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BEHAVIOR AND FIELD DYNAMICS OF THE POTATO LEAFHOPPER (EMPOASCA FABAE (HARRIS)): THE INFLUENCE OF TOMATO AND BEAN INTERCROPPING.

presented by

WILLIAM JAMES ROLTSCH

has been accepted towards fulfillment of the requirements for

Ph.D. degree in ENTOMOLOGY

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Date Feb- 15, 1988

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## BEHAVIOR AND FIELD DYNAMICS OF THE POTATO LEAFHOPPER (<u>EMPOASCA FABAE</u> (HARRIS)): THE INFLUENCE OF TOMATO AND BEAN INTERCROPPING.

BY

WILLIAM JAMES ROLTSCH

## **A DISSERTATION**

## Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

## DOCTOR OF PHILOSOPHY

Department of Entomology

### ABSTRACT

# BEHAVIOR AND FIELD DYNAMICS OF THE POTATO LEAFHOPPER, (<u>EMPOASCA FABAE</u> (HARRIS)): THE INFLUENCE OF BEAN AND TOMATO INTERCROPPING

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#### BY

## WILLIAM JAMES ROLTSCH

Intercropping is considered to be an agricultural practice which can reduce insect pest damage to food crops. Lower pest densities in intercrops versus monocultures have been commonly observed, but few studies have attempted to quantify the mechanism behind such differences. This study investigated the population dynamics of the potato leafhopper (PLH), <u>Empoasca fabae</u> (Harris), on its bean host plant in monoculture and on bean intercropped with tomato.

Studies of this system were conducted under field and laboratory conditions. Field studies investigated PLH abundance in relation to companion plant (tomato) density, host plant (bean) canopy density, and host plant quality. Laboratory studies quantified leafhopper movement, feeding and oviposition on bean with the inclusion of various companion plant leaves.

PLH egg and nymph field densities on bean foliage were significantly different between treatments, being inversely related to tomato density. Based upon the similarity in PLH egg and nymphal density patterns throughout the field season, the analysis showed that lower levels of oviposition on bean interplanted with tomato were responsible for treatment differences. Adults did not respond to differin bean canopy density, however they did responded ences positively to bean guality, defined by total foliar nitroqen. In laboratory studies, PLH feeding was reduced 43% in the presence of tomato. Feeding on bean was reduced because resided extensively on tomato, yet fed very little on PLH In oviposition choice tests there were significantly it. (P<0.05) fewer eggs laid on bean in treatments including tomato or cabbage. PLH arrestment and frequency of movement within the observation cages were not markedly changed in the presence of bean with tomato leaves versus However, an overall pattern of bean leaf control. the increased movement frequency did occur with the inclusion of leaves of other companion plants.

Results support a dual hypothesis regarding the basis for lower PLH densities on bean and tomato intercrops. PLH utilization of bean, including feeding and oviposition, is directly reduced by tomato, and changes in host plant (bean) quality resulting from bean/tomato interactions.

# ACKNOWLEDGMENTS

I wish to extend my sincere thanks to: my advisor, Dr. Stuart H. Gage for his support and patience during the course of this project; and my thesis committee members, Drs. Thomas Edens, Alan Putnam, Gene Safir, and Mark Whalon for their helpful suggestions regarding my research, and thesis review. I also which to thank Dr. James Bath, former departmental chairperson, for his interest and support of my research and assistantship.

Thanks is also given to Mr. Gregory Anderson for his many diligent hours of field and laboratory assistance, as well as to Mr. Jose Velarde for his help in maintaining the field site at the Kellogg Biological Station, through thick and thin.

A very special thanks is given for the love, support, and patience of my wife, Irene; and encouragement by my parents, William H. and Amy J. Roltsch, and sisters and their families.

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PREFACE

This study began because of an interest in alternate approaches to agricultural pest management. The premise was that insect herbivores were more likely to be maintained at acceptable levels if certain plant assemblages were selected to foster appropriate community interactions. Background knowledge of insect life histories, and information on the potential influence of non-host vegetation on herbivores were necessary to initiate research in this area. Except in a few isolated situations, such information was unavailable, particularly that relevant over large geographic areas. The potato leafhopper, bean, and tomato system was selected based upon information obtained through a screening process of several plant combinations. Results indicated that tomato was responsible for reduced numbers of potato leafhoppers on bean interplanted with tomato.

All field studies were conducted at the Kellogg Biological Station, near Hickory Corners, Michigan. Laboratory studies were conducted on the Michigan State University campus.

This dissertation is presented in manuscript form. A general introduction discusses issues of ecosystem diversification, the role of intercropping in pest control, and chemical ecology of Solanaceous plants. It is followed by a manuscript reviewing the life history and phylogeny of the potato leafhopper. Two subsequent manuscripts pertain to field and laboratory investigations of the potato leafhopper

within the context of intercropping. All manuscripts are written in accordance with the journal guidelines of the Entomological Society of America.

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#### INTRODUCTION

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### **INTRODUCTION**

The theory that stability of plant and animal communities is a direct function of species diversity was considered dogma for many years in ecology (Risch 1980). It was believed that as a result of food web interactions across trophic levels, natural ecosystems were less likely to fluctuate radically (a measure of stability) with progressive increases in habitat diversity (MacArthur 1955, Graham 1956, Elton 1958). Investigations of predator/prey relationships and reports by foresters that pure, even-aged tree stands were subject to more insect outbreaks than their diverse counterparts, were used to support the theory (Huffaker 1958, Chumakova 1960, Gibson and Jones 1977). In addition, consideration of the theory extended into agriculture. It was believed that stability could be brought about within agriculture systems through unspecified diversification (Pimental 1961, Pimental et al. 1963, van Emden 1965).

When the theory of "ecosystem diversity and stability" was more closely evaluated, a lack of correspondence between diversity and stability was noted (Watt 1965, van Emden and Williams 1974, May 1976). That is, it has been determined that progressive increases in diversity do not necessarily insure greater stability. Furthermore, there are two main problems with the concept as it related to agriculture

(Risch 1980). First, it is of little importance that populations are stable if densities are high enough to cause economic damage. Secondly, the collection of evidence from agriculture, comparisons between natural systems, laboratory studies, and mathematical models, simply does not indicate that species richness per se provides increased stability. This is not to say that diversity is unimportant. There are many examples in the area of biological control demonstrating significant reductions in pest abundance fostered by the presence of various plant and animal species within a habitat (De Bach 1964, Huffaker 1971, Huffaker and Messenger 1976, Taniqoshi 1983). However, the results are due to specific interactions requiring specific system components. In essence, the theory of stability being a direct function of the degree of diversity, missed its mark by emphasizing the number of interactions rather than the significance of those interactions.

Studies of the influence of intercropping on herbivore and natural enemy communities may provide important insights into understanding the factors responsible for pest outbreaks and the specific kinds of plant diversification that may facilitate pest control. Intercropping (mixed-cropping) involves the simultaneous growth of multiple crops or wild plants in the same field (Perrin and Phillips 1978). The different kinds of intercropping are: mixed intercropping (plants are not in rows), row intercropping (one or more crops planted in rows), strip intercropping (alternate

multiple row patterns), and relay intercropping (second crop planted when the first crop approaches maturity). In part, intercropping research has been pursued because it provides format for utilizing potentially important ecological а interactions for pest control. However, to date the most clear advantage in intercropping lies in reducing the risk of crop failure, particularly in subsistence farming (Kass 1978, Horwith 1985). Its potential value in modern mechanized agriculture and as a means of controlling insect pests has also been discussed (Risch et al. 1983, Horwith 1985). These authors believe that with significant changes in mechanization, intercropping can be a viable alternative in developed countries. Furthermore, it was noted that based on a survey of pest abundance in 150 intercropping studies; of the insect pests were less abundant in the inter-53% crop, 18% were more numerous in the intercrop, 9% showed no difference, and 20% showed a variable response (Risch et al. 1983).

The basis for comparative research of intercropping systems versus their monoculture counterparts has been linked to several hypotheses (Root 1973, 1975). The "enemies hypothesis" predicts that herbivore populations can be better controlled in species-rich plant associations due to greater numbers of natural enemies. The reasons for this are related to the improved spatial and temporal distribution of multiple food resources for natural enemies including pollen, nectar, and alternate hosts. Regarding the

importance of natural enemies, it has been argued (Price et al. 1980), that predators and parasites should be more important in perennial than annual systems. This is because their hosts are more predictable (more easily found) in space and time. Also, perennial plants commonly produce chemical defense substances which act in a quantitative fashion, reducing herbivore growth rates in contrast to killing them outright (Feeny 1976, Rhodes and Cates 1976). Therefore, plant survival against herbivores in perennial systems would appear to be contingent upon the joint host plant defense chemistry and natural presence of enemies. In contrast, annual plant species are less likely to be found in the same location over time, and produce substances which kill all but a few co-evolved phytophagous species. These phytophagous species have circumvented their host plants defenses, and in some cases sequester plant substances to ward off attack by natural enemies (Price et The belief that natural enemies demonstrate al. 1980). higher rates of establishment in perennial systems has been supported by empirical evidence (Clausen 1978, Hall and Ehler 1979, Hall et al. 1980). However, the viewpoint that predators and parasites have little potential in annual systems may be a misconception. As pointed out by Risch (1983), this may be a function of wrongly applying perennial crop biological control theory to annual crop pest problems. It has been recently suggested that natural enemies that are

generalists with high dispersal ability may be more effective control agents in annual cropping systems than specialists (Ehler 1979, Newsom et al. 1980).

In contrast to the "enemies hypothesis", the "resource concentration hypothesis" predicts that herbivores maintain higher population densities in resource-dense areas because the concentrated resources are easier to locate, and more importantly, if the resource is particularly suitable they will stay longer (Root 1973, 1975). Overall, it is expected that in pure stands of host plant species, herbivores will have a higher rate of accumulation, tenure, and reproductive success. Other authors have elaborated on this hypothesis by stating that colonization is affected by visual and chemical stimuli from host and non-host plants, and that this is related to the absolute density and spatial arrangement of host and companion plants (Bach 1980, Risch 1983, Risch et al. 1983). Furthermore, these authors mention that pest survivorship may be increased in monoculture systems as a function of resource concentration. Risch et al. (1983) also point out that for annual cropping systems, the resource concentration hypothesis can better explain reductions in pest loads in intercrop systems than the enemies hypothesis.

Few studies have investigated in detail, the dynamics of pest populations in intercropping systems versus monocultures. Therefore, mechanisms responsible for observed differences have been identified for only a few systems.

The importance of growth form in colonization was indicated when vertically grown cucumber plants had greater densities of the chrysomelid beetle, Acalymma vitata (Fab.), than horizontally grown plants (Bach 1981). Shade has been determined to play an important role in influencing insect densities as well. Studies on a chrysomelid complex attacking plants in typical Central American intercrops (squash, maize, and bean), determined that shade produced by corn, directly influenced colonization by some beetle species (Risch 1980, 1981). The capability of a companion plant to directly influence the herbivore of the associated plant species is evident. Upon evaluating the effects of tomato, Lycopersicon esculentum Mill, on the diamond back moth, <u>Plutella xylostella</u> (L.), tomato appeared to be directly responsible for reducing pest densities on cabbage intercropped between rows of tomato (Buranday and Raros 1975). In that study, there were 50% fewer eggs found on cabbage intercropped with tomato during sample dates occurring 25 days or later following the transplanting of crops into the field. Also, there was no indication, based on yield data, that cabbage growth, size or quality was altered by tomato and thereby accounting for the observed differences in pest densities. In another study where tomato and bean were intercropped, Spodoptera sunia Guenee, a lepidopterous pest of both crops, had little impact on tomato (the primary production plant) when intercropped with bean(Rosset et al. 1985, 1987). In that system, bean acted as

a trap crop because of its greater acceptability by the pest. These studies are cited because they are among the few intercropping studies that have provided evidence of a basis for the observed differences between treatments. In the majority of intercropping studies, the qualitative state of host plants has not been considered (Bach 1981, 1984). Depending on the system, insect populations have been observed to increase or decrease when their host plants are stressed by low water or low or high nitrogen availability (Rhoades 1983, Scriber 1984).

With continued developments in the area of insect/plant interactions, in which chemical ecology is of major importance, greater insights into the potential utility of intercropping will be obtained. Some plant groups are known to have extensive mechanical and chemical defense systems used against other plant species, pathogens, and herbivores. One of the most extensively studied plant families exhibiting such characteristics is the family Solanaceae (D'Arcy Despite there being few insect species attacking 1986). wild solanaceous plants, many cultivated species exist which frequently sustain considerable damage by insects and plant pathogens. Defenses within this family commonly include are mechanical and chemical. those which Mechanical defenses include prickles, trichomes, and glands, while chemical defenses include alkaloids, saponins, essential oils, etc. (Drummond 1986).

The family Solanaceae is particularly well known as a group with rich alkaloid plant chemistry (Harborne 1986). Levin (1976) found that alkaloids are most broadly found in the family Solanaceae (Hsiao 1986). Of those species included in a survey, 85 % of the solanaceous species have alkaloids. There are principally three groups of alkaloids found in this plant family: 1) steroidal, 2) tropane, and 3) pyrrolidine alkaloids. Although alkaloids are frequently associated with host plant defence, blanket generalizations regarding their presence can not be made, for their effects are relatively specific (Robinson 1979).

Species from which domestic tomato and potato, Solanum tuberosum L., were derived have extensive chemical defense systems. Their secondary plant chemistry would seem to make them (especially tomato) a potentially good choice for intercropping from a pest protection standpoint. Wild species of Solanum contain the alkaloid demissine, which is believed to be an important resistance factor, defending many <u>Solanum</u> species against the Colorado potato beetle. In contrast, solanine, the primary alkaloid in domestic potato, is very similar in structure to demissine. However, it has little influence on the Colorado potato beetle, thereby exemplifying the specific role of alkaloids in host plant defence (Harborne 1986). Tomatine, a major alkaloid in tomato, has been demonstrated to be a strong repellent to the Colorado potato beetle (Harborne 1986). **Resistance** of tomato to the Colorado potato beetle has been found to be

correlated with tomatine content, which varies across varieties. This appears to be a clear example of how plant resistance can be lost during the development of new cultivars (Sinden et. al. 1978). Tomatoes have many other groups of compounds and mechanical defenses that may also be responsible for conferring resistance. Several phenolic compounds in tomato (i.e., chloragenic acid and rutin, a flavonol glycoside) are growth inhibitors of the tomato fruitworm, <u>Heliothis</u> <u>zea</u> (Boddie), (Elliger et al. 1981; Isman and Duffey 1982ab). The ketohydrocarbon, 2-tridecanone has been isolated from the trichomes of tomato. It is toxic to the tomato hornworm, Manduca guinguemaculata (Haworth), tomato fruitworm and an aphid species (Kennedy and Yamamoto 1979, Williams et al. 1980). However, domestic tomato has far lower concentrations than its wild ancestor, Lycopersicon hersutum f. glabratum C.H. Mull. The tobacco flea beetle, Epitrix hirtipennis (Melsheimer), has also been found to be deterred by the presence of chemicals located within wild tomato leaves (Gentile and Stoner 1968). In addition, a number of insect species are trapped by a sticky substance produced by the trichomes of various Lycopersicon and <u>Solanum</u> species. The plant species used for study were typically <u>L. hirsutum</u> Humb. and Bonpl., and <u>S. berthaultii</u> Hawkes. The insect species affected include the greenhouse white fly, Trialeurodes vaporariorum (Westwood), Tetranychus cinnabarinus (Boisduval), two spotted mite, T. urticae Koch,

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and the green peach aphid, <u>Myzus persicae</u> (Sulzer), (Gentile et al. 1968, 1969, and Tingey and Laubengayer 1981).

The study of insect population dynamics within intercropping systems is in its early phase of development. It is obvious that plants in such systems may have very complex secondary chemistry, mechanical defenses and growth forms, capable of significantly altering herbivore densities in contrast to their monoculture counterparts. Many factors play into evaluating the role of pest abundance in intercrops versus their monoculture counterparts and past observations have been insufficient to clearly identify the general significance of intercropping as a means of modifying the density of pest species.

The subject matter of this dissertation pertains to insect/plant interactions within the context of an intercrop The primary motivation for pursuing this topic was system. an interest in developing ecologically based approaches to The overall study plan is presented in pest management. To achieve a state of reduced reliance upon Fig. 1. conventional pesticide control, one means of diminishing insect outbreaks on crops would be through the specific **IDENTIFICATION** of a multi-plant species **SYSTEM**. Such a system would be expected to provide a basis for supporting insect/plant community capable of a higher degree of an self-regulation compared to its monoculture counterparts. In 1983, in the pursuit of a potentially important insect/intercrop interaction, an INTERCROPPING DESIGN of bean and



Fig. 1. An organizational diagram of the research program components involved in the study of the direct influence of tomato and other non-host plants upon the potato leafhopper (PLH), as well as effects of variables created through intercropping.

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tomato within a newly planted apple orchard was developed. Tomato was selected due to its history of insect/plant interactions. Bean was selected because of its common use in intercropping, and compatibility with tomato. Apple represented a perennial, and therefore a persistent, longterm feature to the cropping environment, providing permanent refugia for natural enemies. From this first phase of study, results showed that the potato leafhopper on snap bean obtained higher population densities in plots where bean was planted alone, versus with tomato (Fig.3 in Manuscript II). Based upon that finding, it was hypothesized that, (1) as a companion plant, tomato directly influenced potato leafhopper abundance on bean, and (2) the influence would be linearly related to the density of tomato, up to some high density (saturation level) of tomato. To investigate these hypotheses, laboratory and field studies were designed and conducted (Fig.1). Field research was directed toward quantifying the differences in leafhopper nymph densities and oviposition on snap bean in the presence of tomato, and to provide evidence that could be used with results from laboratory studies to determine the mechanism. This included experiments that were conducted to determine the importance of the confounding variables of variable bean plant growth and plant quality, which differed in correspondence with tomato density. Laboratory studies evaluated specific leafhopper behavioral responses to bean in the presence of non-host plants, and to bean representing several qualitative states, based upon the restriction of nutrients. The responses evaluated included residency time on bean, movement frequency, feeding, and oviposition. Overall, evidence was sought to determine whether tomato directly or indirectly influenced the potato leafhopper. The terms DIRECT and INDIRECT EFFECTS were used for purposes of organization, to delineate between different groups of effects. Direct effects were those which could be immediately traced back to tomato without considering the host plant. This included tomato plant chemistry, natural enemies, and micro-climate effects. Indirect effects were those effects of tomato mediated through changes in the bean host plant, which in turn influenced PLH. These included host plant quality and quantity.

The following manuscripts represent a review of the life history and phylogeny of the potato leafhopper, and an analysis of the interaction between this economically important insect pest, noted for its complex life history and wide host range, and a well accepted host-plant (snap bean) interplanted with a non-host (tomato). These studies represent an approach to investigating a complex pest in a complex agro-ecosystem to obtain a mechanistic view of how the insect might be manipulated in a multi-cropping environment.

## MANUSCRIPT I

A REVIEW OF THE LEAFHOPPER SPECIES <u>EMPOASCA FABAE</u> (HARRIS), (HOMOPTERA: CICADELLIDAE), WITH RESPECT TO ITS BIOLOGY, AND PHYLOGENETIC AND TAXONOMIC STANDING

### **INTRODUCTION**

This introduction to Empoasca <u>fabae</u> (Harris) is presented from a taxonomic, phylogenetic and life history perspective. Although reviews have been written on the general biology of leafhoppers (DeLong 1971, Knight 1983, Nault and Rodrigues 1985), reviews of taxonomic groups within this family are uncommon. A great deal of leafhopper taxonomy remains to be done and is under constant revision, thereby making it difficult to track pertinent literature. This is particularly true for the genus Empoasca, since it represents a very large, cosmopolitan insect genus. Despite the fact that the list of described species in the western hemisphere, and throughout the world, has grown extensively, Delong's (1931a) key to the genus Empoasca in America north of Mexico remains the single most comprehensive key available for this genus (Southern 1982). Southern (1982) noted that nearly 460 nominal species have been assigned to the genus in the Western Hemisphere alone, and more than 85 species have been recorded from South America. Beirne's (1956) publication is very useful for identifying many leafhopper taxa in the northern United States and Canada. However, it is of limited use for identifying species of Empoasca. A number of fine publications on the biology and phylogeny of Empoasca are available, including a bibliography of <u>E. fabae</u> (Gyrisco et al. 1978). The overview

presented herein should be of particular value to those reviewing the literature pertaining to <u>E</u>. <u>fabae</u>, and will hopefully encourage efforts in developing comprehensive summaries of other extensively studied members of this family.

Leafhoppers, family Cicadellidae, are differentiated from related families by the presence of one or more rows of small spines extending the length of the hind tibia. There are approximately 2500 species in North America alone, and they are typically less than 13 mm in length (DeLong et al. Worldwide, it is estimated that about 10,000 1981). leafhopper species have been described, with nearly again that many yet to be described (Viraktamath 1983). This would seem to be a conservative estimate since Nielson (1985) estimates that there are 4,000 genera represented by 15,000 described species, and upwards of 30,000 species yet Much of the fauna in the tropics and to be described. southern continents is unknown.

The classification of Cicadellidae has not reached the stage of development that is comparable with many other groups of insects, such as Coleoptera or Lepidoptera. Development of systematics in the group was slow because leafhoppers were not considered important until the early part of 20th century. At that time they were first recognized as injurious to crop plants, and important vectors of plant pathogens (Nielson 1985).

In the family Cicadellidae, the male genitalia are used as the primary character to identify and classify nearly all

species and most genera. In females, characters of similar value are almost completely lacking. The structure of the aedeagus among leafhopper species varies from a simple, symmetrical tube-like structure to an asymmetrical organ of diverse form.

Despite the usefulness of the male genitalia for species identification, Nielson (1985) points out that closely related sympatric species that are difficult to differentiate by aedeagal morphology or by other morphological means are common in the Cicadellidae. For example, several taxa in the genera Circuliger, Carneocephala, and Macrosteles have similar aedeagal types but are biologically distinct species. In some instances aedeagal morphology has been noted to vary within a species. For example, a correlation between day length and morphometrics of the aedeagus within the same species in the genus Euscelis was noted by Muller (1957). As discussed later, in the case of Empoasca fabae, the inclusion of apodemal structures in addition to characteristics of the genitalia used in identifying members of the Empoasca fabae complex, has been instrumental in shaping the current understanding of the distribution and phylogeny of E. fabae (Ross and Moore 1957). As a result, what was once considered to be Empoasca fabae in collections from North and Latin America actually represented an entire complex of species that could be reliably differentiated by apodemes of the basal abdominal tergites.

Currently, there is still no consensus of the number of subfamilies of Cicadellidae. Nielson (1985) notes that Evans(1966), Ross(1957), Wagner(1951), and Linnavouri(1959) have grouped the various subfamilies into taxonomic divisions: Typhlocybides, Iassides, Cicadellides, Eurymelides, Xerophloeides, Macropsides, and Tartessides. The subfamilies and their evolutionary standing is presented in Table 1. The relationship among many subfamilies of leafhoppers is not continuous, suggesting that the gaps between them are represented either by undiscovered or extinct species.

Nost of the subfamilies considered phylogenetically primitive occupy Australia and the adjacent Indo-Malayan land bridge, while the more advanced subfamilies, Deltocephalinae and Typhlocybinae, are cosmopolitan (Nielson 1985). As the subfamily Typhlocybinae is presently constituted, its members are remarkably uniform morphologically compared to Deltocephalinae, which presently exhibits wide variation in size and external features. Speciation in both groups has been extensive; each has a large number of taxa and together have more species than the remaining subfamilies combined. As indicated by their wide ranges, each possesses a high degree of plasticity and adaptability to a broad range of host plants in all zoogeographical regions (Nielson 1985).

Relationships between certain taxa and their biotic and abiotic environments are becoming evident. Most leafhopper species are restricted to a single generation per year. All

Table 1. A list and evolutionary ranking of the generally recognized subfamilies of Cicadellidae (based on Nielson 1985).

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SUBFAMILIES	EVOLUTIONARY RANKING
BURYMELINAE	
AUSTROGALLOIDIINAE	Most primitive
BUACANTHELLINAE	(originated in Australia
MYERSLOPIINAE	or New Zealand)
STENOCOTINAE	
POGONOSCOPINAE	
THAUMATOSCOPINAE	
XBROPHLOEINAE	Primitive
ULOPINAE	
<b>STEGELYTRINAE</b>	
Megophthalminae	
KRISNINAE	
HYLICINAE	
AGALLIINAE	
MACROPSINAE	
LEDRINAE	
TARTESSINAE	Intermediate
COELIDIINAE	
CICADELLINAE	
NIRVANINAE	
GYPONINAE	
IASSINAE	
IDIUCEKINAE BUACANMUINAB	
BVACANININAE Dupdpidutninae	
NDADFORINAF	
MAKILIGINAP	
CEPHALELINAE	Advanced
PENTHIMIINAE	
HECALINAE	
XESTOCEPHALINAE	
APHRODINAE	
DORYCEPHALINAE	
NEOCOELIDIINAE	
NIONIINAE	
MILESWANINAS	
BITHUNIINAE NBODNIINAE	
ngubali nag	
TYPHLOCYBINAE	Most Advanced
DELTOCEPHALINAE	
DELTOCEPHALINAE	

species in the family Cicadellidae, and for that matter in the order Homoptera, are phytophagous (DeLong et. al. 1981). Generally, the host plant range of most leafhopper species is very limited, which dictates the existence of a relatively well defined habitat associated with each species. For example, species of the subfamily Idiocerinae occurring in the nearctic region, breed on willows and poplars. Members of the tribes Balcluthini and Deltocephalini of the subfamily Deltocephalinae, feed and propagate almost entirely on Graminaceae (Nielson 1985). Knight's (1983) review of leafhoppers of Southeast Asia Pacific area gave an account of the host plants known for a number of subfamilies. Most members of the Ulopinae usually occupy the base of plants or roots and are slow moving. Members of the subfamily Euacanthellinae live in marshes. The Macropsinae are mostly arboreal and have a restricted host plant All of the Tartessinae in Australia occur on range. xerophytic trees and shrubs; those in New Guinea on forest trees and shrubs.

Relative to the total number of leafhopper species, few are pests, and it is estimated that less than 1% of the described species are recognized as pests, either as a direct result of feeding or the transmission of a disease. They are commonly known for their ability to carry and transmit phytopathogenic diseases, including viruses, mycoplasmas, spiroplasmas, and bacteria (Nielson 1985, Nault 1985). Compared to aphids, which are strictly phloem
feeders, leafhoppers are known to exploit the phloem, xylem, mesophyll, or all three tissues in some cases (Backus 1985).

At present there are 151 vector species in 65 genera assigned to eight subfamilies. The subfamilies Cicadellinae and Deltocephalinae comprise most of the vector species. Over 60% of the vector genera and species belong to Deltocephalinae, and they transmit over 70% of the known pathogens (Nielson 1985). It should be noted that these two groups are among the most phylogenetically advanced groups In the subfamily Cicadellinae the high of leafhoppers. propensity for disease transmission may be a direct function of feeding characteristics and the associated body structures. All species are restricted to feeding in the plant xylem. This is made possible by the presence of a highly developed, musculated clypeus allowing for sap to be withdrawn from the xylem. This structure is a major taxonomic feature of this group. Furthermore, it should be pointed out that the xylem is an ideal site for the propagation of many plant diseases (Nielson 1985).

The subfamily Typhlocybinae, within which the genus Empoasca exists, represents the second largest subfamily of Cicadellidae (Knight 1983). In North America there are over 700 species, of which over 300 belong to the genus Erythroneura (DeLong et al. 1981). As pointed out by Nielson (1985), subfamily designation of leafhopper groups has been important for separating major groups, and justified since the gaps separating the subfamilies of leafhoppers are

relatively narrow compared to the separation of family groups in other taxa such as Fulgoroidea.

Characteristics used to differentiate members in Typhlocybinae from other subfamilies pertain to the absence of cross veins in the wings except for those in the apical portion, and indistinct veins in the basal area (Beirne 1956). In addition, they are small, fragile, macropterous insects, and the ocelli are often absent. Member species are primarily arboreal although many species are associated with herbaceous plants (Knight 1983). Members of this subfamily are predominately mesophyll feeders, as exemplified by all species in the tribe Erythroneurini. Yet the tribe Empoascini is predominately comprised of phloem feeders (Vidano and Arzone 1983). Feeding traits are variable even within a genus. For example, in the genus Empoasca, E. fabae is a well known phloem tissue feeder while E. abrupta is a mesophyll feeder.

Although members in the family Cicadellidae most commonly have only one generation per year, Vidano and Arzone (1983) note that species of Typhlocybinae in the temperate zones typically have three generations. Only four species in the subfamily Typhlocybinae are known vectors of plant pathogens (Nielson 1985). <u>Empoasca devastans</u> Distant (currently <u>Amrasca devastans</u> (Distant), Ghuari 1983), transmits a disease termed "little leaf of brinjal" in S.E. Asia (Knight 1983). Sohi (1983) noted that <u>Empoasca papayae</u> Oman was a vector of bunchy top virus of papaya in Puerto Rico, and <u>Alebroides nigroscutellatus</u> (Distant) (formerly <u>A.</u> <u>dravidanus</u>) was a vector of purple top and witch's broom disease of potato.

Detailed surveys of past taxonomic studies of the subfamily Typhlocybinae are presented by Ahmed (1983) and Sohi (1983). Worldwide, the subfamily Typhlocybinae contains six tribes: Alebrini, Dikraneurini, Erythroneurini, Typhlocybini, Empoascini and Zyginellini. Following Young's (1952) description of Typhlocybini which included the genus Empoasca, Mahood and Ahmed (1968) erected the tribe Empoascini, to which the genus Empoasca was then transferred. The tribe Zyginellini was erected by Dworakowska (1979). However, Ahmed disputed the validity of separating the genera from Typhlocybini and their placement in Zyginellini. Prior to the creation of the tribe Empoascini, Beirne (1956) distinguished Typhlocybini from other tribes in the subfamily Typhlocybinae by the presence of vein IV in the hind wing and characteristics of the submarginal vein in the He also noted that compared to representatives hind wing. in the tribe Erythroneurini, they are not usually strongly marked nor brightly colored.

### BIOLOGY OF THE GENUS EMPOASCA

Ross et al. (1964) stated that there were six to seven hundred species of leafhoppers worldwide that belong to the genus <u>Empoasca</u>. New World species are represented by 20 to 30 species complexes for which those in the temperate regions appear to have their origin from ancestors in the tropics. Delong (1931a) notes that the genus Empoasca can be distinguished from allied genera by the absence of an appendix in the forewings and the presence of one apical cell in the hind wing which is closed by a submarginal vein. Beirne (1956) differentiated the genus from the other Typhlocybini genera that he addressed by noting the presence of a submarginal vein at the apex of the hind wing. The taxonomic characteristics for Empoasca are well illustrated by DeLong (1931a) and Ross (1959). DeLong (1931a) recognized four subgenera in his revision of North American species of Empoasca: Kybos, Hebata, Empoasca, and Idona. The primary character for differentiating among groups pertained to the shape of the head's vertex.

Although the potato leafhopper is the predominant species of Empoasca attacking crops in the North Central and North Eastern United States and Canada, DeLong (1938) pointed out that other species of Empoasca could be readily confused with <u>E. fabae</u> on wild plant species and apple. Until DeLong's (1931b) clarification of the apple leafhopper fauna (including <u>E. fabae</u> and <u>E. maligna</u> (Walsh)), there

existed a great deal of confusion in the literature with regard to species composition on apple. In the southwestern and western United States various truck and field crops are more commonly attacked by species of <u>Empoasca</u> adapted to arid environments and only to a limited extent by <u>E. fabae</u>. For the most part these species included, <u>E. filamenta</u> DeL., <u>E. arida</u> DeL. and <u>E. abrupta</u> DeL. DeLong (1938) discussed regional variation in <u>Empoasca</u> species composition in the western United States. In addition to these species, <u>E. solana</u> DeL. has an extensive range throughout the tropics, subtropics, southern United States and extending up the Mississippi river valley. In California since 1952, it has been recognized as a pest of cotton and more recently bean and sugar beet (Moffitt and Reynolds 1972).

While some species of <u>Empoasca</u> are highly adapted to temperate regions, others such as <u>E. fabae</u> and <u>E. solana</u> DeLong are members of species complexes containing representatives having more recently adapted to the temperate zones. As a result they demonstrate what is considered to be a less evolved state, exemplified by limitations in overwintering over the full extent of their annual range (Ross et al. 1964).

The <u>Empoasca</u> complex is based upon the finding that specimens previously collected in North and Latin America, that were consider to be <u>E</u>. <u>fabae</u>, actually represented a number of species that were remarkably similar in general morphology and even in terms of the characteristics of the

male genitalia used to identify E. fabae (Ross and Moore 1957, Ross 1959, Ross et al. 1964). Upon close examination of these collections it was observed that the apodemes of the 1st and 2nd abdominal sternites, and 3rd tergite were distinctly different among certain members of the collec-In fact they could be easily separated into groups, tion. with very few intermediate forms present. Relative to other Empoasca species, the presence of well developed apodemal structures in this region of the body is unique to the Empoasca complex. By 1964 twenty six species were recognized in this complex. Overall, as Ross and Moore (1957) pointed out, member species of the <u>fabae</u> complex could be described as ranging in body length from 3.5 to 4 mm, having a pale green color (when alive), whitish markings on head and thorax, male genitalia with simple aedeagus, hook of tenth segment with a slender sclerotized ventral point and an enlarged base, style with only a few short lateral setae and with tip oblique.

Interestingly, <u>E</u>. <u>Fabae</u> represents the only nearctic species in the complex, whereby its distribution is limited to temperate, North America. The remaining species distribution is predominantly in the tropics and subtropics of South and Central America. Ross (1959) stated that it appears that the <u>fabae</u> complex is of tropical origin and that most of its evolution is based on ancestors living in that zone. Because of the trans-Caribbean distribution of some of the species, Ross (1959) felt that speciation was

based upon the dispersal of vagrants as opposed to disruptive climatic changes over portions of the range of an ancestral species. However, in a fascinating account of species origins, Ross (1964) hypothesized that <u>E. fabae</u> could be traced back to an <u>E. mexara</u>-like ancestor having evolved into a species whose range extended well into North America. It is then believed that a portion of the northern population became isolated by an extensive arid zone and speciation restricted to a temperate climate occurred, i.e., <u>E. fabae</u>. It should be noted that the current known distribution of <u>E. mexara</u> is in Central America (particularly Mexico).

### THE BIOLOGY OF EMPOASCA FABAE

The potato leafhopper, Empoasca fabae Harris, is a pest of numerous crop plants, particularly potato, alfalfa, soybeans and field beans. Its host plant range is well over 100 plant species (Poos and Wheeler 1943, 1949). Empoasca fabae does not overwinter within North-Central and Eastern United States (Poos 1932). It is only known to over-winter along the coast of the Gulf of Mexico and migrates with the southerly prevailing winds into the North-Central and North Eastern United States and Canada in late May or early June, depending on weather conditions (Medler 1957, Pienkowski and The first arriving adults are primarily Medler 1964). fertile females (DeLong 1938, 1971). In field and lab studies Decker et al. (1971) determined the sex ratios of established populations to be 1:1. Although it was thought that the North American range of E. fabae was limited to areas east of the Rocky Mountains, DeLong (1938) noted that populations did exist in California. As pointed out by Ross (1964), in contrast to the eastern population, migrations associated with the western population have not been reported. Furthermore, some degree of reproductive incompatibility was apparent between those collected in California and in the Eastern United States.

It was believed that potato leafhopper populations died in their northern range each year, never to return South. However, southward migratory flights have been detected from June to September during intermittent periods during which the winds are from the north-northeast (Taylor and Reling 1986). The prevailing winds during that time of year are from the west.

Adult longevity is highly variable. In a three year study DeLong (1938) noted that adults commonly survived upwards of 30 days in greenhouse conditions and occasionally they lived as long as 92 days. It can be closely estimated from Hogg's (1985) data, that for treatments representing fluctuating diurnal temperature ranges (13-24° C, 18-29° C, and 23-34° C), 50% survivorship was 200, 90 and 40 days respectively. When calculated on a degree-day (DD) basis as opposed to calender time, convergence of 50% survivorship among the temperature treatments did not occur.

The majority of oviposition occurs between 2000 and 2400 hr, and it is enhanced by a lengthened photoperiod (Kieckhefer and Medler 1964). DeLong (1938) estimated that the average preoviposition period was 6.4 days, and the average number of eggs laid per female per day was 2.7, ranging from 2.1 to approximately 6, depending on summer temperatures in Ohio. The incubation period during midsummer was approximately 10 days. In that study females frequently produced as many as 200 nymphs. Decker et al. (1971) also estimated oviposition rates to be 2.7 eggs per day per female. In Decker's study, fecundity ranged between 34 and 57 eggs per female, and it was noted that by transferring females with an aspirator, oviposition was affected

negatively for upwards of four hours. From data presented by Hogg (1985), the oviposition rate from low to high temperature treatments was estimated to be .8, 1.2, and 1.6 eggs per day respectively during the first 600 DD. On a degreeday scale the rate of oviposition up to 600 DD was nearly identical among temperature regimes. Hogg's data were of particular interest since Kieckhefer and Medler (1964) demonstrated a significant reduction in the rate of oviposition with relatively small changes in constant ambient temperature around an optimal temperature of 23.5° C. No nymphs emerged from plants tested at 15° C and 31.5° C. It would appear that constant diurnal temperatures artificially varied oviposition rates as compared to the more realistic fluctuating temperatures in Hogg's (1985) study. From Hogg (1985), mean natality for individuals living to the upper age limit in the low to high temperature treatments was estimated to be 132, 102 and 82 eggs per female respectively. Simonet and Pienkowski (1980) determined that the lower and upper thresholds for egg development were 7.6 and 29° C respectively. Hogg (1985) demonstrated that under fluctuating diurnal temperatures, the potato leafhopper can develop well, even with temperatures periodically reaching 34° C.

Adult activity appears to be greater in the evening. Dysart (1962) determined that 50% of a days flight activity occurred 30 min. after sunset. Eighty-five percent of those caught were males. It appears that certain life history events in relation to movement are unique to each sex.

Adler (1982) determined that large populations of <u>E</u>. <u>fabae</u>, prevalent at dusk on Pennsylvania roads and adjacent soil surfaces, were 99% males. In terms of leafhopper distribution characteristics within fields, populations have been noted to aggregate at field margins and within elevated areas (Kieckhefer and Medler 1965).

The potato leafhopper has five nymphal stadia. The minimum and maximum developmental time from egg hatch to adult ranged from 8 to 25 days in generations occurring throughout the growing season over three years (DeLong 1938). Time spent in each stadia was nearly equal for the first four stadia and nearly double in the fifth (DeLong 1938, Simonet et al. 1978). Simonet and Pienkowski (1980) determined that the lower and upper developmental thresholds for nymphal development is 8.8° C and 29° C respectively. However, as in the case of egg development, Hogg's (1985) study refutes the upper threshold value.

Poos and Wheeler (1943, 1949) conducted an extensive evaluation of <u>E</u>. <u>fabae</u> host plant range. The diversity of host plants was staggering; including deciduous trees such as Maples (<u>Acer</u> spp.), Oaks (Quercus spp.), Sumac (<u>Rhus</u> spp.), and cherry (<u>Prunus</u> spp.), to herbaceous annuals such as Pigweed (<u>Amaranthus</u> spp.), sugar beet (<u>Beta vulgaris</u> L.), and Dahlia (<u>Dahlia</u> spp.). Poos and Wheeler (1943) state that oak and hickory were of special significance as principal hosts when <u>E</u>. <u>fabae</u> migrates northward at the beginning of the season along the Atlantic Coastal Plain.

The extent that potential host plants are utilized (based on lab studies) in nature is variable. Lamp et al. (1984a) demonstrated that leafhopper development can occur on piqweed under laboratory conditions, yet none were found on piqweed in and around alfalfa fields harboring extensive populations of leafhopper adults and nymphs, which were found on various other weed host species as well as alfalfa. Host plant species have a substantial influence on oviposition and the developmental rates of E. fabae. Kieckhefer and Medler (1964) determined that E. fabae has greater ovipositional acceptance for broadbean over alfalfa, while both alfalfa and broadbean were more readily accepted than soybean and field pea. While studying development on four host plant species, Simmons et al. (1984) determined that  $\underline{E}$ . fabae developed most rapidly on broadbean and slowest on soybean. Furthermore, utilization of a plant as a host by E. fabae is highly dependent on a host plants phenological state, and variables associated with host plant distribution (Poos and Wheeler 1949, Mayse 1978, Lamp et al. 1984, Wells et al. 1984).

The potato leafhopper feeds on host plant phloem tissue, causing damage through the physical destruction of these tissues and possible introduction of toxins. DeLong (1971) reviewed the basis of feeding related plant damage. Whether a toxin is released during feeding is still disputed. Superficially, potato leafhopper damage results in the yellowing and stunting of alfalfa, reddening and stunting of

clovers, and yellowing, curling, puckering, stunting and burning of bean and potato leaves. For the evaluation of leafhopper caused damage of beans, Chalfont (1965) presented a six point rating system using these characteristics. Hopperburn ratings are correlated with nymphal counts, the later of which Wolfenberger and Sleesman (1961) believe should be used as a method for evaluating resistance. However, leafhopper counts do not always provide an adequate comparison of resistance between varieties. Eckenrode and Ditman (1963) showed that while one variety of lima bean was host to a lower density of potato leafhoppers, its yield was reduced to a greater extent than were the yields of other varieties with higher leafhopper densities. Studies related to the evaluation of potato leafhopper sampling methods, damage impact and threshold determination are common (Cherry et al. 1977; Mayse et al. 1978; Cancelado and Radcliffe 1979; Simonet and Pienkowski 1979; Wilson et al. 1979; Fleischer et al. 1982; Cuperus et al. 1983; Luna et al. 1983; Flinn and Hower 1984; Walgenbach et al. 1985; Womack 1984; Walgenbach and Wyman 1984, 1985; Walgenbach 1985; Hower and Flinn 1986). To better assess the complex interactions between the potato leafhopper and its cultivated host plants, several models have been developed pertaining to potato leafhopper dynamics on alfalfa and potato (Flinn et al. 1986, Johnson et al. 1987, Onstad et al. 1984, Walgenbach et al. 1985)

Literature on host plant defense mechanisms against E. fabae indicates that trichomes are a major resistance factor. However, the mechanism through which they operate is guite different between plant species. In potatoes, glandular trichomes on wild species encase mouthparts and tarsi with a viscous exudate that rapidly hardens (Tingey and Gibson 1978). In soybeans, trichome density apparently affects nymphal feeding and possibly adult oviposition (Robbins et al. 1979, Singh et al. 1971, Turnipseed 1977). In common bean, Phaseolus vulgaris, trichomes are hooked, and impale leafhoppers. The early instar nymphs are more greatly affected (Pillemer and Tingey 1976, 1978). Although resistance in alfalfa has typically been related to the development of tolerant varieties, trichome secretory glands condition resistance to potato leafhoppers (Maxwell and Jennings 1980).

Environmental factors and host plant phenology may be important in determining the level of host resistance expressed (McKinney 1938). Pillemer and Tingey (1978) showed that bean leaves grown in the greenhouse (more shaded) had a lower density of trichomes and exhibited less of an influence on <u>E. fabae</u> than did those plants grown in the field. In potato, it has been found that the phenological stage is important when leafhoppers are migrating into the field, such that higher infestations occur on older plants (DeLong 1938, Sanford 1982). Although the cause for this is unknown, preliminary evidence by DeLong (1938) indicated an association between host plant sugar content and <u>E</u>. <u>fabae</u> field densities. Additional studies have shown that various sugars (glucose and lactose) can act as phagostimulants of <u>E</u>. <u>fabae</u>, while secondary plant compounds in some plants act to suppress feeding (Dahlman and Hibbs 1967, Dahlman et al. 1981).

In relation to its close relative, <u>E. kraemeri</u>, the bionomics of the two species appear quite similar (van Schoonhoven et al. 1985). Several of the most noticeable differences to date are that <u>E. kraemeri</u> has anywhere from four to seven stadia, and the host plant range, although extensive, does not appear nearly as large as <u>E. fabae</u>'s.

In summary, <u>Empoasca fabae</u> is a member of a large successful genus and subfamily of leafhoppers found around the world. An extensive amount of taxonomic work remains to be done in the genus <u>Empoasca</u>. <u>Empoasca fabae</u> and to a lesser extent <u>E. kraemeri</u>, and <u>E. Solana</u> represent the few species of this genus whose biology has been studied in some detail.

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# MANUSCRIPT II

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## INFLUENCE OF BEAN/TOMATO INTERCROPPING ON POPULATION DYNAMICS OF THE POTATO LEAFHOPPER, <u>Empoasca fabae</u> (Homoptera: Cicadellidae)

### ABSTRACT

The influence of tomato and bean interplanting upon the potato leafhopper (PLH), <u>Empoasca</u> <u>fabae</u> (Harris), was studied. A field design incorporating multiple densities of tomato was used to evaluate the overall influence, and determine which life stage was principally affected. A scparate study identifying the relationship between bean foliar density and PLH colonization was also conducted. Lastly, a laboratory study was conducted to analyze the potential influence of host plant quality (based on total plant nitrogen) upon acceptability for oviposition by PLH.

Reduced PLH densities on bean in bean/tomato interplantings were observed. Differences in nymphal counts between treatments were a function of oviposition, as opposed to differential nymphal mortality from natural enemies or host plant resistance. Although bean foliar density based on differences in plant size varied across treatments in the interplanting study, it did not appear to account for differences in PLH densities. In a separate study evaluating the effect of bean foliar density, no differences were observed in adult PLH densities per plant among treatments, which varied greatly in plant and therefore foliar density. Lastly, reduced bean host plant acceptability was observed when choice tests using beans grown under different fertilization regimes were conducted. Although tomato may have

been directly responsible for reduced PLH densities in the interplantings, the additional effect of host plant quality was also demonstrated.

### INTRODUCTION

The potato leafhopper (PLH), <u>Empoasca fabae</u> (Harris), is a polyphagous insect species occurring in North America. The known number of host plants of PLH is well over 100 species (Poos and Wheeler 1943, 1949). These host plants many different families of perennial and annual represent herbs, as well as some deciduous trees and shrubs. Although the population dynamics of PLH are highly dependent on host plant species, other factors of potential importance include host plant density, host plant spatial arrangement, interference by non-host plants through vegetational diversification, plant quality and natural enemy abundance. Such factors are likely to be interrelated. For instance, plant quality and microclimate (a product of vegetational density) can be a function of both plant density and species divers-Various researchers (Bach 1980, 1981, 1984, Risch ity. 1981, Risch et al. 1983) have discussed these variables in terms of representing the underlying factors that provide a basis for the "resource concentration" and "enemies hypothesis" set forth by Root (1973, 1975).

In a study evaluating the influence of row spacing (i.e., plant density) upon the arthropod fauna of soybean, PLH nymph and adult densities were strongly affected by plant

growth characteristics (Mayse 1978). In that study, plant treatments varied in leaf area, stem structure, biomass and yield by plant and by ground surface area.

PLH is also influenced by effects resulting from vegetational diversification. Lamp et al. (1984) noted that PLH was less abundant in unmanaged alfalfa plots containing multiple plant species in contrast to nearly pure alfalfa stands. The basis for these findings is not clear. However, <u>E. kraemeri</u>, a close relative of the potato leafhopper, was found to be directly influenced by the presence of several grass weed species, <u>Eleusine indica</u> (L.) and <u>Leptochloa filiformis</u> (Lam.), (Altieri et al. 1977).

The potential importance of host plant "quality" relative to host plant acceptability by PLH, has been recognized for many years. Poos and Wheeler (1949) observed PLH developing on the succulent growth of plant species previously not considered to be hosts. The succulent state of these plants was unusual, and was apparently a function of weather conditions that were unusual for the time of Variation in PLH populations among bean plants has year. been attributed, in part, to host plant vigor (i.e., relative growth among treatments) (Wells et al. 1984). One explanation is that certain sugars are phagostimulants (Dahlman et al. 1981). Relative sugar concentrations in bean and potato have been associated with PLH colonization patterns (DeLong 1938).

Although PLH has been studied extensively, little has been reported on the importance of its parasites. This lack of information may indicate that they are not a particularly important factor in PLH population dynamics. More is known about the range of predatory species attacking PLH, however, little information is available regarding their potential importance (Martinez and Pienkowski 1982).

Research on the interactions between insect species and plants in the family Solanaceae is common because of the extensive alkaloid chemistry and plant volatiles associated with this plant group. This is particularly true for tomato, <u>Lycopersicon</u> <u>esculentum</u> Mill., potato, <u>Solanum</u> tuberosum L., and the species from which they were derived (D'Arcy 1986). As a companion plant (one which affords protection for others planted in proximity (Tahvanainen and Root 1972)), tomato is known to influence insect/host-plant interactions. Under laboratory conditions, Phyllotreta Cruciferae Goeze fed less on host plant leaves adjacent to tomato than alone (Tahvanainen and Root 1972). In the field, eggs and adults of the diamond-back moth, <u>Plutella</u> <u>Xylostella</u> (L.), occurred at lower densities on cabbage intercropped with tomato than in monoculture (Buranday and Raros 1975). In that study, tomato appeared to directly affect the pest. Variation in plant quality did not seem to be a factor since there was no difference in yield between treatments, implying little change in the gualitative state of the host plant due to differential competition or

interference between plant species. In terms of chemical constituents of tomato and other members of Solanaceae, advances have been made in characterizing their effect on herbivores (Harborne 1986). The alkaloid tomatine is known to suppress potato leafhopper consumption when added to feeding solutions in the laboratory (Dahlman and Hibbs 1967).

Research envolving a bean/tomato/leafhopper system was stimulated by field observations directed at uncovering differences in insect/host-plant associations brought about through interplanting. Preliminary results indicated that PLH was highly influenced by bean/tomato intercropping, showing reduced densities on intercropped bean. In terms of yield advantages and insect pest control, considerable advantages have been found in intercropping bean and tomato in Central America (Rosset et al. 1985, 1987).

The objective of this study was to evaluate the influence of tomato intercropped with bean (<u>Phaseolus</u> <u>yulgaris</u> L.) upon PLH life stages occurring on bean over a range of tomato densities. Furthermore, the influence of bean foliage density and plant quality (based on total nitrogen) was studied to provide insight into the observed differences in the intercropping investigation.

Root's (1973,1975) "resource concentration" hypothesis states that herbivores (esp. specialists<sup>1</sup>) are most likely to be more abundant in pure stands of their host plants. Typically this has been viewed to be a function of movement rates in and out of host plant habitat. Although the present study does not address movement per se, other laboratory based studies were conducted which specifically addressed PLH movement with and without tomato and other non-host plants (see Manuscript III). Even though PLH is difficult to study in detail under field conditions, the advantages in investigating this species were: (1) much was known about the life history and host plant range of this polyphagous species since it is a commonly studied pest, (2) its natural occurrence in field plots was nearly guaranteed, (3) it was easy to rear in lab cultures, and (4) polyphagous species have been studied less in intercropping systems than monophagous species.

<sup>&</sup>lt;sup>1</sup> Some authors define herbivores as specialists or generalists based on their host plant range, relative to the plant species within a particular habitat (Risch et al. 1983, Letourneau 1986).
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## METHODS

PRELIMINARY FIELD STUDY: During 1983, snap bean and tomato were intercropped within a newly planted apple orchard (Fig. The bean and tomato monoculture and diculture field 1). design included two densities of tomato (Castlehy 105) interplanted with a single bean (Kentucky Wonder, rustresistant) density, one bean monoculture, and a tomato monoculture divided into two densities. Each plot contained eight rows of a monoculture or eight paired rows of a diculture on a trellis composed of wooden stakes 2.2 m in length, and nylon string. Tomato densities were 45 and 70 cm within row and 2 m between rows. Bean density was 20 cm within row and 2 m between row. Rows of bean and tomato in the diculture treatments were 15 cm apart with 1.8 m between each pair of rows. The four treatment plots were replicated as blocks in two sites within the orchard. The purpose of using two densities of tomato in this preliminary study was to insure a successful interplanting treatment of bean and tomato, whereby tomato would not overwhelm bean growth. During this study, the apple trees were believed to have little potential influence on the bean/tomato plantings since they were very small (ca. 1.5 m in height), sparsely distributed and contained little foliage. Data for nymph populations in the bean monoculture and two bean/tomato dicultures were analyzed by a two-factor (i.e., date and



tomato densities "D 1" and "D 2", and tomato monoculture Treatments were blocked within two locations of the orchard. The treatments were: bean Fig. 1. Plot diagram of apple orchard interplanted with monoculture, bean/tomato dicultures with two different with two within row spacings. tomato and bean in 1983.

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treatment) randomized block ANOVA (Snedecor and Cochran 1967). Prior to analysis, data were transformed ( $\sqrt{x+.5}$ ), for compliance with assumptions of analysis of variance.

BEAN/TOMATO INTERPLANTING STUDY: During 1985 and 1986 the experimental design consisted of four blocks of unstaked bean and tomato. Each block consisted of four rows of snap bean (Blue Lake var.) planted at a density of 15 cm within row, and 1.5 m between rows, and tomato (Sunny var.) planted at four densities down the length of each block at a distance of 35 cm from each bean row. Together with a treatment of bean alone at one end of each block, there were five treatments per block (Fig. 2). This design was selected to spatially separate those treatment replicates with no tomato from those with the highest tomato densities, thereby minimizing interactions between them throughout the To facilitate distribution of random effects over season. treatments, the orientation of the four blocks ("gradients") was alternated in a north/south direction. Each block was separated by a 24 m alleyway which was mowed to maintain short (less than 10 cm) weed stubble. Plot preparation consisted of tilling the soil, and applying nitrogen (urea) at a rate of (72 KG/hectare). Water was applied through a drip irrigation system. In 1985 water was not always available as required for irrigation. In 1986, little supplemental water was required due to adequate rainfall, particularly in late summer.



Fig. 2. Bean and tomato intercropped in plots forming increasing densities of tomato over the length of each of four blocks. Rows of bean are represented by stars, and circles identify tomato plants.

In 1985, bean plants within each treatment were sampled to estimate leafhopper nymphs and natural enemy populations Ten whole-plant on 15 dates after true leaf initiation. samples per treatment per block were made using direct observation from julian date 193 (12 July) through julian date 208 (27 July). Thereafter ten half-side plant samples were taken. Egg parasitoids of PLH were monitored using 10 by 20 cm yellow plastic cards treated with Tangle-Trap<sup>®</sup>. These cards were hung within and above bean leaves collected from the field and held in a rearing room to obtain egg counts, as described later. Tomato was also sampled by direct observation on seven dates throughout the season to estimate natural enemy occurrence. Four tomato plants in each treatment replicate were sampled by detailed inspection of one-half of each plant.

In 1986, bean plants were sampled on 10 dates following initiation of the first true leaves. For the first two sample dates, all leaves were sampled, and on subsequent dates three trifoliate leaves from each of 30 plants per treatment were sampled by direct observation. Tomato was not sampled in 1986 because results from 1985 indicated that it was not warranted.

Oviposition by PLH was evaluated throughout the season in 1985 by removing leaves from each treatment in each of the four blocks, placing them in florists waterpics and retaining them within a rearing chamber provided with supplemental lighting (16:8, day:night). Daily observations

were made for newly hatched nymphs. To obtain additional oviposition information, three trifoliate stage plants were grown in four inch pots and placed in the field within each treatment and removed weekly during 1985 and 1986 seasons.

During both years bean plant leaf area was estimated weekly. Initially, measurements were obtained using a LI-COR® leaf area meter. Later, they were obtained by visually comparing trifoliates with photo-copies of leaves of known size. In 1985, four bean plants were measured per treatment within each block, for a total of 16 plants per treatment. In 1986, six plants were measured per treatment within each block. On four dates in 1985, tomato leaf areas were also measured, using the leaf area meter. On each date, leaf areas were taken on one tomato plant in each treatment per block, for a total of four plants per treatment.

Beans were harvested during both years. Within each treatment, four/1 m row portions of beans were marked with ribbon and repeatedly harvested and weighed. This was done both years. Pods measuring 8 cm or longer were harvested. Tomatoes were harvested in 1985 but not in 1986. Four randomly selected tomato plants were repeatedly harvested in each treatment.

**REGIONAL PLH POPULATION DENSITY:** Adult populations were sampled in two alfalfa strips located 30 m east and west of the two outside intercropping study blocks. This was done to provide a record of the regional PLH population through-

out the season. These population estimates were used to assist interpretation of results obtained in the intercropping study across sample dates and between years. Each alfalfa strip was divided into four sections measuring 4 by 10 m. Beginning in early June, one strip was cut every one to two weeks throughout the summer. This maintained a consistent alfalfa age structure throughout the season within each strip. The adult PLH densities were sampled using a large plastic can (with an attached catch jar) that was inverted and placed over alfalfa for 5 min as described by Cherry et al. (1977). On any given sample date, all but the most recently cut section in each strip were sampled. In each strip, a sample  $(.3 \text{ m}^2)$  was taken within each section. Repeated sampling of all three sections per strip continued until the standard error was 20% or less of the mean, to provide population density estimates with similar accuracy over all sample dates.

HOST PLANT DENSITY STUDY: In 1986 the influence of leaf area density on PLH colonization was evaluated in field plots of bean planted at three densities. Each density was replicated three times. A square area divided into nine plots was tilled and fertilized to accommodate three replicates of each of three treatments. Each plot measuring 3 by 6 m contained four rows of bean plants. Within row treatment plant spacings were 8, 22 or 44 cm, and treatments were randomly assigned to each plot. A three meter bare soil alleyway separated all treatment plots. Plants were sampled on 8 and 15 September. The late sample dates were a result of late season (end of July) planting, and cool August temperatures resulting in slow growth. Twenty plants were carefully inspected for adult leafhoppers in each replicate. The plants were small enough to allow observation of each leaf without disturbing the leafhoppers present. Down-wind plots were sampled first so that if leafhoppers were disturbed they would fly to previously sampled plots.

THE ROLE OF PLANT QUALITY ON HOST PLANT SELECTION: In the course of studying the effects of bean/tomato intercropping on <u>E</u>. <u>fabae</u>, it was hypothesized that bean plant quality, which varied across treatments, was an important determinant of leafhopper colonization. Three indicators were used to rank bean quality: leaf area per plant, yield, and total nitrogen. Data for the first two methods of evaluating the influence of plant quality on <u>E</u>. <u>fabae</u> host plant selection were obtained from the intercrop field study, while the latter were obtained from oviposition choice tests conducted in a greenhouse using plants grown under different fertiliz-ing regimes.

Bean plants in the latter study were grown in soil within four liter plastic pots. Three groups of plants were grown under different nutrient (15-30-15 NPK, Miracle-Gro® plant food) regimes. Tests were conducted in cages measur-

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ing 1.6 by 1.0 by 0.7 m in height. They were constructed of untreated pine lumber and saran screen. Humidity was maintained above 40% at all times, and temperatures were between 21 to 29° C . Two plants representing each nutrient level were placed in a cage forming a circle. In the first three tests, 10 adult females were released into the cage to oviposit in bean over a 48 h period. The fourth test consisted of 30 females placed in the cage for 120 h. Following each test, leafhoppers were removed from each plant during an inspection. All plants were then sprayed with water to dislodge any leafhoppers that were missed during inspection, and held in a rearing room until the eggs hatched and nymphs could be counted. For the nitrogen analysis, two trifoliates or petioles were removed from each plant and dried at 65° C.

Total nitrogen was determined (standard Kjeldahl analysis) using leaf tissue in the first two tests, while leaf petioles were used for nitrogen analysis of the third and fourth tests. Petioles were used because immature whiteflies (considered a contaminant) were present on the leaf surface of the plants used in the third test. A chisquare analysis was conducted on each of the four tests for two reasons: 1) total plant nitrogen in each designated level varied between tests, and 2) leaves were analyzed in the first tests, and petioles in the others.

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FIELD DATA ANALYSIS: During 1985 PLH densities were estimated using a half bean plant sample. However, the unit of measurement used during data analysis was the number of leafhopper inhabitants per unit resource (leaf area) in contrast to the total number of occupants per plant. This was calculated by dividing leafhopper nymph counts per halfplant sample by the average leaf area per half-plant per replicate. In 1986 the sample unit was three trifoliates per plant, negating the need to convert from an estimate per plant to leaf area.

To compare nymph densities across treatments, the experimental design was analyzed as a split-plot, such that direction represented the main-plot effect and treatments designated by tomato density represented the sub-plot The blocking term in data analysis is based on effect. pairing field blocks 1 and 2, and 3 and 4 together, whereby each pair contained field blocks oriented in opposite north/south directions (Fig.2). Since tomato density represented a continuous independent variable, the linear and curvilinear (quadratic and cubic) effects were analyzed within the context of the split-plot design (Cochran and Cox 1957). Data collected during each date were analyzed the analysis represented the separately. Data used in average nymph density per m<sup>2</sup> in 1985, and average nymph count per three trifoliates in 1986 for each of the four replicates per treatment. The model residuals (predicted minus actual values) were used as an indicator of a lack of

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compliance with ANOVA assumptions of independently and normally distributed error. Requirements were met by using a square root transformation ( $\sqrt{X+0.5}$ ) on PLH counts.

The mean leaf area per plant for each treatment replicate (used as a measure of bean plant quality) could directly integrated into the statistical model not be because multicollinearity existed between it and tomato density (Freund and Littell 1981). This was evident when leaf area was incorporated into the model as a covariate, whereby linear dependence with tomato density was demonstrated by the generation of a singular X'X regression matrix. This relationship existed between the variables throughout the season. Since bean leaf area could not be entered into the statistical model as an independent covariate, a split-plot analysis was conducted first by using tomato density as the sub-plot independent variable and then replacing it with bean leaf area for a second analysis for each sample date. To analyze the relationship between bean leaf area and tomato density an additional analysis was conducted using leaf area as an independent variable and tomato density as a dependent variable. A11 analyses were conducted with standard programs of the Statistical Analysis System (SAS), (SAS Institute, 1985). Treatment means in 1983 were analyzed using a Waller-Duncan K-ratio t-test (Waller-Duncan 1969).

## RESULTS

**PRELIMINARY FIELD STUDY:** In 1983, PLH population densities were considerably larger on bean in monoculture than in the diculture plots (Fig. 3). In addition, monoculture bean plants exhibited extensive curling and chlorosis leaf because populations were so large that year. Populations peaked during early August (julian date 220) followed by a continuous decline into September. Nymph densities among the two diculture treatments were nearly identical to each other. An analysis of the nymph densities, grouped by treatment over all dates, showed that PLH densities were significantly greater in the monoculture plots than in either of the two intercrop densities. Densities in the two intercrop treatments were not significantly different (P<0.05, Waller-Duncan preceded by ANOVA, [F=84.5; df=2,27; P<0.05]).

NYMPH POPULATIONS IN BEAN/TOMATO INTERPLANTING STUDY: In 1985 and 1986 PLH nymph densities were lower in treatments representing successive increases in tomato densities (Figs. 4 and 5)<sup>2</sup>. Summary statistics comparing tomato density and PLH density are presented for both years (Table 1)<sup>2</sup>.

<sup>&</sup>lt;sup>2</sup> See appendix A, fig.1 for illustration of PLH counts on a per plant basis (compared to leaf area) for 1985.

<sup>&</sup>lt;sup>3</sup> See appendix A, fig. 2 and 3 for a graphical analysis  $\circ \pm$  all sample dates.











three trifoliate Fig. 5. Number of potato leafhopper nymphs per three trifolis bean sample on monoculture and tomato diculture plots in 1986.

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ANOVA LAble Table 1. density ANOVA tables for potato leafhopper nymph densities versus tommto Data are presented for 1986 and 1986 field studies over successive julian dates. Table 1. density.

				1986 DA	TA ANAL	XSI S				
		207	210	214	218	221	224	228	232	239
Source	70				values	1				
Block	T	7.1*	18.0*	26.5*	*6.8	2.3	7.6*	8.2*	*8.6	10.5*
Direction	-	1.2	6.2*	16.3*	28.0*	2.6	22.1*	9.2*	6.7*	2.1
B1*D1r	-	4.	1.6	3.5	9.3*	5.7*	5.2*	1.8	2.4	1.5
Treatment	m									
Trt		10.3*	34.0*	52.3*	39.0*	16.3*	26.2*	110*	94.5*	22.0*
Trt =		9.	2.9	3.2	4	2.2	12.7*	22.0*	20.1*	1.8
Trt =		1.1		e.		. 2	1.3	1.9	1.1	. 7
Trt*Dir	-	5.	<b>9</b> .	9.	<b>eo</b> •	8.2*	9.4*	1.7*	8.7*	1.8
Model r"		.64	. 86	. 89	.87	.76	.87	. 91	. 92	61.
			-	1986 DA	TA ANAL	<u>XSIS</u>				
		184	188	192	195	198	202	205	209	216
Source	DP			6	va ] ues	1				

Values followed by (\*) are significant at P<0.05. Analysis on date 192 was

17.3\*

20.8\* 18.4\* • -

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Although leafhopper nymph densities were low in all treatments during both years (especially in 1986), there was a consistent progression of fewer nymphs with increasing tomato densities, as indicated by linear and quadratic effects of tomato densities on nymph densities. This occurred throughout periods of peak abundance during both years. In 1986, a marked difference was noted between the monoculture and all diculture treatments, while among the diculture treatments the difference was considerably less. This became particularly apparent when the monoculture treatment was eliminated from the statistical analysis. As a result, although a significant linear treatment effect on nymph densities was still noted for julian dates 205, 209 and 216, the sums of squares for treatment were reduced by 82, 75, and 81%, respectively. Overall, the relatively large difference in leafhopper density between the monoculture and diculture treatments, and the small difference between diculture treatments explain the consistent quadratic effect expressed during analysis of 1986 data. For all analyses the model  $r^2$  ranged from .64 to .92 when tomato density was used as the independent variable (Table 1). Significant direction effect was evident during both years. That is, blocks oriented with the monoculture plot in the south, had larger populations of PLH.

Additional data analyses considered the correspondence between bean leaf area and tomato density, and PLH density and bean leaf area. A representative example of these

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relationships along with PLH and tomato densities are illustrated in Figure 6. When the above analysis was repeated, substituting bean leaf area for tomato density, significant linear effects were noted for all of 1985, and quadratic effects paralleling those for tomato density were noted in 1986. The model r<sup>2</sup> was consistently less than that for tomato, however for each date it was at least within 0.2 of the model r<sup>2</sup> produced while using tomato density as the independent variable. When bean leaf area by treatment was regressed on tomato density, the two were determined to be inversely related on nearly all sample dates.

Based upon limited tomato leaf area data collected in 1985, it was evident that the proportional difference in tomato leaf area between treatments was considerable throughout the entire season, although it declined as the season progressed. Relative to the high density intercrop, tomato leaf area proportions, starting with the lowest density, were .16, .25 and .50 on julian date 191, and .38, .54 and .82 of the highest tomato density treatment on day 228, the last day measured.

NATURAL ENEMY POPULATIONS: Populations of predators of the potato leafhopper and other phytophagous species were very low throughout the 1985 season (Table 2). In addition, only eight egg parasitoids (family Mymaridae) were found on the 14 color cards used to capture them following emergence from PLH eggs in leaf cuttings. There was no indication that



Fig. 6. Graphical analysis of the relationships between bean, tomato and PLH nymph density within the bean/tomato intercrop during julian date 205, 1986. 1) nymph density by tomato treatment, 2) bean plant leaf area by tomato treatment, and 3) nymph density by bean plant leaf area. Units of measurement are: tomato plants per row meter, nymph density per 3 trifoliate sample, and leaf area (m<sup>\*</sup>) per bean plant.

and spider predators on bean and tommato plants sampled intercrop treatments representing different densities of tomato interplanted with bean. monoculture and four bean l Table 2. Insect throughout 1986

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BEAN	(TS)
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PREDATOR	(NUMBER

Spiders **
Chrysopidae ***
Nabidae **
Ant hocor idae *
Coccinellidae **
Treatment (Tomato plants per row meter)

3.9	2.5	1.7	2.3	1.4
e.	1.9	2.0	4.7	2.0
1.6		9.	æ.	
6.	9.	1.2	<b>.</b>	9.
6.	<del>.</del>	1.6	1.1	1.7
0	.35	.65	1.10	2.20

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-		1.1	6.
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-	• •	0	•
c		0	•
	1.1	3.6	1.3
25	. 55	1.10	2.20

Whole bean plants were sampled for the first 5 dates; thereafter, one-half of each plant was sampled. <sup>D</sup> Tommto was sampled on seven dates throughout the season. <sup>3</sup> Bean was sampled on 15 dates during 1985. ar adults and nymphs art eggs \* adults

natural enemy populations were different among treatments, suggesting that they were not responsible for the differences in leafhopper densities among treatments.

OVIPOSITION MONITORING: A sequential decline in egg densities occurred across treatment plots, whereby highest egg counts were obtained from potted bean plants located in the monoculture plots (Fig. 7). The relative densities of leafhopper eggs matched well with nymph counts (Fig. 4) across treatments when considering that the lag period associated with leafhopper egg development is approximately seven days during mid-summer temperatures. In addition, these data were supported by very similar results obtained when egg data were collected from leaf cuttings of the actual field plants. These data showed that differences in leafhopper populations across treatments were largely due to differential levels of oviposition, thereby emphasizing the influence of intercrops upon adult activity.

**REGIONAL PLH POPULATION DENSITY:** PLH population patterns in nearby alfalfa strips were considerably different between 1985 and 1986 (Fig. 8). In 1985 the population grew slowly early in the summer and persisted at a relatively constant density until well into September. In 1986 there was a large population buildup that persisted until early August, followed by an abrupt decline. In 1985, there was little rain during June and July, and the strips had to be



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Fig. 8. Mean adult potato leafhopper densities per .3  $\rm m^2$  soil surface in two alfalfa strips. Sample SEM is <20% for each date.

irrigated. Overall plant vigor appeared to be maintained at a relatively high level. In 1986, irrigation was not necessary. In fact, rain occurred very frequently during August. On julian date 216, the first sign of fungal (Ervnia (Brefeld) Humber) infected adult leafhoppers radicans occurred on bean. This was very likely an important factor in the decline of leafhoppers in alfalfa. On several dates following the decline of leafhoppers on alfalfa, neighboring field plots of bean and potato were sampled, and in all cases those populations were also found to be small. Therefore, it was apparent that the regional populations of leafhopper had declined in early August 1986 and that low August populations were not unique to the intercropping plots.

THE EFFECT OF BEAN PLANT DISTRIBUTION ON COLONIZATION: In a test conducted to evaluate the impact of host plant density on the potato leafhopper colonization, mean adult E. <u>fabae</u> counts between treatments were not significantly different during both sample dates (Table 3). Plants during the first sample period were very small. There was only one trifoliate per plant that was developed 50% or more. Plant quality among treatments was considered to be very similar. This assumption was based on general observation and similar average leaf areas per plant among treatments.

Table 3. Mean adult potato leafhopper counts per 20 plants in bean plots representing three different canopy densities.

TREATMENT Plant density (NO. Per Row m)	NO. Adui	OF LTS	₹ PLANT Leaf Area
	T	±SD	
LOW (1.7)	1.7a	1.2	-
MED. (3.4)	1.7a	1.5	-
HIGH (12.5)	3.6a	2.5	-
	 ۹ ۵۵	 9 R	115 mª
	3 0a	0 0	194 m <sup>p</sup>
HIGH (12.5)	3.4a	2.5	.136 mª
	TREATMENT PLANT DENSITY (NO. PER ROW m) LOW (1.7) MED. (3.4) HIGH (12.5) LOW (1.7) MED. (3.4) HIGH (12.5)	TREATMENT NO.   PLANT DENSITY NO.   (NO. PER ROW m) ADUI   Image: Constraint of the state of	TREATMENT   PLANT DENSITY NO. OF   (NO. PER ROW m) ADULTS   X ±SD   LOW (1.7) 1.7a 1.2   MED. (3.4) 1.7a 1.5   HIGH (12.5) 3.6a 2.5   LOW (1.7) 3.0a 2.6   MED. (3.4) 3.0a 0.0   HIGH (12.5) 3.4a 2.5

No means are significantly different. (P<0.05; oneway ANOVA [F=1.9; df=2,6; P<0.05] [F=0.4; df=2,6; P<0.05].

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GREENHOUSE STUDY OF THE EFFECT OF PLANT QUALITY: Based on a greenhouse study of the effect of plant quality (relative to total plant nitrogen) on E. fabae oviposition, it was leafhoppers laid more eggs on plants determined that containing higher levels of nitrogen. In the first three tests, over 70% of the eggs were laid in foliage containing the highest levels of nitrogen (Table 4). In the fourth test, similar numbers of eggs were laid on the high and intermediate treatment, while the lowest nitrogen treatment was the least accepted for oviposition. An evaluation of percent total nitrogen was conducted on bean in two treatments of the intercropping study. During 1986, on julian date 218, leaf petiole samples were taken from the monoculture and the second most dense diculture treatment (1.1 tomato/row m) in each block and analyzed for total nitrogen. The treatment means were 1.8% and 1.3% nitrogen, respectively.

PLANT YIELDS: Bean yield was reduced significantly (P<0.05) by increased tomato density (Table 5). Paralleling leaf area for 1986, bean yield of the lowest density diculture treatment (1.1 tomato/row m) was far lower then the monoculture yield. Although a tomato treatment without bean was not present, in 1985 the tomato yield on a per plant basis was similar for all but the highest tomato density.

In 1986, a plot containing only tomato was added to the end of each intercrop block, as an extension of the high

TRIAL NO.	FERTILIZER TREATMENT	TOTAL a % NITROGEN	% OVIPOSITION	No. EGGS
1	HIGH	4.3	74 a <sup>C</sup>	27
	LUW	1.0	26 D	
2	HI GH	4.5	71 a	7
	LOW	1.4	29 a	
3	HIGH	1.7	76 a	20
•	MED	1.1	18 b	
	LOW	. 9	6 b	
	HIGH	1 8	40 a	160
	MED	1.0	43 8	4
	LOW	. 8	17 b	

Table 4. Greenhouse study of potato leafhopper oviposition in relation to bean plant total nitrogen ; conducted as four separate trials.

<sup>a</sup> Measure of nitrogen in trial one and two are based on leaf nitrogen, while others are based on petiole nitrogen. <sup>b</sup> Ten female leafhoppers were released into cages for 48 h in first three trials. Thirty leafhoppers were released for 120 h in fourth trial. <sup>C</sup> Data within trials analyzed by a G test (Sokal and Rholf

<sup>C</sup> Data within trials analyzed by a G test (Sokal and Rholf 1982). Percentages followed by the same letter are not significantly different (P<0.05) by an STP test.
sting of	ifferent	
udies consi	esenting d	
1986 st	s repr	
985 and	reatment	
yields in 1	ntercrop t ith bean.	
tomato	four i opped w	
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Average b	monocultur of tomato	
Table 5.	a bean i densities	

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		BEAN	YIELD <sup>a</sup>		QMATO YIELD
Treatment (Tomato plants per row meter)	1985 Yield (KG)	Percent of Monoculture	1986 Yield (KG)	Percent of Monoculture	1985 Yield (KG)
0	5.6 a	100	5.5 a	100	1
.35	4.4 ab	19	3.3 b	60	33.5 a
. 55	3.6 b	64	3.4 P	61	32.2 a
1.10	2.0 c	36	3.3 b	61	26.0 b
2.20	1.2 c	21	2.6 c	47	12.6 c
a KG of bean per	4 row mete	£			
Means followed by	same lette	r within a c	olumn ar	e not significantl	y different
(P<0.05, Waller-	Duncan pre	ceded by a	blocked	ANOVA). From lef	t to right:
[F=5.2; df=4, 12;	P<0.05], [F	"=4.3; df=4,1	2; P<0.05	], [F=3.8; df=3,9;	P<0.05].

density tomato/bean treatment. Unfortunately, septoria leaf spot (<u>Septoria lycopersic</u> Spegazzini) caused such extensive defoliation of tomato plants in all treatments during mid August that harvest was not feasible. While the timing of the disease had little effect on events relative to PLH, it did prevent the calculation of land equivalent ratios.

### DISCUSSION

In 1985 there was clearly an inverse relationship between tomato and leafhopper densities. Although bean plant size was also inversely related to tomato density, plant quality could not be used to provide a more likely explanation since leafhopper densities among treatments showed a gradual (near linear) progression. A gradual difference in PLH densities among treatments, resulting from a direct effect of tomato, would be expected since the first two diculture treatments had very low tomato densities and therefore were expected to have a small effect. However, in 1986 there was a large difference in leafhopper densities between the monoculture and all diculture treatments, while little change occurred among the diculture treatments. This association, which could not be explained solely in terms of a direct tomato effect, was paralleled by differences in bean host plant size, which was considered to reflect differences in bean quality among treatments. Based on these results, the effect of host plant quality appeared to be an important factor. Results from ovipositional studies comparing plants grown under low versus high soil fertility, also support the claim that the observed differences in leafhopper field populations were partially due to differences in bean plant quality among treatments.

In terms of the experiment where bean alone was planted at three different densities, PLH was not highly responsive to foliar densities of bean. Even if a statistically significant separation of means had occurred through greater replication during the first sample period, it is noted that the plants had only one partially expanded trifoliate, therefore the value of any conclusions under that extreme condition would be limited. During the second sample period the plants had three to four expanded trifoliates, and PLH counts in all three treatments were nearly identical. Overall, this test provided no evidence that PLH was only responding to differences in foliar densities of bean across treatments in the intercrop study.

Results from this study support the resource concentration hypothesis, in that the presence of tomato did affect leafhopper colonization of bean. However, the basis for this result is hypothesized to have been a combined function of the qualitative status of bean resulting from tomato/bean interaction, and a direct influence of leafhopper activity by the presence of tomato.

Overall, it is apparent that the potato leafhopper is highly sensitive to the qualitative status of its host plants and perhaps less in their distribution. Host plant quality has been implicated as an important factor in several studies involving the potato leafhopper. In a study of soybean insects, Kretzschmar (1948) noted that potato leafhopper densities were five times greater in weed-free, widely spaced fields, than in weedy, closely spaced fields. The role of non-host vegetation may be argued as the basis for those results. However, Mayse (1978) reported similar

results in weed-free plots of soybean planted at three different row spacings. In that study, although a decisive explanation for the results was not available, host plant quality may have been one factor. Upon review, support for this is drawn from differences in yield, and the speculation that the qualitative state of the soybean plants was reflected by yield differences across treatments. Further support for the importance of host plant quality was provided by Wells et al. (1984), who found larger populations of the potato leafhopper on dry bean that exhibited enhanced growth following canopy closure in treatments using a foil mulch. Also, Poos and Wheeler (1949) found potato leafhopper populations on plants that were previously not considered to be host plants, but which were in a stage of development that was atypical for the time of year due to weather.

With few exceptions, the potential influence of the qualitative status of the host plant is seldom incorporated into studies of intercrop systems (Bach 1981, 1984). This is unfortunate since in some cases it is an important determinant of insect pest densities. Even though the inhibition of pests may be a function of what is considered to be a reduced qualitative status of their host plant, reflected by productivity (yield), this should not necessarily be viewed in a negative sense, for the land equivalent ratio<sup>4</sup> (LER),

<sup>&</sup>lt;sup>4</sup>. For an excellent presentation of the LER concept, see J. Vandermeer (1981).

may be greater for the intercrops. In those systems where the qualitative status of the host plant plays a key role in determining pest densities, pest impact will be unpredictable between locations until the influence of host plant quality upon herbivore population dynamics is understood. This is due to regional variation in weather, soil etc. playing an important part in the qualitative state of host plants, and therefore crop susceptibility. Interestingly, it has been reported that tomato yield is little affected when interplanted with bean, and the two can provide a very high over-yield (Rosset et al. 1987).

Plant quality is a relative term and for that reason is difficult to define. It is represented here by productivity (yield) and total plant nitrogen. It should be realized that these relationships (e.g., nitrogen and yield) do not always coincide. Vogtmann et al. (1984) found that nitrogen source (i.e., compost or commercial fertilizers) can qualitatively influence plant nitrogen (NO<sub>3</sub> in particular). Furthermore, it was found that if the appropriate cultivars were selected, plant productivity was equal among treat-It is of interest to speculate that perhaps the same ments. situation may occur when intercropping with particular plant varieties, whereby certain gualitative characteristics of the host plant may be changed, yet productivity is high and acceptability by pests is low. While specific plant combinations can directly impact the potato leafhopper, as in the case of several grass species negatively influencing

<u>E. kraemeri</u> (Altieri et al. 1977), PLH is highly sensitive to the qualitative status of its host plants. Results from this study indicate that a direct tomato influence and host plant quality are capable of reducing PLH densities on bean. Since host plant quality varies extensively among vegetationally heterogeneous habitats (e.g., alfalfa stands and vegetable intercrops), future research should consider this factor along with any direct effects of plants associated with a herbivores' host plant.

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# MANUSCRIPT III

POTATO LEAFHOPPER, <u>EMPOASCA FABAE</u> (HOMOPTERA: CICADELLIDAE), MOVEMENT, OVIPOSITION AND FEEDING RESPONSE PATTERNS IN Relation to host and non-host vegetation.

#### ABSTRACT

Studies were conducted to evaluate the influence of non-host vegetation upon bean host plant acceptance by the potato leafhopper (PLH), <u>Empoasca fabae</u> (Harris), with emphasis on the influence of tomato. Cage environments in the laboratory and greenhouse were used to observe PLH movement and arrestment, and evaluate performance criteria, including feeding and oviposition.

The presence of tomato vegetation suppressed feeding by 43%, and in oviposition choice tests only 28% of the eggs were laid on bean in proximity to tomato. Reduced feeding was a result of considerable residence time on tomato. Cabbage also reduced PLH oviposition when in proximity to bean. In choice tests only 32% of the eqgs were laid on bean in proximity to cabbage. There were no differences in the average length of time on bean during each arrestment bout in treatment cages containing a combination of bean and companion plant leaves versus the control containing two bean leaves. When evaluating leafhopper movement frequency from surface to surface (i.e., the two leaves and cage surfaces), no differences were found when comparing the bean and tomato treatment with the bean control. However, an overall trend of increased movement frequency did occur with the inclusion of leaves of many other companion plants. The importance of evaluating insect/plant interactions based on multiple criteria are discussed.

## INTRODUCTION

The potato leafhopper (PLH), Empoasca fabae (Harris), is a member of the subfamily Typhlocybinae (family Cicadellidae). Despite its presence within a phylogenetically advanced group in which most family members have highly restricted host plant ranges, PLH has an exceptionally large host plant range (Poos and Wheeler 1943,1949). This species has well over 100 known host species representing many different plant families. Because of the extensive host plant range, including both tree and herbaceous plant species, PLH occurs in a wide variety of habitats. Except for economically important plants, the acceptability of host plants for oviposition and as a food source by adults and nymphs is not well understood (Poos and Wheeler 1949, Lamp et al. 1984a, Simmons et al. 1984).

Disparities exist between host plant suitability for nymphal development and acceptance by adults. For example, pigweed (<u>Amaranthus retroflexus</u> L.) is capable of supporting PLH nymphs to maturity in the lab, yet in the field, nymphs were not found on this weed species (Lamp et al. 1984a). Furthermore, under the same field conditions they were found on other weed species, determined to be equally or even less suitable for nymph development than pigweed in laboratory studies. The role that less acceptable and non-host plants

may play in primary host plant utilization within a diverse vegetational environment has been suggested as being important (Lamp et al. 1984b). Whether interactions are due to host-plant spatial distribution, reduced plant quality competition or interference), (through plant improved natural enemy/pest ratios, differences in canopy microclimate, or directly through chemical and mechanical properties of the companion plants themselves is not understood. A close relative of PLH, E. kraemeri Ross and Moore, has been reported to be repelled by the presence of several grass species, Eleusine indica (L.) and Leptochloa filiformis (Lam.), (Altieri 1977). Feeding by PLH and other insect species is affected by the presence of tomatine, a common alkaloid in tomato (Dahlman et al. 1967, Hsiao 1986).

Studying insect behavior and evaluating an organism's performance (i.e., oviposition, feeding, etc.) in relation to an environment's plant species composition may aid in understanding host plant utilization patterns and facilitate predictions of PLH activity in various plant community scenarios. The present study originated from field studies demonstrating that PLH attained lower population densities through reduced oviposition on bean plants intercropped with tomato, compared to bean planted alone (see manuscript II). In that study populations were sequentially reduced over a range of treatments representing a series of increased tomato plant densities. In addition, studies have indicated that domestic tomato and particularly wild tomato, Lycopersicon hirsutum Mull, negatively influence a number of insect species (D'Arcy 1986). Plant compounds and structures (e.g., trichomes) of specific cultivars may adversely affect potential pests of tomato, while non-pests of tomato may respond aberrantly to their respective host plants when in close proximity to tomato (Gentile and Stoner 1968, Gentile et al. 1968, Tahvanainen and Root 1972, Williams et al. 1980, Dahlman and Hibbs 1967, Dimock and Kennedy 1983).

The objective of this study was to examine the response of female potato leafhoppers to leaves of a known primary host plant and other minor or non-host plant species under caged conditions, thereby providing a better understanding of the basis for which bean/tomato intercropping influences PLH, as well as to evaluate the potential of other non-host plants to do so as well. It was hypothesized that PLH would exhibit a unique behavioral pattern toward its bean host plant depending upon the inclusion of different companion vegetation. To investigate this hypothesis, leafhopper movement and performance were evaluated. This was accomp-(1) the direct observation of female lished through: leafhopper behavior in small cages and residency time in large cages, (2) monitoring feeding, and (3) quantifying oviposition in choice and no-choice tests.

SHORT-TERM OBSERVATIONS OF FEMALE PLH MOVEMENT: Observations were conducted to guantify PLH behavior (displacement and arrestment) when exposed to leaves of various plant species, with and without bean (a primary host plant). Responses of female PLH obtained from the lab culture were recorded for a short period of time (15 min), immediately after an individual was introduced into a cage with leaves positioned at each end. Cages consisted of a transparent cylinder made of polyethylene terephthalate<sup>1</sup>, and end pieces from plastic petri dishes (Fig.1). Materials to prevent escape, minimize leaf damage, and provide ventilation and easy assembly were included in their construction. No discernable odor was present in the cages, and following each use at the end of a test day, all cages were washed and rinsed in distilled water.

An individual female leafhopper was released into a cage and observed for 15 minutes. Due to the number of companion plant species evaluated, test groups were arbitrarily selected to be run on the same day. Tomato, radish, squash, and bean composed one test group, while pepper, corn, cabbage, and bean were present in the other. These plant species were chosen based on their representation of separate taxonomic groups. Seven cages were prepared for a day's run of tests. One cage was set up with two bean

<sup>&</sup>lt;sup>1</sup>Polyethylene terephthalate is commonly used for beverage containers.





leaves (control), while the other cages contained either a bean leaf and non-bean companion leaf, or two companion leaves of the same plant species at opposite ends of a cage. For each treatment, three replicates were conducted per day, and a total of 18 female leafhoppers across dates were observed per treatment, one at a time. Observations were conducted from 0800 to 1800 h on each date, and a female was used only once.

Displacement and arrestment on leaf or cage surfaces was recorded each minute. Displacement involved either walking from one surface to another, or relocating on the same or another surface following flight. The leafhopper was considered to be in a state of arrestment from the time she contacted a surface (leaf or cage) until she relocated onto a different surface by either flying or walking. Although the occurrence of multiple events within any one minute period was noted, the time duration of any event less than one minute was not explicitly recorded. Arrestment time on bean leaves was nearly always greater than one minute. Therefore, since tenure on bean was the primary reason for monitoring arrestment duration, discretizing (i.e., blocking time) on a one minute basis was justified. Results include: 1) total number of whole minute periods out of 15 that an individual remained on a surface, 2) duration of "arrestment" for each encounter, and 3) frequency of transitions from one surface to another.

Observations were conducted in a room illuminated only with cool-white fluorescent 40 watt bulbs positioned 1.2 m over the observation table and approximately .8 m from each cage. Room temperature ranged from 23 to 27.5° C, and the relative humidity ranged from 55 to 74%. Each cage/plant treatment was assigned randomly to a location on the table surface for each set of tests run on a given day. Tomato was grown in 12 liter pots, bean plants in 4 liter pots, and all others in 8 liter pots. Plants were lightly fertilized each week with Miracle-Gro<sup>®</sup> (15-30-15) plant food. All plant species used in this study are presented in Table 1.

LONG-TERM OBSERVATION OF FEMALE LEAFHOPPER ACTIVITY, INCLUDING FEEDING: Leafhopper residency and feeding was evaluated over the course of a day (12 h), within the same cages described above. This was done to determine if departures in behavior occurred relative to those observed during the 15 minute study, and to determine if feeding was altered by the presence of tomato.

These tests were limited to treatments of bean and tomato. On a given day each treatment (two bean leaves, bean and tomato, or two tomato leaves) was represented by three replicates. The experiment consisted of fifteen replicates of each of the three treatments. Leafhoppers were placed in the cages at 0800 h and their location within the cage was recorded every 30 min. until 2000 h. To monitor feeding over the course of a day, plastic strips of cage

PLANT	CULTIVAR	T LEAF AREA	a x weight
SNAP BEAN ( <u>Phaseolus vulgaris</u> L.)	BLUE LAKE	1445 cm <sup>2</sup>	5.2 g
CABBAGE ( <u>Brassica oleracea</u> L.)	EARL I ANA	3785	28.2
CORN ( <u>Zea mays</u> L.)	SILVER SWEET hybrid, white	-	-
PEPPER ( <u>Capsicum annuum</u> L.)	CALIFORNIA Wonder	1890	16.9
RADISH ( <u>Raphanus sativus</u> L.)	CRIMSON GIANT	2900	15.3
SQUASH ( <u>Cucurbita moschata</u> Duch.)	BURPEE'S BUSH TABLE QUEEN	41 42	23.4
TOMATO ( <u>Lycopersicon</u> <u>esculentum</u> Mill.)	SUNNY	6641	61.2

Table 1. Species, variety and size of plants used in experiments.

Phenology of those plants used in testing ranged from early flowering to initial fruit set. <sup>a</sup> Above ground biomass.

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material measuring 1.2 by 7.0 cm were placed on the bottom inside of both ends of the cage to collect droplets of excreta. Since each leaf assumed a vertical position at the end of a cage, the excreta produced by each leafhopper fell to the bottom. These strips, held in place by a small piece of cellophane tape, were removed and placed under a 10x dissecting microscope. The total number of excreta droplets were counted. As before, individuals were evaluated separately, and each leafhopper was used only once. All plants used for study were grown as previously described.

LEAFHOPPER TENURE WITHIN A LARGE CAGE ENVIRONMENT: Leafhopper residency time (tenure) within the context of a large cage (Fig. 2) and whole plant environment was studied to further quantify the influence of tomato upon leafhopper movement. A measure was obtained of PLH residency time within the canopy of three treatments represented by two bean plants, two bean plants plus a tomato plant, or one tomato plant. Three large cages were constructed to house the treatments and monitor residency as a reflection of catch rate on cage surfaces. Each cage was composed of a plywood base and top frame, pine vertical supports, saran screen, transparent vinyl and Velcro<sup>®</sup>. All plywood materials were painted four months prior to use with a tan latex paint in order to eliminate odors characteristic of plywood. The sticky panels (30 % of the cage surface), were of clear vinyl coated with Tangle Trap<sup>®</sup>. Tests were conducted



Fig. 2. A cage with sticky, vinyl panels for monitoring PLH residency on selected plant environments.

outdoors on a grass yard from late August through mid September. Fifteen female leafhoppers were released into the lower plant canopy of each cage at 1400 h of day one of each of three trials. During each 46 h test, cage panels were checked every two hours throughout the day from 0800 to 2000 hours for captured leafhoppers. Leafhoppers were inactive from 2000 to 0800 hours during late summer conditions, eliminating the need for nighttime observation. Preliminary tests indicated that with no plants present, nearly all leafhoppers were caught within two hours. The maximum plant canopy temperature within the cages for each respective test period was 28, 30, and 25° C. Tomato plants were approximately 60 cm in height when the tests were conducted.

CHOICE AND NO-CHOICE OVIPOSITIONAL TESTS: To evaluate the impact of companion plants on potato leafhopper oviposition, choice tests were conducted within cages in a greenhouse. Cages used for choice and no-choice oviposition tests were constructed from 5 by 5 cm untreated pine lumber covered with saran screen mesh. Each cage measured 1.6 by 1 by .7 m in height. They were placed in a greenhouse and supplemental lighting (40 watt, cool-white fluorescent) was provided from a distance of 2 to 3 meters on either side. Temperature ranged from 17 to 28° C and humidity was maintained above 40%.

Choice tests were performed using all previously evaluated companion plants, except corn. During each test the diculture treatment (i.e., bean and companion plants) was placed at one end of a cage while a bean control was located at the other end of the cage. Two types of choice tests were conducted using tomato. First, the leaf area of the bean control was set equal to the combined leaf area of the bean/tomato diculture treatment by using variable numbers of bean plants (i.e., 2 to 4 plants). This test controlled for total vegetation between treatments. For the second series using tomato, as well as for tests using other companion plants, the bean leaf surface in the control and diculture treatments were equal. Therefore the combined leaf area of the diculture treatment was more than the bean control. All tests were conducted in each of two cages within a greenhouse. The placement of the bean control versus the diculture treatment was alternated from the north to the south end of a cage, between trials. For all choice tests 10 females were placed in each cage on days one and two (i.e., 20 total PLH's). Each test lasted 72 h, and except for tomato, tests of each plant species were replicated eight times. Tomato tests were replicated 12 times.

No-choice oviposition tests were conducted using only tomato as the companion plant with bean. Two kinds of nochoice ovipositional tests were conducted. The first was conducted in the laboratory, under the same conditions that the small cage observation study was done. Four cages,

identical to those used for rearing  $(.13 \text{ m}^2)$ , were located 1 m from each other, and treatments consisting of one bean plant or a bean and tomato plant were assigned to each. The tomato and bean plants used in this study were grown in .6 liter plastic pots. Five female leafhoppers were place in each cage for 48 h. This test was conducted on five dates. The second series of no-choice tests was conducted in the greenhouse using the same large cages used for the choice tests. Two bean plants and one tomato were arranged in one cage, while two bean plants were placed in the other. The tomato plant was positioned so that its nearest leaves were several cm from touching the bean leaves, and care was taken to avoid shading the bean plants by the tomato plant. Treatments were alternated among cages from one test to the next. Five females were placed in each cage on days one and The tests ran for 72 h, and were replicated eight two. times.

POTATO LEAFHOPPER CULTURE: Adult female PLH, 1 to 3 weeks of age were used in all tests to assure that they were past their preovipositional phase (DeLong 1938). They were obtained from a culture maintained on broad bean (<u>Vica faba</u> L.). The parent stock of the culture was collected annually from various hosts including snap bean, alfalfa, and potato. Culture cages were .13 m<sup>3</sup> in size and kept in a room maintained at 23 to 29° C, 45 to 80% RH and a light/dark cycle of 16:8 h. STATISTICAL ANALYSIS: All data were tested for compliance with assumptions of the analysis of variance. Based on these results either analysis of variance tests or a rank transformation procedure was used. The latter approach is appropriate for data that would be analyzed through traditional nonparametric methods. It involved the ranking of data within test days and applying an analysis of variance (Conover and Iman 1981). Treatment means were tested using Waller-Duncan K-ratio t-test (Waller and Duncan 1969). All analyses were conducted by employing the standard programs of the Statistical Analysis System (SAS) (SAS Institute, 1985).

#### RESULTS

**MOVEMENT OBSERVATION STUDIES:** Although tests were run on two separate test groups (A: tomato, radish, squash, and bean no. 1 control; and B: pepper, corn, cabbage and bean no. 2 control), results were combined to facilitate data summary. To justify this, bean controls used in each test group were compared using a Wilcoxon two-sample test (Sokal and Rohlf 1981). The two controls were not significantly different (P>0.20), so data from treatments of both test groups were combined for further analysis. The degree of uniformity of leafhopper performance among the two controls is apparent in figures 3 and 4. Throughout the results, the summary of both test group controls are presented as bean no. 1 and bean no. 2.

Figure 3 shows that for all cage treatments containing bean leaves (i.e., controls and combination treatments), the mean number of minutes in which leafhoppers were present on the combined leaf surfaces, in contrast to the cage surface, was not significantly different among treatments<sup>2</sup>. For treatments consisting entirely of non-host leaves (i.e., no bean leaves present), with the exception of tomato and pepper, significantly less time was spent on plant surfaces. The least amount of time was spent on cabbage. Although tomato and pepper are not among those in the extensive host

<sup>2</sup>See Appendix B, Table 1 for means and standard deviations.



Fig. 3 Mean time spent on leaf surfaces during a 15 min exposure, in observation cages containing either two bean leaves, two companion leaves, or one bean and one companion leaf. Bars with same letters are not significantly different in total height (P<.05; Waller-Duncan preceded by rank transformation and one-way ANOVA; [F=5.0; df=13,227; P<0.05]).



Fig. 4. Mean number of surface to surface (leaf 1, leaf 2, or cage) transitions during 15 min, in observation cages containing either two bean leaves, two companion leaves, or one bean and one companion leaf. Bars with same letter are not significantly different (P<0.05; Waller-Duncan preceded by a one-way ANOVA [F=2.9; df=13,238; P<0.05]).

plant lists by Poos and Wheeler (1943, 1949), leafhoppers were observed feeding on tomato and occasionally ovipositing in both tomato and pepper during the course of several studies.

In terms of the partitioning of time on leaf surfaces in treatments containing a bean and companion plant leaf, the actual amount of time spent on the bean leaf was not significantly different between treatments (P<0.05 Waller-Duncan; rank transformation). It was apparent that the previously reported, combined leaf surface time in the bean/cabbage treatment, was less because of little time having been spent on cabbage and not due to reduced time on bean (Fig.3). Although not significantly different, leafhoppers tended to reside more on bean in the bean/squash cages compared to the other treatments. Furthermore, PLH spent very little time on squash or cabbage leaves.

Among the plants used in this study, the presence of companion leaves did not significantly (P<0.05) alter the duration of an arrestment bout (i.e., duration of a given encounter) on a bean leaf, relative to the controls containing only bean<sup>3</sup>. All mean arrestment times were within 25 % of each other.

The number of surface to surface transitions was significantly (P<0.05) greater than the controls for only a limited number of treatments (Fig.4). However, the overall

<sup>3</sup>See Appendix B, Fig. 1 and table 2 for details.

trend indicated a general increase in movement for nearly all treatments containing companion plant leaves.

DAY-LONG OBSERVATION RESULTS: When the location of PLH was observed every 30 min. within the small cages, the frequency ±SD) of repeated observations on the same bean leaf (x surface in the bean control ( $\bar{x}=6.6\pm5.2$ ), was not significantly different (ANOVA, blocking by date, P<0.05) from the number of consecutive sightings on bean in the tomato/bean treatment  $(\bar{x}=5.8 \pm 5.3)$ . This analysis was important since it was assumed that there was a relationship between repeated observations and the duration of arrestment on bean. Results indicated that the mean number of repeated observations, therefore arrestment, extended several hours over the course of a day. Therefore, relative to the 15 min trials, the duration of arrestment was considerably longer on bean (for both bean controls and bean/tomato treatments) when leafhoppers were allowed to perform for an extended period. However, the relative differences between treatments were very similar to those obtained in the 15 minute continuous observation results.

The transition frequency  $(\bar{x} \pm SD)$  among all three treatments (bean, bean/tomato, and tomato), was significantly greater (ANOVA, Waller-Duncan, P<0.05) in the tomato treatment ( $\bar{x}$ =10.6 \pm 2.3) than in either the bean control ( $\bar{x}$ =4.3  $\pm 2.3$ ) or bean/tomato treatment ( $\bar{x}$ =5.4  $\pm 2.4$ ). In part, these results differed substantially from those obtained during the 15 minute study (Fig. 4). That is, in the 15 minute study there were no differences in transition frequency between any of these treatments. Compared to the bean control and bean/tomato treatment, PLH transition frequency increased significantly under long-term exposure within cages containing only tomato. Table 2 illustrates the average partitioning of leafhopper residence time during the 12 hour study. No significant time differences were observed between treatments for residence on vegetation versus cage surfaces. Within the bean/tomato cage a considerable amount (ca. 4.3 h) of time was spent on the tomato leaf surface (Table 2).

FEEDING RESULTS: Leafhopper feeding was significantly different between treatments (Table 2). Total excreta production was far greater in control cages containing two bean leaves than in the bean/tomato and tomato treatments. When evaluating the difference between the bean/tomato treatment versus the bean control, it was not apparent that these results were due to a limit in the amount of food that could be obtained from the single bean leaf in the bean/tomato treatment, since greater than 300 droplets were produced from individual leaves in 6 of 15 trials in the bean control. The average amount of feeding on a bean leaf within the diculture treatment was similar to that occurring on an individual leaf in the bean control.

	TREATMENT				
	BE	AN	BEAN/TOMATO		TOMATO
	T	±SD	(Bean)	(Tomato)	
TIME (h) ON Individual Leaves	5.5	<u>+</u> 2.8	6.1 <u>+</u> 3.0	4.3 <u>+</u> 2.7	4.2 +2.4
TIME (b) ON Leaf Surfaces Combined <sup>a</sup>	10.7	<u>+</u> .7 a	10.4	<u>+</u> 1.0 a	8.4 <u>+</u> 1.2 a
DROPLETS PER Leaf Per Cage	189.	4 ±150	181 ±15	5 34 ±51	57 ±110
<u>TOTAL</u> (DROPLETS PER CAGE) <sup>D</sup>	378.8	±241 a	215 ±	163 b	114 ±151 b

Table 2. Average time leafhoppers spent on leaves, and excreta production (droplets) over 12 h, in small cages containing two bean or tomato leaves, or one bean and one tomato leaf.

[F=0.9; df=2,38; P<0.05]. [F=6.8; df=2,38; P<0.05]. b

LEAFHOPPER TENURE WITHIN THE LARGE CAGE ENVIRONMENT: The capture rate of leafhoppers was used to reflect tenure within the bean and tomato habitats represented in each treatment. On two out of the three test dates (2 and 13 Sept.), the capture rate curves for leafhoppers in the bean versus bean/tomato treatments were nearly identical (Fig. 5). However, on 23 August the capture rate in the bean-/tomato treatment was more similar to the tomato treatment. The capture rate in the tomato treatment was consistently greater, thereby reflecting the lowest tenure time across treatments.

The data are also useful in interpreting the mobility of female PLH. In the presence of readily accepted host plants, female PLH reside on them for considerable lengths of time without extensive movement (i.e., movement in meters). At the end of each test, all but one or two leafhoppers were accounted for, indicating that the results were a function of leafhoppers departing from the foliage present in the cage.

BEAN/TOMATO, SQUASH, RADISH, PEPPER, CABBAGE CHOICE TESTS: Representing equal total leaf areas across treatments, the initial series of bean versus bean/tomato ovipositional choice tests showed no significant difference (P<0.05) between treatments, based on the number of eggs per plant per treatment. The egg count (mean  $\pm$ SD) per bean plant in



Fig. 5 Leafhoppers remaining on plant treatments within cages containing bean, tomato, or bean and tomato plants. Fifteen female leafhoppers were released into each cage and their rate of capture on the sides of the cage was monitored for 48 h.

the bean treatment was 32.0 +11.1, and 27.5 +14.2 eggs per plant in the bean/tomato treatment.

In subsequent choice tests using equal numbers of bean plants among treatments, resulting in greater total foliar area in the bean/companion-plant treatment relative to the bean control, significantly (P<0.05) more eggs were laid per bean plant in the bean control than in the bean/tomato treatment (Table 3). An effect of tomato was evident since bean foliage was equivalent between the diculture treatment and control, demonstrating that PLH were responding to factors other than resource (bean) availability.

There were also significantly (P<0.05) fewer eggs laid in the bean/cabbage treatment relative to its bean control (Table 3). Oviposition in the bean/pepper, squash and radish treatments was not significantly (P<0.05) reduced. Furthermore, the combined treatment means for the squash test showed that a very large number of eggs were laid during each squash/bean test relative to other treatments (Table 3).

BEAN/TOMATO NO-CHOICE OVIPOSITIONAL TESTS: The first series of no-choice oviposition tests were conducted in small cages, using young tomato plants grown in .6 liter plastic pots. Mean  $\pm$ SD oviposition in the bean control ( $\bar{x}$ =15.1  $\pm$ 11.2) versus bean/tomato ( $\bar{x}$ =13.8  $\pm$ 14.3) treatment was not significantly different (P<0.05).
TREATMENT <sup>a</sup>	$\overline{\mathbf{x}}$ NYMPHS <sup>b</sup> PER REP.	(%)	±SD	NO.(REPS.)	
TOMATO/BEAN	17.3 a	(28)	12.5	12	
BEAN	45.6 b	(72)	17.3		
PEPPER/BEAN	23.0 a	(43)	20.4	8	
BEAN	30.9 a	(57)	23.8		
SQUASH/BEAN	45.0 a	(50)	15.8	8	
BEAN	46.1 a	(50)	23.5		
RADI SH/BEAN	30.5 a	(39)	22.1	8	
BEAN	47.6 a	(61)	28.8		
CABBAGE/BEAN	16.4 a	(33)	26.9	8	
BEAN	33.6 b	(67)	19.5		

Table 3. Potato leafhopper oviposition choice tests. Paired comparisons represented: bean with companion plants compared to a bean control.

<sup>a</sup> Number of bean plants in companion treatments and bean controls were equivalent. <sup>b</sup> Means within choice tests followed by the same letter are not significantly different (P<.05; five, ANOVA's each blocked by date). [F=29.0; df=1,11; P<0.05]; [F=0.8; df=1,7; P<0.05] [F=0.0; df=1,7; P<0.05]; [F=2.16; df=1,7; P<0.05]

[F=4.15; df=1,7; P<0.05].

The second series of no-choice tests were run under similar conditions (i.e., same plant and cage size) to those described for the second series of tomato/bean choice tests. Oviposition was significantly (P<0.05) greater in cages containing bean ( $\bar{x}$ =46.0, SD=±23.8) as opposed to those containing bean and tomato ( $\bar{x}$ =22.2, SD=±14.6).

### DISCUSSION

The events involved in host plant utilization by an insect have been generally grouped as follows: finding, consuming (Miller and Strickler 1984). examining and Finding not only involves an organism making contact, but also the maintenance of proximity to its host. Examining relates to testing processes prior to consumption, while consumption is the act of utilizing a host (e.g., feeding, oviposition etc.). This study evaluated the interaction of the potato leafhopper with a host and non-hosts by obtaining three kinds of information which are related to certain of these general host plant utilization events. That is, movement is most closely aligned with the finding process, residency with the examining process, and feeding and oviposition with the consumption process. Although these kinds of information only loosely identify the processes involved, they provide a multilateral analysis of the influence of vegetational diversity upon an insect herbivore.

Among bean controls and diculture treatments (except cabbage), the potato leafhopper resided on foliage (in contrast to the cage surface) nearly equally across treatments when exposed for short time periods (15 min.). However, of the time spent on foliage within the diculture cages per se, over 25% was spent on the companion plant surface. The squash and cabbage treatments were exceptions. The importance of this in terms of whether this time would be spent productively (actively feeding, ovipositing etc.) in a system containing only bean, is not entirely clear since the bean control consisted of two leaves versus one in the diculture treatments. It may be hypothesized that increased time spent on bean controls was a result of bean leaf area representing a greater proportion of the total surface area within a cage. However, the hypothesis that PLH processes are altered by the presence of particular companion plant leaves was strongly supported by the day long observation study. Time spent on tomato throughout the day was considerable and resulted in far less overall feeding in cages containing both bean and tomato compared to those containing only bean leaves. Whether feeding was reduced due to a suppressant effect or to a diversion effect is unknown. However, the latter appears most likely since feeding on the bean leaf, within the bean/tomato treatment, was equivalent to the per leaf feeding in the bean control. Since tomatine has been identified as a feeding suppressant of the potato leafhopper when incorporated into feeding solutions, it would be of interest to determine if "food searching" thresholds are altered when residing on tomato (Dahlman and Hibbs 1967). Again, this possibility is supported by the similarity of average per leaf feeding on bean, in the control and bean/tomato treatments. The small cage observation and feeding studies would have been enhanced by the use of a second control consisting of a single bean leaf, to control for bean leaf area.

Oviposition choice tests also demonstrated the potential of tomato, as well as cabbage in reducing oviposition. The two kinds of oviposition tests using tomato (i.e., equal total leaf areas between treatments in contrast to equal bean leaf area plus tomato) indicated a lack of influence (either positive or negative) by vegetational concentration. Tests directed at the combined influence of tomato and cabbage could prove useful in decreasing oviposition even further if the effects are synergistic.

Risks associated with increases in transition frequency due to non-host plant vegetation need to be considered under field conditions. The general pattern of increased transition frequency within cages containing non-host plant foliage indicates that additional movement may commonly be an important result of introducing companion plants. However, in the case of tomato this appeared to not be true. In the 15 min observation study, the day-long observation study, and the outdoor large cage leafhopper residency study, the difference in leafhopper movement between the bean control and the bean/tomato treatments were small or non-existent.

In this study one test provided inconsistent results concerning the potential influence of tomato. The small cage, no-choice oviposition test indicated that tomato had no influence on oviposition, while both the choice and nochoice tests conducted within large cages in the greenhouse indicated a significant negative effect. This may be explained by the fact that the tomato plants used in the nochoice test were small and at an early stage of phenological development. In terms of the influence of host plant phenology upon the PLH, the importance of phenology has been pointed out for bean and potato (DeLong 1938, Sanford 1982).

Results from field studies (see manuscript II), combined with those reported here indicate that the influence of bean/tomato intercropping on PLH involves a combination of altered host plant quality, through plant competition or interference, and the direct influence of tomato. These results indicate that tomato can reduce potato leafhopper feeding and oviposition. The means by which this occurs may be based upon a kind of diversion. Residency time data corresponded most closely to these findings, whereas movement frequency data provided the least support for influence by tomato.

The importance of using more than one criterion to evaluate the impact of companion plants upon a herbivore is clear. That is, it is inappropriate to assume a particular outcome (i.e., more or fewer insects) based upon an evaluation of a single criterion, since one response when combined with various other events may lead to different outcomes. For instance, even though leafhoppers moved more frequently in the presence of squash, the majority of their time was spent on bean in the bean/squash combination tests.

Furthermore, it was demonstrated in the oviposition choice test that little difference existed between the bean control and bean/squash treatment.

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## CONCLUSIONS

Information from intercropping studies, and insect/plant interactions in general, provides strong support for the overall potential of facilitating pest management through intercropping. Although the research presented here does not provide a complete picture of the cause and effect relationships, it does give considerable insight into the complexity of a system representative of intercropping. It is apparent that future work will commonly uncover multiple causes for results encountered in intercropping. For example, in this study it is evident that both host-plant quality and the direct influence of tomato were important factors in reducing leafhopper impact within the inter-It is also apparent that effects can cropped plots. influence one of many activities of a pest, which may result in reduced pest impact. For example, laboratory evidence indicated that the potato leafhopper fed less when tomato was present, while the more commonly studied issue of movement appeared less important.

Illustrated by direct interactions between insect and companion plant species, and interspecific plant interactions affecting herbivores through changes in the host plant, the complexity of intercropping research requires the development of guidelines. Risch (1983) addressed this need

by emphasizing the importance of pest-free controls to provide clear comparisons among treatments because of the effect of pest damage over the course of the season. In this study, an influence of plant damage over the season was not an issue of particular importance, since the potato leafhopper populations during 1985 and 1986 were not large enough to cause any signs of plant feeding damage (leaf burn, leaf curl, and/or chlorosis).

In the opinion of this author, at least one additional guideline is needed. That being the incorporation of noncompetitive spacing arrangements of the intercrop plants as well as their respective monocultures. At least some intercrop treatments within an experimental design should have plants that are qualitatively similar to those grown in monoculture. This would allow the separation of direct and indirect companion plant effects. Furthermore, yield data (and other measures of plant performance) should always be collected and reported. This is often lacking in many studies.

The topic of intercropping has been controversial. Its practicality within a mechanized system of crop production is often questioned. Issues of economics are also raised. For example, concern is expressed toward the simultaneous production of two crops of unequal value and its impact on profits. Furthermore, there exists a reluctance in believing that intercropping or similar forms of manipulating agricultural systems can significantly reduce pest impact.

This viewpoint continues to plague the field of biological control, whereby there are those who believe that the currently documented examples of biological control are little more than attractive oddities. Perhaps when viewed within the broad context of all factors playing into agricultural viability (i.e., in terms of economics and long term sustainability), the currently perceived problems associated with intercropping will be offset by an array of benefits, including reduced pest abundance and reduced reliance on pesticides.

The manipulation of an agroecosystem's vegetational composition is likely to provide striking, easily interpreted results in a limited number of cases. Such results arise from what could be classified as "big effects". They can be achieved even with little knowledge of a system's dynamics. In most fields of science they are pursued early on, and act to justify further investigation within the general area of inquiry. However, in the long run advances are realized in smaller steps. I believe this to be generally true in pest management research and the role that crop diversification can play in managing pests. On an insect behavior basis, important effects resulting from manipulating an insect's environment are frequently not going to be recognized by striking responses such as immediate death, rapid aversion, etc. At the population level, the identification of important effects are not going

to be solely reflected by changes in one kind of response (e.g., immigration and emigration) in all systems.

Pronounced successes in pest control through intercropping and similar methods will require the cooperative interaction of individuals in all areas of crop protection and production. To provide continuity, a systems approach is necessary so that all important components are identified and goals can be appropriately set. An important role of modeling within the context of a SYSTEMS APPROACH is that of identifying system components that are most responsible for system's performance, and most in need of continued a research. The importance of using modeling as an aid in system identification has been generally overshadowed by emphasis on precise predictions. It can provide a common ground among researchers and an organized and disciplined exploration into identifying properties of a system.

Overall, this study supports the viewpoint that the value of intercropping in pest control is through specific interactions brought about by the appropriate selection of plants, and not by general, nonspecific diversification. **BIBLIOGRAPHY** 

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POTATO LEAFHOPPER FIELD STUDY



Fig. 1. Number of potato leafhopper nymphs per bean plant in monoculture and tomato diculture plots in 1985.

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Fig. 2. Graphical analysis of 1985 intercrop, <u>E. fabae</u> nymph populations and bean plant growth by replicate over successive dates. 1) nymph density by tomato treatment, 2) bean plant leaf area by tomato treatment, and 3) nymph density by bean plant leaf area. Units of measurement are: tomato plants per row meter, nymph density per leaf area  $(m^2)$ ; leaf area  $(m^2)$  per bean plant.



cont.





Fig. 3. Graphical analysis of 1986 intercrop, E. fabae nymph populations and bean plant growth by replicate over successive dates. 1) nymph density:tomato treatment, 2) bean plant leaf area:tomato treatment, and 3) nymph density:bean plant leaf area. Units of measurement are: tomato plants per row meter, nymph density per 3 trifoliate sample, leaf area  $(m^2)$  per bean plant.







Table 1. 1985 intercrop field study data. PLH nymph counts represent an average per half bean plant, based on a 10 plant sample per treatment per block. Bean leaf area was obtained from four plants per treatment per block. Variables are: Julian date, Treatment, Block, Plants samplied per replicate for nymphs, Nymph count, and Bean leaf area  $(m^2)$ .

193	0.00	1	10	0.00	.045
193	0.00	2	10	0.00	.061
193	0.00	3	10	0.00	.014
193	0.00	4	10	0.00	.040
193	0.35	1	10	0.00	.061
193	0.35	2	10	0.00	.007
193	0.35	3	10	0.00	.005
193	0.35	4	10	0.00	.012
193	0.55	1	10	4.35	.030
193	0.55	2	10	0.00	.021
193	0.55	3	10	0.00	.007
193	0.55	4	10	0.00	.036
193	1.10	1	10	0.00	.038
193	1.10	2	10	0.00	.012
193	1.10	3	10	0.00	.009
193	1.10	4	10	0.00	.025
193	2.20	1	10	9.12	.025
193	2.20	2	10	0.00	.019
193	2.20	3	10	9.12	.009
193	2.20	4	10	0.00	.037
198	0.00	1	10	0.00	.104
198	0.00	2	10	0.95	.128
198	0.00	3	10	0.00	.039
198	0.00	4	10	0.00	.105
198	0.35	1	10	0.00	.039
198	0.35	2	10	2.40	.060
198	0.35	3	10	0.00	.015
198	0.35	4	10	0.00	.053
198	0.55	1	10	3.51	.028
198	0.55	2	10	0.00	.013
198	0.55	3	10	0.00	.021
198	0.55	4	10	3.51	.051
198	1.10	1	10	0.00	.056
198	1.10	2	10	0.00	.031
198	1.10	3	10	0.00	.035
198	1.10	4	10	0.00	.090
198	2.20	1	10	7.92	.020
198	2.20	2	10	0.00	.012
198	2.20	3	10	0.00	.017
198	2.20	4	10	0.00	.056
203	0.00	1	10	12.47	.104
APPENDIX A

203	0.00	2	10	11.76	.128
203	0.00	3	10	12.47	.039
203	0.00	4	10	0 95	105
203	0.35	1	11	30 87	039
203	0 35	2	10	9 75	060
203	0.35	2	10	0 00	015
203	0.35	4	10	7 35	053
203	0.55	1	10	24 51	028
203	0.55	2	10	0 00	013
203	0.55	ร้	10	0.00	021
203	0.55	Ă	10	0.00	051
203	1 10	1	10	32 00	056
203	1 10	2	10	52.00	.030
203	1 10	2	10	0.00	035
203	1 10	J	10	0.00	.033
203	2 20	1	10	7 92	.030
203	2.20	2	10	7.92	.020
203	2.20	2	10	0.00	.012
203	2.20	3	10	0.00	.01/
203	2.20	1	10	3.32	.030
207	0.00	2	10	34.32	.205
207	0.00	2	10	20.67	.0/1
207	0.00		10	0.00	.047
207	0.00	4	10	3.12	.001
207	0.35	7	10	1.92	.150
207	0.35	2	10	21.60	.10/
207	0.35	3	10	2.07	.050
207	0.35	4	10	3.92	.0/0
207	0.55	Ţ	10	17.15	.1/3
207	0.55	2	10	4.80	.054
207	0.55	3	10	0.00	.125
207	0.55	4	10	0.72	.214
207	1.10	1	10	12.47	.201
207	1.10	2	10	5.27	.049
207	1.10	3	10	0.00	.083
207	1.10	4	10	2.75	.108
207	2.20	1	10	7.35	.083
207	2.20	2	10	0.00	.060
207	2.20	3	10	0.00	.081
207	2.20	4	10	5.76	.254
210	0.00	1	10	43.07	.103
210	0.00	2	10	40.47	.036
210	0.00	3	10	75.20	.024
210	0.00	4	10	30.87	.041
210	0.35	1	10	28.67	.075
210	0.35	2	10	28.67	.054
210	0.35	3	10	6.27	.029
210	0.35	4	10	16.32	.038
210	0.55	1	9	36.72	.087
210	0.55	2	10	21.60	.027
210	0.55	3	10	26.55	.062

APPENDIX A

210	0.55	4	10	1.47	.107
210	1.10	1	10	18.00	.100
210	1.10	2	10	44.40	.025
210	1.10	3	10	6.80	.041
210	1.10	4	10	5.76	.054
210	2.20	1	10	24.51	.041
210	2.20	2	10	6.27	.030
210	2 20	3	10	0 72	040
210	2 20	Ă	10	0.15	127
214	2.20	1	10	75 20	157
214	0.00	Ť	10	15.20	.15/
214	0.00	2	10	30.87	.184
214	0.00	3	10	36.72	.093
214	0.00	4	10	37.95	.189
214	0.35	1	10	75.20	.118
214	0.35	2	10	28.67	.073
214	0.35	3	10	32.00	.129
214	0.35	4	10	14.72	.119
214	0.55	1	10	27.60	.042
214	0.55	2	10	23.52	.123
214	0.55	3	10	22.55	.121
214	0.55	Ā	10	14 72	142
214	1 10	1	10	37 95	113
214	1 10	2	10	27.55	061
214	1 10	2	10	0 75	.001
217	1 10	3	10	7 35	.040
214	7.10	4	10	1.35	.001
219	2.20	Ť	10	23.52	.101
214	2.20	2	10	9.12	. U 2 4
	2.20	3	10	4.80	.025
214	2.20	4	10	2.40	.023
218	0.00	1	10	124.2	.157
218	0.00	2	10	16.32	.184
218	0.00	3	10	99.4	.093
218	0.00	4	10	27.60	.189
218	0.35	1	10	168.5	.118
218	0.35	2	10	0.95	.073
218	0.35	3	10	11.76	.129
218	0.35	4	10	4.35	.119
218	0.55	1	10	109.8	.042
218	0.55	2	10	15.12	.123
218	0.55	3	10	13.22	.121
218	0.55	4	10	22.53	.142
218	1.10	1	10	33.65	.113
218	1.10	2	- q	26.25	061
218	1.10	จึ	10	18 72	048
219	1 10	Ă	10		061
219	2 20	1	10	7 22	101
210	2 20	2	10	A 13	024
210 210	2 20	4 2	10	3.13	
210	2.20	3 •	10	20.02	.023
270	2.20	4	TO		.023
<b>221</b>	0.00	1	TU	T0/./	. 350

221	0.00	2	10	29.76	.128
221	0.00	3	10	47.12	.193
221	0.00	4	10	41.76	.156
221	0.35	1	10	114	.147
221	0.35	2	10	30.87	.135
221	0.35	3	10	55.76	.190
221	0.35	4	10	27.60	.211
221	0.55	i	10	28.67	.176
221	0.55	2	10	7.35	.174
221	0.55	3	10	10.40	.139
221	0.55	4	10	27.60	.211
221	1.10	1	10	48.51	.153
221	1.10	2	10	18.87	.063
221	1.10	3	10	10.40	.035
221	1.10	4	10	17.15	.050
221	2.20	1	10	4.80	.045
221	2.20	2	10	22.55	.052
221	2.20	3	10	4.80	.029
221	2.20	4	10	19.76	.035
224	0.00	i	10	116.2	.350
224	0.00	2	10	33.15	.128
224	0.00	3	10	89.76	.193
224	0.00	4	10	18.00	.156
224	0.35	1	10	71.76	.147
224	0.35	2	10	16.32	.135
224	0.35	3	10	32.00	.190
224	0.35	4	10	19.76	.211
224	0.55	1	10	37.95	.176
224	0.55	2	10	5.27	.174
224	0.55	3	10	24.51	.139
224	0.55	Ă	10	18.00	211
224	1.10	1	10	32 00	153
224	1 10	2	10	18 87	063
224	1 10	2	10	3 92	035
223	1 10	A	10	11 76	050
224	2 20	1	10	27 60	045
224	2.20	5	10	14 72	052
224	2 20	วิ	10	7 35	029
224	2 20	Ă	10	7 35	025
223	0 00	1	10	76 95	219
228	0 00	2	10	45 75	194
228	0.00	2	10	52 80	345
228	0.00	Ă	10	30 87	241
228	0.35	1	10	37.95	336
228	0.35	2	10	18.87	. 205
228	0.35	3	10	7.35	.177
228	0.35	Ă	10	17,15	367
228	0.55	1	10	15.51	363
228	0.55	2	10	8 51	105
228	0.55	2	10	14.72	198
V	~ • • • •	<b>.</b>	- V		

228	0.55	4	10	18.87	.373
228	1.10	1	10	22.55	.213
228	1.10	2	10	11.07	.087
228	1.10	3	10	2.07	.119
228	1.10	4	10	7.92	.176
228	2.20	1	10	6.27	.156
228	2.20	2	10	4.35	.067
228	2.20	3	10	0.95	.089
228	2.20	4	10	4.35	.070
232	0.00	1	10	66.75	.219
232	0.00	2	10	30.87	.194
232	0.00	3	10	37.95	.345
232	0.00	Ă	10	37.95	.241
232	0.35	1	10	47 12	336
232	0.35	2	10	15 51	205
232	0.35	ร	10	19 76	177
232	0.35	Ă	10	14 72	367
232	0.55	1	10	29 67	. 307
232	0.55	2	10	20.07	. 303
232	0.55	2	10	12 47	100
232	0.55	3	10	11 07	.170
232	0.55	1	10	11.07	.3/3
232	1 10	2	10	1 4 7 7 2	. 213
232	1.10	2	10	14./2	.08/
232	1.10	3	10	0.00	.119
232	1.10	4	10	3.51	.1/0
232	2.20	Ť	10	3.12	.150
232	2.20	2	10	8.51	.067
232	2.20	3	10	2.07	.089
232	2.20	4	10	3.12	.070
239	0.00	1	10	28.67	.316
239	0.00	2	10	30.87	.323
239	0.00	3	10	15.51	.201
239	0.00	4	10	20.67	.297
239	0.35	1	10	13.20	.379
239	0.35	2	10	15.51	.289
239	0.35	3	10	5.27	.335
239	0.35	4	10	15.51	.239
239	0.55	1	10	25.52	.276
239	0.55	2	10	19.76	.267
239	0.55	3	10	15.51	.156
239	0.55	4	10	15.51	.087
239	1.10	1	10	10.40	.158
239	1.10	2	10	9.75	.099
239	1.10	3	10	0.00	.057
239	1.10	4	10	7.92	.134
239	2.20	1	10	1.47	.098
239	2.20	2	10	5.27	.099
239	2.20	3	10	1.47	.053
239	2.20	4	10	2.75	.053

## APPENDIX A

Table 2. 1986 intercrop field study data. PLH nymph counts represent an average per three trifoliates per plant, based on 30 plants per treatment in each block. Average bean leaf area was obtained from six plants per treatment in each block. Variables are: Julian date, Treatment, Block, Plants sampled per replicate for nymphs, Average nymph count, and average bean leaf area  $(m^2)$ .

188	0.00	1	30	0.46	.017
188	0.00	2	30	1.92	.019
188	0.00	3	30	0.22	.024
188	0.00	4	30	1.15	.023
188	0.35	1	30	0.25	.019
188	0.35	2	30	0.88	.016
188	0.35	3	30	0.19	.016
188	0.35	4	30	0.48	.015
188	0.55	1	30	0.25	.014
188	0.55	2	30	0.27	.015
188	0.55	3	30	0.22	.020
188	0.55	4	30	0.68	.016
188	1.10	1	30	0.08	.012
188	1.10	2	30	0.48	.014
188	1.10	3	30	0.08	.018
188	1.10	4	30	0.75	.020
188	2.20	1	30	0.02	.015
188	2.20	2	30	0.58	.020
188	2.20	3	30	0.19	.020
188	2.20	4	30	0.79	.017
192	0.00	1	27	0.95	.017
192	0.00	2	30	1.34	.024
192	0.00	3	30	•	.019
192	0.00	4	0	•	.023
192	0.35	1	30	0.75	.019
192	0.35	2	30	0.19	.016
192	0.35	3	30	•	.016
192	0.35	4	0	•	.015
192	0.55	1	30	0.88	.014
192	0.55	2	30	0.51	.015
192	0.55	3	0	•	.020
192	0.55	4	0	•	.016
192	1.10	1	30	0.42	.012
192	1.10	2	30	0.42	.014
192	1.10	3	0	•	.018
192	1.10	4	0	•	.020
192	2.20	1	30	0.15	.015
192	2.20	2	25	0.58	.020
192	2.20	3	0	•	.020
192	2.20	4	0	•	.017
195	0.00	1	30	0.84	.051

195	0.00	2	30	0.42	.071
195	0.00	3	30	0.11	.084
195	0.00	4	30	0.25	.062
195	0.35	1	30	0.64	.061
195	0.35	2	30	0.05	.052
195	0.35	3	30	0.08	.038
195	0.35	4	30	0.19	.072
195	0.55	1	30	0.11	.023
195	0 55	2	30	0 98	043
195	0.55	2	30	0.50	047
105	0.55		30	0.11	049
105	1 10	1	30	0.22	.040
105	1.10	7	30	0.02	.020
132	1.10	4	30	0.34	.042
132	1.10	3	30	0.11	.044
132	1.10	4	30	0.15	.047
132	2.20	Ţ	30	0.15	.031
195	2.20	2	30	0.15	.050
195	2.20	3	30	0.15	.058
195	2.20	4	30	0.11	.097
202	0.00	1	30	2.14	.128
202	0.00	2	30	0.95	.159
202	0.00	3	30	2.58	.182
202	0.00	4	30	1.31	.146
202	0.35	1	30	2.20	.124
202	0.35	2	30	0.42	.107
202	0.35	3	30	0.72	.083
202	0.35	4	30	0.79	.097
202	0.55	1	30	0.64	.065
202	0.55	2	30	0.34	.094
202	0.55	3	30	0.98	.116
202	0.55	4	30	0.88	.124
202	1.10	1	30	0.64	.086
202	1.10	2	30	0.05	.098
202	1.10	3	30	0.64	.066
202	1.10	4	30	0.56	.119
202	2.20	1	30	0.56	.057
202	2.20	2	30	0.34	.088
202	2.20	3	30	0.81	.082
202	2.20	4	30	0.25	.098
205	0.00	1	30	2.17	.128
205	0.00	2	30	2.17	.159
205	0.00	3	30	1.80	.182
205	0.00	Ă	30	3 16	146
205	0.00	1	30	1 80	124
205	0.33	2	30	1 71	107
205	0.33	2	30	1.11	. 101
205	0.33	Å	30	1 10	
20J	0.JJ 0 EE	1	20	1 00	• V7 / A2E
203 205	V.JJ A EE	2	30	1 20	.003
203	0.33	4	30	1.20	.034
203	V. 35	3	30	0.81	.116

205	0.55	4	30	1.31	.124
205	1.10	1	30	0.68	.086
205	1.10	2	30	0.64	.098
205	1.10	3	30	0.64	.066
205	1.10	4	30	1.00	.119
205	2.20	1	30	0.81	.057
205	2.20	2	30	0.98	.088
205	2.20	3	30	0.56	.082
205	2.20	4	30	1.05	.098
209	0.00	1	30	1.80	.238
209	0.00	2	30	1.20	.182
209	0.00	3	30	2.20	.238
209	0.00	4	30	1.10	.258
209	0.35	1	30	1.15	.232
209	0.35	2	30	0.75	.214
209	0.35	3	30	1.05	.176
209	0.35	4	30	0.81	.175
209	0.55	1	30	0.79	.139
209	0.55	2	30	0.62	.216
209	0.55	3	30	0.75	.192
209	0.55	4	30	1.05	.164
209	1.10	1	30	0.25	.101
209	1.10	2	30	0.11	.114
209	1.10	3	30	0.48	.191
209	1.10	4	30	0.84	.136
209	2.20	1	30	0.81	.080
209	2.20	2	30	0.19	.145
209	2.20	3	30	0.95	.156
209	2.20	4	30	0.48	.188
216	0.00	1	30	2.83	.397
216	0.00	2	30	1.45	.370
216	0.00	3	30	3.16	.505
216	0.00	4	30	1.26	.390
216	0.35	1	30	1.47	.385
216	0.35	2	30	1.42	.351
216	0.35	3	30	1.10	.311
216	0.35	4	30	0.88	.266
216	0.55	1	30	0.91	.113
216	0.55	2	30	1.08	.209
216	0.55	3	30	0.79	.272
216	0.55	4	30	1.08	.276
216	1.10	1	30	0.81	.111
216	1.10	2	30	0.51	.203
216	1.10	3	30	1.05	.215
216	1.10	4	30	1.42	.231
216	2.20	1	30	0.84	.137
216	2.20	2	30	0.46	.213
216	2.20	3	30	0.88	.235
216	2.20	4	30	0.34	.221
<u></u>					

## APPENDIX B

POTATO LEAFHOPPER BEHAVIOR STUDY



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bout on bean leaves significant treatments. ANOVA; [P=0.4; diculture were not one-vay arrestment ments and and treati transformation controls an 0f between duration df=7,136; P<0.05]) bean rank Differences the Fig. 1. Mean (P<0.05; **buome** 

APPENDIX B

Table 1. Mean number of minutes a leafhopper spent on each plant surface during the 15 min small cage, observation study. A treatment contained two leaves.

TREATMENT	MEAN	+SD	
Bean (control 1)	7.7	6.7	
Bean (control 2)	8.2	6.3	
Bean/Tomato	<b>.</b> .		
Bean Tomato	5.4 1.8	5.9 4.3	
Momete		5 7	
Tomato	8.2	5.7	
Bean/Pepper			
Bean	4.7	6.0	
Pepper	2.4	3.7	
Pepper	8.3	4.9	
Bean/Corn			
Bean	6.2	5.7	
Corn	1.6	3.9	
Corn	3.5	5.5	
Bean/Squash			
Bean	7.3	5.4	
Sguash	. 2	.9	
Squash	3.4	4.5	
Bean/Radish			
Bean	5.2	6.3	
Radish	1.6	4.1	
Radish	2.2	4.7	
Bean/Cabbage			
Bean	4.9	5.3	
Cabbage	. 2	.7	
Cabbage	.4	1.9	

A total of 18 individual leafhoppers were observed for each treatment.

## APPENDIX B

Table 2. Mean number of minutes during an arrestment bout on bean leaves, for those treatments containing bean (i.e. bean controls, and bean/companion-leaf treatments). A treatment contained two leaves.

TREATMENT	MEAN	<u>+SD</u>
Bean (control 1)	8.3	7.1
Bean (control 2)	9.2	6.2
Bean/Tomato	8.8	5.7
Bean/Pepper	8.9	5.0
Bean/Corn	9.3	5.6
Bean/Squash	9.0	5.8
Bean/Radish	7.9	6.6
Bean/Cabbage	6.9	5.9

An arrestment bout is the duration of time from arrival on a surface to relocation upon another surface. For each treatment a total of 18 individual leafhoppers were observed for 15 min within the small cages.