" rather than in sampling physically larger
quadrats such as 4Q or 6Q.

Because R.N.P. of a given quadrat often changes with mean density, this study
must be repeated at several mean densities before any conclusions can be drawn
about which quadrat size (if any) is most efficient for sampling BLB eggs at all
densities [see Appendix 6 for data from sampling several mean densities using
quadrat Q4]. Further, because large numbers of eggs are located more than 14 cm
from soybean plants, future sampling should utilize only quadrats that extend more
than 14 cm out from the row if estimates of absolute egg abundance are desired. Previously published studies found less than 7% of total eggs located more than 14 cm from a soybean plant (Waldbauer & Kogan 1975).

Finally, in future experiments control cores should be subjected to the same conditions (e.g., freezing) as those experienced by experimental cores. Published reports suggest that freezing for several weeks does not alter percent egg recovery, but no published data are available on the effects of 6 months of freezing.
APPENDIX 6

PARTIAL LIFETABLE FOR BEAN LEAF BEETLE IN IOWA SOYBEAN

Objectives

To quantify fecundity of overwintered and F1-generation bean leaf beetle (BLB) females.

To quantify survivorship of F1- and F2-generation BLB immatures.

To estimate costs of sampling required for future lifetables.

Procedures

Experimental site comprised halves of two fields at Johnson Research Farm (5 km S of Ames, IA). Soil type in each was Webster silty clay loam. Fields were contiguous with an established alfalfa stand (2 ha), and were being used for a concurrent study of soybean planting date. On 3 May 1990, half (0.5 ha) of each field was planted to soybeans (cv. 'Corsoy 79') with 76 cm (30 in) row spacing and planting density approx. 10.8 seeds per 30 cm (11 seeds/ft). On 30 May 1990, remaining halves were planted to 'Corsoy 79' soybeans at the same density. Lifetable sampling was conducted in the late-planted halves, which were divided into a total of 14 plots (strata) each approx 700 m². To reduce cumulative habitat destruction, only 7 strata (chosen randomly) were sampled for overwintered adults and F1 eggs from 8 June-11 July 1990. The remaining 7 strata were not disturbed until being sampled for F1-generation adults and F2-generation eggs and adults from 5 July-24 August 1990.

Sampling and calculation procedures used for each BLB stage are summarized in Table A6.1.

Estimating overwintered adult longevity. On 4 June (prior to seedling emergence), 15 screen cages were erected at the experimental site. Ten cages (1.8 by 0.9 m) were
covered with saran screen; 5 cages (3.0 by 0.6 m) were covered with aluminum screen. All cages were positioned with long axes parallel to soybean rows, with each cage centered over a row. Bottom edges of cages were buried to preclude BLB invasion. On 13 June, 7 cages (5 saran, 2 metal) were infested with overwintered BLB adults collected via sweepnet from an alfalfa field at Ross Research Farm. Each cage was infested at the rate of 10 BLB adults per row-m. Beginning on 18 June 1990, number of BLB surviving in each infested cage was counted twice weekly by entering the cage and examining soybean foliage and cage interior. Two uninfested (control) cages were also sampled. Sampling was terminated when survivors were no longer found (18 July 1990).

For each infested cage, number of survivors was graphed against Julian date. The area under each survival curve was calculated via the ENT671 computer program, and divided by the number of beetles initially placed in the cage. The result was an estimate of mean longevity among the beetles in a given cage. Results from each of the 7 cages were averaged to produce a grand mean of longevity per overwintered beetle.

**Sampling overwintered and F1 adults.** From seedling emergence (8 June 1990) to soybean growth stage V6 (8 July 1990), 7 direct-count samples (1 per stratum) were taken twice weekly. Direct-count sampling consisted of counting all BLB adults in a 5-m section of row. From soybean growth stages V7 (11 July 1990) to R6 (24 August 1990), 35 beatcloth samples (5 per stratum) were taken weekly. Beatcloth sampling consisted of placing a muslin cloth (1 m by 76 cm) on soil surface between 2 soybean rows with long axis parallel to rows, bending soybean plants from 1 m of one row over the cloth, vigorously shaking and beating plants for 30 secs to dislodge beetles, and counting the number of BLB falling onto the cloth. Maturity (teneral or adult) was determined for beetles in beatcloth samples.

Beetles were classified by sample date as belonging to the overwintered or F1
generation. Adult counts decreased to zero on 5 July 1990. Teneral counts began increasing on 11 July 1990. Therefore, all beetles sampled prior to 5 July were classified as overwintered, and all beetles in beatcloth samples after 5 July were classified as F1 generation. Separate graphs of abundance vs. Julian date were made for each generation. Areas under each abundance curve were calculated using the ENT671 computer program. To estimate total number of BLB sampled, area under the overwintered generation abundance curve was divided by the mean longevity of overwintered beetles (from the caging experiment described above). Area under the F1-generation abundance curve was divided by 20 days, a published estimate of F1 adult longevity.

**Sampling F2 adults.** In mid-August, soybean plants began to lodge, decreasing the accuracy of beatcloth samples. To obtain an estimate of absolute abundance of F2 adults, 28 emergence cages were set out on 16 August 1990. Each cage comprised a hollow rectangular wooden base (1 row-m by 38 cm) topped with a metal screen pyramid (height 40 cm). Long end of each cage was pressed flush against soybean stems. Bottom edges of bases were buried to preclude BLB movement in or out. Three cages were placed in each of 7 strata (21 cages total). The remaining 7 cages were used as controls. Control cages were placed over portions of the experimental site from which BLB had been excluded throughout the season [i.e., portions that had been covered by 7 of the large uninfested screen cages; see "Estimating overwintered adult longevity".]

Beginning 22 August 1990, each emergence cage was examined twice weekly for BLB. Any BLB in cages were removed by lifting up cage bottom and inserting an aspirator. Sex and maturity (teneral or adult) of BLB were determined, then cage bottom was re-buried. Sampling was terminated when adult emergence ceased (26 September 1990).

Mean total BLB capture was computed for the 21 experimental emergence cages. A separate mean was computed for the 7 control cages.
Measuring cumulative egg degree-days. From 6 May-5 October 1990, daily mean soil temperature at 3 cm depth was recorded via a LI-1200S automated weather station (Li-Cor, Inc., Lincoln, NE). Daily mean soil temperature was converted to daily BLB degree-days by subtracting the minimum cardinal temperature (11.5°C). Degree-day accumulations for each date were calculated by adding each date's degree-days to those of all preceding dates.

Sampling F1 and F2 eggs. From 12 June-11 July 1990, 7 egg samples (1 per stratum) were taken twice weekly. From 11 July-21 August 1990, 7 egg samples (1 per stratum) were taken weekly. Egg sampling consisted of pushing a hollow rectangular sheetmetal corer (10 row-cm by 28 cm) into the soil to a depth of 8 cm. Short end of the corer was pressed flush against soybean stems while pushing into soil. Each corer and the soil core it enclosed were dug out of the surrounding soil, scraped to remove soil adhering to exterior of corer, placed in a labelled plastic bag, and transported to a freezer.

Soil cores were stored at -15°C until technicians were available to extract eggs (up to 5 months storage). BLB eggs were extracted by rinsing each soil core through a #30 sieve, retaining eggs and small debris in a #50 sieve, then decanting into a 1 l separatory funnel containing 700 ml of MgSO₄ solution of specific gravity 1.25 (in which eggs float). Debris with a specific gravity > 1.25, along with most of the MgSO₄ solution, were drained out of the bottom of the separatory funnel. Eggs and low-density debris remaining were agitated with a weak solution of Sparkleen detergent (3.5 g Sparkleen/l H₂O), then allowed to settle. BLB eggs were drained out the bottom of the funnel in a few ml of solution, then were counted using a dissecting microscope.

To quantify the precision and accuracy of the egg extraction and counting process, eggs were extracted from 18 control cores to which known numbers of eggs had been added [see Appendix 5 for details].
Eggs were classified by sample date as belonging to the F1 or F2 generation. By 11 July 1990, egg counts had fallen to zero, but increased rapidly after 19 July. Therefore, all eggs sampled prior to 11 July were classified as F1, and all eggs sampled after 11 July were classified as F2 generation. Separate graphs of abundance vs. cumulative egg degree-days were made for each generation. Areas under each abundance curve were calculated using the ENT671 computer program. To estimate total number of eggs sampled, area under each abundance curve was divided by the mean duration of the egg stage (121.2 egg degree-days).

**Life table calculations.** The calculated numbers of BLB that survived to each sampled life stage (egg or adult) were used to develop a partial lifetable in the format of Harcourt (1969). Life table columns were calculated as follows.

- $l_x$: The number of survivors per 10 cm of row. Calculated as described above (see Table A6.1 for summary).
- $d_x^F$: Factor which caused mortality in a given stage. Only adult sex ratio is listed. No effort was made to determine mortality factors for immature stages.
- $d_x$: Number of individuals dying during a given stage. $d_x$ for stage “n” = ($l_x$ for stage “n”) - ($l_x$ for stage “n+1”). Total mortality for a generation was calculated by summing the $dx$ values for all stages.
- $100q_x$: Percent mortality during a given stage. $100q_x = 100 \times (d_x / l_x)$. Overall % mortality for a generation was calculated by dividing the total generation mortality by the initial $lx$, and multiplying the result by 100.
- $s_x$: Proportion of individuals surviving a given stage. $s_x$ for stage “n” = ($l_x$ for stage “n+1”) / ($l_x$ for stage “n”)

**Egg sampling cost predictions.** For all egg sample dates, log of sample variance was regressed against log of sample mean. A dummy variable was included in the data
set to test the effect of egg generation (F1 or F2). Regression coefficients were used to predict sample variances within the range of mean egg densities sampled. Based on predicted sample variances, sample sizes required to attain various levels of precision were calculated from the formula:

\[ n = \frac{s^2}{C^2 \cdot \bar{x}} \], where \( C = \frac{\text{S.E.M.}}{\bar{x}} \)

Results

Table A6.1 summarizes the estimates of absolute abundance for the various generations and stages. A partial life table (egg and adult stages only) for the F1 and F2 generations is presented in Table A6.2. Each overwintered female apparently oviposited an average of 327 eggs, of which 9.0% survived to the F1 adult stage. Each F1 female apparently oviposited an average of 66 eggs, of which 6.8% survived to the F2 adult stage. The trend index over two generations (i.e., the ratio of F2 adults: overwintered adults) was 45.3. The trend index from F1 to F2 adults was 2.5.

Slopes of linear regressions of log variance against log mean for egg samples were significantly different for F1- vs. F2-generation eggs \( (r= 2.811, \ 1 \ d.f., \ P= 0.031) \). Therefore, separate regressions were performed for samples of F1-generation (Fig. A6.1) and F2-generation (Fig. A6.3) eggs. Regression coefficients were used to predict sample variances for mean egg densities ranging from 0-10 eggs/10 row-cm. Predicted variances were then used to predict the number of quadrats (10 by 28 cm) that would have to be sampled (per field per sample date) to achieve various levels of precision (Figs. A6.2 and A6.4).
\[ \log Y = \log 3.097 + (1.626 \times \log X) \]

\[ R'^2 = 0.964 > 0.4 \]

Mean egg density (per 10 cm. of row)

Figure A6.1. Regression of variance vs. mean for F1-generation eggs

Mean egg density (per 10 cm. of row)

Figure A6.2. Sampling requirements for F1-generation eggs (from Taylor's power law)
\[
\log Y = \log 2.510 + (1.042 \times \log X)
\]

\[R^2 = 0.967\]

Figure A6.3. Regression of variance vs. mean for F2-generation eggs

Figure A6.4. Sampling requirements for F2-generation eggs (from Taylor's power law)
Table A6.1. Derivation of $l_x$ values used in the life table.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Stage</th>
<th>Sampling used to estimate absolute abundance</th>
<th>Independent variable against which abundance data were graphed</th>
<th>&quot;A&quot; (Area under the graph of abundance)</th>
<th>&quot;B&quot; (Duration of the stage)</th>
<th>$l_x$ (the abundance of the stage per meter of row)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overwintered</td>
<td>Adult</td>
<td>Direct counts and beatcloth samples in strata 1 - 7</td>
<td>Julian date</td>
<td>2.30 beetle-days</td>
<td>16.28 days (from longevity of caged beetles)</td>
<td>0.14 beetles</td>
</tr>
<tr>
<td>F1</td>
<td>Egg</td>
<td>Egg sampling in strata 1 - 7</td>
<td>Cumulative degree-days</td>
<td>4,215.3 degree-days</td>
<td>121 degree-days (from Zeiss et al. 1994)</td>
<td>34.78 eggs</td>
</tr>
<tr>
<td>F1</td>
<td>Adult</td>
<td>Beatcloth samples in strata 8 - 14</td>
<td>Julian date</td>
<td>51.94 beetle-days</td>
<td>20.0 days (from Isely 1930)</td>
<td>2.60 beetles</td>
</tr>
<tr>
<td>F2</td>
<td>Egg</td>
<td>Egg sampling in strata 8 - 14</td>
<td>Cumulative degree-days</td>
<td>13,838.6 egg-degree-days</td>
<td>121 degree-days (from Zeiss et al. 1994)</td>
<td>114.18 eggs</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Emergence traps in strata 8 - 14</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>6.40 beetles (mean total catch per trap)</td>
<td></td>
</tr>
</tbody>
</table>
Table A6.2. Partial life table for bean leaf beetle in Iowa soybean.

<table>
<thead>
<tr>
<th>Generation</th>
<th>x</th>
<th>$I_x$ (per m of row)</th>
<th>$d_xF$</th>
<th>$d_x$</th>
<th>$100q_x$</th>
<th>$s_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overwintered</td>
<td>Adult</td>
<td>0.14</td>
<td>Sex ratio 0.04</td>
<td>24.82</td>
<td>0.752</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Female adult</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F1</td>
<td>Egg</td>
<td>34.78</td>
<td>32.18</td>
<td>92.52</td>
<td>0.075</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>2.60</td>
<td>Sex ratio 0.88</td>
<td>33.85</td>
<td>0.662</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Female adult</td>
<td>1.72</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F2</td>
<td>Egg</td>
<td>114.18</td>
<td>107.78</td>
<td>94.39</td>
<td>0.056</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>6.40</td>
<td>Sex ratio 3.03</td>
<td>47.37</td>
<td>0.526</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Female adult</td>
<td>3.37</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Discussion

Because there are few published data on dynamics of BLB field populations, it is difficult to gauge the accuracy of the values presented in Table A6.2. Estimated fecundity of overwintered females is at the high end of the range reported for laboratory populations, and therefore seems excessive. Sampling probably underestimated overwintered females or overestimated F1 eggs. Any lifetable is only as reliable as the sample data from which it is derived. For studies of population dynamics, sample data are generally considered sufficiently precise if the relative variability (S.E.M./mean) of the data is ≤10%. In contrast, relative variabilities of the adult beetle samples in this study averaged 68% for direct counts, 23% for beatcloth samples, and 18% for F2 emergence cages. Relative variabilities of egg samples averaged 64% for F1 eggs and 43% for F2 eggs.

To allow BLB population dynamics to be compared and contrasted among locations and years, future studies of BLB population dynamics must achieve more precise estimates of absolute abundance. Sampling methods should be improved where possible (e.g., by using quadrat sizes with lower variability). In addition, sample sizes should be increased. Figs. A6.2 and A6.4 illustrate the cost of increasing sample sizes in egg sampling. Similar calculations should be made for other sampling techniques.
APPENDIX 7
FORTRAN CODE FOR WSPLICE2 AND WSPLICE3

Introduction

Two FORTRAN computer programs, WSPLICE2 and WSPLICE3, are presented. Each program can splice together two weather data files that conform to the standards of DSSAT, the Decision Support System for Agrotechnology Transfer. Specifically, WSPLICE2 and WSPLICE3 can splice weather data files that conform to DSSAT versions 2.1 and 3.0, respectively. For each WSPLICE version, the intended application is to create a hybrid file of weather data that begins with actual observations of past weather but concludes with predicted values for future weather. The hybrid weather data file then could be used as an input for DSSAT crop simulation models to generate forecasts of future crop development. This would improve curative management of bean leaf beetle by improving the accuracy of forecasts of soybean susceptibility to beetle injury.

Both programs are available on the Internet via either Gopher or FTP in the "Software" directory of Iowa State University's Entomology Gopher/FTP server (gopher.ent.iastate.edu). Each program is available both as FORTRAN source code and as an executable version suitable for DOS microcomputers. A publication describing the use and structure of these programs is currently under preparation:

1. WSPLICE2

PROGRAM WSPLICE2

* THIS PROGRAM SPLICES WEATHER DATA FILES FOR DSSAT V2.1 *
* Written By: Steven Knapp (sknapp@iastate.edu) *
* Modifications by Scott Williams (swilliam@iastate.edu) 10/18/94 *

c Identifier from first column
CHARACTER*4 IDENT

REAL DATA(5)

integer JDAY, YEAR, ENDDAY, CURDAY, TEMPDAY, MO, $ DAY, YR, FDATE

character ICHR

character*12 INFIL, INFIL2

character*70 HEADER

real CDATE

integer IDL

character*2 INSTW1, INSTW2

character*2 STATW1, STATW2

real XLAT1, XLAT2

real XLONG1, XLONG2

real PARFC1, PARFC2

real PARDT1, PARDT2

character*70 JUNK1, JUNK2

logical YESPAR

PRINT *, 'This program splices any two weather files that'
PRINT *, 'meet the specifications of DSSAT version 2.1.'
PRINT *
PRINT *, 'A new file named "TEMP0000.W00" will be created.'
PRINT *, 'This file will not contain any columns of data'
PRINT *, 'that are not found in BOTH input files.'
PRINT *
PRINT *, 'Before running one of the DSSAT crop growth models'
PRINT *, 'be sure to create an entry for this new file in the'
PRINT *, 'appropriate directory. For example, for SOYGRO'
PRINT *, 'create an entry for "TEMP0000.W00" within the SOYGRO'
PRINT *, "WTH.DIR" file.'
PRINT *
PRINT *, 'Note: Continuing with this splicing program will'
PRINT *, 'overwrite any existing file named "TEMP0000.W00".'
PRINT *, 'If you have a previous file that you wish to save,'
PRINT *, 'you should rename it via the DOS RENAME command'
PRINT *, 'before continuing.'
PRINT *
c Allow user the ability to exit the program, default is continue.

1 PRINT *, 'Okay to continue and overwrite any previous '
PRINT *, '"TEMP0000.W00" file (Y,N)?'
READ '(A)', ICHR
IF (ICHRS .EQ. 'N') .OR. (ICHRS .EQ. 'n')) STOP
IF (.NE. 'y') .AND. (ICHRS .NE. 'Y')) GO TO 1
PRINT *
c GET FILE NAMES

PRINT *, 'Enter the name of the first weather file to use:'
READ '(A)', INFIL
PRINT *
PRINT *, 'Enter the name of the second weather file to use:'
READ '(A)', INFIL2
PRINT *
c GET SPLICE DATE

5 PRINT *, 'Enter the date through which the first file should'
PRINT *, 'be used, in mm/dd format. [Example: 01/06]'
PRINT *, 'Enter 00/00 to process all of file #1.'

5 If they enter the date in an invalid format, prompt them again
READ (UNIT=5,FMT='(I2,1X,I2)',ERR=5) MO, DAY
PRINT *
IF ((MO .GT. 12) .OR. (DAY .GT. 31)) THEN
  GO TO 5
END IF

OPEN BOTH INPUT FILE AND OUTPUT FILE

OPEN (UNIT=12, FILE='TEMP0000.W00', STATUS='UNKNOWN')
OPEN (UNIT=13, FILE='INFIL', STATUS='OLD', ERR=200)
OPEN (UNIT=14, FILE='INFIL2', STATUS='OLD', ERR=201)

GET AND COPY HEADER FROM FIRST FILE

READ (UNIT=13, FMT=1004,END=200, ERR=205) INSTW1,
$  STATW1,XLAT1,XLONG1,PARFC1,PARDT1,JUNK1
READ (UNIT=14, FMT=1004,END=201, ERR=206) INSTW2,
$  STATW2,XLAT2,XLONG2,PARFC2,PARDT2,JUNK2

YESPAR = .TRUE.
IF ( (PARDT1 .eq. 0.0) .OR. (PARDT2 .eq. 0.0)) THEN
  YESPAR = .FALSE.
  PARDT1 = 0.0
END IF

WRITE(UNIT=12,FMT=1004,ERR=207) INSTW1,
$  STATW1,XLAT1,XLONG1,PARFC1,PARDT1,JUNK1

READ (UNIT=14, FMT='(A)', END = 201,ERR=206) HEADER

GET YEAR AND COPY HRST RECORD

ENDDAY = 0
READ (UNIT=13,FMT=1000,END=200,ERR=208) IDENT, YR, FDATE,
$  (DATA(IDL),IDL=1,5)
IF (MO .NE. 0) THEN
  ENDDAY = JDATE(MO,DAY,YR)
  IF (ENDDAY .LT. FDATE) GO TO 204
  WRITE (*,'(A36,F5.2)') Tile #1 will be processed through: ',
$  CDATE(ENDDAY,YR)
ELSE
  PRINT *,'File #1 will be completely processed.'
END IF
PRINT *
IF (YESPAR) THEN
    WRITE(UNIT=12,FMT=1001,ERR=209) IDENT, YR, FDATE,
$    (DATA(IDL),IDL=1,5)
ELSE
    WRITE(UNIT=12,FMT=1005,ERR=209) IDENT,YR,FDATE,
$    (DATA(IDL),IDL=1,4)
ENDIF

IF (FDATE .EQ. ENDDAY) GO TO 20

Copy records

10 READ (UNIT=13,FMT=1002,END=15,ERR=210) TEMPDAY,
$   (DATA(IDL),IDL=1,5)
IF (TEMPDAY .EQ. 0) GO TO 10
CURDAY = TEMPDAY

IF (YESPAR) THEN
    WRITE(UNIT=12,FMT=1001,ERR=211) IDENT, YR, CURDAY,
$   (DATA(IDL),IDL=1,5)
ELSE
    WRITE(UNIT=12,FMT=1005,ERR=211) IDENT,YR, CURDAY,
$   (DATA(IDL),IDL=1,4)
ENDIF

IF (CURDAY .EQ. ENDDAY) GO TO 20
GO TO 10

File ends on another day other than ENDDAY

15 IF (MO .NE. 0) THEN
   PRINT *,
$       ' First file ended before the specified date was found.'
   PRINT *
   c If the date was not found in the first file,
   c Delete the output, close both files, and get a new date.
   CLOSE(UNIT=13,STATUS='KEEP',ERR=200)
   CLOSE(UNIT=12,STATUS='DELETE',ERR=203)
   GO TO 5
END IF
   PRINT *
   PRINT '((A),F5.2,(A))', ' File #1 ended on ',CDATE(CURDAY,YR),','
ENDDAY = CURDAY
GO TO 21

c File ENDED 21-END 20-reached date.

20 PRINT *,'File #1 reached entered date successfully.'
21 PRINT *,'Beginning processing on file #2.'
CLOSE(UNIT=13, ERR=200, STATUS='KEEP')
PRINT *

c Search 2nd file for ENDDAY+1

IF (ENDDAY .EQ. 365) THEN
   CURDAY = 0
   GO TO 500
END IF

30 READ (UNIT=14,FMT=1002,END=202,ERR=213) TEMPDAY,
   $ (DATA(IDL),IDL=1,5)
   IF (TEMPDAY .EQ. ENDDAY+1) GO TO 35
   GO TO 30

35 CURDAY = TEMPDAY

   IF (YESPAR) THEN
      WRITE(UNIT=12,FMT=1001,ERR=211) IDENT, YR, CURDAY,
         $ (DATA(IDL),IDL=1,5)
   ELSE
      WRITE(UNIT=12,FMT=1005,ERR=211) IDENT, YR, CURDAY,
         $ (DATA(IDL),IDL=1,4)
   ENDIF

c Once found, start copying after that.

40 READ (UNIT=14,FMT=1002,END=500,ERR=212) TEMPDAY,
   $ (DATA(IDL),IDL=1,5)
   IF (TEMPDAY .EQ. 0) THEN
      GO TO 40
   END IF
   CURDAY = TEMPDAY

   IF (YESPAR) THEN
      WRITE(UNIT=12,FMT=1001,ERR=211) IDENT, YR, CURDAY,
         $ (DATA(IDL),IDL=1,5)
ELSE
WRITE(UNIT=12,FMT=1005,ERR=211) IDENT,YR, CURDAY,
$(DATA(IDL),IDL=1,4)
ENDIF

GO TO 40

*********************************
| Error reports |
************************************************

200  PRINT *, 'Problems developed with file:',INFIL,'.'
PRINT *, 'Possible causes:'
PRINT *, '- File does not exist'
PRINT *, '- File is in another directory'
PRINT *, '- File is empty'
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=13,STATUS='KEEP')
GO TO 520

201  PRINT *, 'Problems developed while processing file:',INFIL2,'.'
PRINT *, '- File does not exist'
PRINT *, '- File is in another directory'
PRINT *, '- File is empty'
CLOSE(UNIT=14,STATUS='DELETE')
CLOSE(UNIT=13,STATUS='KEEP')
GO TO 520

202  PRINT '(A$F5.2,A,I3,A,A,1)', 'The month/day ',
$ CDATE(ENDDAY+1,YR), (Julian Date ',ENDDAY+1,')','
$ 'not found in ', INFIL2,'.'
PRINT *
CLOSE(UNIT=14,STATUS='KEEP',ERR=200)
CLOSE(UNIT=12,STATUS='DELETE',ERR=203)
GO TO 5

203  PRINT *,'An error occured in writing TEMPO000.W00.'
PRINT *,'Possible cause:'
PRINT *,'- Disk is full'
GO TO 520

204  PRINT *,'The file ',INFIL,' does not begin before the ',
$ 'day requested.'
CLOSE(UNIT=13,STATUS='KEEP',ERR=200)
CLOSE(UNIT=12,STATUS='DELETE',ERR=203)
GO TO 5
205 PRINT *,'An error occurred while reading the header', $  ' from ','INFIL,':'
  PRINT *,Possible cause:
  PRINT *,'- Data file may have been improperly formatted'
  CLOSE(UNIT=13,STATUS='KEEP')
  CLOSE(UNIT=12,STATUS='DELETE')
  CLOSE(UNIT=14,STATUS='KEEP')
  GOTO 520
206 PRINT *,'An error occurred while reading the header', $  ' from ','INFIL2,':'
  PRINT *,Possible cause:
  PRINT *,'- Data file may have been improperly formatted'
  CLOSE(UNIT=13,STATUS='KEEP')
  CLOSE(UNIT=12,STATUS='DELETE')
  CLOSE(UNIT=14,STATUS='KEEP')
  GOTO 520
207 PRINT *,'An error occurred while writing the', $  ' header to TEMP0000.WOO.'
  PRINT *,Possible cause:
  PRINT *,'- Not enough space to create TEMP0000.WOO'
  CLOSE(UNIT=13,STATUS='KEEP')
  CLOSE(UNIT=12,STATUS='DELETE')
  CLOSE(UNIT=14,STATUS='KEEP')
  GOTO 520
208 PRINT *,'An error occurred while reading the', $  ' first data record from ','INFIL,':'
  PRINT *,Possible cause:
  PRINT *,'- Data file may have been improperly formatted.'
  CLOSE(UNIT=13,STATUS='KEEP')
  CLOSE(UNIT=12,STATUS='DELETE')
  CLOSE(UNIT=14,STATUS='KEEP')
  GOTO 520
209 PRINT *,'An error occurred while writing data', $  ' to TEMP0000.WOO.'
  PRINT *,Possible cause:
  PRINT *,'- Not be enough space to create TEMP0000.WOO'
  CLOSE(UNIT=13,STATUS='KEEP')
  CLOSE(UNIT=12,STATUS='DELETE')
  CLOSE(UNIT=14,STATUS='KEEP')
  GOTO 520
210 PRINT *,'An error occurred while copying', $  ' records from ','INFIL,':'
  PRINT *,Last day successfully processed was day,CURDAY
PRINT *, 'Possible cause:'  
PRINT *, 'Data file may have been improperly formatted'  
CLOSE(UNIT=13,STATUS='KEEP')  
CLOSE(UNIT=12,STATUS='DELETE')  
CLOSE(UNIT=14,STATUS='KEEP')  
GOTO 520

211 PRINT *, 'An error occurred while copying',  
$ ' records to TEMP0000.WOO.'  
PRINT *, 'There may not be enough space to create',  
$ ' TEMP0000.WOO'  
CLOSE(UNIT=13,STATUS='KEEP')  
CLOSE(UNIT=12,STATUS='DELETE')  
CLOSE(UNIT=14,STATUS='KEEP')  
GOTO 520

212 PRINT *, 'An error occurred while copying',  
$ ' records from ', INFIL2',.'  
PRINT *, 'Last day successfully processed was day', CURDAY  
PRINT *, 'Possible cause:'  
PRINT *, 'Data file may have been improperly formatted'  
CLOSE(UNIT=13,STATUS='KEEP')  
CLOSE(UNIT=12,STATUS='DELETE')  
CLOSE(UNIT=14,STATUS='KEEP')  
GOTO 520

213 PRINT *, 'An error occurred while skipping over',  
$ ' records from ', INFIL2',.'  
PRINT *, 'Last day successfully processed was day', CURDAY  
PRINT *, 'Possible cause:'  
PRINT *, 'Data file may have been improperly formatted'  
CLOSE(UNIT=13,STATUS='KEEP')  
CLOSE(UNIT=12,STATUS='DELETE')  
CLOSE(UNIT=14,STATUS='KEEP')  
GOTO 520

Description of file completion

500 PRINT *, 'Splicing successful!'  
PRINT *, 'A new file TEMP0000.WOO has been created.'  
PRINT *, 'It contains:'  
PRINT '(A,A,A,F5.2,A,F5.2,A)',  
$ ' Data from file ', INFIL2 ', from date ',
$ CDATE(FDATE,YR), to CDATE(ENDDAY,YR),''
PRINT '(A,I3,A,I3,A), Julian date 'FDATE,
$ to', ENDDAY,'''

IF (CURDAY .GT. ENDDAY) THEN
  PRINT '(A,A,AA,F5.2,A,F5.2,A),
  $ Data from file 'JNFIL2,' from date
  $ CDATE((ENDDAY+1),YR), to ',CDATE(CURDAY,YR),'.
  PRINT '(A,a3A,I3,A)',' Julian date '3NDDAY+1,
  $ to', CURDAY,'.'
END IF

Close files

510 CLOSE(UNIT=12,STATUS='KEEP',ERR=203)
  CLOSE(UNIT=14,STATUS='KEEP')

520 STOP

FUNCTION JDATE(MO,DAY,YR)
****************************
* JDATE : A function that returns the julian date *
* JDATE(MO,DAY,YR) *
* MO : Month : Integer *
* DAY : Day : Integer *
* YR : Year : Integer *
****************************
INTEGER MO, DAY, YR, TJDATE, I, DBASE(12)
LOGICAL LEAP

C Jdate conversion table
DATA (DBASE(I), I= 1, 12) /0, 31, 59, 90, 120, 151, 181, 212,
$ 243, 273, 304, 334/
TJDATE = DBASE(MO)

C Leap Year Adjustment
IF (LEAP(YR) .AND. (MO .GT. 2)) TJDATE = TJDATE + 1
JDATE = TJDATE + DAY
END

FUNCTION CDATE(JDAY,YR)
*********************************************************************************
* CDATE : A function that returns the calendar date *
* CDATE(JDAY,YR)
* JDAY : Day : Integer
* YR : Year : Integer
*********************************************************************************

INTEGER JDAY, YR, DBASE(12)
REAL CDATE
LOGICAL LEAP

C Jdate conversion table
DATA (DBASE(I), I= 1, 12) /0, 31, 59, 90, 120, 151, 181, 212,
$ 243, 273, 304, 334/

C Begin with December, searching for correct month.
I = 13
3000 I = I - 1
C A near impossible error, J-date was less than or equal to 0 zero
IF (J .EQ. 0) THEN
  PRINT *, 'An error has occured while translating a J-date'
  STOP
END IF
C Get Jdate equivalent of the begining of the month
TJDATE = DBASE(I)
C Compensate for Leap Year
IF (LEAP(YR) .AND. (I.GT. 2)) TJDATE = TJDATE + 1
C If not yet in correct month, go back further.
IF (JDAY .LE. TJDATE) GO TO 3000
C Send date back as 01.12 for Jan 12th
CDATE = I + (JDAY-TJDATE)/100
END
FUNCTION LEAP(YR)
  c This is a function to determine when a year is a leap year, and when
  c it is not. Function type is logical.
  c This was put in a function to allow for easy updates to the
  c leap year rules.

 INTEGER YR
 LOGICAL LEAP

 IF ((MOD(YR,4) .EQ. 0) .AND. (YR .NE. 0)) THEN
   LEAP = .TRUE.
 ELSE
   LEAP = .FALSE.
 END IF
 END
2. WSPLICE3

PROGRAM WSPLICE3

C ******************************************************************
C * THIS PROGRAM SPLICES WEATHER DATA FILES FOR DSSAT V3.0 *
C * Modified to include new startup text 7/14/94 *
C * Written By: Steven Knapp (sknapp@iastate.edu) *
C * Modified to comply with Fortran 77 standard by *
C * David Willmore (willmore@iastate.edu) on 9/20/94 *
C * Modified a wee bit more by *
C * Scott Williams (swilliam@iastate.edu) on 10/19/94 *
C ******************************************************************

C Test character string
CHARACTER*5 CHTST

C Which columns have data
LOGICAL DATA(7)

C Date information
CHARACTER*6 CHDTA(7)

INTEGER ENDDAY, CURDAY, TEMPDAY, MO, DAY, YR, YR2, YR3

INTEGER OFFSET

C Beginning, Ending Day & year information for each file
INTEGER BEGD1, BEGY1, ENDD1, ENDY1
INTEGER BEGD2, BEGY2, ENDD2, ENDY2

C Generic Y/N response character
CHARACTER ICHR

C Input file names
CHARACTER*12 INFIL, INFIL2

C Header string and general text
CHARACTER*70 HEAD, HEAD2

C Calendar date from JDATE
REAL CDATE

C Integer for Implied DO loops
INTEGER IDL

LOGICAL LEAP

C ******************************************************************
C * Intro text *
C ******************************************************************
PRINT *, 'This program splices any two weather files that'
PRINT *, 'meet the specifications of DSSAT version 3.0.'
PRINT *
PRINT *, 'The splicing creates a new file named "TEMP0000.WTH"'
PRINT *, 'that are not found in BOTH input files.'
PRINT *
PRINT *, 'Before running one of the DSSAT crop growth',
$ ' models,'
PRINT *, 'be sure to create an entry for this new file in the'
PRINT *, 'appropriate directory. For example, for CROPGRO'
PRINT *, 'create an entry for "TEMP0000.WTH" within the CROPGRO'
PRINT *, '"WTH.LST" file.'
PRINT *
PRINT *, 'Note: Continuing with this splicing program will'
PRINT *, 'overwrite any existing file named "TEMP0000.WTH".'
PRINT *, 'If you have a previous file that you wish to save, '
PRINT *, 'you should rename it via the DOS RENAME command '
PRINT *, 'before continuing.'
PRINT *

C Allow user to exit the program, default is continue.

1 PRINT *, 'Okay to continue and overwrite'
PRINT *, 'any previous "TEMP0000.WTH" file (Y,N)?'
READ '(A)', ICHR
IF ((ICHRI.EQ. 'N') .OR. (ICHRI.EQ. 'n')) STOP
IF ((ICHRI.NE. 'y') .AND. (ICHRI.NE. 'Y')) GO TO 1
PRINT *

C Get file names

PRINT *, 'Enter the name of the first weather file to use:'
READ '(A)', INFIL
PRINT *
PRINT *, 'Enter the name of the second weather file to use:'
READ '(A)', INFIL2
PRINT *

C Get the date for the splice

5 PRINT *, 'Enter the date through which the first file should'
PRINT *, 'be used, in mm/dd format. [Example: 01/29]'
PRINT *, 'Enter 00/00 to process all of file #1.'
READ (UNIT=5,FMT='(I2,1X,I2)',ERR=5) MO, DAY
PRINT *
IF ((MO .GT. 12) .OR. (DAY .GT. 31)) GO TO 5

C Open both input files, output file and copy header
C of first file to output file.
C Read up to 2nd to last line of header

OPEN (UNIT=12, FILE='TEMPOOOO.WTH', STATUS='UNKNOWN')
OPEN (UNIT=13, FILE=INnL, STATUS='OLD', ERR=200)
OPEN (UNIT=14, FILE=INnL2, STATUS='OLD', ERR=201)

6 READ (13, '(A70)', END = 200, ERR=205) HEAD
IF (HEAD(1:5) .NE. '@DATE') THEN
  WRITE (12,'(A70)') HEAD
GOTO 6
ENDIF

7 READ (14, '(A70)', END = 201, ERR=206) HEAD2
IF (HEAD2(1:5) .NE. '@DATE') GOTO 7

C Determine which columns are to be used
DO 8 IDL=6,70
  IF ((HEAD(IDL:IDL) .EQ. '') .OR.
      $   (HEAD2(IDL:IDL) .EQ. '') .OR.
      END IF
  DATA(1) = (HEAD(11:16) .NE. ' ')
  DATA(2) = (HEAD(17:22) .NE. ' ')
  DATA(3) = (HEAD(23:28) .NE. ' ')
  DATA(4) = (HEAD(29:34) .NE. ' ')
  DATA(5) = (HEAD(35:40) .NE. ' ')
  DATA(6) = (HEAD(41:46) .NE. ' ')
  DATA(7) = (HEAD(47:52) .NE. ' ')

8 CONTINUE

C Write header line of first file to the splice file
WRITE(12,'(A70)',ERR=207) HEAD

C Get year and copy first record from first file
C Also set BEGD1 and BEGY1 to the day and year of the first record
ENDDAY = 0
9 READ (UNIT=13, FMT=1000, END=204, ERR=208) CURDAY,
$ (CHDTA(IDL), IDL=1,7)
BEGY1 = CURDAY / 1000
BEGD1 = CURDAY - (BEGY1 * 1000)

C This if statement handles if we're looking for a specific
C date or just scanning all the way through to the end of the file
IF (MO .NE. 0) THEN
   ENDDAY = JDATE(MO,DAY, BEGY1)
   WRITE (*,'(A36,F5.2)',ERR=209)
   $ 'File #1 will be processed through: ',
   $ CDATE(ENDDAY, BEGY1)
C In this case, ENDD1 should be the same as ENDDAY
ENDD1 = ENDDAY
ELSE
   PRINT *, 'File #1 will be completely processed.'
END IF

PRINT *
DO 10 IDL=1,7
10 IF (.NOT. DATA(IDL)) CHDTA(IDL) = ' ' 
    WRITE(12,1000, ERR=209) CURDAY, (CHDTA(IDL), IDL=1,7)
IF (BEGD1 .EQ. ENDDAY) GO TO 20

C Copy records
C Use TEMPDAY as a temporary value so we don't destroy the
C Last date successfully read.
11 READ (UNIT=13, FMT=1000, END=15, ERR=210) TEMPDAY,
$ (CHDTA(IDL), IDL=1,7)
IF (TEMPDAY .EQ. 0) GO TO 11
CURDAY = TEMPDAY
DO 12 IDL=1,7
12 IF (.NOT. DATA(IDL)) CHDTA(IDL) = ' ' 
    WRITE(12,1000, ERR=211) CURDAY, (CHDTA(IDL), IDL=1,7)
YR = CURDAY/1000
ENDY1 = YR
IF ((CURDAY-YR*1000) .EQ. ENDDAY) GO TO 20
GO TO 11

C File ends on some day before ENDDAY
15 IF (MO .NE. 0) THEN
   PRINT *
   $ ' First file ended before the specified month/day was found.'
   PRINT *
C If the date was not found in the first file,
C Delete the output, close both files, and get a new date.
   CLOSE(UNIT=13,STATUS='KEEP',ERR=200)
   CLOSE(UNIT=14,STATUS='KEEP',ERR=201)
   CLOSE(UNIT=12,STATUS='DELETE',ERR=203)
   GO TO 5
END IF
PRINT *
ENDDAY = CURDAY - (YR*1000)
PRINT '(A,F6.2,A)',' File #1 ended on ',CDATE(ENDDAY,YR),'.'
ENDD1 = ENDDAY
ENDY1 = YR
GO TO 21
C File ENDED 21-END 20-reached date.
20 PRINT *,^116 #1 reached requested date successfully.'
21 PRINT *,'Beginning processing on file #2.'
   CLOSE(UNIT=13, ERR=201,STATUS='KEEP')
   PRINT *
C Search 2nd file for the new ENDDAY
C ENDDAY is set to ENDDAY + 1, or day 1 if ENDDAY is 365 or 366
   ENDDAY = ENDDAY + 1
   OFFSET = 0
   IF ((ENDDAY .EQ. 366) .OR. (ENDDAY .EQ. 367)) THEN
      ENDDAY = 1
      OFFSET = 1
   END IF
30 READ (UNIT=14,FMT=1000,END=202,ERR=213) TEMPDAY,
   $ (CHDTA(IDL),IDL=1,7)
   BEGY2 = TEMPDAY / 1000
   IF ((TEMPDAY - BEGY2*1000) .EQ. ENDDAY) GO TO 35
   GO TO 30
C Once found, copy the data for this day and set BEGD2
35  BEGD2 = TEMPDAY - BEGY2*1000
     TEMPDAY = TEMPDAY - (BEGY2-ENDY1-OFFSET)*1000
     DO 37 IDL=1,7
37    IF (.NOT. DATA(IDL)) CHDTA(IDL) = '     '
     WRITE(12,1000,ERR=211) TEMPDAY, (CHDTA(IDL),IDL=1,7)
     ENDDY2 = BEGY2
     YR3 = BEGY2
     CURDAY = TEMPDAY
     C  Okay, now copy the rest of the records.
40    READ (UNIT=14, FMT=1000,END=500,ERR=212) TEMPDAY,
     $ (CHDTA(IDL), IDL=1,7)
     IF (TEMPDAY .EQ. 0) GO TO 40
     CURDAY = TEMPDAY
     YR3 = CURDAY / 1000
     C  Adjust the day to the current year.
     CURDAY = CURDAY - (BEGY2-ENDY1-OFFSET)*1000
     DO 45 IDL=1,7
45    IF (.NOT. DATA(IDL)) CHDTA(IDL) = '     '
     C  Rid new file of any extra leap days
     IF ( ( ( CURDAY+1000*(BEGY2-ENDY1-YR3-OFFSET) ) .NE. 366)
     $ .OR. LEAP(YR3-BEGY2+ENDY1) ) THEN
       WRITE(12,1000,ERR=211) CURDAY, (CHDTA(IDL),IDL=1,7)
       ELSE
       PRINT *,'A leap day from file #2 was deleted as it ','
       $ 'did not map into a leap year in the combined file.'
       ENDIF
     C  (Debugging statement follows)
     C  PRINT *, 'DATE', CURDAY
     GO TO 40
     C  ***********************
     C  * Error reports      *
     C  ***********************
200   PRINT *, 'Problems developed with file: ',INFIL
     PRINT *, 'Possible causes:'
     PRINT *, '/ File does not exist'
     PRINT *, '/ File is in another directory'
PRINT *,' - File is empty'
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=13,STATUS='KEEP')
GO TO 520

201 PRINT *, 'Problems developed with file: ',INFIL2
    PRINT *, ' - File does not exist'
    PRINT *, ' - File is in another directory'
    PRINT *, ' - File is empty'
    IF (INFIL .EQ. INFIL2) THEN
        PRINT *, 'File name is same as file #1'
    END IF
    CLOSE(UNIT=12,STATUS='DELETE')
    CLOSE(UNIT=14,STATUS='KEEP')
    GO TO 520

202 PRINT '(A,F5.2,A,I3,A,LA)', ' The month/day ',
    $ CDATE(ENDDAY,YR), (Julian Date ',ENDDAY,'), not found in ',
    $ INFIL2,'.'
    PRINT *
    CLOSE(UNIT=14,STATUS='KEEP,ERR=200)
    CLOSE(UNIT=12,STATUS='DELETE',ERR=203)
    GO TO 5

203 PRINT *,'An error occurred in writing TEMP0000.WTH.'
    PRINT *,' - Disk is full'
    GO TO 520

204 PRINT *, 'The file ',INFIL,' does not begin before the ',
    $ ' date requested.'
    CLOSE(UNIT=13,STATUS='KEEP,ERR=200)
    CLOSE(UNIT=12,STATUS='DELETE',ERR=203)
    GO TO 5

205 PRINT *, 'An error occurred while reading the header',
    $ ' from ',INFIL,'.'
    PRINT *, 'Possible cause:'
    PRINT *, ' - Data file may have been improperly formatted'
    CLOSE(UNIT=13,STATUS='KEEP')
    CLOSE(UNIT=12,STATUS='DELETE')
    CLOSE(UNIT=14,STATUS='KEEP')
    GOTO 520

206 PRINT *, 'An error occurred while reading the header',
    $ ' from ',INFIL2,'.'
    PRINT *, 'Possible cause:'
    PRINT *, ' - Data file may have been improperly formatted'
    CLOSE(UNIT=13,STATUS='KEEP')
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=14,STATUS='KEEP')
GOTO 520

207 PRINT *, 'An error occurred while writing the',
$ ' header to TEMPO000.WTH.'
PRINT *, 'Possible cause:'
PRINT *, ' Not be enough space to create TEMPO000.WTH'
CLOSE(UNIT=13,STATUS='KEEP')
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=14,STATUS='KEEP')
GOTO 520

208 PRINT *, 'An error occurred while reading the',
$ ' first data record from ',INFIL,'.'
PRINT *, 'Possible cause:'
PRINT *, ' Data file may have been improperly formatted.'
CLOSE(UNIT=13,STATUS='KEEP')
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=14,STATUS='KEEP')
GOTO 520

209 PRINT *, 'An error occurred while writing data',
$ ' to TEMPO000.WTH.'
PRINT *, 'Possible cause:'
PRINT *, ' Not be enough space to create TEMPO000.WTH'
CLOSE(UNIT=13,STATUS='KEEP')
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=14,STATUS='KEEP')
GOTO 520

210 PRINT *, 'An error occurred while copying',
$ ' records from ',INFIL,'.'
PRINT *, 'Last day successfully processed was day',CURDAY
PRINT *, 'Possible causes:'
PRINT *, ' Data file may have been improperly formatted'
CLOSE(UNIT=13,STATUS='KEEP')
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=14,STATUS='KEEP')
GOTO 520

211 PRINT *, 'An error occurred while copying',
$ ' records to TEMPO000.WTH.'
PRINT *, 'Possible cause:'
PRINT *, ' Not be enough space to create TEMPO000.WTH'
CLOSE(UNIT=13,STATUS='KEEP')
CLOSE(UNIT=12,STATUS='DELETE')
CLOSE(UNIT=14,STATUS='KEEP')
GOTO 520
212 PRINT *, 'An error occurred while copying',
$ ' records from ', INFIL2, '.
PRINT *, 'Last day successfully processed was day', CURDAY
PRINT *, 'Possible causes:
PRINT *, ' Data file may have been improperly formatted'
CLOSE(UNIT=13, STATUS='KEEP')
CLOSE(UNIT=12, STATUS='DELETE')
CLOSE(UNIT=14, STATUS='KEEP')
GOTO 520
213 PRINT *, 'An error occurred while skipping over',
$ ' records from ', INFIL2, '.
PRINT *, 'The last day successfully processed was', CURDAY
PRINT *, 'Possible cause:
PRINT *, ' Data file may have been improperly formatted.'
CLOSE(UNIT=13, STATUS='KEEP')
CLOSE(UNIT=12, STATUS='DELETE')
CLOSE(UNIT=14, STATUS='KEEP')
GOTO 520

C **********************************
C * Description of file completion *
C **********************************
500 PRINT *, 'Splicing successful!
PRINT *, 'A new file TEMPOOOO.WTH has been created.'
PRINT *, 'It contains:
$ ' Data from file ', INFIL, ' from date ', CDATE(BEGD1, BEGY1),
$ '19', BEGY1, ' to ', CDATE(ENDD1, ENDY1), ' 19', ENDY1, '.*
PRINT '(A,J3,A,J3,A)', ' Julian date ', BEGD1, ' to ', ENDD1,'.*

C Adjust the curday to the right year, set ENDD2 and ENDY2
ENDD2 = CURDAY - (CURDAY / 1000) * 1000
CURDAY = CURDAY + 1000*(BEGY2-ENDY1-YR3)
ENDY2 = YR3

$ ' Data from file ', INFIL2, ' from date ',
$ CDATE(BEGD2,BEGY2),
$ ' 19', BEGY2, ' to ', CDATE(ENDD2, ENDY2 + OFFSET),
$ ' 19', ENDY2, '.*
PRINT '(AJ3,AJ3,A3A)', ' Julian date 'BEGD2,' to ' ENDD2.',
PRINT '(AJ2,AJ2A)V The years of data are labeled 19',
$ BEGY1,' through 19', (ENDY1+YR3-BEGY2+OFFSET)', '

CLOSE files

510 CLOSE(UNIT=12,STATUS='KEEP',ERR=203)
CLOSE(UNIT=13,STATUS='KEEP',ERR=200)
CLOSE(UNIT=14,STATUS='KEEP',ERR=201)

520 STOP

C  ******************************************************
C  * File formats  *
C  ******************************************************

1000 FORMAT(5,7(A6))
1001 FORMAT(5)
1002 FORMAT(8X,I3,1X,J75.2,3(1X,J5.1),1X,F6.2)
1003 FORMAT(8X,I3)

END

C  ******************
C  * End of program *
C  ******************

FUNCTION JDATE(MO,DAY,YR)
C  ******************************************************
C  * JDATE : A function that returns the Julian date  *
C  * JDATE(MO,DAY,YR)                                *
C  *  MO : Month : Integer                           *
C  *  DAY : Day  : Integer                          *
C  *  YR : Year  : Integer                          *
C  ******************************************************

INTEGER MO,DAY,YR,TJDATE,I, DBASE(12)
LOGICAL LEAP

C   Jdate conversion table
DATA (DBASE(I), I= 1, 12) /0, 31, 59, 90, 120, 151, 181, 212,
$ 243, 273, 304, 334/
TJDATE = DBASE(MO)

C Leap Year Adjustment
IF (LEAP(YR) .AND. (MO .GT. 2)) TJDATE = TJDATE + 1
JDATE = TJDATE + DAY
END

FUNCTION CDATE(JDAY,YR)

*****************************************************
C * CDATE : A function that returns the calendar date *
C * CDATE(JDAY,YR) *
C * JDAY : Day : Integer *
C * YR: Year : Integer *
*****************************************************
INTEGER JDAY,YR,DBASE(12)
REAL CDATE
LOGICAL LEAP

C Jdate conversion table
DATA (DBASE(I), 1= 1. 12) /0, 31, 59, 90, 120, 151, 181, 212,
$ 243, 273, 304, 334/
C Begin with December, searching for correct month.
I = 13
3000 I = I - 1
C A near impossible error, J-date was less than or equal to 0 zero
IF (I .EQ. 0) THEN
  PRINT *,'An error has occurred while translating a J-date'
  STOP
END IF
C Get Jdate equivalent of the beginning of the month
TJDATE = DBASE(I)
C Compensate for Leap Year
IF (LEAP(YR) .AND. (I .GT. 2)) TJDATE = TJDATE + 1
C If not yet in correct month, go back further.
IF (JDAY .LE. TJDATE) GO TO 3000
C Send date back as (for example) 01.12 for Jan 12th
CDATE = I + (JDAY-TJDATE)/100
END

FUNCTION LEAP(YR)

************************************************************************
C * This is a function to determine when a year is a leap year, and when *
C * it is not. Function type is logical. *
C * This was put in a function to allow for easy updates to the *
C * leap year rules. *
LOGICAL LEAP
INTEGER YR

IF ((MOD(YR,4) EQ 0) .AND. (YR NE 0)) THEN
   LEAP = .TRUE.
ELSE
   LEAP = .FALSE.
END IF
END