AN APPROACH TO ALFALFA WEEVIL MANAGEMENT IN MICHIGAN

Thesis for the Degree of M. S.
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RICHARD A. CASAGRANDE
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AN APPROACH TO ALFALFA WEEVIL MANAGEMENT IN MICHIGAN

By

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INTRODUCTION

The alfalfa weevil, <u>Hypera postica</u> (Gyllenhal) (Coleoptera, Curculionidae), has been a serious pest of alfalfa in the United States since 1904 when it was first introduced near Salt Lake City, Utah (Titus, 1907). It spread throughout the west but was never found east of the Great Plains until 1950 when it was discovered in Maryland (Bissell 1952). The east coast population spread much more rapidly than the western one, and this difference, in addition to several others noted by Blickenstaff (1965), Koehler and Gyrisco (1961), and Armbrust et. al., (1970) indicates the two strains were possibly introduced from different areas of Europe (where it is native). The first report of the alfalfa weevil in Michigan was in 1966 (Dowdy 1966). Since that time it has spread rapidly throughout the state and by 1971 was present in potentially damaging numbers throughout the entire lower peninsula.

The alfalfa weevil is the most serious pest of alfalfa in Michigan, primarily because of larval feeding damage. Larvae skeletonize the leaves and reportedly have the potential to destroy a stand if large numbers are present after a field is cut by continually eating back the new growth.

To date alfalfa weevil damage in Michigan has been reduced primarily by insecticide use. Of Michigan's 1.25 million acres of alfalfa, 206,000 acres were treated with pesticides for weevil control in 1970 (Anonymous, 1971) at a cost of 8 - 12 dollars per acre for materials, equipment, and labor (Janes and Ruppel, 1969), not including an unknown cost to the environment associated with the production, distribution, and side effects of these pesticides.

My overall objective has been to develop an effective management program for the alfalfa weevil in Michigan which would minimize insecticide use and provide for satisfactory alfalfa production. To this end I have spent three field seasons studying the weevil. The first (1969) was devoted primarily to learning about the weevil, the crop, and the parasites and developing objectives and sampling techniques for further research. The 1970 season provided sound information on the life history of weevils and parasites with relation to cropping practices and allowed for the development of a preliminary management scheme which was implemented and evaluated in 1971.

It is not the intent of this thesis to provide a chronological record of these three years of research. Instead I am presenting only those results which are pertinent to the development, implementation, and evaluation of the management program in the hope that this might provide the basis for a state-wide program and suggest means for evaluation and subsequent refinement of such a program.

DESCRIPTION OF FIELDS STUDIED

In 1970 two fields were studied, one at Gull Lake, and one at Collins Road. Both were mature stands of Vernal alfalfa and neither had been treated with insecticides for at least one year. The field at Collins Road was a fairly clean, dense stand of alfalfa, situated on level ground. A 100 X 200 foot research plot was located near its center. The Gull Lake field was of similar density with slightly less weeds and was situated on a slight south slope, although the research plot selected within this field (100 X 200 foot) was on relatively level ground. On 26 May one half of the Gull Lake plot was cut, leaving the remainder of the field uncut, and on 28 May the Collins Road plot was similarly cut. Neither field showed any degree of larval feeding damage at cutting date.

In 1971 all research was conducted at Gull Lake. Three fields were selected for close study. Field A, the same field studied in 1970, was a somewhat sparse, four year old, stand of Vernal alfalfa about three acres in size. Field B was a two year old stand of Saranac alfalfa, somewhat denser than field A and 2.5 acres in size. Field C was a three acre stand of one year old Saranac alfalfa that was of moderate density and vertually free of weeds, the latter feature being in marked contrast with the other fields. Field C was sprayed on 30 April with malathion to kill ovipositing adult weevils, thus establishing a low density of eggs.

On 28 May 25% of field B was cut in the form of a strip (fifteen feet wide) extending for the length of the field. On 3 June another such strip was cut in field B and fields A and C were cut as well. In the center of field C a strip eight feet wide was left uncut, extending from one end of the field to the other. In field A a similar strip was left in the center (measuring three feet wide) and a three foot strip was left uncut along each of two sides of the field as well. Fields B and C showed a very slight degree of larval feeding damage at the time of cutting, but field A was considerably damaged.

LIFE HISTORY IN MICHIGAN

Obviously the first step in the development of a pest management program is a complete knowledge of the life history of the pest. The life history of the alfalfa weevil was reasonably well understood in 1969 as outlined in Extension Bulletin E-639 (Janes and Ruppel 1969). This was based on some limited field observations and on projections based on data collected in neighboring states (particularly Ohio). Since the basic biology of the weevil was known, I was able to concentrate on those specific aspects influenced by Michigan's northern climate.

Alfalfa weevils are active in the very early spring and have been observed in flight even on warm winter days (Prokopy and Gyrisco 1965). I have not observed any such activity in Michigan before mid-April, however considerable evidence of a much earlier period of flight activity has been observed for three consecutive years. During the first week in April of 1969, large numbers of alfalfa weevils were observed on the sand dunes along the Lake Michigan shoreline in Berrien County (D. L. Haynes, pers. comm.). On 8 April and 27 April, 1970 I made similar observations at the same location and on 1 April, 1971, I again found large numbers of weevils on the sand at Grand Haven, Michigan. A week later I returned to

Grand Haven, finding weevils there and at several other locations as far south as Holland, Michigan. These weevils were apparently flying on the warmer days of late March and early April and were concentrated at the shoreline by the cold air over the water.

In 1970 and 1971 several of these weevils were collected and returned to the laboratory for observation. It was found in both years that, although they fed readily on greenhouse alfalfa immediately after their capture, no oviposition occurred until two weeks after the initiation of feeding. Weevils which were given water but no food did not oviposit at all despite the availability of suitable oviposition sites. Since no alfalfa was yet available in the field when these weevils were collected, it was concluded that a feeding period was required before oviposition could occur.

This was found to be in agreement with Snow's observations (1928) that sexual maturation of diapausing overwintering alfalfa weevils does not occur until they feed after breaking diapause.

Samples taken in research plots at the Entomology Research Station on Collins Road in East Lansing, Michigan (hereafter referred to as Collins Road) and at the Kellogg Gull Lake Laboratories Experimental Farm in northeastern Kalamazoo County, Michigan (hereafter referred to as Gull Lake) in early April, 1970, showed that most alfalfa weevils did not overwinter in the alfalfa fields. According to Hamlin et. al., (1949) and Manglitz (1958) many alfalfa weevils overwinter in woods, hedgerows, and field borders. These overwintering weevils apparently fly about on warmer days and, after the first new growth occurs in the alfalfa fields, begin to concentrate in these fields. As shown in Figure 1, weevils were first found in the Gull Lake alfalfa field in 1970 on 17 April (the first sample date after the new alfalfa growth began). Although the weevils were present in the field on 17 April, no significant oviposition was observed until 30 April despite suitable oviposition sites in dead stems from the time of their arrival. Similarly in 1971, although the new green alfalfa was available as early as 8 April, no oviposition was observed until 20 April. This seems to indicate that the weevils in alfalfa fields, like the weevils from Lake Michigan, require a feeding period before oviposition begins.

Once oviposition begins, the egg density increases quite rapidly and the peak egg density occurs about the third week of May (Figures 2 and 3) after which the rate of hatching exceeds that of oviposition and egg density subsequently declines to nearly zero by late June. As these eggs hatch, the first instar larvae begin feeding on the alfalfa buds but cause little noticeable damage to the crop. The first visible damage occurs just before the time of the peak larval density

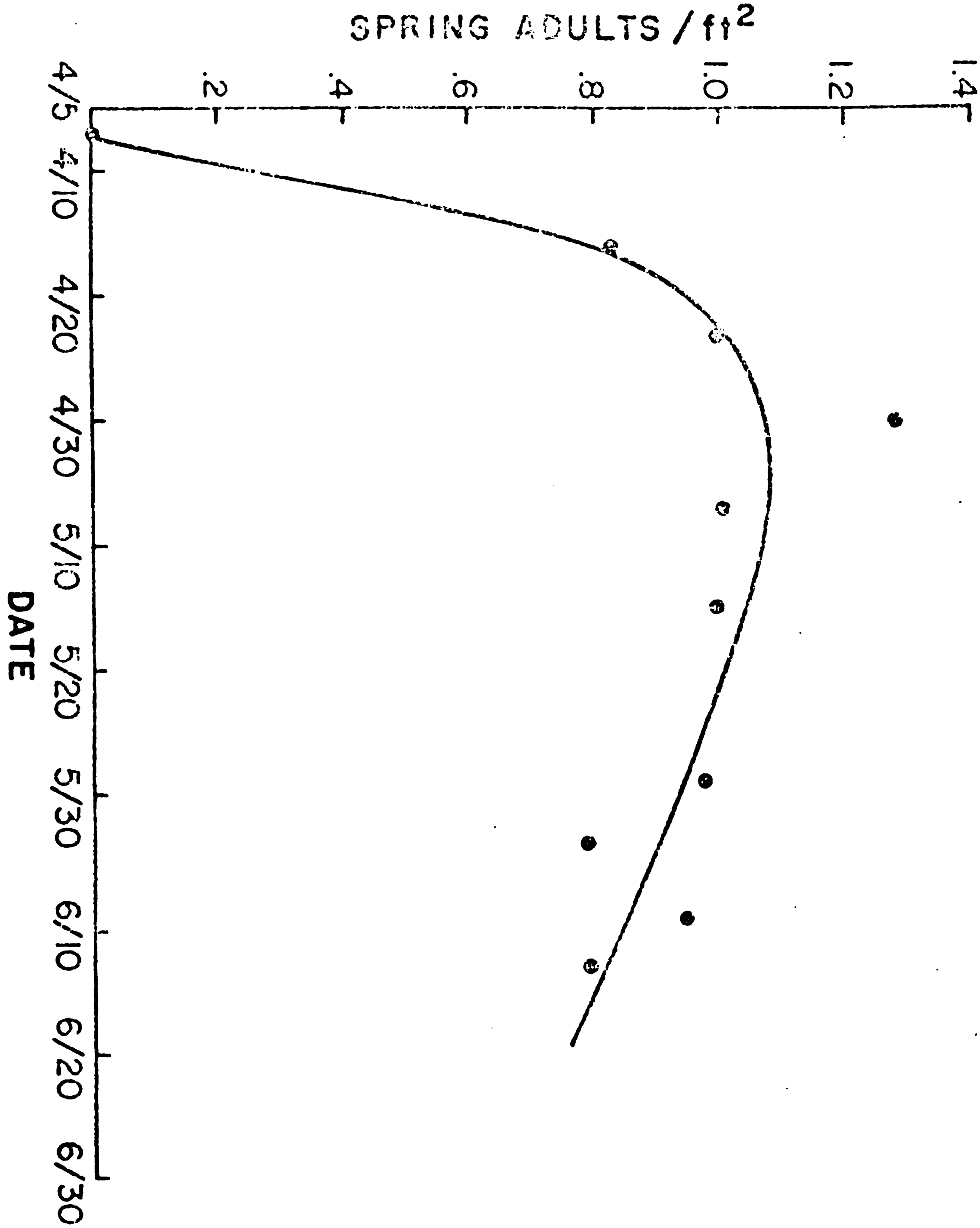

Figure 1. --Density of adults in the alfalfa field studied at Gull Lake in 1970.

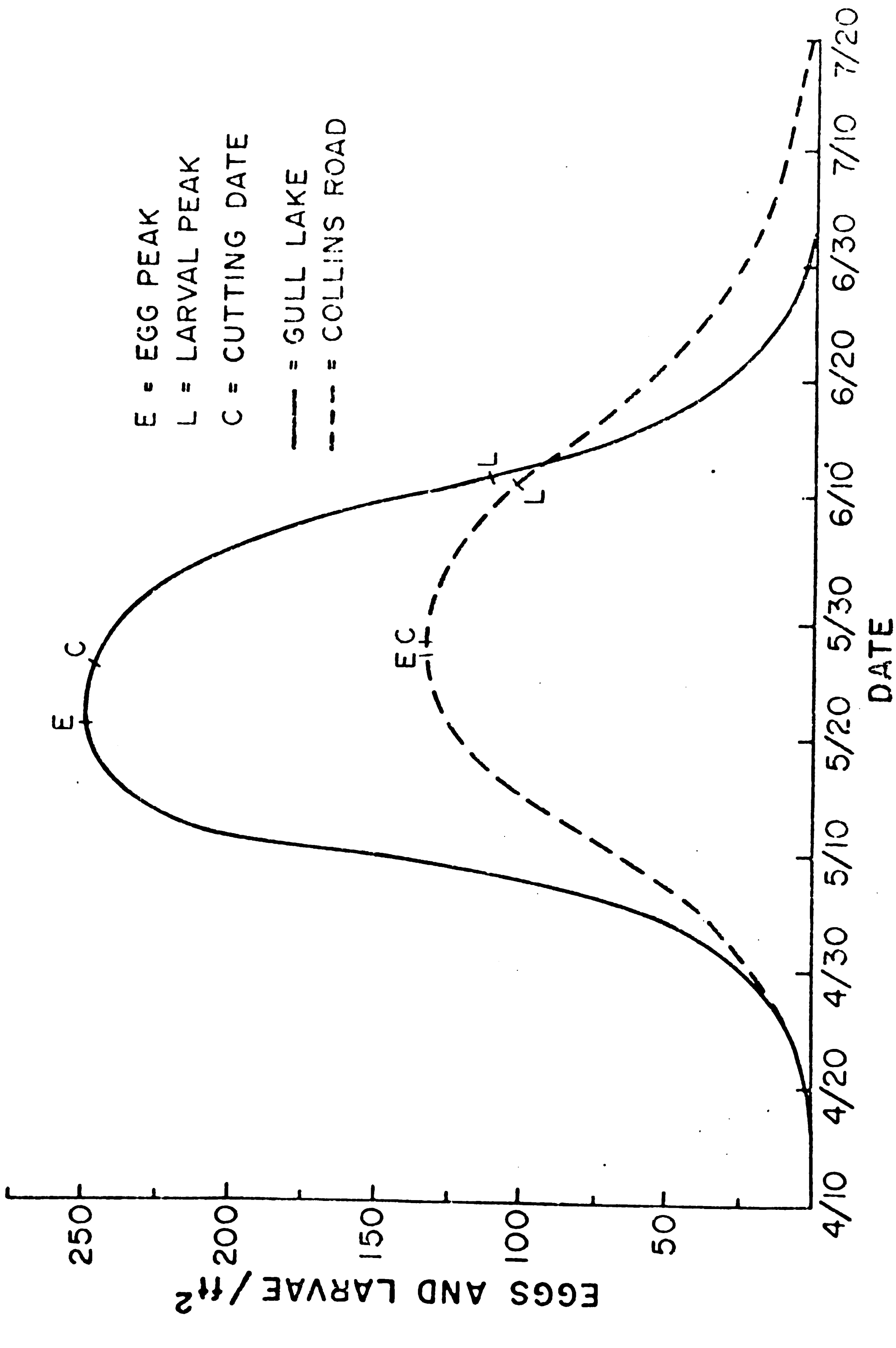

Figure 2. --Density of eggs and larvae combined throughout the 1970 season.

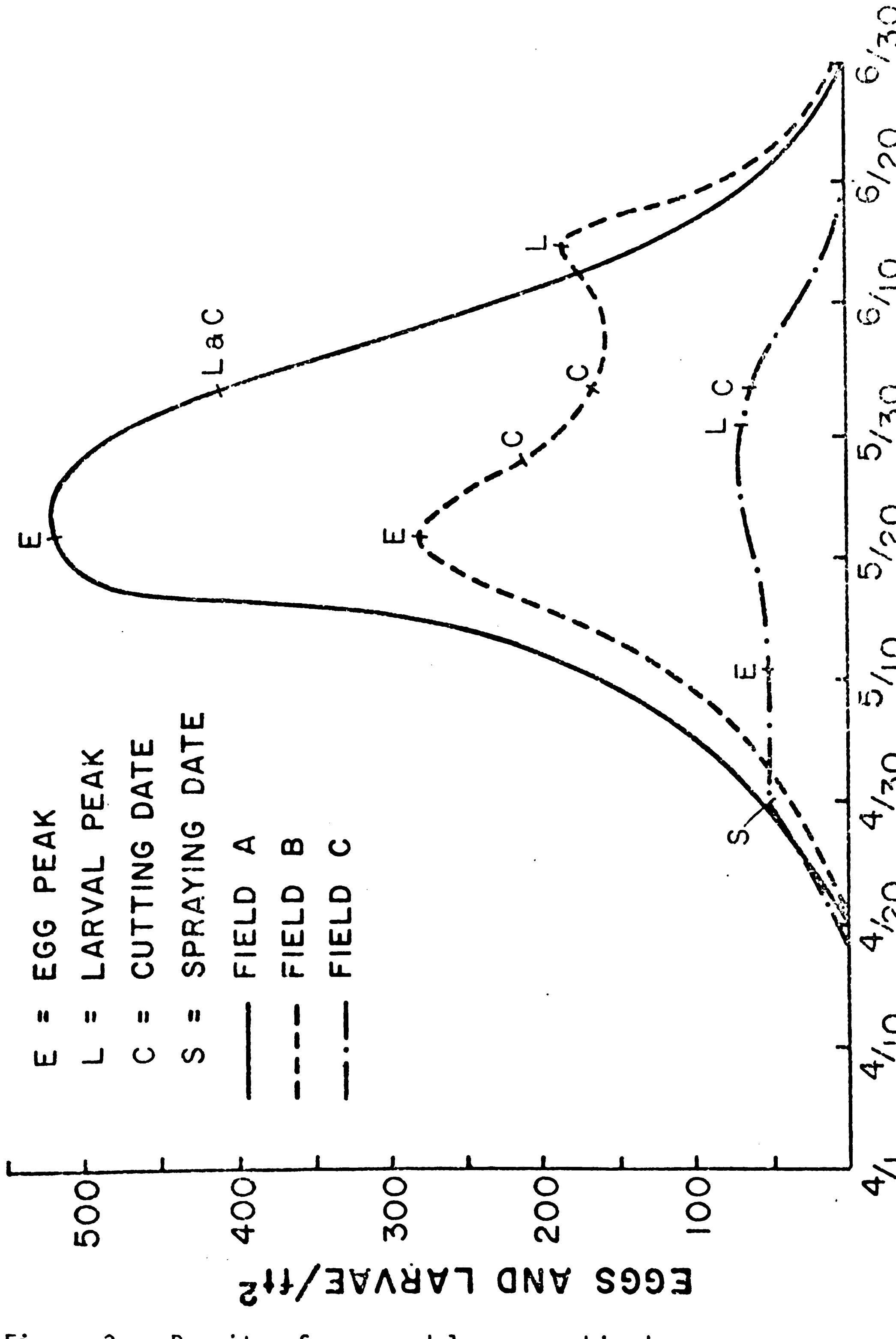

Figure 3. --Density of eggs and larvae combined throughout the 1971 season.

(about the first to second week of June at these sites) when the earliest larvae reach the third and fourth instars and begin eating a great deal. Larvae pass through four instars in about two weeks and pupation lasts about five days. After emergence adults feed for a few days and leave the field, not to return until the following spring.

It should be noted that the dates given for peak egg and larval densities apply generally to the Lansing and Gull Lake areas and would vary considerably to the north and south. In addition there can be a great deal of variation between even adjacent fields, depending primarily on the density of the stand and the slope of the field. At Gull Lake in 1971, the larval populations in one of the fields with a sparse stand of alfalfa on a southwest facing slope reached its peak twelve days before a level field with a denser stand. Furthermore a field with a steeper southern slope and sparser stand had an even earlier larval population, preceeding the former by approximately one week.

Overwintering Eggs

Of considerable interest to a management program is the question of overwintering eggs. In Delaware adult weevils return to alfalfa fields in the fall, where after feeding for a while they lay considerable numbers of eggs, most of which hatch early the following spring, causing early damage to the alfalfa (Burbutus et. al., 1967). Similar observations have been made in Virginia (Woodside et. al., 1968), New Jersey (Dively 1970) and New York (Armbrust et. al., 1966), but at the more northerly sites, generally fewer eggs were noted to survive the winter. Ruppel and Janes (1969) predicted that only a few overwintering eggs were expected to survive Michigan's winters. But Armbrust (1966) found that in New York overwintering survival varied from 8.8% to 91.6%, depending on a number of factors including snow cover and field location. Townsend and Yendol (1968) noted considerable differences in survival between eggs laid in upright and in lodged alfalfa stems in Pennsylvania. Thus there was considerable evidence that micro-climate was important in determining overwintering survival.

To determine how fall-laid eggs survived Michigan's winters, a fairly comprehensive study was initiated in October, 1969. Ten samples of all the stems in a square foot of alfalfa were taken at the Gull Lake and Collins Road fields twice each month. All stems were split open and the eggs were counted. Also recorded was the viability of eggs, the depth of snow cover on each sample date, whether stems with egg masses were lodged or erect, the height of egg masses in erect stems, and the diameter of stems with egg masses. In addition, percent parasitism of eggs was noted. These observations, which were continued through January, 1970, showed one important fact. In Michigan, alfalfa weevils simply do not oviposit in the fall. The results presented in Table 1 indicate that very few eggs were laid in the fall and of these few, only a small number remained viable through the winter.

Meanwhile, Niemczyk, (1970) published the results of his observations in Ohio. He found considerable fall oviposition and overwintering survival in southern Ohio, but in the north fewer eggs were laid in the fall, and of those laid, relatively few survived the winter.

Subsequent samples I took in mid-April, 1971 showed a continuation of this trend into Michigan. On the Ohio-Michigan border in Lenawee County there was a mean density of 7.9 overwintering eggs/square foot in four alfalfa fields while the mean density at Gull Lake and Collins Road was 2.2 and 1.4 eggs/square foot respectively.

The data I collected, when combined with that presented by Niemczyk, indicates a trend toward less fall oviposition and less winter survival as one moves north. It does not seem surprising that very few eggs survive the cold of the winter, but the reason for decreasing fall oviposition with increasing northerly latitude is less apparent.

A review of the literature suggested several possible explanations but the key factor seemed to be adult diapause. Guerra and Bishop (1962) showed that alfalfa weevil females

TABLE 1. Overwintering Eggs (1969-1970)

Gull Lake				Collins Road			
Date	Eggs/ft^2	Parasites/ft^{2*}	Egg Viability	Date	Eggs/ft^2	Parasites/ft^2	Egg Viability
1 Oct	1.6	0.0	94%	3 Oct	0.8	0.0	100%
15 Oct	0.7	0.0	100%	15 Oct	1.0	0.0	40%
1 Nov	1.3	0.0	-	4 Nov	0.0	0.0	-
14 Nov	2.2	1.3	57%	14 Nov	0.0	0.0	-
2 Dec	0.0	0.0	-	2 Dec	0.0	0.0	-
12 Dec	2.7	2.0	57%	12 Dec	0.0	0.0	-
8 Jan	0.0	0.0	-	8 Jan	0.0	0.0	-
16 Jan	0.8	0.8	0%	23 Jan	1.1	0.0	-
7 Apr	2.5	0.0	0%	10 Apr	0.0	0.0	-
16 Apr	2.7	1.2	4%	17 Apr	0.0	0.0	-
23 Apr	3.0	3.1	0%	24 Apr	0.0	0.0	-

* Anaphes praetensis

undergo a true ovarian diapause. Huggans and Blickenstaff (1964) noted that field populations of weevils consisted of both diapausing and non-diapausing adults and felt that this trait could be selected for. The fact that very few eggs are laid in the fall in Michigan can thus be explained by the selective pressure for diapausing adults exerted by the severe winter. Those few adults which do not enter diapause feed in the early fall and oviposit, but most of these eggs do not survive the winter and the tendency for fall oviposition is selected out. This explanation also seems adequate to explain the gradient in fall oviposition indicated by Niemczyk (1970). In the southern part of Ohio where eggs can survive the winter there is much fall oviposition, but farther north relatively fewer weevil eggs survive the winter, resulting in a shift of the population toward spring oviposition. The majority of weevils in Michigan leave the alfalfa fields shortly after emergence and enter diapause, not to emerge until the next spring. These are comparable to the "ditch bank" weevils which Snow (1928) observed to remain sexually immature until spring.

The length of diapause of those weevils which do undergo diapause was found by Huggins and Blickenstaff (1964) to be determined by the photoperiod exposure in the larval stage. They noted, as did Rosenthal and Koehler (1968), that longer daylength exposure in larvae results in longer diapauses by the adults. There is a one hour difference in daylength between southern Ohio and central Michigan during the peak larval periods on mid-May (Ohio) and mid-June (Michigan) (List, 1951) so it is probable that photoperiod determines diapause and hence time of oviposition. Additional data on photoperiod responses would be interesting, but at present the best estimate of the duration of diapause in Michigan is the 170 days (at twelve hours larval photoperiod) noted by Huggins (1964). A 170 day diapause would be more than adequate to prevent fall oviposition in Michigan, as weevils could not become active until January. After breaking diapause in January these weevils remain sexually immature until after they initiate feeding in April.

Parasites in Michigan

Several parasites have been introduced into Michigan in recent years. Many of these have been recovered and are thought to be established, however by 1971 only *Bathyplectys curculionis* (Thompson) (Ichneumonidae) was present in densities high enough to have any effect on weevil populations. In May of 1970 and early June of 1971 *Microctonus aethiops* (Nees) (Braconidae) was recovered at Gull Lake following releases made in 1969 (Stehr and Casagrande 1971). *Bathyplectys anurus* (Thompson) (Ichneumonidae) and *Tetrastichus incertus* Ratzburg (Eulophidae) were recovered at Collins Road in 1970 following releases in 1969. In addition *Tetrastichus incertus* was also recovered at Gull Lake in 1971 where it was released in 1968.

Two other parasites, which were not introduced into Michigan, were discovered in the research plots. These are both egg parasites and at present do not appear to be of any real significance. In sampling for overwintering eggs many *Anaphes praetensis* (Foerster) were recovered. These are recorded in Table 1 along with the egg density. Since overwintering eggs are not significant in this area of Michigan these parasites probably will not be of much importance, except to add to the already severe selective pressure exerted by the Michigan winter. The other egg parasite recovered, *Patasson luna* (Girault), was recovered in fair numbers from eggs collected in July. This was found to exert up to 60% parasitism on 2 July, 1970 but egg densities are very low at that time. This parasite is described by Brunson and Coles (1968) as primarily a parasite of overwintering eggs and is apparently not very important in Michigan.

METHODS OF COLLECTING AND ANALYZING DATA

In order to intelligently interfere with the life cycle of the alfalfa weevil in the form of a management program, it is necessary to first understand the natural population regulators. Once these factors are understood it is possible to try various manipulations that might reduce weevil populations. Thus it was necessary for me at an early date to develop sampling techniques that would allow for an understanding of the sources of natural control. Subsequently, for evaluating management programs, a long term population dynamics study seems to be the best approach and it is for this purpose that I am presenting a discussion on sampling techniques so that it may provide a ready reference for future research.

Sampling for Eggs

Other researchers have sampled for alfalfa weevil eggs by examining all the stems in a unit area or by sampling a certain number of stems selected at random throughout a field. Results have thus been expressed as numbers of eggs per square foot or as numbers per stem. Both of these sample units seem useful, however they serve different purposes. Numbers of eggs per stem might be adequate for predicting larval damage, and indeed, expressing larval density in terms of stem density might lead to a better understanding of larval competition. However, for a population dynamics study it is advantageous to express the density of all stages in the same units and it does not seem logical to express pupal or adult density as numbers per stem since they are more often found on the ground than on the plants. Samples for all stages were thus taken on a unit area basis and stem density was later recorded.

Since many authors, including Armbrust et. al., (1960), Blickenstaff (1966), and Woodside et. al., (1968) expressed egg density in terms of stems, I found it desirable to determine the relationship between stem and egg density in order to interpret their work and to decide on the proper sample unit. I took 34 square foot samples on 18 June, 1970 at Collins Road and recorded the number of eggs and the number of stems in each. The results (Figure 4) indicate that for the normal range of stem densities, the number of eggs is independent of the number of stems in a sample. Thus eggs are distributed by area and not by stems and it is most reasonable to sample according to the same distribution.

In choosing the proper size area for each sample, I decided to make each sample representative of the alfalfa field as a whole. Since each plant is usually several inches from other plants I found a square foot to be the minimum size sample which provided an adequate representation of spatial distribution of the plants. Furthermore, consideration of

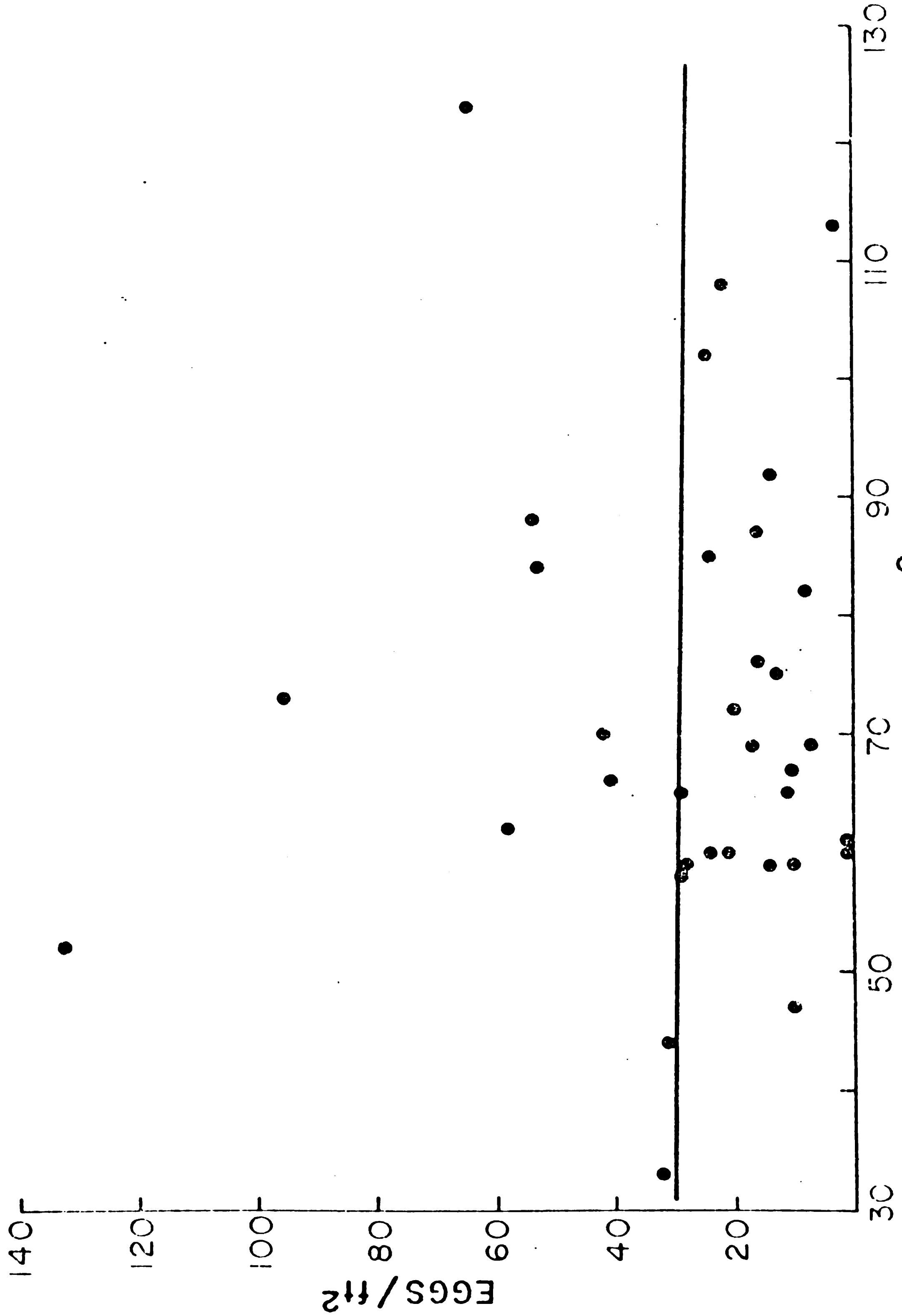

Figure 4. --Relationship between stem density and egg density.

the time and effort required to process square foot samples in light of available resources showed such samples to be practical from an economic standpoint. Thus one square foot was decided upon as the basic sample unit.

Eggs were sampled by removing all stems of all types from the area delimited by a square foot frame placed in a randomly selected location within a plot. Living stems were clipped at ground level and dead stems were also collected and placed in a plastic bag. Stems were later split with a single-edge razor blade and examined for eggs. Data recorded included the numbers of eggs, egg masses, and stems in each sample. Frequent samples of eggs were tested for viability. These were held on moist filter paper in small plastic petri dishes and kept at 75°F. Eggs were treated with .01% captan to retard fungal growth.

Sampling for Larvae

Different methods were used for larval sampling in 1970 and 1971. In 1970 I took one half square yard samples, by placing a sample frame over the foliage, clipping it, and placing it in a plastic bag, taking care not to shake the larvae out. I then placed the samples in large Berlese funnels, each equipped with a 500 watt lamp and collected the larvae in a jar of 70% alcohol for 24 hours. This method of sampling is fast, requires relatively little labor, and provides for consistent results. However, it has a severe shortcoming in that considerably less than 100% of the larvae in the field are counted in a sample. It is not possible to clip and remove the intertwined alfalfa stems from the field without shaking or brushing some larvae from the plants. Careful examination of the ground on two dates revealed that no first or second instars were knocked from the foliage, but 18% of the third and 25% of the fourth instar larvae were lost in this manner. A further reduction occurred with the Berlese funnels from which the percent recovery of the first, second, third, and fourth instar larvae was 27, 90, 70, and 70 respectively. Thus in order to determine the actual density in the field, the results obtained had to be corrected by two factors. This seemed to be a very undesirable means of sampling so in 1971 samples were designed to eliminate these losses and the necessary correction factors.

In 1971 a three-sided (U-shaped) one foot^2 sample frame was constructed of 1/8" x 3/4" flat iron, with a piece of fine white fabric measuring 24" x 24" attached to the back. In taking samples, this frame was slipped between the stems at ground level and the entire square foot of foliage was gently leaned over the cloth, clipped, and placed in a plastic bag. Any larvae which were dislodged from the plants by clipping were easily found on the material and added to the sample. In addition the soil surface and alfalfa crowns within the sample frame were carefully examined and any larvae found were added to the sample. The samples were then returned to the laboratory where each stem was carefully examined and the larvae were removed and preserved in 75% ethyl alcohol. Before discarding the sample, it was individually washed in 95% alcohol to remove any larvae missed. The few larvae which were found were counted and added to the other larvae from the sample.

This method of sampling requires considerably more effort than the method used in 1970, but has the advantage of allowing complete recovery of all the larvae from the field.

Sampling for Pupae

In 1971, the same samples were taken for larvae and pupae. After all the foliage was clipped and placed in the sample bag, the crowns of the plants and the litter were carefully examined for pupae and any found were added to the sample. Samples were then taken back to the laboratory where they were frozen and held until they could be processed by hand and the pupae and larvae counted.

Sampling for Adults

Anyone who doubts the effectiveness of evolution in providing for effective coloration and behavioral adaptations should try sampling for adult alfalfa weevils. For almost seventy years the problems of sampling for adult weevils have hampered researchers in this country. Probably the best technique that I have used for determining absolute adult density involves the use of a square foot metal frame 4" high on each side and sharpened on the bottom edge. The frame is pressed into the soil and adults on the foliage within the frame are shaken off into it and the stems are then clipped at ground level and removed. A very sharp lawn-weeding tool is then used to cut the roots of each plant, the crowns are removed and examined for adults, and the soil within the frame is swept up with a small wisk broom, placed in a plastic bag, and taken back to the laboratory where the adults are separated from the soil by floatation in water. Although this technique has not been used extensively, it seems to be quite effective, particularly if the samples are processed while the adults are still alive.

Adults were not sampled in the 1971 study on age specific mortality because it was thought that pupal density would provide an adequate estimate of adult density. Since there are no pupal parasites, apparently low predation, and low pupal mortality, the large effort involved in sampling for summer adults (particularly with separating emergence from dispersal) seemed not worthwhile.

Precision of Data

Most researchers working on population studies agree that the standard error of a sample should approximate 10% of the mean. This is an arbitrary figure which seems to be a reasonable compromise between accuracy of results and effort required in sampling. In the egg data I collected in 1970 I found that the magnitude of the standard error is dependant upon the magnitude of the mean. Thus to keep the standard error at 10% of the mean it is necessary to take larger samples at low densities than at high. Using the results of 1970, I determined that ten 1 foot^2 samples would provide for quite precise data at the expected peak egg densities. Taking into consideration the time and expense involved in taking and processing each square foot sample, the large number of fields studied and frequency of sampling, I concluded that for 1971 I could not take more than ten samples per field without reducing the number of fields or sample frequency. Although this sample size seemed adequate for high densities, it was not expected to provide great precision at low densities. However, a precise knowledge of density was far more important to me at higher densities then at the low and thus samples consisting of ten square feet seemed to be an adequate compromise between precision and excessive expense. Similarly a constant sample size of ten 1 foot^2 samples was chosen for larvae and pupae with the realization that the results would likely be less precise than the egg data because of lower densities.

Figure 5 shows the means and variances of samples taken in 1971. A regression line fit to the data points on this figure shows the relationship between means and variances to be

$$\log S^2 = 0.3692 + 1.458 \log \bar{X}$$

The variance for a given mean can either be read directly off Figure 5 or calculated according to the equation

$$S^2 = .6234 + \text{antilog}\ (1.458 \log \bar{X})$$

which incorporates the necessary conversion factor for transforming logarithmic data back to arithmetic as described by Bliss (1967).

Table 2 shows the precision of the estimates of peak density in each field for each stage sampled during the 1971 season.

TABLE 2. Precision of Sample Data for 1971 (Standard Errors Expressed as Percentages of Means at Peak Densities)

	Field A	Field B	Field C
Eggs	9.1%	10.5%	16.4%
Larvae	11.2%	12.2%	15.4%
Pupae	19.2%	3.7%	27.5%

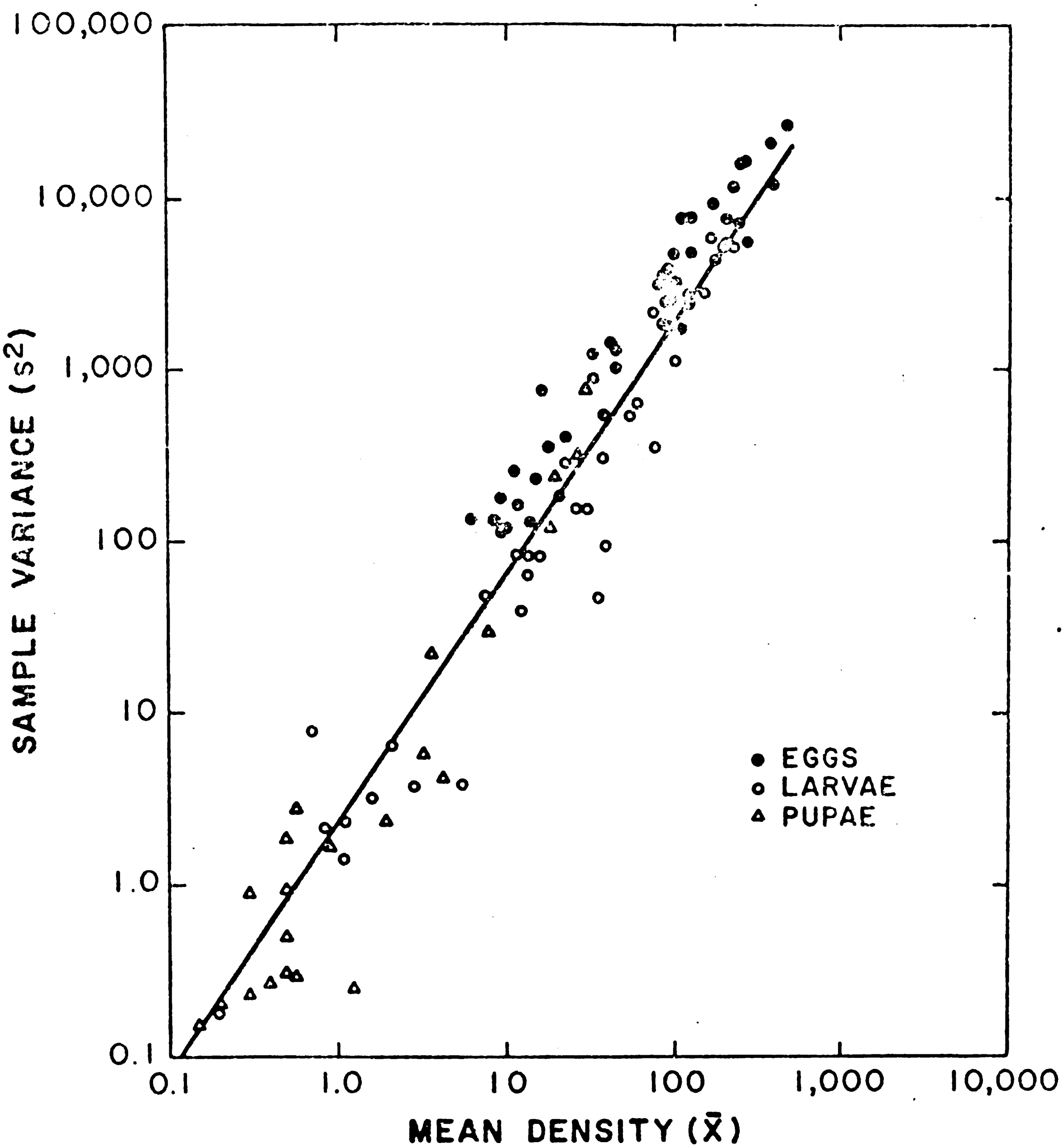

Figure 5. --Variance of samples for immature weevils.

Developmental Times of Eggs, Larvae, Pupae and Parasites

In order to make any calculations on age mortality or to compare densities between fields or years, it is necessary to determine the total incidence for the season of whatever stage is under consideration. I accomplished this by using the method of T. R. E. Southwood (1966) in which the density is plotted on a graph throughout the season and the area under the curve is divided by the developmental time, giving the total incidence per unit area for the season.

Developmental times of alfalfa weevil life stages are readily available in the literature in papers by Sweetman and Wedemeyer (1933), Koehler and Gyrisco (1961) and Roberts et. al., (1970). In addition H. D. Niemczyk kindly provided some additional unpublished egg data that he collected. The combined results of all these sources (presented in Table 3) show that developmental times are determined by temperature exposure. Since field temperatures change dramatically from mid-April to July (and occasionally equally as dramatically from one day to the next), I decided to calculate developmental times in terms of degree days, thus eliminating the variation caused by temperature changes.

In order to calculate degree day requirements, it is first necessary to determine a lower temperature threshold, above which degree days are accumulated. This is typically done by plotting percent development per day over different

TABLE 3. Developmental Times

Temp. (°C.)	Days as Eggs	Days as Larvae	Days as Pupae
6.9[a]	90.5	-	-
10.0[a]	44.5	-	-
12.0[c]	49.3	80.5	37.9
12.8[a]	29.0	-	-
13.3[d]	29.0	-	-
15.0[a]	19.3	-	-
17.0[b]	19.8	28.6	-
18.9[a]	13.0	-	-
20.0[c]	13.4	20.5	11.5
21.1[d]	11.0	-	-
22.0[b]	9.3	15.2	9.9
23.7[b]	8.5	-	-
25.3[b]	7.2	-	-
26.7[d]	9.0	-	-
27.0[b]	6.9	10.6	6.7
28.0[c]	6.0	9.8	6.4
28.7[b]	6.2	-	-
30.3[b]	5.8	-	-
32.0[b]	5.5	8.1	5.1
36.0[c]	5.1	9.6	4.9
37.0[b]	4.0	10.9	-

a Niemczyk and Flessel (1970)
b Sweetman and Wedemeyer (1933)
c Koehler and Gyrisco (1961)
d Roberts et. al., (1970)

temperatures, finding the point at which the regression line crossed the X axis, and defining that point as the lower threshold (that temperature below which no development can occur). This method seems objectionable to me for two reasons. First I do not think one can justify extending a regression line past data points and secondly, I do not think it is biologically meaningful to establish an exact threshold such as 44.5°F. (7.2°C.) (Roberts et. al., 1970) on the assumption that no development occurs below that temperature. It seems quite possible to me that different physiological processes could have different thresholds and hence it might not make sense to establish a fixed threshold.

Thus I decided to use whatever threshold would provide the best results for degree day requirements for each stage. This was accomplished by arbitrarily substituting different thresholds and calculating degree days for each different experimental temperature in Table 3. The mean number of degree days and standard error was then calculated for all temperatures at each threshold and these standard errors were plotted against the thresholds (Figure 6). The bottom point of each curve was associated with the threshold which gave the most consistent results and was thus selected as the lower temperature threshold for development. Thus the thresholds for eggs, larval, and pupal development were determined to be 9°C., 11.5°C., and 9°C. respectively. Using

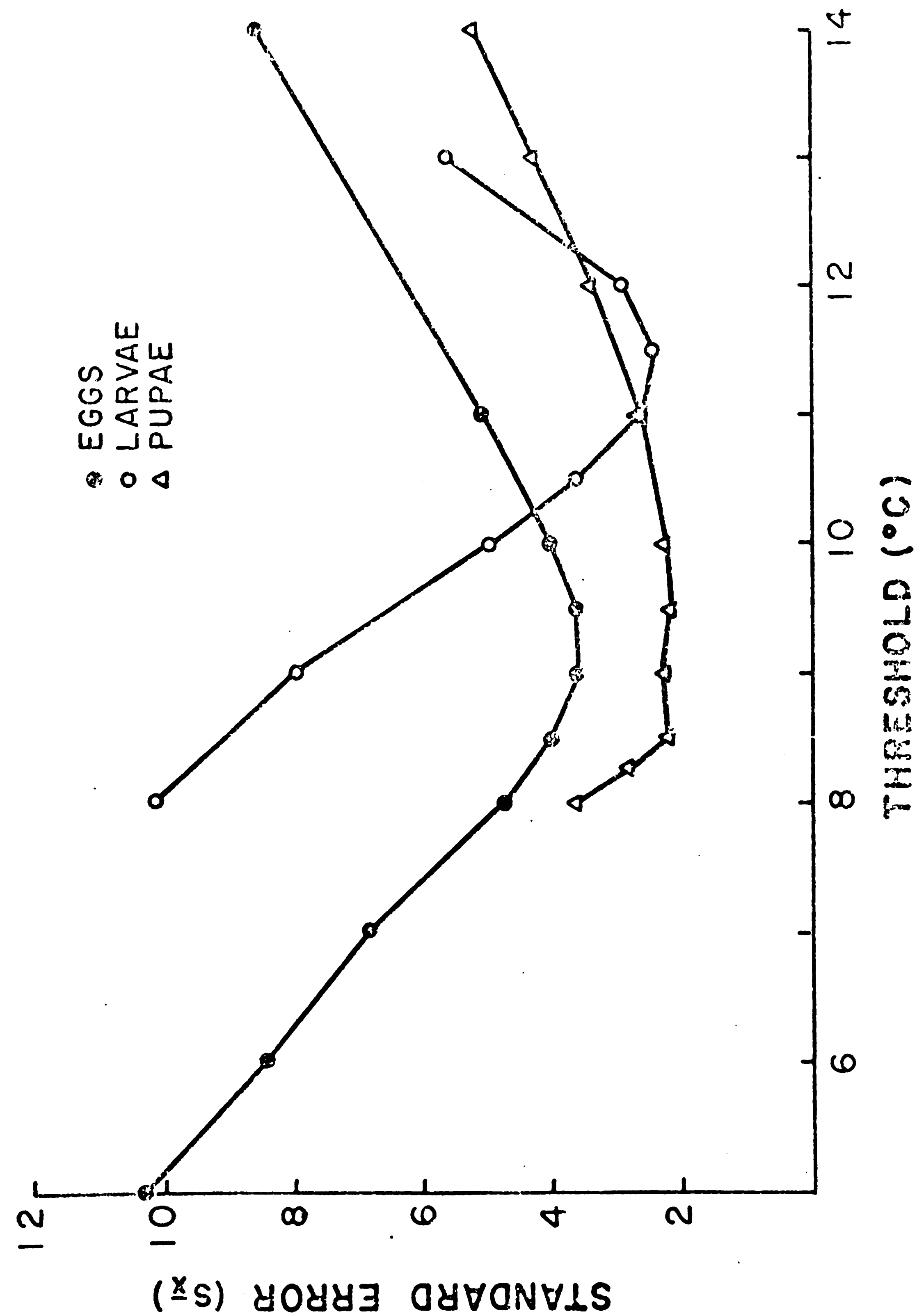

Figure 6. --Standard errors that result from the use of different thresholds in computing degree day requirements from Table 3.

the data again in Table 3, the mean degree day requirements above these thresholds were determined to be 130.6 for eggs, 171.6 for larvae, and 73.8 for pupae.

With this information available, it was then necessary to calculate the rate of degree day accumulation within the fields. Temperature records were kept during 1971 by using a hygrothermograph located at the ground surface within an alfalfa field. Degree day accumulation was calculated from the daily maximum and minimum temperatures by using the sine curve method described by Baskerville and Emin (1969) with a computer program written by Gordon Baskerville (unpublished). Calculations were made by using 48°F. (9°C.) and 52°F. (11°C.) as thresholds and the rate of degree day accumulation for the entire season was determined for each threshold. Unfortunately such hygrothermograph records were not kept during 1970 so I looked up the daily maximum and minimum temperatures for Gull Lake and East Lansing in the Climatological Record (published by the U. S. Department of Commerce). Then using hygrothermograph records for June 1970, measured at the surface of a mixed field of alfalfa and oats by S. H. Gage, I developed conversion factors for converting the standard temperature records to surface temperatures in an alfalfa field. Using the equations:

Maximum temperature at surface = air temperature X .73 + 16.34

Minimum temperature at surface = air temperature X .65 + 22.5

I then corrected the air temperatures from the Climatological Record to the temperatures at the surface of the field and proceeded to determine the rate of degree day accumulation for both thresholds again using the computer program written by G. Baskerville.

The effectiveness of this technique for determining developmental times was checked on two occasions during the 1971 season by inserting freshly laid eggs into alfalfa stems in the field and checking them daily to determine the time until hatch. Eggs laid on 15 May hatched on 26 May (144 degree days later) and eggs laid on 4 June hatched on 12 June, requiring 132 degree days. These values are in close agreement with the predicted requirement of 130.6 degree days for egg hatch.

Not much information was available on the developmental times of larvae parasitized by Bathyplectys curculionis, however Armbrust et. al., (1970) showed that they spend less time in the feeding stage than unparasitized larvae. Using his results I determined that parasitized larvae spend 84% as long in the feeding stage as unparasitized larvae. Using the larval threshold of 11.5°C. I thus determined that parasitized larvae require 144.1 degree days for development as opposed to the 171.6 required for unparasitized larvae.

Methods of Analysis

Cutting an alfalfa field has a complex effect on alfalfa weevils and parasites. It not only causes the removal of eggs and mortality of larvae and immature parasites as described by Hamlin et. al., (1947), but it also causes a reduction in oviposition by both weevils and parasites. In order to evaluate these effects for different cutting dates, I found it necessary to analyze graphs of density plotted against time for each stage in each field. The results, presented in Tables 4 and 5, are the product of this analysis which seems best explained by discussing a complete example.

The total incidence in the uncut portion of field A was calculated by the method of Southwood (1966) which involved measuring the area under the outer curve in Figure 7 (130,952.62 egg degree days) and dividing by the developmental time of eggs (130.6 degree days). The result 1002.7 eggs/foot^2 is the average number of eggs laid in each square foot of field A during the period studied.

Marking the time of cutting (506 degree days) on this curve allowed the determination of density at cutting time, showing that 160.0 eggs/foot^2 were exposed to cutting (16% of the total incidence).

To determine how many eggs hatched before cutting I subtracted the developmental time of eggs (130.6 degree days) from the time of cutting (506 degree days). Thus any eggs

TABLE 4. Results of 1970

	Gull Lake[1]	Collins Road[2]
EGGS		
Hatched Before Cutting Date	332.6	175.3
Exposed to Cutting	230.0	129.5
Removed by Cutting	180.5	86.1
Laid in Cut Part After Cutting	39.2	23.0
Laid in Uncut Part After Cutting	236.7	135.0
Total Incidence in Uncut Part	812.4	434.0
Total Incidence in Cut Part	398.5	232.5
LARVAE		
Pupated Before Cutting Date	0.0	0.0
Exposed to Cutting	12.0	7.5
Killed by Cutting	12.0	7.5
Hatched in Cut Part After Cutting	43.4	45.0
Hatched in Uncut After Cutting	94.7	100.1
Total Incidence in Uncut Part	111.5	105.3
Total Incidence in Cut Part	45.0	43.4

[1]cut on 26 May
[2]cut on 28 May

TABLE 5. Results of 1971

	Field A[2]	Field B[1]	Field B[2]	Field C[2]
EGGS				
Hatched Before Cutting Date	729.2	259.6	436.0	91.1
Exposed to Cutting	160.0	195.0	114.0	4.0
Removed by Cutting	125.0	176.2	78.0	0.0
Laid in Cut Part After Cutting	87.5	74.8	59.8	5.5
Laid in Uncut After Cutting	126.1	151.3	111.9	5.4
Total Incidence in Uncut Part	1002.7	646.5	646.5	99.2
Total Incidence in Cut Part	842.2	359.9	543.6	101.0
LARVAE				
Pupated Before Cutting	44.0	0.0	1.0	3.0
Exposed to Cutting	217.0	24.0	39.2	61.6
Killed by Cutting	118.3	24.0	39.2	35.9
Hatched in Cut After Cutting	16.1	54.2	30.1	3.0
Hatched in Uncut After Cutting	38.7	154.7	120.8	2.9
Total Incidence in Uncut Part	237.1	165.9	165.9	68.5
Total Incidence in Cut Part	76.5	67.1	34.8	23.6
PUPAE				
Emerged Before Cutting	0.0	0.0	0.0	0.0
Exposed to Cutting	0.2	0.0	0.0	0.0
Total Incidence in Uncut Part	87.8	89.2	89.2	31.4
Total Incidence in Cut Part	8.5	5.1	4.1	2.1
PARASITIZED LARVAE				
Pupated Before Cutting	1.0	0.0	2.1	3.0
Exposed to Cutting	15.2	6.8	5.9	9.2
Killed by Cutting	2.7	-	4.9	6.6
Input in Cut After Cutting	12.1	16.0	13.7	1.2
Input in Uncut After Cutting	16.1	36.4	30.9	3.9
Total Incidence in Uncut Part	26.5	40.3	40.3	19.5
Total Incidence in Cut Part	19.9	21.7	17.5	6.6

[1]cut on 28 May
[2]cut on 3 June

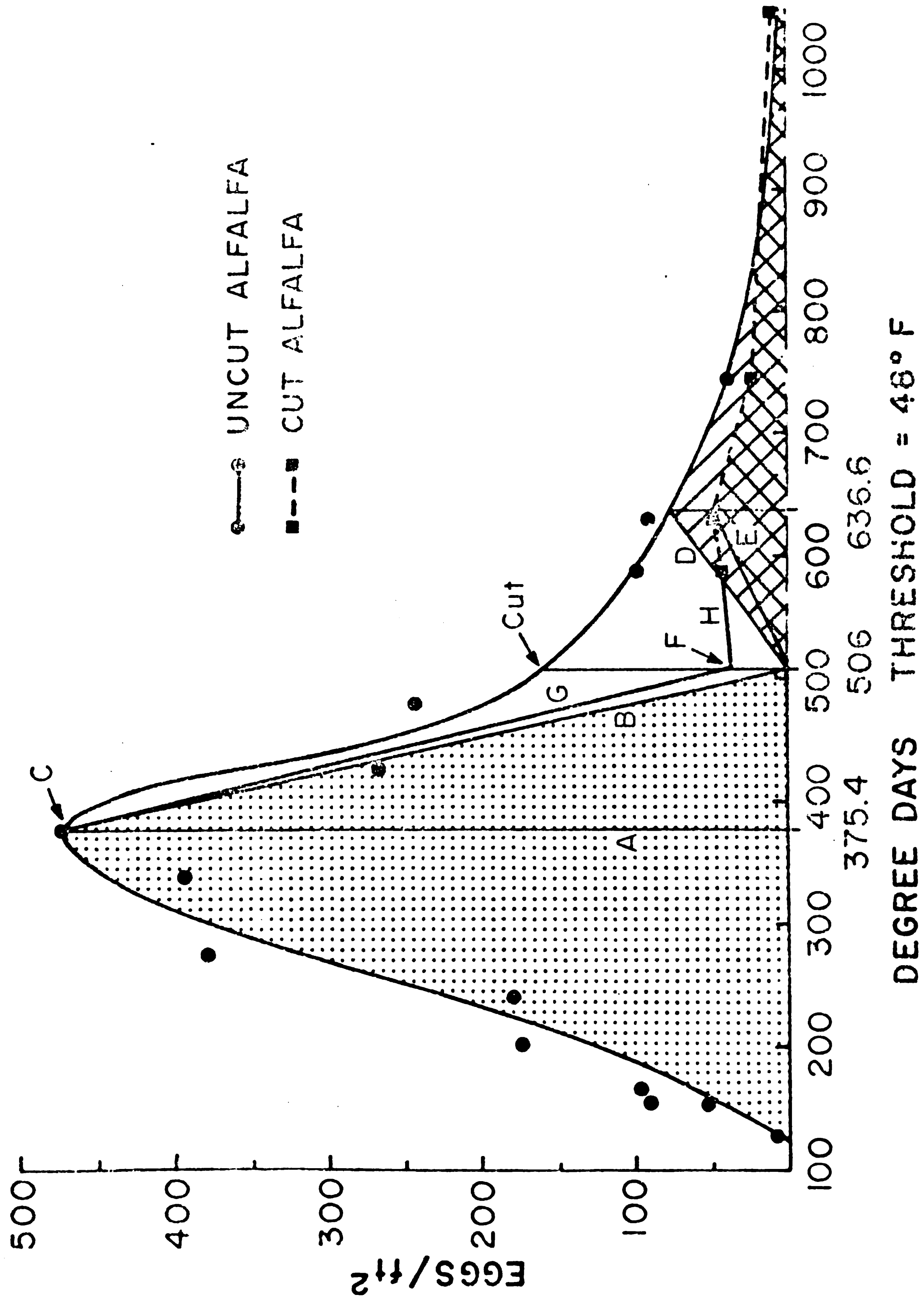

Figure 7.-- Density of eggs in field A throughout the 1971 season.

laid before 375.4 degree days (line A) had time to hatch (130.6 degree days) before cutting. To determine the total incidence of these eggs it was necessary to allow for the hatching of eggs laid before line A and so a line was extended from point C (the intercept of line A and the curve) to zero at 506 degree days (time of cutting). Thus the shaded area of Figure 7 results from eggs which hatched before cutting. Dividing this area (95,233.5 egg degree days) by the developmental time of eggs (130.6 degree days) shows that 729.2 eggs/foot^2 or 73% of the total incidence hatched before cutting and hence were not subject to removal as eggs.

Determination of the numbers of eggs laid after cutting was made in a similar manner. Since the field was cut at 506 degree days and the developmental time of eggs is 130.6 degree days, those eggs present at 636.6 degree days must have been laid after cutting. Line D shows the rate of oviposition from the time of cutting until 636.6 degree days (where it again joins the curve of density versus time in the uncut portion of the field). The area with the cross-hatching slanting to the right (//) (16,468.7 egg degree days) thus shows the amount of oviposition following the cutting date in the uncut portion of the field to be 126.1 eggs/foot^2. Line E similarly shows the rate of oviposition in the cut portion of the field after cutting, and the left-slanting cross-hatched (\\) area (11427.5 egg degree days) shows that 87.5 eggs/foot^2 were laid in the cut portion of the field after cutting.

Calculation of the number of eggs removed by cutting was accomplished by subtracting the egg density measured immediately after cutting (35.0 eggs/foot^2) from the density at cutting time (160.0 eggs/foot^2). Thus 125.0 eggs/foot^2 were removed by cutting (12% of the total incidence).

Finally the total incidence of eggs in the cut portion of the field was determined by plotting the number of eggs left by cutting (35.0 eggs/foot^2) at point F on Figure 7 and connecting points C and F with line G. This line shows the rate of hatch of those eggs laid before cutting which were not subsequently removed by cutting. Line H, which connects point F to the first measured egg density in the cut portion of the field shows the combined effects of oviposition and hatching for the period immediately following cutting. The total incidence of eggs in the cut portion of the field was then calculated by measuring the area under the curve formed by following the curve of density in uncut alfalfa to point C, then along the lines G and H until meeting the first data point for the cut part of the field, and then following the curve formed by connecting the remainder of the data points in cut alfalfa. This showed the total incidence of eggs in the cut alfalfa to be 842.2/foot^2 (84% of the uncut total).

Figure 8 was analyzed in the same manner as Figure 7 to determine the effect of cutting on larvae in field A. The

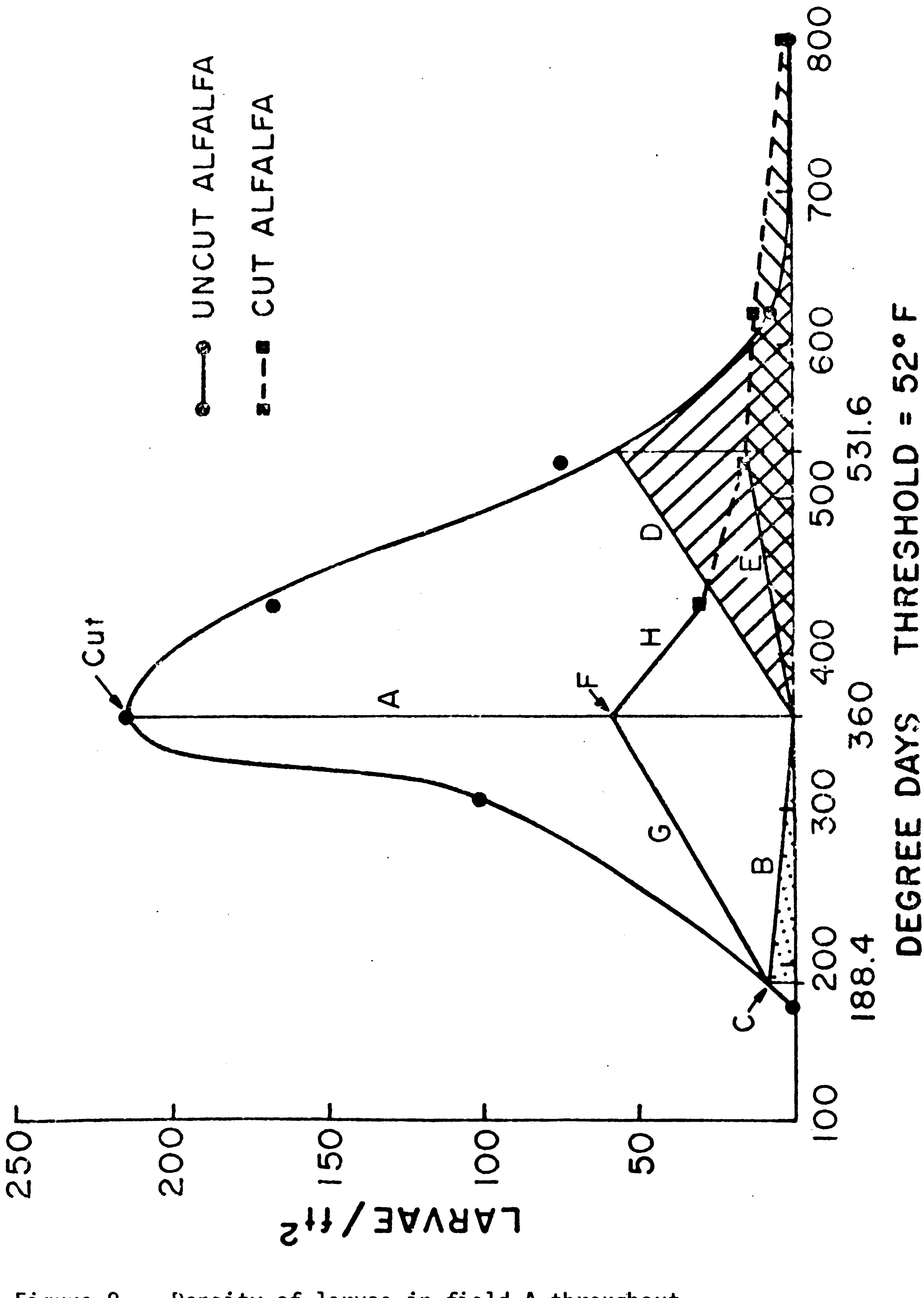

Figure 8. --Density of larvae in field A throughout the 1971 season.

only difference is that it was not possible to immediately measure the larval mortality caused by cutting because this occurs over a period of several days. Thus in order to calculate the number of larvae killed by cutting, the rate of larval mortality was calculated during the four days following cutting for both cut and uncut alfalfa and the difference in mortality between the two was attributed to cutting. This was calculated as follows:

larval density at cutting date	$217.0/ft^2$
larval density in uncut part 4 days later	$167.8/ft^2$
input (of larvae) in uncut part in 4 days	$26.0/ft^2$
output (of pupae) in uncut part in 4 days	$0.8/ft^2$
larval density in cut part 4 days later	$30.0/ft^2$
input (of larvae) in cut part in 4 days	$7.0/ft^2$
output (of pupae) in cut part in 4 days	$1.3/ft^2$

mortality in cut part: $217 - (30 + 1.3 - 7.0) = 192.7$

mortality in uncut part: $217 - (167.8 + .8 - 26) = \underline{74.4}$

larvae killed by cutting: 118.3

Using the total incidence method for larvae provides an estimate of the number of median age larvae which occurred throughout the season (Southwood 1966). This estimate is not to be confused with the number of eggs hatching or fourth instar larvae pupating.

Pupae were relatively easy to work with since virtually none occurred in any of the fields before the cutting dates; hence the total incidence in the cut and uncut portions of field A was determined by measuring the area under the two curves in Figure 9 and dividing by 73.8 degree days (the developmental time of pupae).

The parasitized larvae in Figure 10 were handled in exactly the same manner as the larvae in Figure 8 except that the number pupating in cut and uncut strips during the four days immediately following cutting was considered to be equal.

This assumption was made for two reasons: first of all, no reliable estimate of the rate of parasite pupation was available; and secondly, Hamlin et. al., (1947) showed that almost no parasitized fourth instar larvae are killed by cutting and thus no difference in pupation rate would be expected. Thus the number of parasitized larvae killed by cutting was calculated as follows:

density of parasitized larvae on cutting date	$15.2/ft^2$
density of parasitized larvae in uncut part 4 days later	$10.1/ft^2$
input (of parasitized larvae) in uncut part in 4 days	$6.1/ft^2$
density of parasitized larvae in cut part 4 days later	$3.3/ft^2$
input (of parasitized larvae) in cut part in 4 days	$2.0/ft^2$

reduction in cut part: 15.2 - (3.3 - 2.0) = 13.9

reduction in uncut part: 15.2 - (10.1 - 6.1) = <u>11.2</u>

parasitized larvae killed by cutting: 2.7

Tables 4 and 5 were completed using the same type of analysis just described for each field studied in 1970 and 1971.

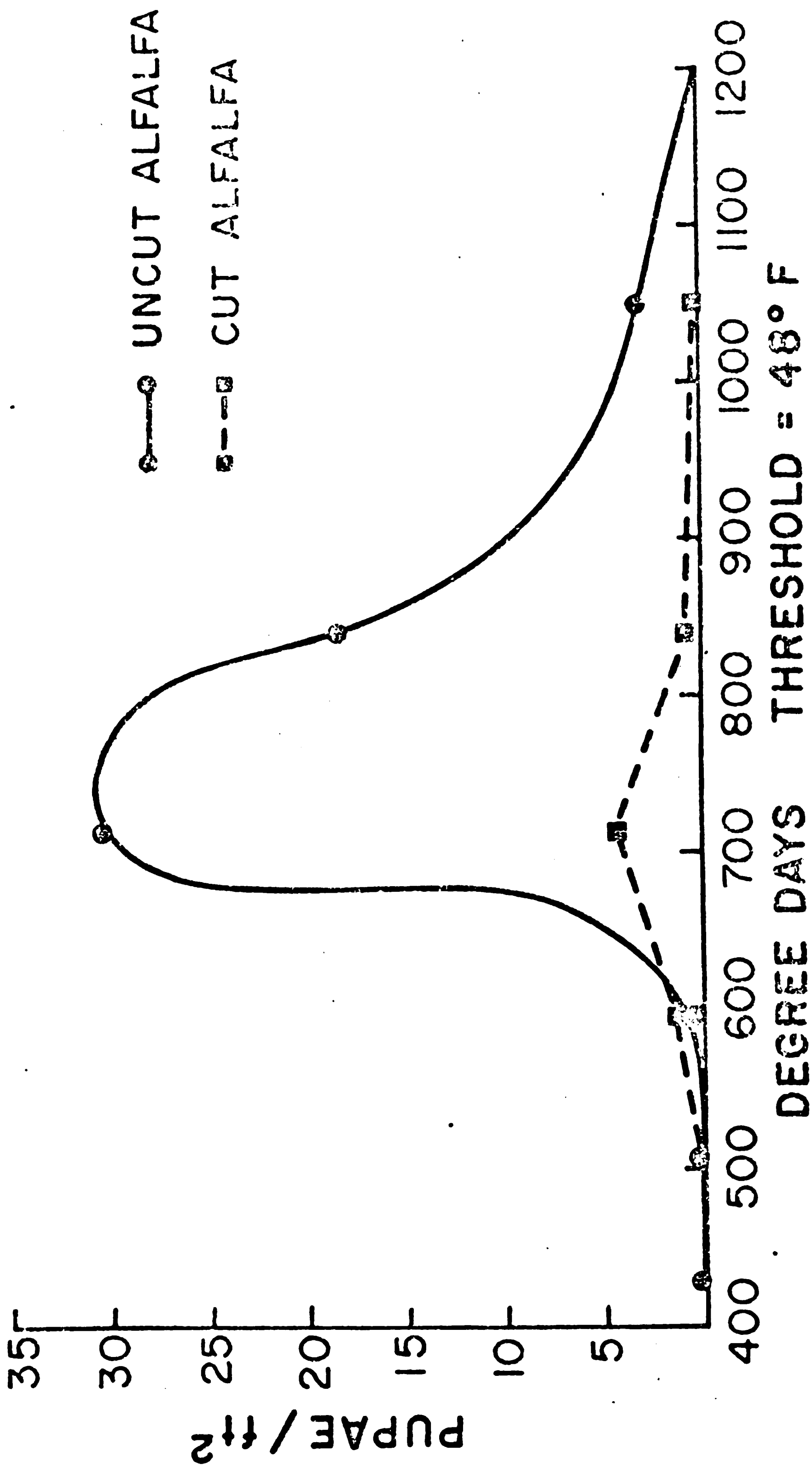

Figure 9. --Density of pupae in field A throughout the 1971 season.

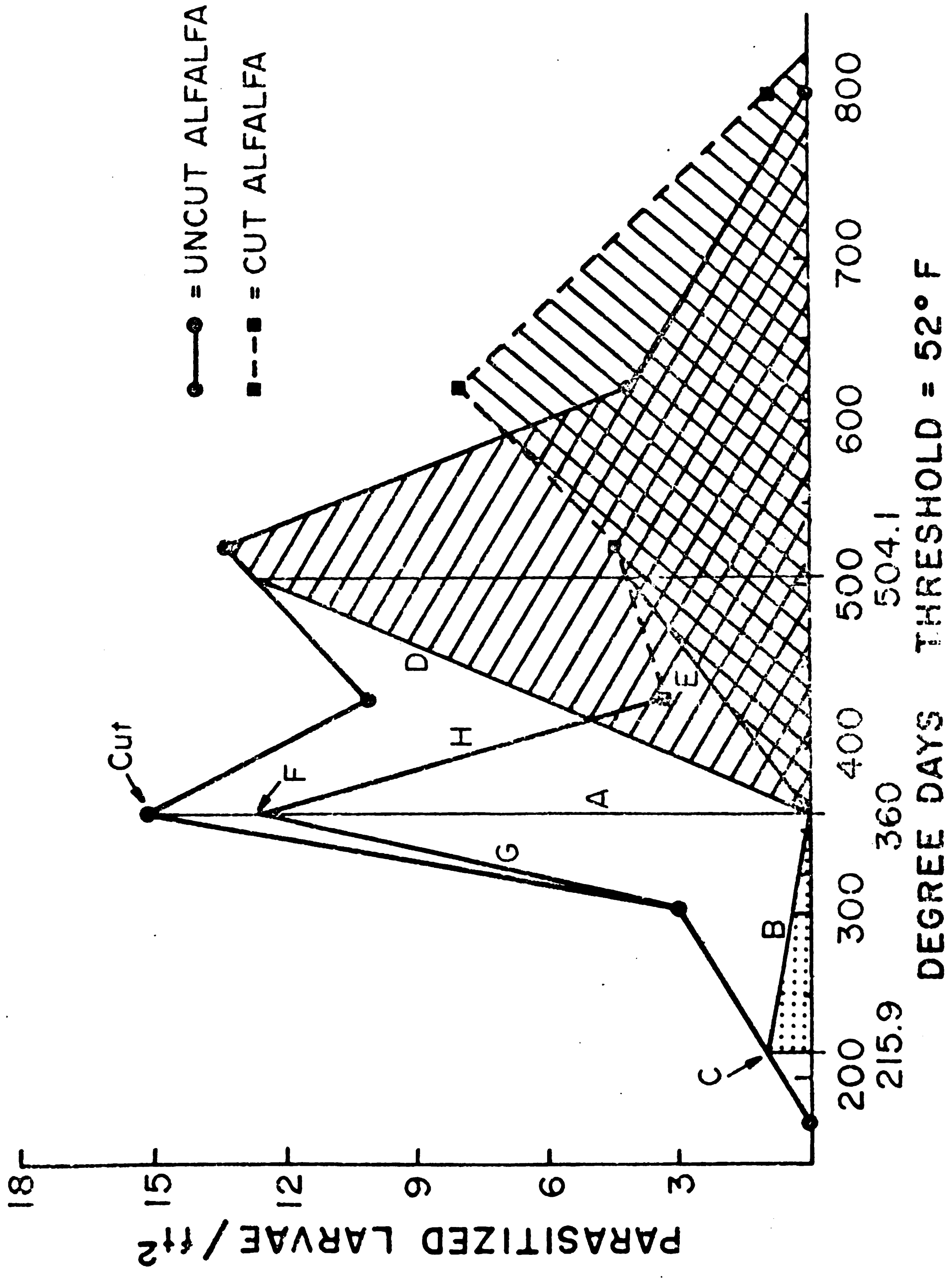

Figure 10. --Density of parasitized larvae in field A throughout the 1971 season.

AGE SPECIFIC MORTALITY

In order to determine and understand the effects of cutting on weevils and parasites, I considered the problem from two aspects. First I studied the uncut strips, determining the interactions of weevils and parasites and the manner in which both responded to density in a situation uncomplicated by cutting. Once these general responses were understood, it was possible to make direct comparisons of mortality in cut and uncut portions of the fields and to interpret the results.

Density Dependant Mortality

Among the uncut strips there was a considerable range of egg densities. From Table 5 it can be seen that the total incidence of eggs in field A was 1002.7 eggs/foot^2 while fields B and C had 646.5 and 99.2 eggs/foot^2 respectively. These differences apparently resulted directly from differences in density of ovipositing adult weevils (12.2, 8.4 and 0.8 per 20 sweeps in fields A, B, and C respectively, on 24 May). Of these eggs there was a density dependant survival to median age larvae of 23%, 26%, and 69% in fields A, B, and C respectively. An even further reduction occurred in the number of pupae where the pupal densities were 9%, 14%, and

32% of the egg densities in fields A, B, and C respectively. The total incidence of pupae in fields A, B, and C (87.8, 89.2, and 31.4 respectively) further shows the extent of density dependant larval mortality since field B produced more pupae than field A despite the much greater egg density in field A.

The total incidence of larvae parasitized by <u>Bathyplectys curculionis</u> (26.5, 40.3, and 19.5 in A, B, and C respectively) reflects to a greater extent the same larval mortality and also a difference in density of ovipositing adult parasites (3.3, 2.0, and 0.8 per 20 sweeps in fields A, B, and C respectively on 24 May).

Effect of Cutting on Weevils

Total egg density is reduced by cutting because eggs are removed and oviposition is reduced following cutting. As seen in Figure 2, in 1970 both fields were cut very near the peak egg densities. As a result approximately 20% of the total incidence of eggs in uncut alfalfa was removed in the cut portions of the field. Of even greater importance in reducing the total incidence in the cut portion of the field was the reduction in oviposition caused by cutting which accounted for a further reduction of 25%.

Cutting parts of field B on two different dates in 1971 showed that the time of cutting is important in determining egg reduction. Figure 3 and Table 5 show that cutting near the peak egg density causes a greater removal of eggs and a greater reduction in oviposition than does cutting at a later date. As a general rule, the longer the period between peak egg density and cutting date, the smaller the reduction of egg density caused by cutting. Field C, which was cut long after the peak egg density (Figure 3) actually produced more eggs in the cut than in the uncut part.

In addition to causing a reduction in egg density, cutting an alfalfa field causes larval mortality. Not only are larvae mechanically killed by the cutting process, but they are also subjected to heat, desiccation, and starvation following cutting. Hamlin et. al., (1947) found that nearly all first and second and many third instar larvae are killed when a field is cut during hot, dry weather. In 1970 all the larvae present on the cutting dates in both fields were killed by cutting. Since cutting in that year took place near the time of peak egg density, which preceeded the peak larval density by two weeks, there were very few larvae present at cutting time and almost all of these were early instars.

In 1971 parts of field B was cut on two different dates, both times well in advance of the peak larval density (Figure 3). At both cutting dates all larvae present were killed, although a relatively small number were present at the time of cutting. Cutting at peak larval density in field A exposed the greatest number of larvae (92% of the total uncut incidence), but only 73% of them were killed. When field C was cut after the peak larval density (Figure 3) 90% of the total uncut larval incidence was exposed to cutting but only 59% of them were killed.

In summary, when cutting is made early, a greater percentage of exposed larvae are killed than when cutting is made at or past the peak of larval density. However, when the field is cut late a greater number of larvae are exposed to cutting and although a smaller percentage may be killed, the total mortality caused by cutting is actually greater. Thus the greatest number of larvae were killed by cutting at peak larval density.

In 1971 cutting had little direct effect on pupae since no pupae were yet present at the cutting dates (except field A which had 0.2/foot^2). Thus the differences in pupal density between cut and uncut parts of fields are attributed to the direct effects of cutting on eggs and larvae.

Effect of Cutting on Parasites

Hamlin et. al., (1947) found that although cutting causes a large reduction in populations of alfalfa weevil larvae, it causes somewhat less of a reduction in the numbers of larvae parasitized by *B. curculionis*. This occurs because most parasites are found in larger larvae (Hamlin et. al., (1947) and Brunson and Coles (1968) which are much more likely to survive cutting than the smaller larvae (Hamlin et. al., 1947).

This was generally found to be the case in the fields studied at Gull Lake in 1971. For example, in field A 73% of the larvae present on the cutting date were killed by cutting but of those larvae which were parasitized, only 17% were killed.

The rates of parasitism in the cut and uncut parts of the fields indicate that after cutting adult parasites were more active in the uncut strips than in the cut parts of the fields. In the three fields studied in 1971 an average of 43% as many larvae were parasitized after cutting in the cut parts as in the uncut strips.

MANAGING ALFALFA

In 1970 several fields surrounding my research plot at Gull Lake were cut about ten days earlier than the one I was studying. All of these fields required repeated insecticide applications. The fields that I cut at East Lansing and Gull Lake both grew back with little alfalfa weevil damage without insecticide treatment and another one at Gull Lake cut the same day as mine grew quite well with only a single stubble spray.

Similarly at Gull Lake in 1971 one field was cut on 20 May and another on 23 May. These fields were not closely studied, but were very near field B, and were of similar stand density and were planted on level ground so field B probably serves as a reasonable indicator of weevil activity in these fields. As can be seen from Figure 3, egg density was very near its peak at cutting time, however there were very few larvae yet present in the field. As a result, when the field was cut, many eggs were removed and probably all the larvae present were killed and the fields started regrowing without damage. However in two weeks most of those eggs left in the stubble had hatched and had produced sufficient numbers of large larvae to cause considerable damage to the alfalfa when it was 5-6" high. These fields were thus sprayed to reduce larval damage.

The three fields under close study in 1971 were cut at considerably later dates than in 1970 with respect to weevil activity (Figure 3) and all of them grew back without any significant damage to the second crop. Field A, however, was probably cut a little too late because it started showing signs of considerable larval feeding a few days before cutting. Since most eggs and early instar larvae are killed by cutting, the greatest kill of weevils could be accomplished at a time when the population of eggs and early instars is the greatest. This seems to be well after the egg peak and probably near the peak larval density. However by the time the larval density reaches its peak, many larvae have become quite large and start noticeably damaging the field. Furthermore, cutting at a later date does not utilize the reduced rate of oviposition following cutting.

Thus the problem seems to be in deciding between cutting early and having damage to the second crop and cutting late and having damage to the first. There is a period between these extremes when it is possible to avoid damage altogether as occurred in fields B and C in 1971 and in both fields in 1970. At the time these fields were cut, larval damage was just becoming apparent. This damage had not reached a degree where it could be of any economic importance and yet it was certainly greater than the damage caused by larvae coming from occasional overwintering eggs. In each of these fields the damage in the uncut portion became progressively worse after cutting date and after about two weeks the crop was very severely damaged with the exception of field C in 1971 which had a low weevil density and only experienced moderate damage. It is apparent that cutting prevented this damage in the fields I studied.

Thus larval damage provides a simple key to determining the proper cutting date for weevil control. If the field is cut when larval feeding damage just begins, it should not experience any significant damage to either the first or second crops.

The parasite Bathyplectys curculionis should be given consideration in a management program. In addition to reducing the number of alfalfa weevil larvae which survive to pupation, a high parasitization rate by these parasites also reduces the duration and amount of larval feeding (Armbrust et. al., 1970).

Cutting does reduce the number of parasitized larvae in the field, although it causes a greater reduction in unparasitized larvae. This reduction of parasites, although undesirable, seems to be unavoidable as long as the field is cut. It is possible to leave uncut strips in a field to increase parasite production, but results of 1971 indicate a ten to twenty-fold increase in the number of weevil pupae produced in such strips while the increase in parasites was always less than three-fold and averaged close to two-fold. Apparently there is no mass migration of adult parasites into such strips because the average rate of parasitism in these strips (20%) was considerably lower than in the cut portions of the field (33%). The additional parasites produced in the strips left uncut are insignificant in comparison to the parasite production of the entire field and do not justify the expenses of loss of alfalfa yield and additional weevil production. In short, it does not seem worthwhile to leave uncut strips for parasite production in a management program.

Another consideration in alfalfa management for weevil control is stand density. Hamlin et. al., (1947) reported that weevil damage occurred at an earlier date and was generally more severe in sparse stands of alfalfa. They found that this occurred because sparse fields are considerably warmer than more dense stands and there was less foliage for the weevils to consume and hence a greater percentage of damage. Observations in 1971 confirmed these reports and also indicated that the slope of the field is important since a south-facing slope experiences damage earlier than a level field. Sparse stands on a south-facing slope are particularly vulnerable to severe damage early in the season. On 23 May such a field was already quite damaged at Gull Lake and a very sparse stand on a south slope near Paw Paw was observed to be almost completely defoliated on 25 May. No significant damage occurred to dense level stands at Gull Lake until approximately two weeks later.

Thus it is important in a management program to maintain a good dense stand of alfalfa. Sparse fields or those on south-facing slopes should be watched carefully early in the season and cut as soon as damage is observed.

Of primary concern in this management program is the quality and quantity of the alfalfa produced. Cutting date is important in determining both the quantity and the quality of an alfalfa harvest as well as the overwintering survival of the plants. Current recommendations suggest cutting the field in the bud stage. In a management program it is important to have a variety which is ready for cutting at the proper time for weevil control. In 1970 both fields were of Vernal alfalfa and both were in the bud stage when cut on 27 and 28 May. In 1971 field A (Vernal alfalfa) was in the bud stage when it was cut (3 June) which was probably a few days late for weevil control in that particular field. Fields B and C (Saranac) were in the late bud stage on cutting date (3 June) which seemed to be about the proper time for weevil control. Although Saranac alfalfa matures at an earlier date than Vernal, in the fields I studied the variety was not an important factor because both varieties were in the bud stage on the dates which seemed ideal for cutting for weevil control.

Summary of Management Practices

Summarizing all the results to date on alfalfa management, it seems that fields should be closely watched from mid-May through the first week in June for larval feeding damage. Those fields with sparse stands and those on south slopes are likely to be damaged first and hence should be watched most closely (at least once every three days). As soon as larval feeding damage becomes apparent in each field, it should be cut. Since hot, dry weather is most suitable for making hay and for killing weevils, an effort should be made to cut on a good day, even if it entails waiting a few days after the first damage occurs. The field should be entirely cut, cleanly and as close to the ground as possible and the hay should be removed as soon as possible which is another reason for waiting for good weather. In the absence of larval feeding damage the field should be cut by the early bloom stage. It is important to maintain a dense stand of alfalfa so fields should be well fertilized and kept relatively free of weeds and plowed when they become too old.

This program, based on timed cutting cannot only prevent damage to the current crop, but can also propagate the parasite Bathyplectys curculionis while leaving only a small number of adult weevils for the subsequent generation.

The final consideration for this management program is that of its success. In 1971 of the thirty-five alfalfa fields on the Gull Lake farm only five were treated with insecticide for control of weevil damage and of these, treatment was probably necessary in only three fields. Two of these were cut at too early a date and encountered larval damage as they were regrowing. The third was the sparse, south-facing slope which was not cut early enough and experienced considerable damage before cutting. The remainder of the fields were cut within several days of the recommended time and experienced very little damage. The overall effect of the management program in 1971 was a tremendous reduction in insecticide use, and in spite of a cold spring and exceptionally dry season, a good yield of high quality alfalfa.

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