Phenology and population dynamics of the alfalfa weevil, *Hypera postica* (Coleoptera: Curculionidae), in central and southern Iowa

by

Todd A. DeGooyer

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INTRODUCTION

Alfalfa, *Medicago sativa* L. is the most valuable cultivated forage crop in the world (Grau et al. 1985) and the most important perennial forage crop in North America (Michaud et al. 1988, Fick and Mueller 1989). Over 11 million ha of land in the U.S. (Melton et al. 1988) and 4-5 million ha of land in Canada (Goplen et al. 1980) are committed to alfalfa production. Alfalfa is predominantly grown in the northeastern and northcentral regions of the U.S. (Bolten et al. 1972) and the southcentral prairie provinces of Canada (Goplen et al. 1980). In Iowa, 769,000 ha of alfalfa were harvested in 1989 (Show and Holden 1990).

The number of alfalfa cuttings varies throughout its production range in North America. In the prairie provinces of Canada, only 1 or 2 cuttings are harvested (Goplen et al. 1980). Alfalfa usually is harvested 3 to 4 times a year in the midwestern U.S. (Iowa Crop and Weather Weekly crop report 1992). Irrigated stands in Arizona and California have 6 to 10 alfalfa harvests annually (Scheaffer et al. 1988).

Alfalfa usually is cut during the late-bud to early-flower stages of growth. Harvest at these stages allows for maximum quality and quantity of yield (Harcourt and Guppy 1975). Alfalfa is fed as hay, silage, greenchop, pellets or cubes to a variety of livestock, but it also is grown for pasture and seed production (Fick and Mueller 1989).

The perennial nature of alfalfa makes it a very important crop in terms of energy and soil conservation. It functions in crop rotation, fixing nitrogen for subsequent crops, improving soil structure and fertility, and reducing pest problems for other crops. But, alfalfa's perennial nature also permits insect pests to cause greater damage than they might cause if associated with annual crops (Grau et al. 1985).

The alfalfa weevil, *Hypera postica* (Gyllenhal), is one pest that benefits from alfalfa

production. The larval stage of this insect injures alfalfa plants by using its chewing mouthparts to feed on leaflets of the first cutting. In some instances, when large weevil populations are in a field or when weevil phenology is delayed, injury to regrowth of the second-cutting alfalfa also is possible (Foster 1986). Extensive alfalfa weevil injury can cause direct reduction of yield and loss of photosynthetic capability of the alfalfa plant (App and Manglitz 1972).

The alfalfa weevil, an introduced pest from Europe or Eurasia, occurs as far north as the prairie provinces of Canada and as far south as Arizona and southern California. The seasonal life history of the alfalfa weevil varies greatly throughout its North American geographical range, but it usually has only one generation per year. However, a recent study in Wisconsin has found evidence of a complete second generation (Mohamed et al. 1992).

Climatic conditions for oviposition in the fall and winter, along with egg survival during the winter months (December through March) determine the timing of larval populations. Northern populations of alfalfa weevil, found in eastern Ontario (Harcourt et al. 1977) , Michigan (Casagrande and Stehr 1973), and Wisconsin (Litsinger and Apple 1973b), do not oviposit in the fall and winter because of the cool temperatures. In areas intermediate between these northern and southern locations, the number of weevil eggs laid in the fall and winter vary, depending on climatic conditions. Examples of states in this intermediate area include Illinois (Hsieh and Armbrust 1974) and Ohio (Niemczyk and Flessel 1970). Southern populations of alfalfa weevil, including Alabama (Bass 1967), Oklahoma (Berberet et al. 1980, Stark 1991), and southern California (Summers et al. 1981), exhibit even more variability in terms of timing of oviposition in the winter months.

Although phenology studies have been conducted in neighboring states of Illinois and Wisconsin (Hsieh and Armbrust 1974, Litsinger and Apple 1973b), information

concerning alfalfa weevil population dynamics and phenology is lacking for Iowa. Because Iowa lies in a transitional region between truly northern and more southerly latitudes, it was determined that a study was needed to better understand the biology and ecology of the alfalfa weevil in this region.

Therefore, a sampling study was initiated in Iowa to determine if populations in the state resemble the phenology of those in Wisconsin, which have populations with northern ovipositional behaviors or those populations in southern Illinois, which have more southern ovipositional behaviors, e.g., fall and winter oviposition.

Consequently, the specific objectives of this study were as follows:

1. To use alfalfa weevil phenology for predicting the damaging stages of the pest at different latitudes in Iowa.
2. To determine alfalfa plant development stages in relation to weevil phenology.
3. To validate existing degree-day systems for the alfalfa weevil and modify them, if necessary, for use in Iowa.
4. To assess weevil densities at 4 latitudes in central and southcentral Iowa.
5. To incorporate the information obtained from these population dynamics studies into life tables.

Thesis Format

This thesis contains 2 papers and is organized in the following manner: the general introduction, the literature review, the papers of the thesis, the general summary, the additional references cited, the acknowledgements, and the appendix. Paper I discusses the phenology of the alfalfa weevil at 4 different latitudes in Iowa. In addition, the present alfalfa weevil management program is refined for utility throughout central and southern regions of the state. In paper II, the population dynamics of the alfalfa weevil in central and southern Iowa is examined. The appendix table shows the relationship of degree-days and alfalfa weevil total larval density for

all the sampling dates during the 3-year study. These papers were prepared for submission to scientific journals following the guidelines of the Entomological Society of America.

LITERATURE REVIEW

Background and Geographical Distribution

The alfalfa weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae), is the most important single pest of alfalfa in the United States (App and Manglitz 1972) and North America (Dysart and Day 1976). The western strain of the alfalfa weevil, an introduced pest from Europe or Eurasia (Chamberlin 1924), was first found near Salt Lake City, Utah, in 1904 (Titus 1916). A second alfalfa weevil introduction later identified as the Egyptian alfalfa weevil, *Hypera brunneipennis* (Boheman) occurred in California in 1939 (Wehrle 1939). The Egyptian alfalfa weevil presently is distributed in parts of California and Arizona. The alfalfa weevil was detected for a third time near Baltimore, Maryland in 1951 (Poos and Bissell 1953). This strain, also of Eurasian origin, is known as the eastern strain of the weevil. Since its detection, the alfalfa weevil has spread and is now present in all of the contiguous states (Day 1981) of the U.S. and in 4 Canadian provinces (Dysart and Day 1976). The alfalfa weevil was first reported in southeastern Iowa in 1967 (Stockdale 1967) and has since spread throughout the state (Foster 1986).

Description of the Alfalfa Weevil

Eggs of the alfalfa weevil are oval, lemon-yellow and ca. 0.51 mm in diameter. They turn a yellow-green just before hatching. Newly eclosed larvae are ca. 0.8 mm long with faded yellow, legless bodies and a distinct black head (capsule). As the larvae mature, the body turns lime-green, and a white line forms on the dorsal surface. The head capsules of the larvae remain black throughout the larval stage. Full-grown larvae are ca. 9.5 mm long. Adult weevils are dark brown with a black stripe extending down part of the dorsal surface of the insect. Adults are ca. 6.4 mm long. As the adult weevils age, their bodies darken, and the black dorsal stripes

become less pronounced (Titus 1909, Snow 1928).

The two strains of the alfalfa weevil (eastern and western), along with a close relative the Egyptian alfalfa weevil, are indistinguishable in appearance and have similar life histories (Summers et al. 1981). However, the eastern and western strains can be separated using a Giemsa staining technique (Hsiao and Hsiao 1985). Another difference between the two strains is the eastern and western strains of the alfalfa weevil require a minimum effective development temperature of 8.9^{o}C and 10.6^{o}C, respectively (Hsieh et al. 1974). Genetic studies conducted by Klostermeyer and Manglitz (1978) showed chromosomal differences between the eastern and western strains of the alfalfa weevil. However, no differences were observed between eastern and Egyptian strains.

Life History

The alfalfa weevil typically has one complete generation per year. A partial second generation also can occur in the fall (Essig and Michelbacher 1933, Litsinger and Apple 1973a, Dowell and Horn 1977). Alfalfa weevils are primarily a pest of the first-cutting alfalfa and regrowth of the second cutting (Harcourt and Guppy 1975, Foster 1986).

In Iowa, adult weevils emerge in the spring (late March to early April) from their winter hibernation sites and migrate to alfalfa fields to feed, mate, and lay eggs (Foster 1986). Initially, eggs are deposited in dead alfalfa stems and other plant debris. After alfalfa has begun to grow, eggs are deposited within the green alfalfa stems, usually within the lower 40 cm of the plant (Whitford and Quisenberry 1990). Alfalfa weevil eggs are found in the stem in clusters of ca. 10-14 eggs (Harcourt et al. 1974a, Whitford and Quisenberry 1990), but as many as 50 may be deposited at one time (Ruppel and Stehr 1973). Although most eggs are laid inside alfalfa stems during this time, oviposition into other plant species including some grasses, weeds (Essig

and Michelbacher 1933), and henibit (*Lanium amplexicaule* L.) have been observed (Pass 1967).

Larvae eclose from eggs inside the stems. Then, they exit the stem through the oviposition hole and climb up the stem until they reach the growing point of the plant where they begin feeding. Second instar weevils continue to feed and grow in this general area of the alfalfa plant. After the larvae molt to become third instars, they begin to feed on the expanding leaves of the developing plant. The fourth instars pupate in a net-like cocoon that they have spun. These cocoons usually are attached to the alfalfa plant or can be found in the ground debris. The western strain of the alfalfa weevil has been reported to crawl or drop to the ground before spinning its cocoon (Titus 1910; Essig and Michelbacher 1933; Hamlin et al. 1949). However, several authors have noted a preference in the eastern strain of the alfalfa weevil to spin a cocoon in the foliage (Poos and Bissell 1953; Manglitz and App 1957; Miller and Guppy 1972).

Adults emerge from the cocoons and feed on the alfalfa plants for a few weeks. Climatic conditions determine the adult weevil's next behavior. If the late summer is hot and dry many of the adult weevils move out of the alfalfa field to summer dormancy or aestivation sites. These aestivation sites are usually along alfalfa borders, in or near forested areas, or in ditches (Blickenstaff 1967). The adult alfalfa weevils remain at these aestivation locations until temperatures begin to drop in the late summer or early fall. Weevils have a potential aestivation period from May to October (Litsinger and Apple 1973). After aestivation has been broken, the weevils return to the alfalfa fields where they may feed, lay eggs, and prepare for winter. The other summer behavior, which may occur under cool weather conditions, is the alfalfa weevils may remain in the alfalfa field throughout the summer feeding and sometimes producing a partial second generation . During this type of behavior, the

alfalfa weevil's peak activity occurs after dark (from 2100 hr to 100 hr)(Warner and Ritcher 1974). Adult weevils overwinter in the soil around the alfalfa crowns (Helgesen and Cooley 1976, Foster 1986).

Alfalfa/Alfalfa Weevil Relationship

There are two kinds of injury caused by the alfalfa weevil. The first is defoliation of the stems, which decreases photosynthetic capacity and yield of the alfalfa plant. The second injury is feeding on the regrowth of the second-cutting alfalfa. During this time, larval weevils may feed on the growing terminals of the regrowth, while adults feed on the green surface of the stem (Foster 1986). Extended feeding may damage or even kill plants (App and Manglitz 1972).

The first and second stage larvae feed in and around the growing point of the plant. As the larvae develop (become third and fourth stage larvae), they cause the greatest loss by skeletonizing and defoliating plants. Feeding may occur under windrowed hay in severe infestations. Adult feeding may result in some loss of yield but rarely cause significant yield loss (Summers et al. 1981).

The timing of plant growth and alfalfa weevil egg hatch is crucial, because the growth stage of the plant at the time of larval infestation (egg hatch) is related to the plant's ability to withstand larval feeding injury (Shade and Hintz 1983). The earlier alfalfa is attacked, the greater potential damage from larval feeding (Hintz et al. 1976).

Although the success of alfalfa stand establishment is affected by many environmental elements, the date of crop planting is often the dominating factor (Strand and Fribourg 1973). Using this idea as a precept, Dowdy et al. (1986) demonstrated that early fall-planted alfalfa (August) had a better stand and greater overwintering alfalfa weevils populations than late-fall-planted alfalfa (September or October). The poorer stand establishment of the late-fall-planted alfalfa was not offset by the smaller overwintering weevil population.

Sampling Techniques

To understand the seasonal life cycle of the alfalfa weevil as well as monitor population densities for management programs, sampling techniques have been designed for estimating each developmental stage of the population. Because of the holometabolous nature of alfalfa weevil, different population assessment methods are required for the egg, larval, pupal (cocoon), and adult life stages.

Egg sampling

Various methods have been used to estimate egg populations of the weevil. The first method implemented was direct counts of egg numbers obtained by dissecting alfalfa stems. Pass and VanMeter (1966) attempted to improve egg estimation by devising a blender extraction technique. This technique involved cutting up the alfalfa stems, grinding these stems in a blender, and extracting the eggs from the stem material through a series of sieves and a Buchner funnel.

In formulating his egg sampling program Harcourt et al. (1974a) used criteria of Morris (1955) (viz., the unit is small, easy to collect, stable, and estimates the absolute population well) in developing a 3-stem sampling unit. The 3-stem sampling unit was taken from within a random 1 ft^2 quadrat. Harcourt et al. (1974a) proposed two methods of estimating egg populations by using this sampling unit. The first method involves direct counting of the eggs in the stem. The second technique involved counting the oviposition punctures on the stems and taking this total times the average number of alfalfa weevil eggs laid in a cluster. In using the latter technique, 10 eggs/puncture were found on the average. This average number of eggs per puncture agrees with previous work by many authors (Hamlin et al. (1949), Manglitz and App (1957), Niemczyk and Flessel (1970), and Whitford and Quisenberry (1990).

Larval sampling

Since the larval stage of the alfalfa weevil is the most damaging to alfalfa, the need to obtain a reliable estimate of weevil during this stage was necessary to determine the status of the population. Early population assessment studies on the alfalfa weevil suggested the use of sweep nets for sampling larvae (Blickenstaff 1966). The inadequacy of this population estimation technique was pointed out by a number of authors (Blickenstaff and Huggans 1969, Cothran and Summers 1972).

Instead of employing the sweep-net for quantitative studies of the alfalfa weevil, Armburst et al. (1969) suggested the use of a 1 ft ^{2} sampling quadrat or stem samples to assess weevil populations and that the sweep-net should be limited to survey and control evaluation studies. In developing a stem-sampling program, various sample sizes have been recommended which included 5 10-stem sampling units (Blickenstaff 1966), 1 20-stem sample (Armbrust et al. (1969), 1 5 to 25-stem sample (using a sequential sampling program) (Blickenstaff and Huggans 1969), 16 12-stem sampling units (Miller et al. 1972), 10 50-stem sampling units (Christensen et al. 1977), and 1 30-stem sample (Armbrust 1981).

Using a slight modification of population estimation, Guppy et al. (1975) determined that a 6-stem sampling unit of alfalfa, taken from within 1 ft^2 sampling area, was an appropriate sampling unit for determining larval population density. This work also suggests that for a moderate larval population (ie. 12 larvae per 6-stem sampling unit), 16 sampling units per field would provide an adequate estimation of the larval population. In addition, this paper by Guppy et al. (1975) points out the importance of changing sample size depending on the density of the population.

Another larval sampling techniques uses plant damage characteristics to assess larval alfalfa weevil populations. This technique utilizes visual rating of feeding damage to estimate alfalfa weevil larval populations (Cothran and Summers 1974,

Berberet and McNew 1986).

Cocoon sampling

Cocooning of the alfalfa weevil occurs on the foliage and on the ground. A sampling program for the cocoon stage must therefore be flexible enough to sample both localities. Harcourt and Guppy (1975) developed a sampling method of estimating cocoon populations. The cocoons located in the foliage were estimated using 6-stem sampling units of alfalfa from within a 1 ft ^{2} quadrat, and cocoons located on the ground were estimated by collecting ground litter from within one-quarter ft ^{2} quadrats. After the specimens were collected, they were reared at room temperature to determining various mortality factors.

Adult sampling

Many management programs are centered on alfalfa weevil larvae, the most damaging stage of the pest. But in some instances an estimate of adult weevils is needed. One situation where an estimate of adult numbers is necessary is in the development of life tables. Another situation where adult sampling is needed is in an experimental program for adult control developed in California (Summers et al. 1981).

Early adult sampling has involved a steel die which was driven into the ground 5 cm. Next, all the plants within the sampling unit were cut, the debris on the ground was collected, and 5 cm of soil was removed from within the sampling area (Hamlin et al. 1949). This sampling technique was improved later by using a pyrethrin drench to detect summer adults instead of soil sifting (Manglitz et al. 1978).

Other sampling techniques used a sweep net and/or a D-vac ^{R} suction machine (Dietrick et al. 1959) to obtain alfalfa weevil estimates (Latheef and Pass 1974, Guppy and Harcourt et al. 1977). Sweep-net sampling for weevil adults has been employed extensively in North America (Blickenstaff 1966), but changes in weather conditions, crop development, diel activity (Warner and Ritcher 1974) of the alfalfa weevil have

limited its usefulness (Guppy and Harcourt 1977). More recently, sweep-net sampling has been replaced by vacuum sampling (D-Vac ^{R} or other suction machines), along with the use of the 1 ft ^{2} sampling unit (quadrat) (Guppy and Harcourt 1977).

Mortality Factors

Many mortality factors play an important role in determining the status of alfalfa weevil populations. Most of the agents that reduce population densities act during the larval and prepupal periods (Harcourt et al. 1977). These factors include establishment loss, rainfall, and a number of natural enemies including fungal disease, predators, and a variety of parasitoids.

Infertility

Although few factors affect weevil survival during the egg stage, a small percentage are infertile (Harcourt and Guppy 1976). Latheef et al. (1979) estimated a loss of 12.1% in the alfalfa weevil egg population in Kentucky from infertility.

Establishment loss

The establishment phase of the weevil, which includes the first and second instars, is the phase after larval eclosion from the egg when these individuals are searching for food. In the establishment phase, some small larvae are exposed to situations or conditions where this activity may lead to predation or desiccation. Once the larva reaches the terminal bud, it is protected from these factors. The larva again will be subject to these similar factors during the feeding stage when the larva leaves the terminal bud to feed on the opened leaves (Harcourt et al. 1977). Latheef et al.(1979) found that larval death in Kentucky during establishment and feeding was the principal mortality factor that determined seasonal population density changes.

Emigration

An analysis of the mortality factors of the alfalfa weevil by Latheef et al. (1979) also showed that adult emigration was one of the principle causes of seasonal population

change in alfalfa fields. Climatic conditions play an important role in determining the degree of adult emigration out of the alfalfa field and into neighboring areas (Litsinger and Apple 1973a)

Rainfall

A seemingly less important, but still notable cause of mortality, is heavy rainfall. Rainfall may dislodge larvae and lead to death through drowning or make them more assessable to other factors including establishment loss and predation (Harcourt et al. 1977).

Natural Enemies

Natural enemies contribute to regulation of individuals within an alfalfa weevil population. Three biological factors, disease, predation, and parasitism, play an important role in population regulation.

Disease of the alfalfa weevil The fungal pathogen, *Zoophthora phytonomi* (Arthur) (=*Entomophthora phytonomi* Arthur) (Zygomycetes: Entomophthorales), an important indigenous control agent of the alfalfa weevil, was first discovered in North America by Harcourt et al. (1974b). This disease is caused by a complex of two fungi belonging to the genus *Zoophthora* (Harcourt et al. 1981). Harcourt et al. (1974b) first observed this fungus in the summer of 1973, when large numbers of larvae and prepupae were killed by infectious disease in southern Ontario, Canada.

Alfalfa weevil that are dying from the fungal disease show two completely different patterns of symptoms and produce characteristic cadavers, which are designated Type I and Type II. The fungus attacks all stadia of the larvae (Harcourt et al. 1990). Before death, the Type I diseased larva climbs and crawls under the terminal leaves, then turns a creamy brown color. Rhizoids of the fungus quickly develop, anchoring the dead larva to the leaflet. This guarantees effective dispersal of the conidia, which are deposited as a halo surrounding the insect cadaver. Type II infected larvae,

however, do not produce rhizoids and after they die instead fall to the ground litter beneath the alfalfa canopy (Harcourt et al. 1990). Spores located within the weevil cadavers are released when the cadavers crumble. These spores are dispersed in the ground litter by wind and water. After overwintering, the spores germinate in the spring (Harcourt et al. 1990). The fungus also attacks the prepupal and pupal stages of the weevil. These stages both turn black and contain resting fungal spores (Harcourt et al. 1977). The survival rate of the pupae is relatively high compared to larvae and prepupae, but some pupae become infected by the fungus (Harcourt et al. 1977).

Later work by Harcourt et al. (1984) showed that larval disease was responsible for about 93% of the variation in within-generation mortality (1972-1976) and was the key factor (Morris 1959, Varley and Gradwell 1960) governing population trend. Harcourt et al. (1984) also noted that mortality from disease was density dependent, but overcompensating, creating further instability in the population of weevils. Dry weather was the main factor in deterring the spread of the disease.

Predators After larvae eclose from the egg and until they reach the protected area in the terminal growing point (establishment phase), they are susceptible to predation by some vertebrate (birds) and some invertebrate (ladybird and ground beetles) animals. Once larvae reach the later stage of growth (feeding phase), they again are exposed to these similar pressures (Harcourt et al. 1977).

Parasitoid of alfalfa weevil eggs A wasp parasitoid, *Patasson luna* (Girault) (Mymaridae) may cause slight mortality of alfalfa weevil eggs. Populations of *P. luna* from Italy were first released in Utah in 1911-1913 and again during the period between 1925-1928. Another release of individuals from France occurred in California in 1933-1934. The wasp was not recovered in any areas of the U.S. until the late 1950s, when it was identified in eastern North America. It now has been reported in

many areas of the eastern region and more recently in some of the western states (Dysart and Day 1976). Adult female wasps lay 1 or 2 eggs into the eggs of the alfalfa weevil. More wasp eggs may be deposited in clusters of weevil eggs in the stem. *P. luna* are multivoltine and pass the winter within the alfalfa weevil egg. Dysart and Day (1976) suggested that egg parasitism from this species ranges from 0 to 10 percent in overwintering alfalfa weevil eggs.

Parasitoids of alfalfa weevil larvae Three species of larval parasitoids have been introduced as biological control agents to help manage alfalfa weevil populations. The chief species of larval parasitoids that have been released to aid in reducing the alfalfa weevil were *Bathyplectes curculionis* (Thompson), *Bathyplectes anurus* (Thompson), and *Tetrastichus incertus* (Ratzeburg). *B. curculionis* was first released in Utah in 1911, and *B. anurus*, first released in 1960. *B. anurus* is a univoltine species throughout North America, but. *B. curculionis* may have a partial second generation. Both species are endoparasitic wasps (Ichneumonidae) whose females deposit a single egg into the developing weevil larva. Unlike some *B. curculionus* eggs , *B. anurus* eggs are not encapsulated by the host (Puttler 1967). The parasitic larva continues development while feeding internally on the host, until the weevil larva pupates and spins a cocoon. After the cocoon is spun, the parasite kills the host, spins its own cocoon inside the host cocoon, and completes development (Dysart and Day 1976, Harcourt 1990).

Tetrastichus insertus was first released as a biological control agent against the alfalfa weevil in 1960 and 1962 in the eastern United States and has spread to parts of Delaware, Maryland, and Pennsylvania by 1964. *T. insertus* is a gregarious, multivoltine endoparasitoid that prefers third and fourth instar weevils (Chamberlin 1924). In contrast to the *Bathyplectes* spp., this species of wasp deposits from 2 to 22 eggs in each weevil larva. After 47 to 60 hours the eggs hatch and larvae

immediately begin to feed on the host (Dowell and Horn 1977). Usually from 4 to 7 individuals complete development in about 2 weeks within the host's dead body (Dysart and Day 1976). Also, unlike *Bathyplectes* spp. , *T. incertus* is more abundant in the summer months and therefore is more dependent on the second generation larvae than other members of this feeding guild. Similar to *B. anurus*, *T. insertus* is not encapsulated by the host weevil.

Parasitoids of alfalfa weevil adults Two species of endoparasitic wasps (Braconidae) are biological control agents of weevil adults. *Microctonus aethiopoides* Loan, a bivoltine parasitoid of European origin, was first released against the alfalfa weevil in 1957 (Day et al. 1971, Dysart and Day 1976). *Microctonus colesi* Drea is an univoltine, parthenogenetic parasitic wasp also of European origin and was first found in 1962 (never intentionally released) (Coles and Puttler 1963). The former species is more abundant than the latter. In the middle Atlantic states, *M. aethiopoides* has killed from 70 to 90 percent of the overwintered (adult) weevils, and the second generation has parasitized an average of 7 to 39 percent of new weevils (Dysart and Day 1976, Van Driesche and Gryisco 1979).

Female *M. aethiopoides* lay a single egg in the overwintered, sexually mature alfalfa weevil adult. The larva ecloses from the egg and begins feeding on the internal tissues of the weevil until the wasp larva nears the larval stage of development. At this point, the parasite larva burrows through the side of the adult weevil, drops to the ground, and pupates. When the newly emerged *M. aethiopoides* adult emerges from the pupa, it lays an egg in a newly emerged, sexually immature adult weevil. This resulting larva diapauses as a first instar and overwinters in the alfalfa weevil adult.

M. colesi adults lay an egg in mature weevil larva. After hatch and larval eclosion, the first instar enters diapause and overwinters in the weevil adult in a similar manner as *M. aethiopoides*. *M. colesi* have parasitized from 1 to 18 percent of the "new"

(newly emerged, sexually immature) weevils in the middle Atlantic region (Dysart and Day 1976).

Disease/parasitoid interactions *Bathyplectes curculionis* and *T. incertus* are both direct competitors with the fungal disease, *Z. phytonomi*. Because of their inability to compete successfully for alfalfa weevil hosts with the disease, they seem to have little influence on alfalfa weevil population trends (Harcourt et al. 1977, 1984). Harcourt et al.(1980) found *M. colesi* less compatible to the fungi than other parasitoids because it is vying for the same host resource. However, research done by Loan (1981) suggests that *M. colesi* avoids the disease by attacking the remaining larvae after the epizootic has begun to decline. *M. aethiopoides* attacks also are compatible to the disease because it attacks the adult stage, which does not seem affected by the disease (Harcourt et al. 1980, Loan 1981).

Mortality compensation High mortality of one or more stages of the weevil may lead to lower mortality during other stages. Latheef et al. (1979) found that increased mortality during the larval stages was partially compensated for by having decreased adult mortality, and vice versa.

Management Strategies

Alfalfa weevil management programs

To develop a useful pest management program, an accurate estimate of seasonal occurrences of alfalfa weevil life stages must be determined. Harcourt (1981) proposed a thermal summation model for accurately predicting the peak egg hatch and other important biological events critical to management. These events included maximum numbers of larval and pupal stages, as well as timing of cocooning and adult emergence. By using this model, degree-days (base $9^{O}C$) can be monitored which would, in turn, decrease the amount of sampling needed to assess the population.

An experimental management program which uses this information is being implemented by University of California researchers. Instead of monitoring the alfalfa weevil larval populations in the spring to determine outbreak populations, they observe the weevil populations in the fall. By using accurate fall field counts and daily temperature readings, this information can be incorporated into a computer model which simulates the alfalfa weevil life cycle, and an assessment can be made on whether a population needs to be treated. This program attempts to minimize the damage caused by the weevil larvae in the spring, and requires less sampling, and fall treatment lessens the exposure of chemicals to predators and honeybees (Summers et al. 1981).

Another useful management tool is the development of a sequential sampling program for characterizing insect populations. Harcourt and Guppy (1976) devised a sequential sampling program for the alfalfa weevil based on the Poisson distribution which used the number of oviposition punctures found in 3-stem sampling units of green alfalfa to estimate populations. The main advantage of this plan was that the number of samples to be collected varies according to mean density of the alfalfa weevil population.

Many integrated pest management programs have adopted using a single 30-stem sample (Armbrust 1981) for assessing alfalfa weevil populations within a field and making management decisions (Wedberg et al. 1980, Foster 1986, Barney and Legg 1987, and Higgins et al. 1988). Other information usually required in these programs include the calculation of Celsius or Fahrenheit degree-day accumulations and the measuring of the alfalfa stem height from the 30-stem sample for calculation of the average stem height. The weevil density, alfalfa plant height, and degree-day accumulation information is then used in a recommendation chart to make a management decision.

Legg et al. (1985) have shown no significant difference when using the 30-stem sample between utilizing a random and systematic sampling regime for estimating mean densities or variances. Further studies using this sampling procedure have demonstrated there were no significant differences in mean population assessments if the number of stems per sample was reduced or subsampling the field was employed (Legg et al. 1988). Another recent study has shown that the way alfalfa stems were "picked" affects the efficiency of estimating the actual numbers of alfalfa weevil larvae (Higgins et al. 1991).

Another alfalfa weevil management program uses a combination of degree-day accumulation and plant damage. In this program, management decisions are based on whether 40% of the plant tips (growth terminals) have obvious signs of damage. If there is this percentage of damage or greater, spraying or early cutting of the alfalfa is recommended, depending on the development stage of the alfalfa (Undersander et al. 1991).

Management tactics

After the size of the population has been estimated, and it has been determined that some management tactic is necessary, then there are 3 main control strategies used. The first type of management is chemical insecticides. Although chemical control has been vastly used (Wedberg et al. 1980), 2 other methods, cultural, and biological management, also have been implemented successfully. These management strategies are discussed in more detailed below.

Chemical control The use of chemical insecticides is necessary in some instances to avoid complete destruction of the crop. Because of the cost of insecticides, they are normally applied as a curative means of control rather than a preventive one. It is typically applied before the first cutting of alfalfa, when large numbers of larvae are present (Ruppel and Stehr 1973). The advantage of using

chemical control is that often only one application is necessary (Foster 1986). The main disadvantage is that along with killing the weevil, parasitoids and predators, which help to manage alfalfa weevil populations, also are killed (Wedberg et al. 1980).

Cultural control In some circumstances, chemical management of weevils is not economically feasible. In these situations, other management tactics can be used to effectively to reduce alfalfa weevil numbers. One example of this type of management tactic is cultural control, e.g., early harvest of the alfalfa crop. Early harvest can be used in a situation where weevil injury occurs during the late bud stage of alfalfa development. At this time, the alfalfa is at maximum quality, and harvesting the alfalfa is the most reasonable and economical management tactic. Even if the alfalfa is not quite to the point of harvest, if may be cut early as an economic and environmental alternative to chemical control methods. Cutting the alfalfa during this crucial time kills most of the weevil eggs and larvae (Ruppel and Stehr 1973). But, early harvest during this time is a more feasible tactic in the northern part of the U.S. than the southern part because there is greater variability in the seasonal life history of the alfalfa weevil in the south (Stark 1991).

Another type of cultural control tactic involves manipulation of the stem material to destroy fall-laid eggs. This includes alfalfa stem removal by grazing and burning dead alfalfa stems in the fall to suppress weevil populations. For this type of cultural management, timing of the manipulation is important for maximum effect on the alfalfa weevil with minimum effect on the alfalfa stand density and quality (Higgins et al. 1988).

The third type of cultural control involves the use of host-plant resistance in the development of alfalfa cultivars. At the present time there are already on the market alfalfa cultivars that are tolerant to low levels of alfalfa weevils. These varieties can tolerate some feeding by weevils without an economic loss in yield. Other alfalfa

varieties are presently being developed that contain erect, glandular hairs capable. Secretions from these hairs in some cases have the ability to entrap or impede smaller instars of the weevil. Continued research in this area could lead to the production of commercial varieties of alfalfa with these host-plant resistance qualities within the next few years (Higgins et al. 1988).

Biological control Biological control of the alfalfa weevil involves the use of insect parasitoids, parasites and in some environments predators. One of the most successful biological control agents in Illinois is a parasitoid wasp, *B. curculionis* (Wedberg et al. 1980). Other important alfalfa weevil larval parasitoids used in biological control include *B. anurus* and *T. incertus*. Adult weevil parasitoids, such as *M. aethiopoides* and *M. colesi*, also have had limited success (Dysart and Day 1976). Using mass releases, coupled with establishment, these parasitoids may have a stabilizing effect on alfalfa weevil populations when the fungal pathogen, *Z. phytonomi*, is enzootic (Harcourt 1990).

PAPER I

PHENOLOGY OF THE ALFALFA WEEVIL (COLEOPTERA: CURCULIONIDAE) IN IOWA AND REFINEMENT OF THE MANAGEMENT PROGRAM

ABSTRACT

A 3-year latitudinal study was conducted from 1990 through 1992 to determine the phenology of the alfalfa weevil, Hypera postica (Gyllenhal), in relation to alfalfa growth, at 4 Iowa fields located in a transitional region. Strong phenological differences were noted at the field sites. There was at least some fall and perhaps winter oviposition at all 4 of the sites. At the northernmost sites (Ames and Ankeny), the majority of eggs were deposited in the spring. However, there was greater fall oviposition at the two southernmost sites (Knoxville and Chariton). These differences in phenological behaviors led to greater densities of larvae present earlier in the growing season when plants were smaller at the southernmost sites relative to the northernmost sites. This suggested that alfalfa fields located in the southern part of Iowa have a greater potential for economically damaging densities of alfalfa weevil.

Additionally, an Illinois-based alfalfa weevil management program was tested and found inadequate for making management recommendations for southern Iowa. Management recommendations were revised using our current understanding of alfalfa weevil phenology in Iowa.

INTRODUCTION

The alfalfa weevil, *Hypera postica* (Gyllenhal), is one of the most destructive insect pests on alfalfa. The larval stage of this insect injures alfalfa plants by using its chewing mouthparts to feed on leaflets of the first cutting. Additional injury to regrowth of the second-cutting alfalfa by larvae and newly emerged adults also is possible (Foster 1986). The timing of plant growth and weevil egg hatch is crucial, because the growth stage of the plant at the time of larval infestation (egg hatch) is related to the plant's ability to withstand larval feeding injury (Shade and Hintz 1983). The earlier alfalfa is attacked in the spring, the greater potential for damage from larval feeding (Hsieh and Armbrust 1974 and Hintz et al. 1976). Extensive alfalfa weevil injury can cause direct reduction of yield and loss of photosynthetic capability of the alfalfa plant (App and Manglitz 1972).

The alfalfa weevil occurs throughout the contiguous United States and the prairie provinces of Canada. Its seasonal life history varies greatly throughout its North American geographical range. It usually has one complete life cycle per year. Climatic conditions for oviposition in the fall and winter, along with egg survival during the winter months (December through March) determine the timing of larval populations. Northern populations of alfalfa weevil, found in eastern Ontario (Harcourt et al. 1977) , Michigan (Casagrande and Stehr 1973), and Wisconsin (Litsinger and Apple 1973), rarely have been found to oviposit in the fall and winter because of the cool temperatures. In the region intermediate between these northern and southern locations, the number of weevil eggs laid in the fall and winter vary, depending on prevailing weather conditions. Alfalfa weevil populations located in this intermediate or transitional region show patterns of increasing fall oviposition and winter survival with declining latitude (Niemczyk and Flessel 1970). Examples of

locations in this transitional region include Illinois (Hsieh and Armbrust 1974) and Ohio (Niemczyk and Flessel 1970). Southern populations of alfalfa weevil, including Oklahoma (Berberet et al. 1980) and southern California (Summers et al. 1981), have been found to exhibit even more variability in terms of timing of oviposition in the fall and winter months. Southern weevil populations may deposit eggs from late November to mid March (Summers et al. 1981).

Although phenology and oviposition studies have been conducted in neighboring states (Illinois, Hsieh and Armbrust 1974 and Wisconsin, Litsinger and Apple 1973), information concerning weevil phenology is lacking for Iowa. Alfalfa weevil populations are most damaging in the southern and northeastern parts of Iowa, but their seasonal life histories are considerably different (Foster 1986). Geographically, Iowa lies in a transitional region between areas with northern and southern populations. But inadequate information about alfalfa weevil phenology makes it difficult to effectively manage the pest in this transitional region.

Therefore, a phenological study was conducted in Iowa to determine whether alfalfa weevil populations at different latitudes of the state resemble the phenology of those in Wisconsin and Michigan, which have populations with northern ovipositional behaviors or those populations in Illinois and Ohio, which have more southern ovipositional behaviors, e.g., fall and (or) winter egg laying. By determining the relationship between the phenology of the alfalfa weevil and the alfalfa plant, decisions can be made on the potential for alfalfa damage within this transitional region. In addition to the phenological studies, an alfalfa weevil management program developed for Illinois (Wedberg et al. 1980), was tested to determine its utility for management recommendations in Iowa.

MATERIALS AND METHODS

Description of Field Locations

Alfalfa weevil sampling was conducted in 4 Iowa alfalfa fields including Ames (Story County), Ankeny (Polk County), Knoxville (Marion County), and Chariton (Lucas County) (Fig. 1). Ames was chosen as the northernmost field site because it was located far enough north that the winter climate was noticeably different than the 2 southern locations (Knoxville and Chariton). Each of the other fields was located approximately 40-km apart latitudinally on a north-to-south transect. Samples were collected twice a week from 1 April through the first alfalfa harvest within each field from 1990 through 1992 (Ankeny was sampled only in 1991 and 1992). Fields were divided into sections by the following scheme: (1) each field site was ca. 50-m by 50-m or 25-m by 100-m, depending on the space available; (2) these sites were divided further into 8 equal plots 12.5-m by 25-m; and (3) wire flags were placed in the corners of the fields to delimit the sampling area.

All sampling locations were managed according to conventional practice. However, in 1990 and 1991 heavy rains near first-cutting prevented the normal harvest of the alfalfa in the Knoxville field. A similar situation arose at the Ames location in 1990. Furthermore, at the Chariton location in 1990, economic populations of the alfalfa weevil required the use of an insecticide. Carbaryl (2.1 kg [AI]/ha) was applied for suppression of alfalfa weevil at the perimeter of the sampling site. A buffer zone was left surrounding the site to prevent weevil mortality within the sampling area.

Ames This field was located in the westcentral part of Story County at the Iowa State University (I.S.U.) Johnson Research Farm (93^{O} 37'W 41^{O} 59'N). The sampling site was part of a 3.6 ha field of 'Vernal' alfalfa that was seeded in 1987. The average

alfalfa stand density was 101 $\pm$ 6 and 65 $\pm$ 5 stems/0.1 m^2 for 1990 and 1991, respectively. The soil type was a Webster (a fine-loamy, mixed, mesic Typic Haplaquolls) with a 3-5 degree westerly slope. This field was surrounded by field crops including corn (*Zea mays* L.), soybeans (*Glycine max* L. (Merrill) , and oats (*Avena sativa* L.) that were rotated annually. This field contained few weeds, most of them grass species.

In 1992, the Ames sampling site was changed to the I.S.U. Horticulture Research Farm north of Ames in Story County (93^o 36'W 42^o 00'N). This sample site was part of a 3 ha field of 'Apollo II' alfalfa seeded in 1988. The average alfalfa stand density was 57 $\pm$ 3 stems/0.1 m^2 for 1992. The soil type was a Nicollet-Webster complex (a fine-loamy, mixed, Aquic Hapludolls, Typic Haplaquolls). This alfalfa field was bordered by grassy areas on the north and south sides, an apple orchard on the east side, and a strawberry field on the west side. Only a few weeds species, including dandelion (*Taraxacum officinale* Weber), Canada thistle (*Cirsium arvense* (L.) Scop.), and various grasses, were distributed throughout the field.

Ankeny This field was located in the central part of Polk County at the ARS/USDA Ankeny Corn Insects Research Facility (93^o 37'W 41^o 43'N). The sampling site was part of a 2 ha field of 'Apollo II' alfalfa that was seeded in 1988. Average alfalfa stand density was 41 $\pm$ 5 and 32 $\pm$ 3 stems/ 0.1 m^2 for 1991 and 1992 , respectively. The soil was a Webster with a southerly slope. This field was bordered by pastures and grassy areas. Many weeds species, including dandelion, Shepherd's purse (*Capsella bursa-pastoris* (L.) Medic.), field pennycress, (*Thlaspi arvense* L.) and various grasses, were dispersed throughout the field.

Knoxville The Knoxville site was located in the central part of Marion County on a private-grower's farm (93^o 08'W 41^o 19'N). This sample site was part of a 5.3 ha field of Pioneer PA80, a winterhardy variety of alfalfa with 80% alfalfa and 20%

assorted grass mixture (pasture mix) that was seeded in 1988. The average alfalfa stand density was 78 ± 8, 74 ± 7, and 56 ± 4 stems/0.1 m^2 for 1990, 1991, and 1992, respectively. The soil type was a Ladoga (fine, montmorillonitic, mesic Mollic Hapludalfs) with a 2 to 5 degree southerly slope. This field was bordered by a field of corn (1990 and 1992) or soybeans (1991) on the south side, a farmstead to the east, a road ditch to the north, and a grove of trees to the west. Some weeds species including field pennycress, prickly lettuce (*Lactuca canadensis* L.), and a variety of grasses, were distributed throughout the field.

Chariton This field was located in the central part of Lucas County at the I.S.U. McNay Agricultural Field Station (93° 26'W 40° 58'N). The sample site was part of a 8 ha field of 'Assure' alfalfa seeded in 1987. The average alfalfa stand density was 64 ± 7, 40 ± 5, and 40 ± 4 stems/0.1 m^2 for 1990, 1991, and 1992, respectively. The soil type was a Shelby (fine-loamy, mixed, mesic Typic Argiudolls) with a 5 to 13 degree southeasterly slope. This field was surrounded by farmsteads to the north and south, a road ditch to the west, and more alfalfa to the east. Many weeds were distributed throughout the field including Sheppard's purse, dandelions, and a variety of other grasses.

Larval Sampling Method

Larval samples were collected using a 0.1 m^2 sampling frame which was thrown 4 times within each 12.5-m by 25-m plot. A 6-stem sampling unit was picked from within each sampling frame, giving 32 6-stem sampling units (Harcourt et al. 1975) from each field site on each sampling date. A modification of the palm-tip stem-removal method (Higgins et al. 1991) was used for collecting alfalfa stem samples that contained the larvae. After third instars were found at a sampling site, sampling was modified by moving the sampling frame 0.1 m to the right of where it had landed. This method was used to minimize the dislodging of the larger larvae by the force of

the thrown sampling frame. Larvae were extracted by manually hitting the stems against the side of a deep tray. The growing tip of each plant also was separated to expose first and second instars. After manual extraction was completed, the remaining larvae were extracted mechanically using 32 modified Berlese funnels (Eastman 1980). Four 6-stem alfalfa sampling units were placed in each funnel, and the remaining specimens were collected in 2-dram, screw-top vials containing 70% alcohol. During examination and counting, the larvae were separated into period-1 or establishment-phase larvae (first and second instars) and period-2 or feeding-phase larvae (third and fourth instars) (Harcourt et al. 1977) for each site on each date. Numbers of period-1 and period-2 larvae per 0.1 m^2 were determined by multiplying the average number of larvae obtained per stem times the alfalfa stand density at each site.

Alfalfa Sampling Methods

Alfalfa stem height and developmental stages were monitored over time until the first cutting of alfalfa. Thirty-two 2-stem sampling units were picked (cut at the crown) from within each 0.1 m^2 sampling frame. Each stem was measured from the top of the growing point down to the end of each stem. The presence, location, and number of buds, flowers, and seeds, also were determined for plant staging.

Degree-Day Accumulation

Temperature information (daily highs and lows) was obtained from National Oceanic and Atmospheric Administration (NOAA) weather stations located proximal to each sampling site. This information was used to calculate Celsius degree-days (CDD) from 1 January, using a developmental threshold of 9 ^{o}C. CDD were calculated on each sampling date for each sampling site.

Alfalfa Weevil Management Program

Alfalfa weevil management recommendations, which are presently used in the Illinois program and the Iowa program (a modification of the Illinois program), were validated for their utility in central and southcentral regions of Iowa. The use of the Illinois management program (Wedberg et al. 1980) required the following information: (1) calculation of degree-day accumulations (this management program uses Fahrenheit degree-days, but for consistency Celsius degree-days were used in this paper ; (2) counting of the number of larvae collected in a 30-stem sample; and (3) measuring the alfalfa stem height from the 30-stem sample. After this information was gathered, the next step was to refer to the alfalfa weevil management recommendation tables for determining management decisions.

The recommendation tables require the user to initiate sampling for alfalfa weevil larvae after 93 CDD have accumulated since 1 January. After sampling on the first date has been completed and data calculated, the program then advises the user to either resample in a prescribed number of CDD or spray the alfalfa. Sampling continues until harvest or 288 CDD have accumulated. At this point, a second recommendation table is used that focuses on the change in number of larvae since the last sample.

For the validation process, the earliest occurrence of peak period-1 density at each the 4 locations was determined and chosen as the latest possible time that a sampling program could be initiated to prevent alfalfa damage. Thus, the initiation of larval sampling for an alfalfa weevil management program was determined by the earliest occurrence of peak period-1 larvae at each location. These values were compared with alfalfa weevil management programs from neighboring states. The present Illinois (Wedberg et al. 1980) , Minnesota and Wisconsin, (Undersander et al. 1991) and Iowa (Foster 1986) alfalfa weevil management programs call for sampling

to begin after 93 CDD, 93 CDD (southern Minnesota and Wisconsin), and 149 CDD, respectively. If the management recommendations of neighboring states were not applicable for Iowa, a new management program would be developed.

RESULTS AND DISCUSSION

Larval Density

For 10 of the 11 field-years (field-year = one field / location / year) of the transitional region study, the alfalfa weevil larval populations were determined to be non-economic, based on current thresholds used in Iowa. The peak densities of the non-economic populations ranged from 24 to 82 total larvae / 0.1 m^2 during the 3 years of the study. These low population densities were caused in part by the onset of a fungal pathogen of the weevil, *Zoophthora phytonomi* Arthur (Zygomycetes: Entomophthorales), in 1990 and 1991 (Giles 1992). This pathogen reduced populations to levels at which few larvae could be collected in 1991 and may have been the reason for low population densities in 1992. The only population that reached economic status was at the southernmost site (Chariton) during the first week of May in 1990. This population had a peak density of 481 total larvae / 0.1 m^2, which necessitated the use of insecticide (carbaryl) near the sampling site to suppress the weevil population and prevent economic loss of the first alfalfa cutting.

Larval Phenology

There were strong phenological differences in alfalfa weevil populations at the 4 latitudinal locations of this study. These differences were determined by monitoring the occurrence of (1) the first alfalfa weevil larvae, (2) the peak density of period-1 larvae, and (3) the peak density of total larvae.

Table 1 shows the CDD that had accumulated at the time the first larvae were collected at each location. Using the established development requirement of ca. 156 CDD for egg hatch (Roberts et al. 1970) and extrapolating backwards from the time the first larvae were collected, an estimate of the timing of alfalfa weevil oviposition was calculated at each location. By using this approach, it was determined that there

was at least some fall oviposition and subsequent egg survival at all 4 of the locations. This was determined because substantially less than 155 CDD had accumulated at the time the first larvae were collected. At the Ames site in 1990, however, the first larvae were not collected until after 155 CDD had accumulated. Based on the development requirements for alfalfa weevil egg hatch, only spring oviposition occurred at Ames in 1990. Furthermore, in all 3 years of the study, the populations at Ames tended to require the most CDD accumulations before the first larvae were found in all 3 years of the study. In 1991 and 1992, there were no differences in the occurrence of the first larvae because there was fall oviposition at all of the locations.

Table 2 shows the number of CDD that had accumulated at the time of the peak density of period-1 larvae. Among the locations the most CDD accumulated at the Ames site when this larval peak occurred. Progressively less CDD had accumulated at the field sites with declining latitude in 1990 and 1991. The occurrence of the peak period-1 larval density at the Ames site (292 $\pm$ 5 CDD) and Chariton site (165 $\pm$ 8 CDD) was notably different for the 3-year study. On the average, the two southernmost locations (Knoxville and Chariton) tended to require less CDD in the spring than the at the northernmost locations (Ames and Ankeny) for this occurrence.

The amount of CDD that had accumulated at each of the locations before the occurrence of peak period-1 larval density suggests that there is considerably more fall oviposition at the Knoxville and Chariton sites (Table 2). Fall-laid eggs usually hatch earlier in the spring than spring-laid eggs because partial egg development occurs when eggs are deposited in the fall. Thus, these eggs require less CDD in the spring to hatch (Casagrande and Stehr 1973). However, the majority of oviposition seems to occur in the spring at the Ames and Ankeny sites.

Similar results were obtained when estimating the occurrence of the total peak larval density (period-1 and period-2 larvae combined) at the 4 field sites (Table 3). Once again, the weevil population at the Ames site required substantially more CDD to reach peak larval numbers than the population at the Chariton site. Likewise, there was a trend for the timing of peak larval density to occur when less CDD accumulation with declining latitude. However, there was no notable difference at the two central field locations (Ankeny and Knoxville).

These findings support the phenology work conducted by Niemczyk and Flessel (1970) in Ohio and Roberts et al. (1970) in Illinois. Both groups of researchers found that more eggs were deposited in the southern locations in the fall and winter than in the northern locations in their respective states. Additionally, these results show that there are phenological differences within this transitional region. This is demonstrated by the notable differences in the timing of larval development throughout the study range.

Relationship of Alfalfa Weevil and Alfalfa Plant Phenology

The importance of latitudinal alfalfa weevil phenology was demonstrated further by comparing the insect with alfalfa plant phenology. In comparing the occurrence of the peak larval density (represented by the accumulated CDD) at each location with the average alfalfa stem height, several trends were noted (Fig. 2). The average alfalfa stem height at the occurrence of peak larval density was greatest at the Ames (50 cm) and least at Chariton site (36 cm). Additionally, the average alfalfa stem height was progressively shorter at the occurrence of peak larval density with declining latitude. This phenomenon has important management implications because larger alfalfa plants can tolerate greater larval intensity (weevil density per habitat area) than shorter and less developed alfalfa (Hintz et al. 1976). Thus, southern field locations, where alfalfa plants were smaller (shorter) than northern

locations at the time of peak larval density, had greater potential for economically damaging weevil populations.

Utility of the Illinois Alfalfa Weevil Management Program for Iowa

The assumption for validating the Illinois program was that sampling needed to begin before or near the peak period-1 density. One reason for choosing this period of weevil development was to prevent future economic losses by larger larvae. Another reason was that period-1 larvae are less inadvertently dislodged from the alfalfa plant than larger, period-2 larvae during stem collection, making sampling for period-2 larvae less accurate.

The results of the phenological study showed that the Illinois program was inadequate for use in determining when to begin sampling in the southern part of Iowa. Two examples, which both occurred in 1990, demonstrate this inadequacy. At the Knoxville site, the peak density of period-1 larvae occurred when only 76 CDD accumulated at that site (Table 2). Additionally, at the Chariton site, less than 71 CDD had accumulated when curative management tactics should have been implemented to suppress the alfalfa weevil population. The Illinois program, however, does not recommend sampling until the accumulation of 93 CDD, which would have been late for making a timely management decision at these southern locations. These two examples of the inadequacy of the Illinois program for southern Iowa suggests the need for a revised alfalfa weevil management program for alfalfa producers in the state.

To revise the Iowa management program, the first step was to determine when sampling should be initiated in the central and southern regions of the state. Two graphs were plotted, using period-1 larval data, to determine different strategies for initiating an weevil management program

at different regions throughout the state. The first strategy would use the earliest occurrence (in terms of CDD) of peak period-1 larvae or the presence of an economic population (when treatment is recommended) at each location. For example, at the Chariton and Knoxville locations, sampling to monitor weevil populations would be started before the accumulation of 75 CDD (Table 2). By this time, approximately 20% of the total period-1 larvae would have been present at these locations (Fig. 3). In contrast, sampling when 20 % of the total period-1 larvae had occurred at Ankeny and Ames sites would have initiated after approximately 125 CDD or more had accumulated. Using this "risk averse" approach, more effort (money and time) would be required for more frequent scouting of the alfalfa fields, but the savings benefit could be potentially greater if there was an alfalfa weevil outbreak early in the growing season (75 CDD or less).

The second strategy would use the mean values (average of 3 years) of the occurrence of total period-1 larvae and CDD at each location for determining when sampling would be initiated (Fig. 4). Using the mean value strategy, sampling when 20% of the total period-1 larvae at the Knoxville and Chariton locations would begin after the accumulation of 100 CDD . If this strategy were used for determining when to initiate sampling, it would have been too late at these locations in 1990 to prevent economic losses. At the Ames location, using similar criteria, sampling would not have been initiated until over 150 CDD had accumulated. Clearly, this approach would require some risk-taking because the grower would be using mean values for determining when to initiate a sampling program instead of the earliest recorded presence of peak period-1 larval density or an economic population at each location. The recommendation of this author is that the former of these two strategies be implemented to prevent the chance of loss to larval population growth.

Iowa's present management program (Foster 1986) recommends initiating sampling after the accumulation of 149 CDD for all of Iowa and then using the Illinois alfalfa weevil management program. Based on the findings of this study, alfalfa weevil sampling should be initiated earlier in both the central and southern regions of Iowa. The recommended management program would require the initiation of sampling after the accumulation of 65 CDD south of the decision line, approximately 41^{O} 30'N or Interstate 80) and the accumulation of 121 CDD north of the decision line (Fig. 1).

After the initial sampling has been conducted, the Kansas Alfalfa Weevil Stem Count Method can be used for management of alfalfa weevil. The Kansas program is simple to use and incorporates the alfalfa values into management decisions. This program uses nominal thresholds that only require a grower to calculate the number of larvae/stem and measure the alfalfa stem height. These values then can be plotted to determine the management action based on three different prices of alfalfa ($35/ton (Higgins et al. 1988), $70/ton, and $105/ton (Danielson 1992)).

The results of this study showed that there are important phenological differences in weevil populations in Iowa. The information obtained from this study was used to refine alfalfa weevil management within Iowa. With this better understanding of the ovipositional behaviors of the alfalfa weevil at different latitudes, more effective management decisions can be made.

Table 1.- Occurrence of first collected alfalfa weevil larvae at 4 Iowa field sites.

Year	Ames		Ankeny		Knoxville		Chariton	
	Date	CDD [a]	Date	CDD	Date	CDD	Date	CDD
1990	28-Apr	155	---	---	12-Apr	68 [b]	12-Apr	67 [b]
1991	25-Apr	109	21-Apr	101	07-Apr	97	07-Apr	107
1992	30-Apr	121	30-Apr	94	23-Apr	107	23-Apr	103

[a] Number of degree-days (base 9 ^{o}C) accumulated since 1 January at each site.

[b] Larvae were present in the field before the first sampling date in 1990.

Table 2.- Occurrence of the peak density of period-1 alfalfa weevil larvae per 0.1 m^2 at each of the 3 sites in 1990 and the 4 in sites in 1991 and 1992.

Field sites	Year	Day-Month	Degree-Days [a] ^oC	No. Larvae/ 0.1 m^2
Ames	1990	29-May	316	38
	1991	20-May	285	51
	1992	20-May	275	60
			$\bar{x} = 292 \pm 5$ (SEM)	
Ankeny	1991	20-May	273	51
	1992	14-May	188	41
			$\bar{x} = 231 \pm 8$	
Knoxville	1990	18-Apr	76	32
	1991	11-May	181	21
	1992	16-May	266	24
			$\bar{x} = 174 \pm 10$	
Chariton	1990	28-Apr	152	218
	1991	25-Apr	109	18
	1992	16-May	234	36
			$\bar{x} = 165 \pm 8$	

[a] Number of degree-days (base 9 ^oC) accumulated since 1 January at each site.

Table 3.- Occurrence of peak alfalfa weevil larval density per 0.1 m^2 at each of the 3 sites in 1990 and the 4 sites in 1991 and 1992.

Field sites	Year	Day-Month	Degree Days [a] ^oC	No. Larvae/ 0.1 m^2
Ames	1990	29-May	316	77
	1991	20-May	285	82
	1992	27-May	341	91
			$\bar{x}$ = 314 ± 5 (SEM)	
Ankeny	1991	20-May	273	32
	1992	14-May	188	50
			$\bar{x}$ = 231 ± 8	
Knoxville	1990	08-Apr	169	69
	1991	16-May	298	55
	1992	16-May	266	54
			$\bar{x}$ = 244 ± 8	
Chariton	1990	07-May	170	481
	1991	02-May	164	24
	1992	16-May	234	60
			$\bar{x}$ = 189 ± 6	

[a] Number of degree-days (base 9 ^{o} C) accumulated since 1 January at each site.

Fig. 1. Location of field sites where alfalfa weevil larvae were sampled in Iowa from 1990 through 1992. Included on this map is the decision line for determining when to initiate a sampling program. Above the decision line, sampling should be initiated after the accumulation of 121 CDD. Below the decision line, sampling should be initiated after the accumulation of 65 CDD.

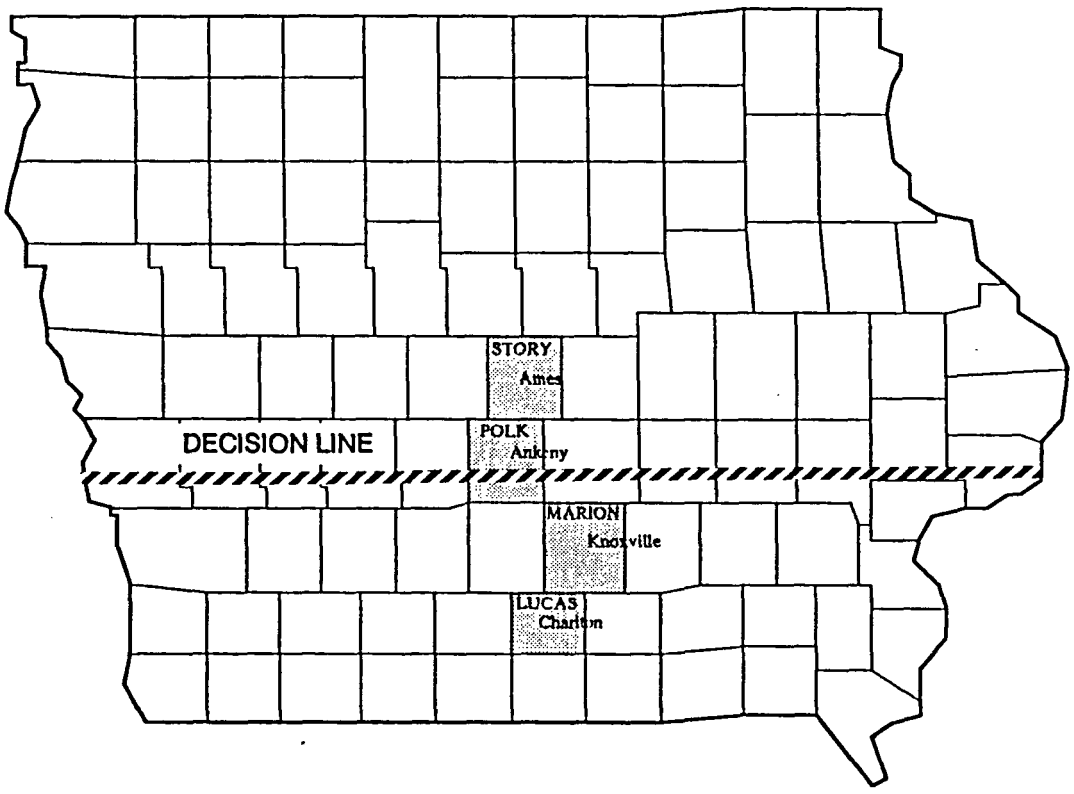

STORY
Ames
DECISION LINE
POLK
Ankeny
MARION
Knoxville
LUCAS
Chariton

Fig. 2. Phenological relationship between the occurrence of peak larval density and the average alfalfa stem height at 4 Iowa sites. The vertical bars represent means $\pm$ SEM (black vertical line).

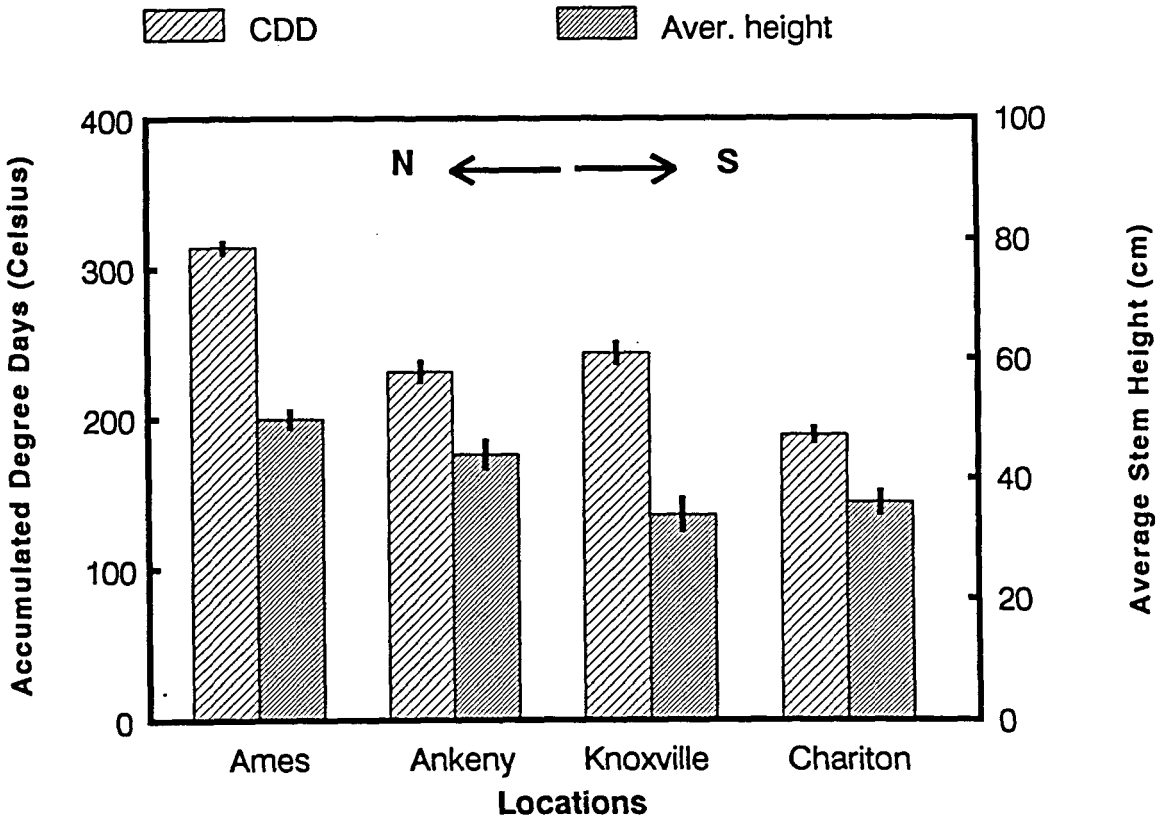
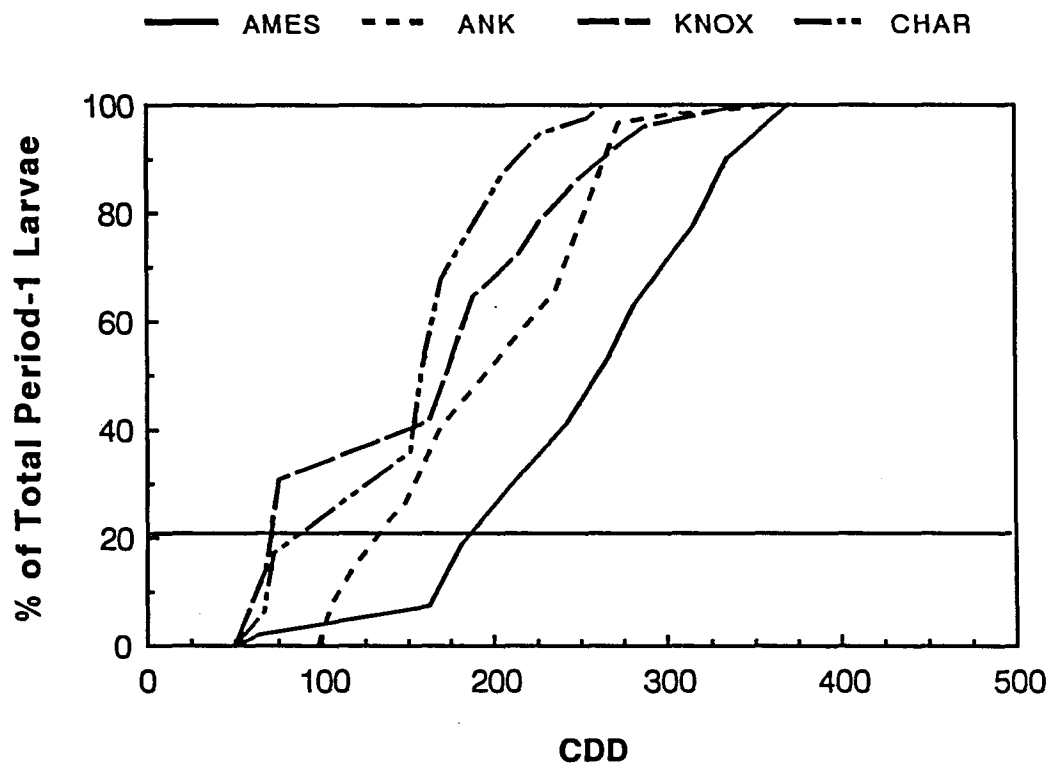
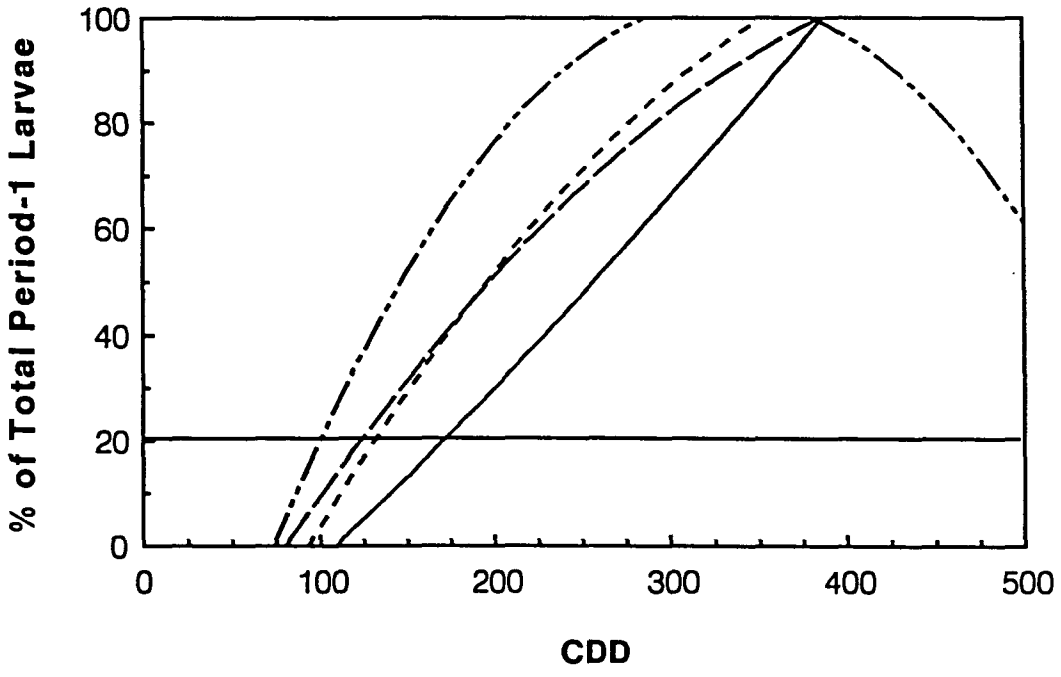

CDD
Aver. height
N
S
400
300
200
100
0
100
80
60
40
20
0
Accumulated Degree Days (Celsius)
Average Stem Height (cm)
Ames
Ankeny
Knoxville
Chariton
Locations

Fig. 3. Phenological development of period-1 alfalfa weevil larvae using the earliest developing population, based on accumulated CDD, from each of 4 Iowa locations. The horizontal line shows when approximately 20 % of the total period-1 have occurred. In this graph, first-cutting was considered 100% for period-1 presence, even though small numbers of period-1 alfalfa weevil larvae were collected after this time.

Fig. 4. Phenological development of period-1 larvae using the mean number of accumulated CDD for developing populations from 1990 through 1992 at each of 4 Iowa locations. The horizontal line shows when approximately 20 % of the total period-1 have occurred. In this graph, first-cutting was considered 100% for period-1 presence, even though small numbers of period-1 alfalfa weevil larvae were collected after this time.


AMES
ANK
KNOX
CHAR
% of Total Period-1 Larvae
100
80
60
40
20
0
0
100
200
300
400
500
CDD


% of Total Period-1 Larvae
100
80
60
40
20
0
0
100
200
300
400
500
CDD

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PAPER II

POPULATION DYNAMICS OF THE ALFALFA WEEVIL, *HYPERA POSTICA* (GYLLENHAL)(COLEOPTERA: CURCULIONIDAE) IN CENTRAL AND SOUTHCENTRAL IOWA

ABSTRACT

Eight life tables were constructed for the alfalfa weevil, *Hypera postica* (Gyllenhal), from populations at 4 Iowa locations in 1991 and 1992. A fungal pathogen, *Zoophthora phytonomi* Arthur, was determined as the key factor regulating within-generation population trends in 1991. This disease caused especially high mortality during larval third and fourth stadia. Other unknown mortality factors were important in regulating population density in 1992. Some of these undetermined mortality agents may have included establishment failure and predation. Two larval parasitoids, *Bathyplectes curculionis* (Thomson) and *Bathyplectes anurus* (Thomson) caused only a small percentage of mortality during both 1991 and 1992. Mortalities occurring during the third and fourth stadia were density-dependent.

INTRODUCTION

The alfalfa weevil, a periodic pest of alfalfa, is an introduced pest from Europe or Eurasia. It was first detected near Salt Lake City, UT in 1904 (Titus 1910) and again found in the early 1950's near Baltimore, MD (Poos and Bissell 1953). As a result of these introductions, the alfalfa weevil is now located in all alfalfa-producing states in the contiguous United States (Day 1981) and in 4 Canadian provinces (Dysart and Day 1976). The alfalfa weevil was first reported in southeastern Iowa in 1967 (Stockdale 1967) and since has spread throughout the state (Foster 1986).

Life History of Alfalfa Weevil in Iowa

Alfalfa weevils overwinter as both adults and eggs. Adult activity begins within the first week of April. Most oviposition occurs between this time and the first cutting of alfalfa. After this period, there is only a small amount of oviposition. With suitable fall conditions, egg laying may occur at that time. Eggs are deposited into dead stems, ground debris and (or) green alfalfa stems, depending on the ovipositional sites available at the time. Fall-laid eggs hatch in early April and spring-laid eggs in early May. Eggs are laid in clusters of approximately 10-14 eggs (Harcourt et al. 1974, Foster 1986).

Larvae eclose from the eggs and crawl up alfalfa stems to the growing terminal where the 1st stadia weevils begin to feed. After the larva reaches one of these protected areas, it will stay and feed until developing into a large larva (third or fourth stadia). At this point in development, the larva moves out of the terminal and begins skeletonizing mature leaflets. Typically, alfalfa weevil have 4 instars and require 4 weeks or more to complete development. After spinning a net-like cocoon in the ground litter or attached on a leaflet on the lower portion of the alfalfa plant, fourth instars pupate. Adults emerge from the cocoons starting in mid-May through early

June. These adults remain in the field for a few weeks, sometimes causing damage to alfalfa regrowth, and then move to summer dormancy sites along fence rows, ditches, and weedy areas near the alfalfa field (Harcourt et al. 1977). Adults may return in early September and do some feeding and may lay some eggs in the fall and early winter before preparing for hibernation (Foster 1986).

Mortality Factors

Although considerable mortality usually occurs during the larval and prepupal stages of alfalfa weevil development, few mortality factors affect survival of the egg stage (Harcourt and Guppy 1976). This is because a large proportion of weevil eggs are deposited within green and dead alfalfa stems, which protects them from predation (Harcourt et al. 1977) and desiccation. However, some mortality does occur during this stage. Two causes of mortality are infertility and parasitism by *Patasson luna* (Gir.) (Hymenoptera: Mymaridae).

Newly eclosed larvae are exposed to predators and establishment failure (larvae are dislodged from the stem and may be unable to relocate a suitable host) while attempting to find alfalfa growth terminals (Harcourt et al. 1977). Larvae may be subject to a fungal pathogen, *Zoophthora phytonomi* (Arthur) (Zygomycetes: Entomophthorales). The disease was the principal mortality factor of large larvae in Ontario (Harcourt et al. 1974). Once larvae become third instars, they move out onto mature leaflets and are again exposed to predators.

Many mortality factors occur during the prepupal and pupal stages. Larvae infected by the *Z. phytonomi*, which remain alive throughout the last stadium, die as prepupae or pupae (Harcourt et al. 1990). After the alfalfa weevil spins its cocoon, the larval parasitoids (*Bathyplectes curculionis* (Thomson), *Bathyplectes anurus* (Thomson) (Hymenoptera: Ichneumonidae), and *Tetrastichus incertus* (Ratz.) (Hymenoptera: Eulophidae) kill the host during this prepupal stage and pupate in the

weevil's cocoon. Prepupae and pupae also are killed by predators.

Microctonus aethiopoides Loan and *Microctonus colesi* Drea (Hymenoptera: Braconidae) are adult parasitoids that deposit their eggs into adults and large larvae third and fourth stadia), respectively. These parasitoids sterilize both the summer and overwintered adults in the spring (Harcourt et al. 1982, Harcourt et al. 1980).

Although the alfalfa weevil is a well-studied pest, e.g., Woods et al. 1978, no studies on this pest and its related population regulation factors have been conducted in Iowa. At the present time, alfalfa weevil biological and ecological information used in Iowa management programs is obtained from neighboring states. With a better understanding of the population dynamics in Iowa, a more effective integrated pest management program can be developed that incorporates these biotic and abiotic regulatory factors.

Therefore, a population dynamics study was conducted (1) to assess alfalfa weevil densities in central and southcentral Iowa, (2) to determine the various mortality factors acting on the weevil populations, and (3) to incorporate this information obtained from these population dynamics studies into life tables for further population analyses.

MATERIALS AND METHODS

Description of Field Locations

Alfalfa weevil sampling was conducted in 4 Iowa alfalfa fields including Ames (Story County), Ankeny (Polk County), Knoxville (Marion County), and Chariton (Lucas County). Each field was located approximately 40-km apart latitudinally on a north-to-south transect. Samples were collected twice a week from 1 April through the first alfalfa harvest within each field from 1990 through 1992 (Ankeny was sampled only in 1991 and 1992). Fields were divided into sections by the following scheme: (1) each field site was ca. 50-m by 50-m or 25-m by 100-m, depending on the space available; (2) these sites were divided further into 8 equal plots 12.5-m by 25-m; and (3) wire flags were placed in the corners of the fields to delimit the sampling area.

All sampling locations were managed according to conventional practice. However, in 1990 and 1991 heavy rains near first-cutting prevented the normal harvest of the alfalfa in the Knoxville field. A similar situation arose at the Ames location in 1990. Furthermore, at the Chariton location in 1990, economic populations of the alfalfa weevil required the use of an insecticide. Carbaryl (2.1 kg [AI]/ha) was applied for suppression of alfalfa weevils at the parameter of the sampling site. A buffer zone was left surrounding the site to prevent weevil mortality within the sampling area.

Ames This field was located in the westcentral part of Story County at the Iowa State University (I.S.U.) Johnson Research Farm (93^{O} 37'W 41^{O} 59'N). The sampling site was part of a 3.6 ha field of 'Vernal' alfalfa that was seeded in 1987. The average alfalfa stand density was 101 $\pm$ 6 and 65 $\pm$ 5 plants/0.1 m^{2} for 1990 and 1991, respectively. The soil type a Webster (a fine-loamy, mixed, mesic Typic Haplaquolls)

with a gentle slope. This field was surrounded by field crops including corn (*Zea mays* L.), soybeans (*Glycine max* (L. Merrill) , and oats (*Avena sativa* L.) that were rotated annually. This field was virtuously weedless except for a few grass species.

In 1992, the Ames sampling site was changed to the I.S.U. Horticulture Research Farm north of Ames in Story County (93^{o} 36'W 42^{o} 00'N). This sample site was part of a 3 ha field of 'Apollo II' alfalfa seeded in 1988. The average alfalfa stand density was 57 $\pm$ 3 plants/0.1 m^{2} for 1992. The soil type was a Nicollet-Webster complex (a fine-loamy, mixed, Aquic Hapludolls, Typic Haplaquolls). This alfalfa field was bordered by grassy areas on the north and south sides, an apple orchard on the east side, and a strawberry field on the west side. Only a few weeds species, including dandelion (*Taraxacum officinale* Weber), Canada thistle (*Cirsium arvense* (L.) Scop.), and various grasses, were distributed throughout the field.

Ankeny This field was located in the central part of Polk County at the ARS/USDA Ankeny Corn Insects Research Facility (93^{o} 37'W 41^{o} 43'N). The sampling site was part of a 2 ha field of 'Apollo II' alfalfa that was seeded in 1988. Average alfalfa stand density was 41 $\pm$ 5 and 32 $\pm$ 3 plants/ 0.1 m^{2} for 1991 and 1992 , respectively. The soil was a Webster with a southerly slope. This field was bordered by pastures and grassy areas. Many weeds species, including dandelion, Shepherd's purse (*Capsella bursa-pastoris* (L.) Medic.), field pennycress, (*Thlaspi arvense* L.) and various grasses, were dispersed throughout the field.

Knoxville The Knoxville site was located in the central part of Marion County on a private-grower's farm (93^{o} 08'W 41^{o} 19'N). This sample site was part of a 5.3 ha field of Pioneer PA80, a winterhardy variety of alfalfa with 80% alfalfa and 20% assorted grass mixture (pasture mix) that was seeded in 1988. The average alfalfa stand density was 78 $\pm$ 8, 74 $\pm$ 7, and 56 $\pm$ 4 plants/0.1 m^{2} for 1990, 1991, and 1992, respectively. The soil type was a Ladoga (fine, montmorillonitic, mesic Mollic

Hapludalfs) with a 2 to 5 degree southerly slope. This field was bordered by a field of corn (1990 and 1992) or soybeans (1991) on the south side, a farmstead to the east, a road ditch to the north, and a grove of trees to the west. Some weeds species including field pennycress, prickly lettuce (*Lactuca canadensis* L.), and a variety of grasses, were distributed throughout the field.

Chariton This field was located in the central part of Lucas County at the I.S.U. McNay Agricultural Field Station (93^{o} 26'W 40^{o} 58'N). The sample site was part of a 8 ha field of 'Assure' alfalfa seeded in 1987. The average alfalfa stand density was 64 $\pm$ 7, 40 $\pm$ 5, and 40 $\pm$ 4 plants/0.1 m^2 for 1990, 1991, and 1992, respectively. The soil type was a Shelby (fine-loamy, mixed, mesic Typic Argiudolls) with a 5 to 13 degree southeasterly slope. This field was surrounded by farmsteads to the north and south, a road ditch to the west, and more alfalfa to the east. Many weeds were distributed throughout the field including Sheppard's purse, dandelions, and a variety of other grasses.

Alfalfa Weevil Population and Mortality Assessment

Density estimates of the egg, larval, and pupal stages were determined using sampling techniques similar to those of Harcourt et al. 1974, Guppy et al. 1975, and Harcourt and Guppy 1975, respectively.

Egg Sampling Method Egg counts were estimated beginning on 1 April of each year by collecting all the ground litter from 8 15 cm^2 samples per field. A blender extraction technique (Pass and Van Meter 1966) was used to separate the eggs from the stems for counting. After the alfalfa began to grow above the ground, 32 sampling units were taken in each field. Samples were collected until first cutting of the alfalfa at each location. Each sample consisted of a 3-stem sampling unit taken from a 0.1 m^2 sampling area. Estimates of the number of eggs per stem and eggs per cluster were determined by dissecting each plant of the 3-stem sampling unit. Collected

eggs were placed in a rearing container at 25 ^{o} C and held to assess egg viability and rate of parasitization by *P. luna*.

Larval Sampling Method Larval samples were collected using a 0.1 m^2 sampling frame that was thrown 4 times within each 12.5-m by 25-m plot. A 6-stem sampling unit was randomly picked from within each sampling frame, giving 32 6-stem sampling units (Harcourt et al. 1975) from each field site on each sampling date. A modification of the palm-tip stem-removal method (Higgins et al. 1991) was used for collecting alfalfa stem samples that contained the larvae.After third instars were found at a sampling site, sampling was modified by moving the sampling frame 0.1 m to the right of where it had landed. This method was used to minimize the dislodging of the larger larvae by the force of the thrown sampling frame. Samples were collected from 1 April until the first cutting of alfalfa at each location.

Larvae were extracted by manually hitting the stems against the side of a deep tray. The growing tip of each plant also was separated to expose first and second instars. After manual extraction was completed, up to 20 larvae from each set of 4 sampling units (24 stems) were placed individually into 5-dram glass vials. Each vial contained a fresh alfalfa terminal that was changed twice weekly. To prevent the larva from escaping, the vial was lightly stuffed with cotton. Larvae then were reared to determine survivorship and mortality factors. The mortality factor assessed for this stage was the fungal pathogen, *Z. phytonomi*. The remaining larvae were extracted mechanically using 32 modified Berlese funnels (Eastman 1980). Four 6-stem alfalfa sampling units were placed in each funnel, and the remaining specimens were collected in 2-dram, screw-top vials containing 70% alcohol. During examination and counting, the larvae were separated into period-1 or establishment-phase larvae (first and second instars) and period-2 or feeding-phase larvae (third and fourth instars) (Harcourt et al. 1977) for each site on each date. Numbers of period-1 and

period-2 larvae per 0.1 m^2 were determined by multiplying the average number of larvae obtained per stem (obtained from both manual and mechanical extraction) times the alfalfa stand density at each site.

Prepupal and Pupal Sampling Method Sampling of prepupal and pupal stages of the alfalfa weevil was initiated on 1 May of each year and continued until first-cutting or when population density dropped off. Sampling involved taking an additional 8 samples from each field by throwing a 0.1 m^2 sampling frame and harvesting all the foliage and ground litter within it. Cocoons were collected by hand and stored in rearing containers at 25^{o}C for emergence or death from 2 larval parasitoids (*B. curculionis* and *B. anurus*) or disease. Emerging adults were counted and frozen for adult parasitoid dissections.

Life Table Construction

Alfalfa weevil population and mortality data were summarized in partial life tables to determine within-generation population change. The following 4 stage intervals were used for the life table analysis: egg, period-1 larvae, period-2 larvae, and pupae. Eight life tables total were developed over the 2-years of the study (a life table for each location each year). Using these tables, 2 composite life tables (for 1991 and 1992) were developed to summarize the information for each year. Life tables were not constructed for 1990 because alfalfa weevil mortality data was not collected.

The following column headings proposed by Morris and Miller (1954), Morris (1963), and Harcourt (1969) were used in constructing the life tables: (1) *x* - age interval at which the sample was taken, (2) *lx* - the number of individuals living at the beginning of the stage noted in the *x* column, (3) *dx* - the number dying within the age interval stated in the *x* column, (4) *dxF* - the mortality factor responsible for *dx*, (5) *100qx* - the percentage of mortality for that stage interval, and (6) *Sx* - survival rate within x. Data values in columns 2 (*lx*) and 4 (*dx*) were rounded to the nearest whole

number.

Population estimates were integrated to form a single *lx* value for each stage interval. Each *lx* value was determined by using the area under a curve method (Southwood 1978), with the trapezoidal solution procedures for determining the integral. Integrals then were divided by the number of degree-days required to complete the development stage (Hsieh et al. 1974).

For this life table analysis all period-1 larval, period-2 larval, and pupal *lx* values were obtained from direct estimates of weevil populations at the 4 Iowa locations. However, because relatively less egg numbers were collected than period-1 larvae, *lx* values for egg density were calculated by collecting eggs from each location and rearing them to determine percentage mortality. The *lx* value obtained from the direct count of period-1 larvae then were divided by the percentage of egg mortality to calculate an *lx* value for the egg-stage interval. Because direct prepupal estimates were not obtained, larval mortality from these parasitoids (*B. curculionis* and *B. anurus*) was included in the period-2 larval stage interval.

RESULTS AND DISCUSSION

Population Densities

Larval population curves were constructed by plotting the mean density of total larvae (all instars combined) against accumulated Celsius degree-days (CDD) (from 1 January) for each year at each location (Fig. 1 (A-D)). These curves were used to compare population levels and trends from year-to-year and location-to-location. The earliest occurrence of the peak larval population was 28 April 1990 at Knoxville and the latest was 31 May 1990 at Ames.

The Ames and Ankeny locations showed little change in occurrence of peaks among 3 years of the study. However, at the Chariton and Knoxville locations there was a considerable difference in occurrence of peaks among the years. The least and greatest number of CDD that were accumulated before the occurrence of peak larval density was 163 and 298 at Knoxville in 1990 and 1991, respectively, a difference of 135 CDD and 18 calender days between the 2 years.

Comparisons of location and year showed substantial differences in the date and CDD accumulations for the occurrence of peak larval density. Differences were attributed to greater fall oviposition at the Knoxville and Chariton sites in 1990. At these locations, eggs began development in the fall or winter before entering diapause and, thus, required less CDD in the spring (relative to the Ames site) before larval eclosion (see paper 1).

The population densities encountered in this study were mostly low. In 10 of the 11 field-years (field-year = one field per location per year) of the study, larval densities were not economic, i.e., the number of larvae per stem was less than the economic threshold used in the Iowa pest management program (Foster 1986). Peak density of the non-economic populations ranged from 24 to 82 larvae / 0.1 m^2. The

only population reaching economic status occurred at Chariton during the first week of May in 1990. This weevil population had a peak density of 481 total larvae / 0.1 m ^{2} or 8 larvae per stem, well over the economic threshold of 2 larvae per stem for 6 in.-tall alfalfa (Foster 1986). This outbreak could be explained by greater than normal fall oviposition in 1989 combined with additional oviposition in the spring (see paper 1).

Survivorship Curves

Surviviorship curves were developed that combined all locations for each year (Fig. 2 (A-C)). These curves indicated that there was little mortality during the egg stage in all 3 years of the study. Substantially greater mortality occurred during the period-1 larval stage. However, the greatest mortality occurred during the period-2 larval and pupal stages. Individual mortalities were explained further by life table analysis.

Life Table Analysis

Within-generation population change was analyzed by combining all 4 locations for 1991 and 1992 to determine the stage of the alfalfa weevil that contributed most to population trend. Mortality data used for determining within-generation population change was obtained from a related study (Giles 1992).

Infertility was the only identifiable cause of mortality during the egg stage in both 1991 and 1992 (Table 1 and Table 2). Although no *P. luna* were found at any time during this study, parasitization rates of 13 % and 46.9 % have been found in Wisconsin for green-stem alfalfa and ground litter, respectively (Hogg and Kingsley 1983).

In 1991, 14.1 % of period-1 larvae and 58.1 % of period-2 larvae were killed by *Z. phytonomi*. At the Ankeny and Knoxville locations, 93 % and 81 % of period-2 larvae were killed by this pathogen, but at the Ames and Chariton locations period-2 larvae were only moderately infected. Greater disease infection at Ames probably was

prevented by early cutting of the alfalfa at this location. The low percentage of infection at Chariton was probably the result of low weevil densities during this year. Diseased prepupae and pupae were not collected within the sampling units for the life table study. However, some diseased prepupae and pupae were found in impromptu collections at these sites. More prepupal and pupal samples were needed to assess the fungal mortality of these stages. Larval parasitoids, combined, caused only 13 % mortality. Residual mortalities (other unknown mortality factors) were relatively low for both larval periods. These mortalities probably were caused by a combination of establishment loss, predation and heavy rainfall experienced during the sampling period.

In 1992, *Z. phytonomi* was a not a major cause of mortality (Table 2). Only 10.9 % of period-1 larval mortality and 10.4 % of period-2 larval mortality were caused by the disease. Because of the low number of diseased larvae, diseased prepupae and pupae were not collected in 1992. Larval parasitoids caused less percentage mortality in 1992 than in 1991. The reason for this decrease was not determined. Most mortality during the larval periods occurred because of unknown factors, probably establishment loss and predation. Harcourt et al. (1977) found that establishment loss was an important cause of mortality for period-1 larvae. In a study related to the population dynamics research, Giles (1992) found large numbers of *Coleomegilla maculata* (Timberlake) (Coleoptera: Curculionidae) present in all 4 of our study sites and observed the lady beetle feeding on weevil larvae during 1992.

Life table data were analyzed to determine the magnitude of the contributions of stage-specific mortality factors. These mortality factors were expressed as k-values (killing powers) (Varley and Gradwell 1960). The k-values were determined by the equation:

k_i = log (*lx* of a stage (k_i)/*lx* of the subsequent stage (k_i + 1)

The total mortalities (K) is equal to the sum of all individual mortalities

$K = k_1 + k_2 + k_3$ (Varley and Gradwell 1965)

where:

k_1 = mortality of eggs because of infertility, etc.

k_2 = mortality of period-1 larvae because of disease, establishment loss, etc.

k_3 = mortality of period-2 and prepupae because of disease, parasites predation, etc.

To identify the key factor (Morris 1959, Varley and Gradwell 1960) that contributes most to changes in population density, a graphical (Varley and Gradwell 1968) and a statistical analysis (Podoler and Rodgers 1975) were used. The first analysis involved plotting individual k-values for each location and year and comparing the individual k-value graphs with a graph of K plotted against the same parameters. The k-value having similar fluctuations as K was identified as the key factor (Varley and Gradwell 1968). The second analysis involves plotting the individual mortalities as k-values (y axis) against total mortalities (x-axis) and calculating the regression coefficient. The k-value which gives the greatest value for the slope was determined as the key mortality factor (Podoler and Rogers 1975).

The results of the graphical and statistical key factor analyses are shown in Fig. 3 and Fig. 4. For both analyses, the key factor was determined as k_3, the death of period-2 larvae from disease and other unknown factors such as predation and establishment loss. In the graphical analysis method, k_3 mortality fluctuations were the most similar in magnitude and direction to the total within-generation mortality (K). For the statistical analysis method, individual k_3 mortality values for each year and location regressed against K gave the slope closest to unity ($b = 0.714359$, $r = 0.8406$). In both analyses, k_2, mortality from disease, establishment loss, etc. and k_1, mortality from infertility, etc. caused relatively small within-generation mortality.

The results of this key factor analysis were comparable to those of Harcourt et al. (1977) and Harcourt and Guppy (1991). Their findings showed that death from *Z. phytonomi* during the larval feeding stage (period-2) was the principal regulator of alfalfa weevil population densities. The disease also was an important regulator in our study in 1991, but the low populations encountered in 1992, combined with below average rainfall levels, were not conducive to initiation and spread of the disease within the alfalfa fields (Giles 1992).

Density Relationships of the Mortality Factors

To assess density relationships of the mortality factors, a procedure proposed by Smith (1973) was used that regressed individual submortalities (k_i) against *lx* density values (Fig. 5 A and B). Mortalities acting on period-2 larvae (k_3) appear to have a density-dependent relationship. However, when the disease and the unknown mortality factors were separated from the total submortality of period-2 larvae, the disease had a density-independent relationship with this interval ($r = 0.11235$). The unknown mortality factors acted in a relatively strong density-dependent manner ($r = 0.8868$). Mortalities acting on the egg stage (k_1) and period-1 larvae (k_2) were density independent.

Contrary to this study, Harcourt et al. (1977) found that the disease acted in a density dependent manner. These differences between our study and that of Harcourt et al. may have been because of low alfalfa weevil densities, which may have inhibited the spread of the disease at the 4 locations. In addition, other unknown mortality factors played a more important role in population regulation. This occurrence interfered with the ability to attribute all mortality during a stage interval to one factor.

This population dynamics study provided valuable biological and ecological information on the alfalfa weevil relevant to Iowa. In the past, alfalfa weevil management programs had been based mainly on information from neighboring states (Illinois and Wisconsin). With a better understanding of the life history of the

weevil and its related mortality factors, a better prediction can be made that allows a more effective integration of management tactics for alfalfa weevil suppression.

Table 1 - 1991 Partial composite life table for 4 locations in Iowa.

x Stage interval	lx No. alive [a] at beginning of x	dxF Factor Responsible for dx	dx No. dying during x	100qx dx as percentage of lx	Sx Survival rate within x
Egg	54 [b]	Infertility	4	4.0	0.960
Larvae					
Period-1	52±12	Disease	7	14.1	
		Unknown	2	3.8	
		Total		17.9	0.821
Period-2	43±11	Disease	25	58.1	
		Larval Parasitoids	6	13.1	
		Unknown	9	21.8	
		Total		93.0	0.070
Pupae	3±1				

[a] Density per 0.1 m^2.

[b] Estimated based on overall survival of eggs collected from all locations.

Table 2 - 1992 Partial composite life table for 4 locations in Iowa.

x	lx	dxF	dx	100qx	Sx
Stage interval	No. alive [a] at beginning of x	Factor Responsible for dx	No. dying during x	dx as percentage of lx	Survival rate within x
Egg	101 [b]	Infertility	4	4.0	0.960
Larvae					
Period 1	97±30	Disease	11	10.9	
		Unknown	28	28.8	
		Total		39.7	0.600
Period 2	58±12	Disease	6	10.4	
		Larval Parasitoids	5	7.9	
		Unknown	46	79.7	
		Total		98.0	0.020
Pupae	2±0.5				

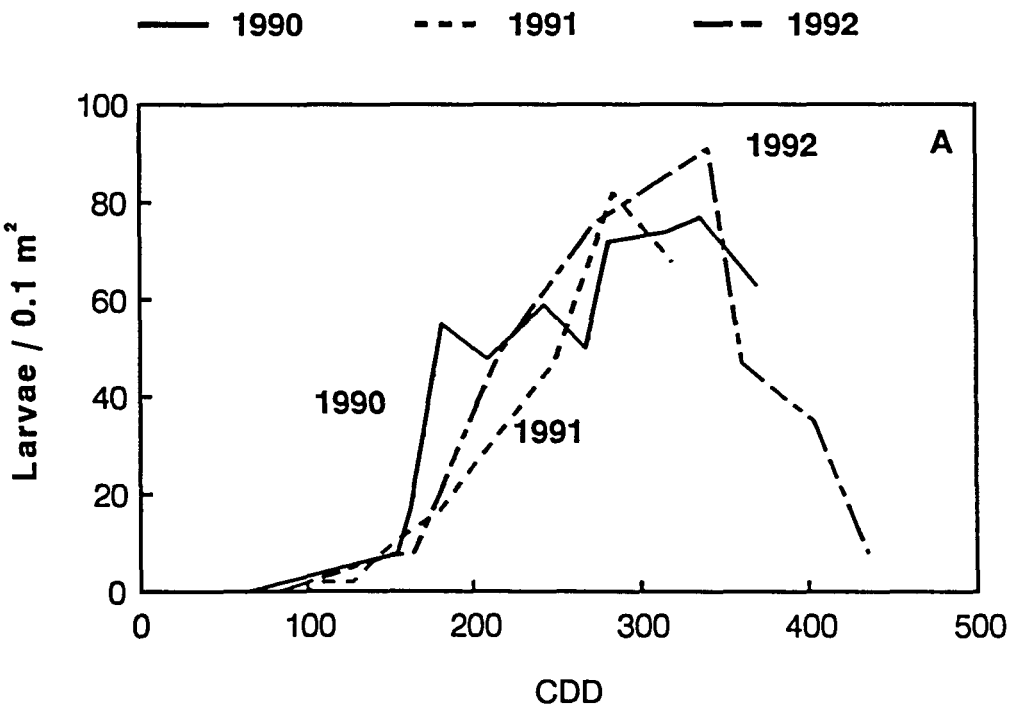
[a] Density per 0.1 m^2.

[b] Estimated based on overall survival of eggs collected from all locations.

Fig. 1 Larval population curves of the alfalfa weevil. Each curve presents the average number of larvae collected at 4 Iowa locations.

(A) Ames (Story County, IA) 1990, 1991, and 1992.

Fig. 1 (B) Ankeny (Polk County, IA) 1991 and 1992.


1990
1991
1992
A
Larvae / 0.1 m²
CDD
0
20
40
60
80
100
0
100
200
300
400
500
1990
1991
1992

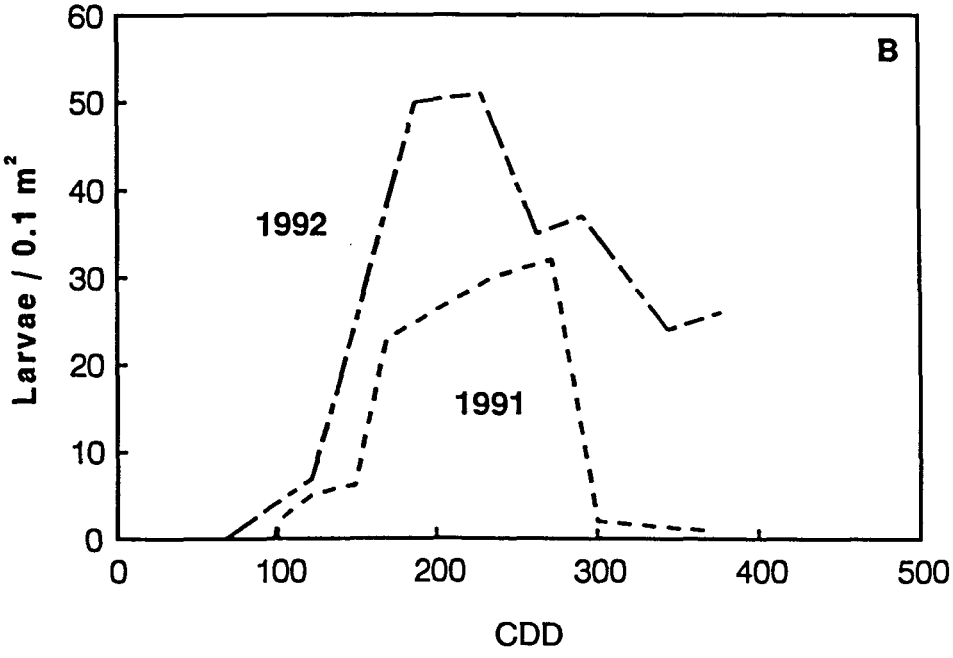
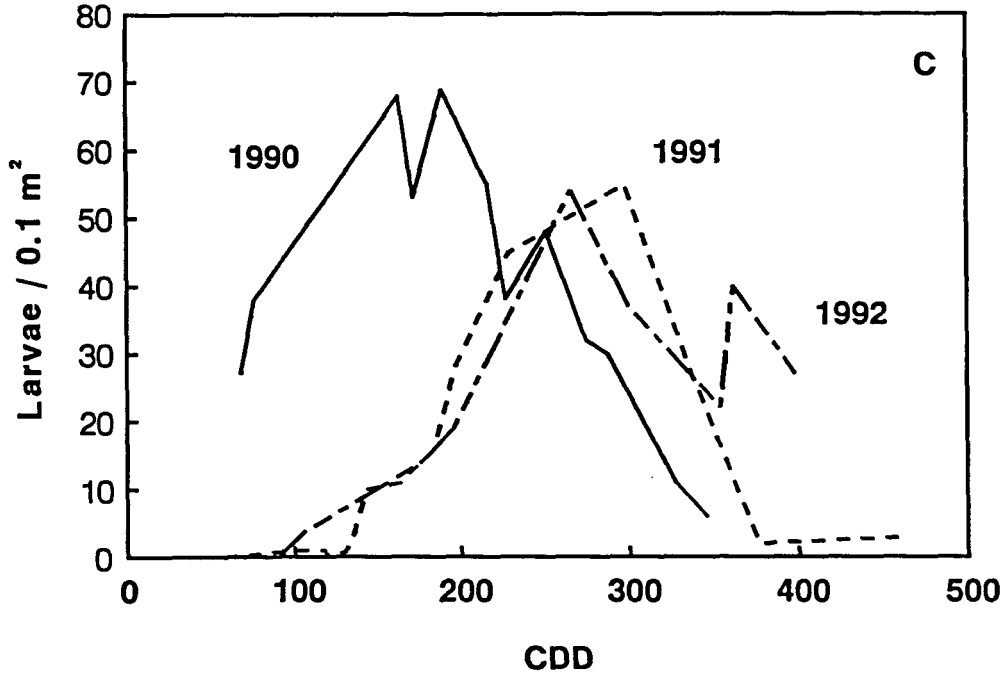

B
Larvae / 0.1 m²
CDD
0
10
20
30
40
50
60
0
100
200
300
400
500
1992
1991

Fig. 1 (continued); (C) Knoxville (Marion County, IA) 1990, 1991, and 1992.

(D) Chariton (Lucas County, IA) 1990, 1991, and 1992.


C
1990
1991
1992
Larvae / 0.1 m²
CDD
0
10
20
30
40
50
60
70
80
0
100
200
300
400
500

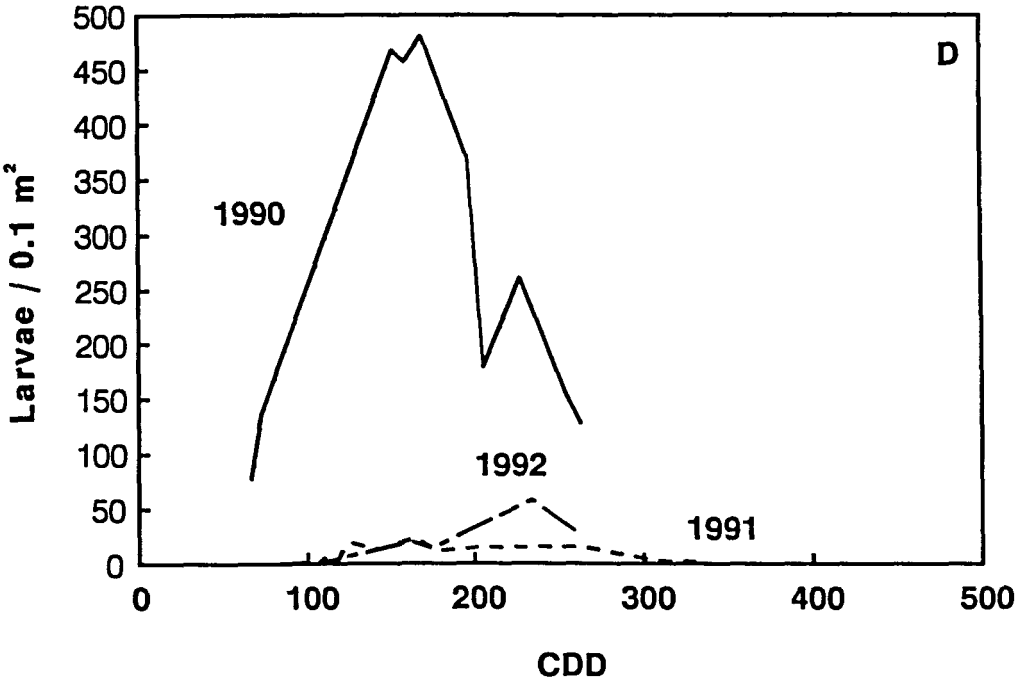
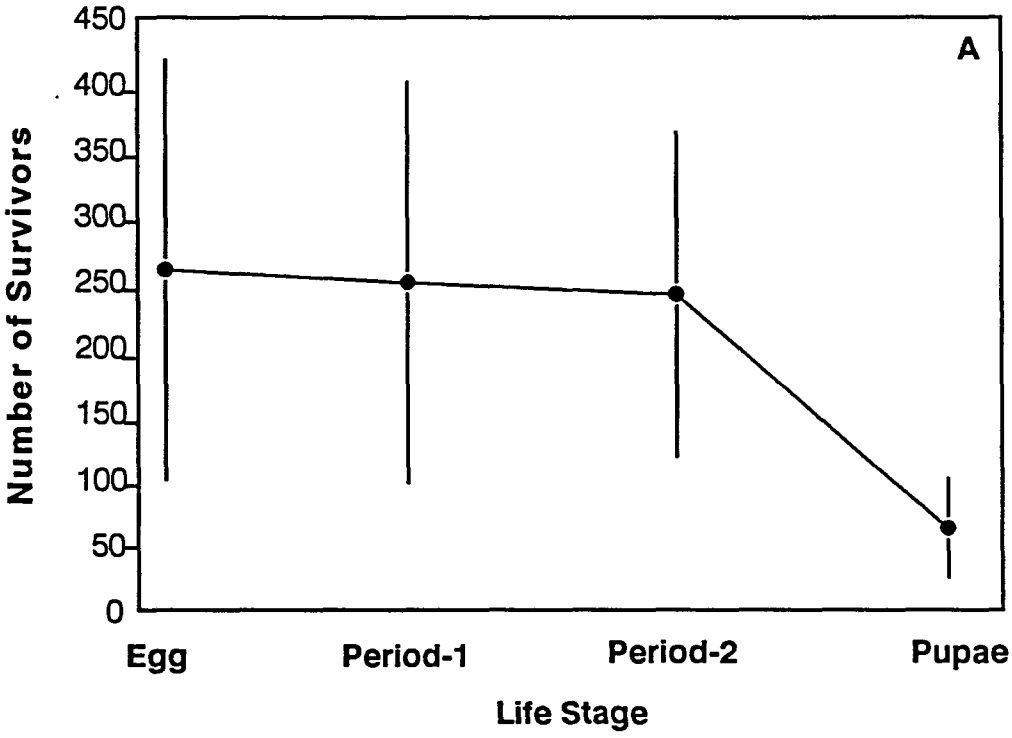

D
1990
1992
1991
Larvae / 0.1 m²
CDD
0
50
100
150
200
250
300
350
400
450
500
0
100
200
300
400
500

Fig. 2 Survivorship curves of the alfalfa weevil. Each curve represents the average of the study locations for each year (1990, 1991, and 1992). Standard errors of the means are shown as vertical lines.

(A) 1990

(B) 1991


A
450
400
350
300
250
200
150
100
50
0
Number of Survivors
Egg
Period-1
Period-2
Pupae
Life Stage

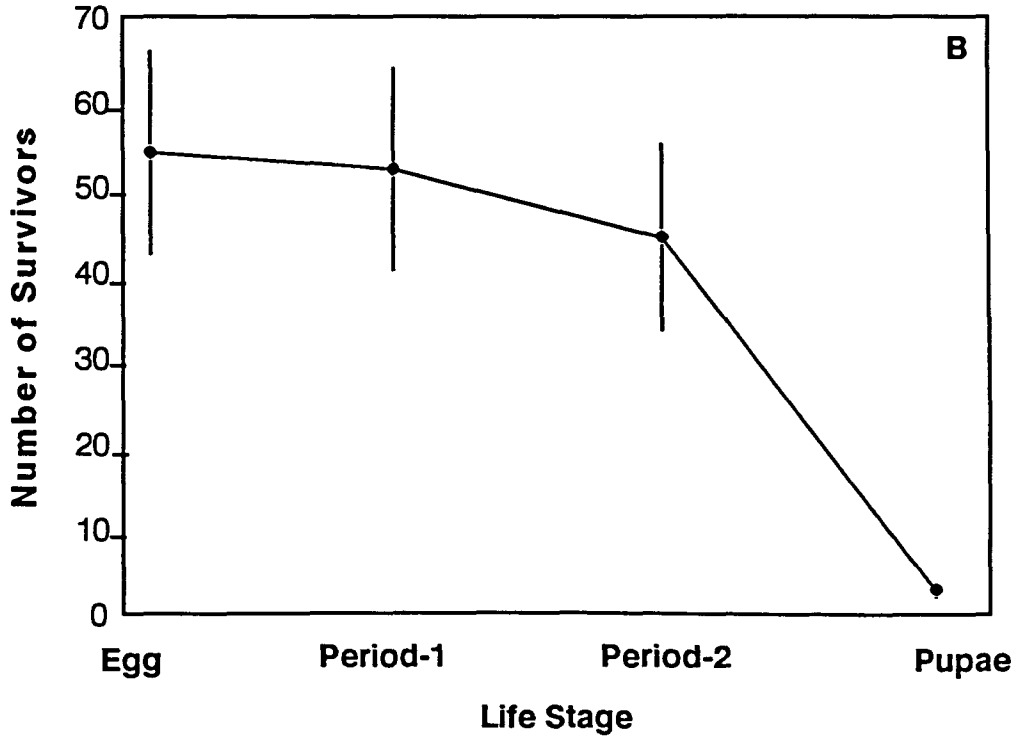

B
70
60
50
40
30
20
10
0
Number of Survivors
Egg
Period-1
Period-2
Pupae
Life Stage

Fig. 2 (continued); (C) 1992.

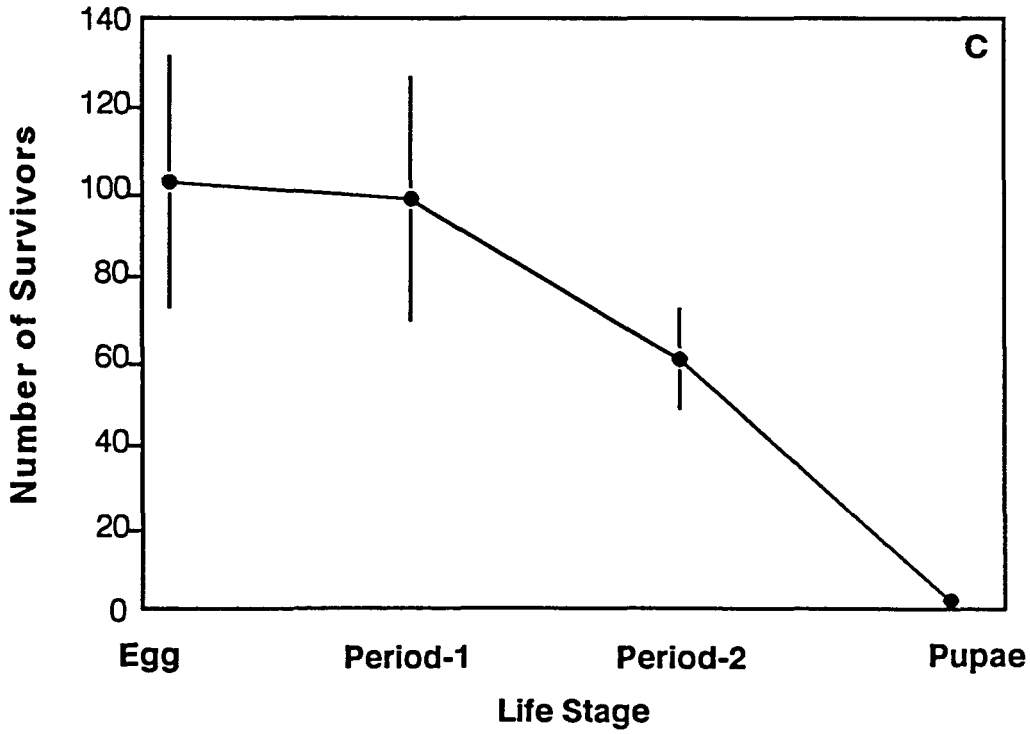

C
140
120
100
80
60
40
20
0
Number of Survivors
Egg
Period-1
Period-2
Pupae
Life Stage

Fig. 3 Determination of the key factor using the graphical method for comparing individual stage mortalities with total mortality at 4 Iowa sites in 1991 and 1992. The individual mortality (k_i) with the fluctuations most similar to the total morality (K) was determined as the key factor or factor that contributes most to change in population density.

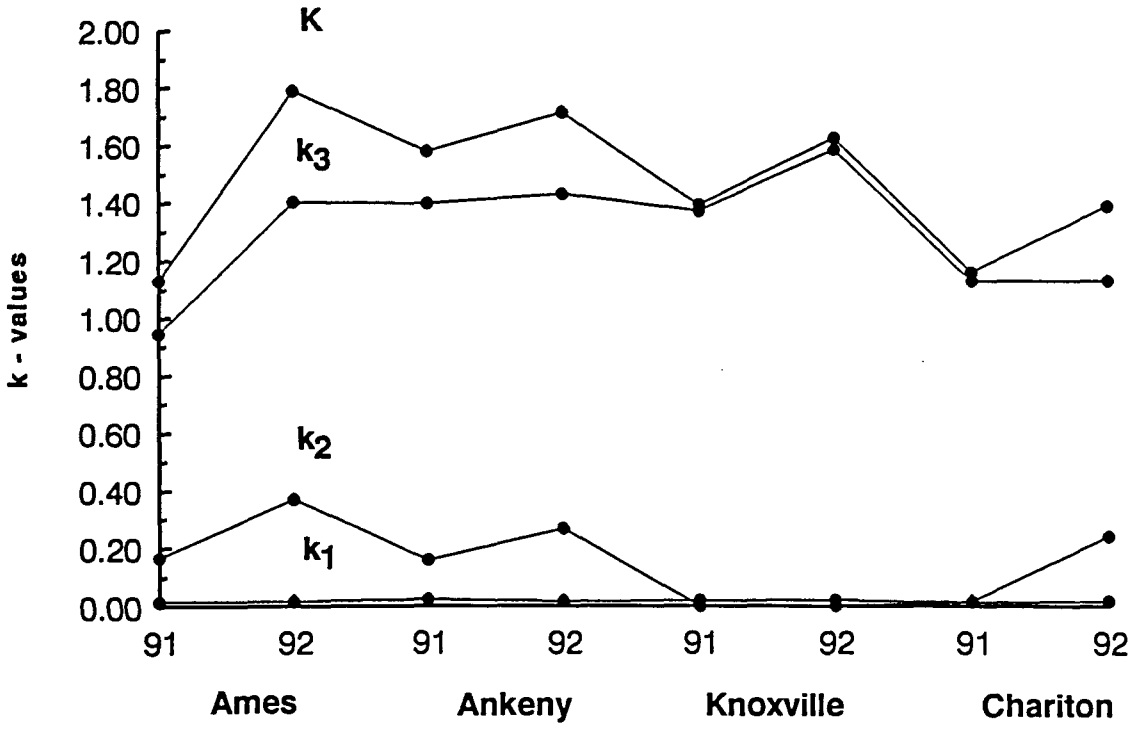

K
k_3
k_2
k_1
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
k - values
91
92
91
92
91
92
91
92
Ames
Ankeny
Knoxville
Chariton

Fig.4 Determination of the key factor using the statistical method for regressing individual stage mortalities against total mortality at 4 Iowa sites in 1991 and 1992. The individual mortality with the slope closest to unity was determined as the key factor.

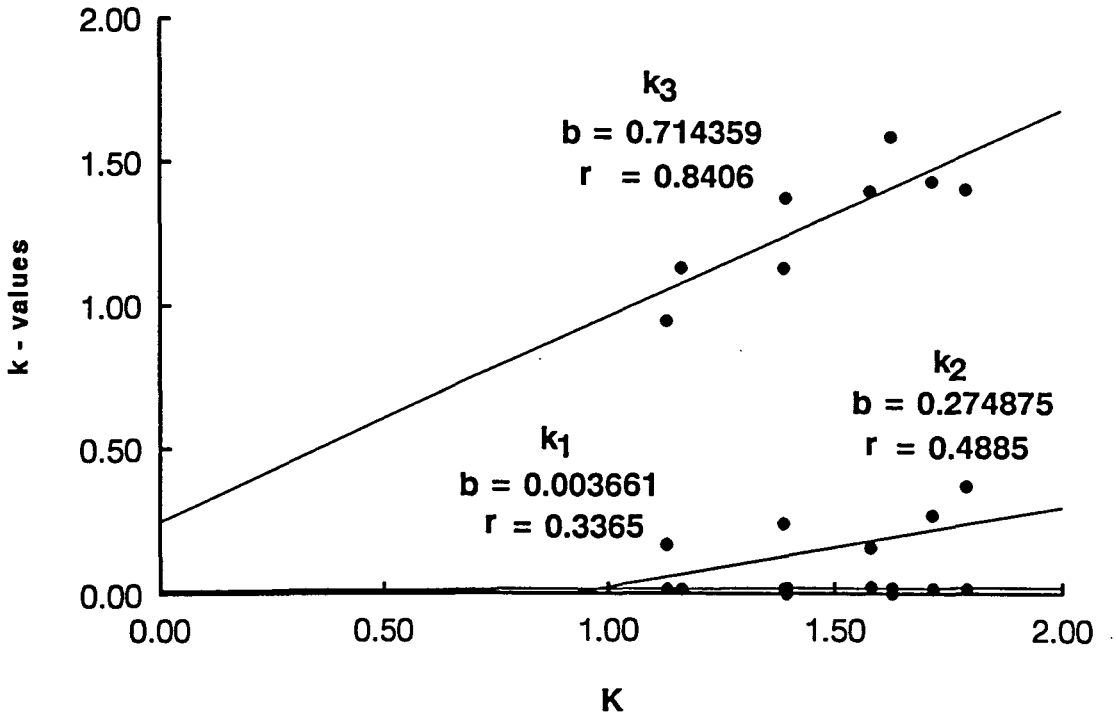
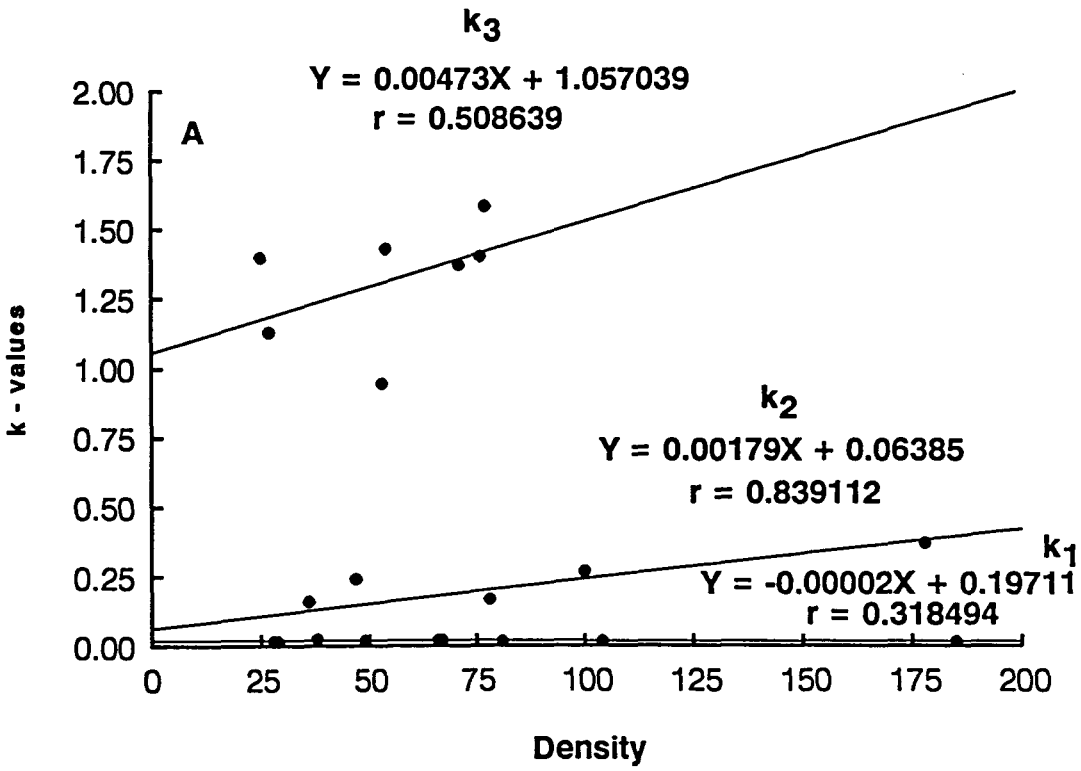
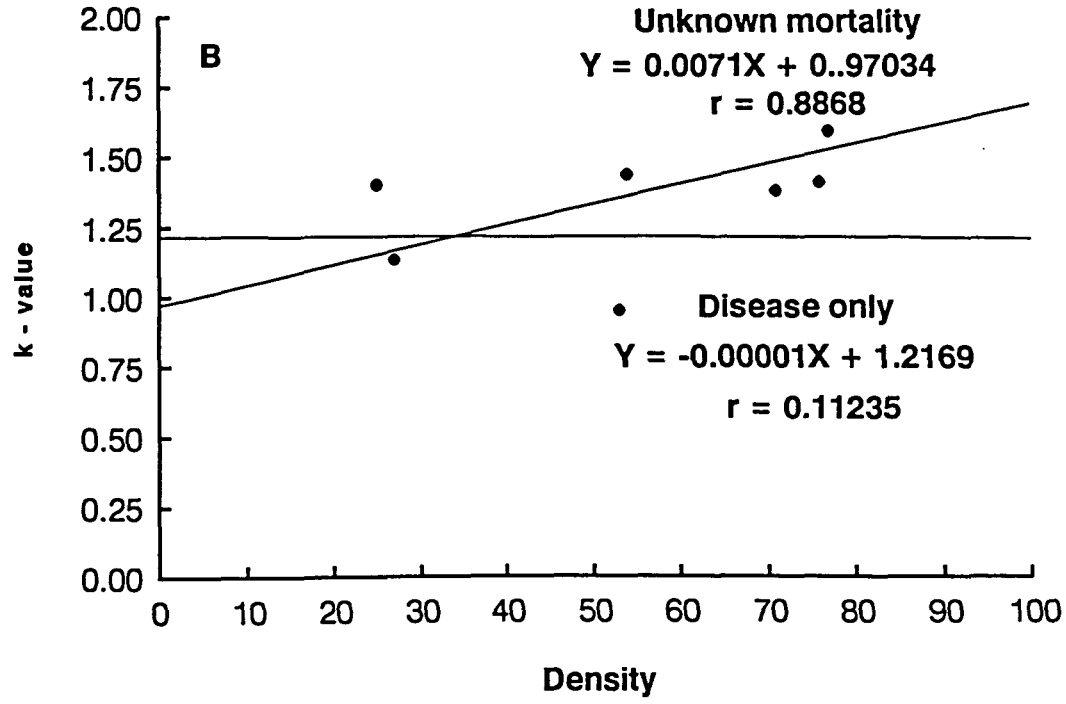

2.00
1.50
1.00
0.50
0.00
k - values
0.00
0.50
1.00
1.50
2.00
K
k3
b = 0.714359
r = 0.8406
k2
b = 0.274875
r = 0.4885
k1
b = 0.003661
r = 0.3365

Fig.5 Density relationships of the stage interval mortality factors.

A) Individual submortalities (k-values) were regressed against density (*lx* values) upon which they act.

B) The individual submortality, k_3, separated into two of its mortality components, disease and unknown factors and regressed against *lx* densities.


k3
Y = 0.00473X + 1.057039
r = 0.508639
A
k2
Y = 0.00179X + 0.06385
r = 0.839112
k1
Y = -0.00002X + 0.19711
r = 0.318494
k - values
Density
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
0
25
50
75
100
125
150
175
200


B
Unknown mortality
Y = 0.0071X + 0..97034
r = 0.8868
Disease only
Y = -0.00001X + 1.2169
r = 0.11235
k - value
Density
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
0
10
20
30
40
50
60
70
80
90
100

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GENERAL SUMMARY

Phenology Study

From this study, it was determined that fall and winter oviposition occurs in the central and southcentral parts of Iowa. However, there was greater oviposition in the fall and winter at the Knoxville and Chariton sites, as demonstrated by the greater densities of AW larvae that were present earlier in the spring growing season. A comparison of AW and alfalfa phenology showed that the timing of peak larval density occurs when alfalfa plants are less developed at the more southern Knoxville and Chariton sites relative to the more northern Ames and Ankeny sites within this transitional region. Not only do these findings suggest that there are phenological differences within this transitional region, but they also demonstrate that there is a greater potential for large, damaging densities of AW due to these combined factors with declining latitudes in Iowa.

The Illinois alfalfa weevil management program was validated for Iowa and found inadequate for determining initiation of sampling in the southern part of the state. Based on this study, management guidelines were refined to improve alfalfa weevil management in the central and southcentral regions of Iowa.

Population Dynamics Study

Life table analysis showed that mortalities occurring during the period-2 larval interval were the key factor or factor most responsible for within-generation population change. The fungal pathogen, *Z. phytonomi* (Arthur) was an important mortality factor during this interval in 1991. Other unknown factors, including establishment loss, predation, and heavy rainfall, were more important mortality factor in 1992. These unknown factors had a density dependent relationship with the alfalfa weevil. Two larval parasitoids, *Bathyplectes curculionis* (Thomson) and *Bathyplectes. anurus* (Thomson) caused only a small percentage of mortality during both years of this study.

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Appendix- Mean larval density per 0.1 m^2 collected at three field sites in 1990 and four field sites in 1991 and 1992.

Field sites	Year	Day-Month	Degree Days [a]	No. Larvae/ 0.1 m^2
Ames	1990	18-Apr	63 (145)	0
		28-Apr	155 (311)	8
		02-May	163 (325)	17
		07-May	182 (359)	55
		10-May	209 (409)	48
		17-May	243 (469)	59
		21-May	268 (514)	50
		24-May	282 (540)	72
		29-May	316 (601)	74
		31-May	336 (636)	77
		04-Jun	370 (698)	63
Ames	1991	18-Apr	96 (205)	0
		21-Apr	100 (212)	0
		25-Apr	109 (229)	2
		28-Apr	127 (261)	2
		02-May	145 (293)	8
		07-May	152 (305)	10
		11-May	181 (357)	17
		16-May	249 (480)	47
		20-May	285 (545)	82
		23-May	319 (607)	68
Ames	1992	23-Apr	81 (178)	0
		05-May	145 (293)	7
		09-May	165 (329)	8
		14-May	216 (421)	49
		20-May	274 (526)	76
		27-May	341 (645)	91
		31-May	361 (682)	47
		05-Jun	404 (759)	35
		08-Jun	436 (816)	8
Ankeny	1991	18-Apr	98 (209)	0
		21-Apr	101 (214)	2
		25-Apr	106 (223)	3
		28-Apr	121 (249)	5
		02-May	140 (284)	6
		07-May	149 (300)	6
		11-May	170 (338)	23
		16-May	236 (457)	30
		20-May	273 (523)	32
		23-May	301 (573)	2
		28-May	368 (695)	1

Appendix (continued)

Field sites	Day-Year	Degree Month	No. Larvae/ Days [a]	0.1 m ^{2}
Ankeny	1992	23-Apr	67 (153)	0
		05-May	122 (251)	7
		09-May	138 (280)	17
		14-May	188 (371)	50
		19-May	229 (444)	51
		23-May	264 (507)	35
		27-May	292 (557)	37
		04-Jun	344 (651)	24
		07-Jun	377 (710)	26
Knoxville	1990	12-Apr	68 (155)	27
		18-Apr	76 (168)	38
		28-Apr	163 (326)	68
		02-May	172 (342)	53
		07-May	189 (373)	69
		10-May	216 (421)	55
		14-May	227 (441)	38
		17-May	251 (484)	48
		21-May	275 (527)	32
		24-May	288 (550)	30
		29-May	328 (623)	11
		31-May	346 (654)	6
Knoxville	1991	03-Apr	58 (137)	0
		07-Apr	97 (207)	1
		11-Apr	118 (245)	1
		14-Apr	120 (248)	0
		18-Apr	131 (268)	1
		21-Apr	135 (275)	3
		25-Apr	143 (289)	10
		28-Apr	164 (327)	11
		02-May	184 (364)	16
		07-May	197 (387)	28
		11-May	229 (445)	45
		16-May	298 (569)	55
		20-May	337 (638)	27
		23-May	377 (711)	2
		28-May	461 (862)	3
Knoxville	1992	16-Apr	90 (194)	0
		23-Apr	107 (225)	4
		05-May	176 (349)	14
		09-May	196 (385)	19
		16-May	266 (511)	54

Appendix (continued)

Field sites	Year	Day-Month	Degree Days [a]	No. Larvae/ 0.1 m^2
Knoxville	1992 (cont.)	19-May	300 (572)	37
		23-May	354 (669)	22
		27-May	362 (684)	40
		02-Jun	399 (750)	27
Chariton	1990	12-Apr	67 (152)	77
		18-Apr	73 (164)	136
		28-Apr	152 (305)	468
		02-May	159 (319)	457
		07-May	170 (338)	481
		10-May	197 (386)	370
		14-May	206 (403)	178
		17-May	228 (441)	261
		21-May	255 (491)	155
		24-May	264 (508)	128
Chariton	1991	07-Apr	77 (170)	0
		11-Apr	107 (225)	1
		14-Apr	110 (230)	6
		18-Apr	118 (245)	3
		21-Apr	122 (251)	16
		25-Apr	127 (260)	19
		28-Apr	142 (288)	14
		02-May	164 (327)	24
		07-May	178 (352)	12
		11-May	201 (393)	15
		16-May	264 (507)	16
		20-May	306 (582)	4
		23-May	336 (636)	2
		26 May	374 (706)	2
Chariton	1992	09-Apr	50 (122)	0
		16-Apr	78 (173)	1
		23-Apr	103 (218)	2
		30-Apr	109 (229)	2
		05-May	161 (321)	21
		09-May	175 (347)	15
		16-May	234 (453)	59
		19-May	262 (503)	28

[a] Number of degree-days (base ^{o} C) accumulated since 1 January at each site.