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This is to certify that the

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Post-harvest Biology of the
Onion Maggot, Hylemya antiqua (Meigen)

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of the requirements for

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POST-HARVEST BIOLOGY OF THE ONION MAGGOT, *HYLEMYA ANTIQUA* (MEIGEN)

By

Francis Andrew Drummond

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ABSTRACT

POST-HARVEST BIOLOGY OF THE ONION MAGGOT, HYLEMYA ANTIQUA (MEIGEN)

By

FRANCIS ANDREW DRUMMOND

This thesis discusses the post-harvest generation of the onion maggot (OM). It focuses on the interactions of the third generation with the spatial and temporal dynamics of onions left in the field after harvest (cull onions). A comparison of the proportion of the second generation OM population that entered diapause with a model of diapause induction suggests that the potential for damage in the spring is largely determined by the density and survival of the third generation flies. Egg density on culls correlates highly with the relative abundance of flies after harvest. Cull type (sprouting, whole, cut, rotting, and cuttops) interact with time to be a major factor in determining the spatial distribution of eggs within a field. Overwintering survival of pupae is high and not significantly influenced by habitat. Life table analysis also indicates that the third generation depends on first instar establishment 300 degree days prior to sub-freezing temperatures in the fall.

To Elizabeth somewhere on Route 66
and to the man who planted trees and grew happiness.

ACKNOWLEDGEMENTS

I am indebted to the man who gave me my first exposure to the science of entomology--John Mathewson--who also provided food and shelter when I was without. Equally so, I thank Dick Casagrande for introducing me to Dean L. Haynes and instilling in me the confidence to initiate graduate study at Michigan State University. To my mother and sister I extend my deepest love for standing by me through thick and thin.

At Michigan State University, I wish to extend my gratitude to Dr. James Bath for fostering an atmosphere of intellectual challenge infused with kindness and understanding--an environment I doubt I would have found elsewhere. I thank my committee members Dr. Lal Tummala, Dr. Mark Whalon, and Dr. Ed Grafius for making sacrifices on my behalf. Appreciation is extended to my colleagues Gary Whitfield, Michael Mispagel, Ed Caswell, Susan Battenfield, Ray Carruthers, Duane Jokinen, and Tom Ellis for providing me with the indispensible catalyst from which ideas are born. Special thanks go to Ken Dimoff, a good friend, who was always eager to answer my questions about mathematics, computer science, and statistics. This study would not appear in its present form without the efforts of the student employees who participated in collecting some of the data. Thank you: Lisa Jonson, Marie Pane, Cathy Stewart, Neal Newman, Faye Hanneway, Vince Fritz, and Jeff Van Zandt.

I will always consider myself lucky to have conducted research with Dr. Dean Haynes. The lessons I learned from him reach far beyond the boundaries of entomology and will shape the rest of my life.

Last, and most importantly, I thank my best friend and colleague, Ellie Groden, from the bottom of my heart for her innumerable contributions to this study.

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INTRODUCTION

Current management strategies for the onion maggot, Hylemya antiqua (Meigen) are based on an intensive use of insecticides. A common application schedule in Michigan consists of a granular furrow treatment at the time of planting and foliar sprays as frequent as three times a week during peak flight activity (Carruthers 1979). One consequence of this approach has been the development of insecticide resistance. This has led to an increased number of applications, higher dosages, and new compounds only to result in resistance again. Hylemya antiqua has developed resistance to almost every insecticide group used for its control (reviews of the chronological path of these events have been given by Carruthers 1979, Haynes et al. 1980, Carruthers 1981, Whitfield 1981). The future of this approach does not appear promising in light of potential ground water contamination (Pimentel 1981) and the economics of pesticide development for small acreage crops (the average cost to develop a new pesticide from initial screening to marketing was estimated at ten million dollars and twenty man-years of research effort during the past decade (Matsumura 1975)).

Integrated pest management addresses the problem of maintaining an existing production system facing a declining effectiveness of control practices. Usually this is accomplished by integrating selective biological and chemical management strategies within an existing production system structure. The high technology of IPM has focused on incremental adjustments within the established structure and has eliminated unnecessary pesticides and has reduced secondary pest outbreaks (Edens and Haynes 1982).

The existing onion production structure has dictated the type of biological research conducted and thus the results for integration into management decisions. In 1976, a multidisciplinary research project was initiated at Michigan State University to investigate the ecological interactions in an onion agroecosystem independent but inclusive of the production system (see Groden 1982 for more details). An approach utilizing various states within a continuum of the onion agroecosystem (chemical-intensive production system, non-chemical intensive production system, and a passive pristine system) identified biological links not discernable within a chemical-intensive production system alone.

The early findings of this study suggested that the absence of many important biological components in the crop production system (Entomopthora muscae (Cohn), Aphaereta pallipes (Say), and Aleochara bilineata (Gyll.)) was not solely related to pesticide use but was influenced by the design of the agricultural production system (Haynes et al. 1980, Carruthers 1981, Groden 1982). Field borders are essential for high levels of infection by E. muscae (Carruthers 1981), and proximal bovine pastures are necessary for high levels of parasitism from A. pallipes (Groden 1982).

It was in this vein that the role of onions left in the field after harvest (culls) were studied as to their possible impact on the onion maggot population. Prior to 1979 the temporal structure of the onion crop production system study of the population dynamics of the onion maggot was confined to generations present during the growing season. Lack of understanding in the process of diapause induction may have also been responsible for the historic bias in the biological investigations of the onion maggot, as the potential for the post-harvest generation to contribute to the overwintering pupal density during some

years but not others was not realized. In fact the epidemic outbreaks of onion maggot damage in the past has only been attributed to (1) soil moisture during the spring and (2) insecticide resistance (Workman 1958).

This thesis reports upon a preliminary analysis of the post-harvest biology endemic to the onion agroecosystem and its consequences concerning population regulation. The major objectives of the study were: (1) to describe the food resource (cull population) available for colonization by the onion maggot, (2) to examine the spatial and temporal dynamics of the onion maggot and the culls, (3) to determine factors affecting survival, and (4) to document the incidence of other arthropod colonizers on culls.

REVIEW OF THE LITERATURE

The past three decades of research aimed at elucidating the biology of the onion maggot, Hylemya antiqua (Meigen) represent an evolution in philosophy and methodology culminating in a more holistic perspective. Basic life history was the major emphasis of investigations from the 1940's to the 1960's (Armstrong 1924, Hammond 1924, Baker and Stewart 1927, Kastner 1929) before insecticides dominated onion maggot research (see Carruthers 1979, Haynes et al. 1980, Carruthers 1981, Whitfield 1981). When biological research was rekindled, the approach had shifted to onion maggot behavior, although often divorced from the ecology of the agroecosystem (Tozloski 1954, Workman 1958, Ellington 1963). These areas of investigation (interaction of the onion maggot with the environment), particularly the relationships between the onion plant and the onion maggot, were initiated by the pioneering work of Perron (Perron and LaFrance 1962, Perron 1972). Recent research shows the complexity of interactions (Loosjes 1976, Carruthers 1979, Groden 1982, Carruthers 1981, Whitfield 1981), all ultimately impinging on the population dynamics of the onion maggot. Reviews of the more encompassing research in onion agroecosystem ecology as it pertains to crop production have been compiled by Loosjes (1976), and Carruthers (1979, 1981). Whitfield (1981) discusses the biology of the onion maggot.

Despite the systems approach to agricultural research in the onion agroecosystem (Haynes et al. 1980), most studies have focused on interactions within the framework of the onion production system (Whitfield 1981, Carruthers 1981, Hammond 1924). Research on the onion maggot has been conducted generally on two generations. The distribution of the onion maggot globally is restricted to the northern hemisphere (Loosjes 1976), although Hennig (1974) made reference

to a finding in Brazil, but this is suspect (Loosjes 1976). The number of flights or generations per year reported around the world range from one to five. Northern Norway has one generation a year (Loosjes 1976). Two generations per year, with a partial third, have been recorded by: Maan (1945) and Loosjes (1976) in the Netherlands; Ellington (1963) in New York; Hammond (1924) in Ontario, Canada; Kastner (1929) in Germany; and Eyer (1922) in Pennsylvania.

The onion maggot produces three generations in Quebec, Pennsylvania, England, and Michigan (Armstrong 1924, LaFrance and Perron 1959, Perron and LaFrance 1960, Eyer 1922, Smith 1922, Carruthers 1979, Whitfield 1981). Reports of four and five generations per year are not as common, but Loosjes (1976) makes reference to occurrences of four generations per year in Turkey and four with a partial fifth generation in southern France. Perron et al. (1955) mentions a partial fourth generation in Quebec.

Despite these local properties of the onion maggot's biology, little research has been conducted on the onion maggot after the second generation pupates. Some of the early researchers indicated that a third generation existed. Armstrong (1924) reported on the occurrence of three generations of onion maggots in Montreal. He recorded that third generation flies emerged to be from August 21 to October 3, 1923, and 2.3% of the total seasonal egg input was laid in May, 36.1% in June, 8.9% in July, 39.6% in August, and 13.1% in September. It appears that he did not continue sampling after harvest. Maan (1945) mentions that third generation adults live for three to four weeks.

In 1957, Workman (1958) found an infestation of onion maggots in the fall of the year at the college experimental farm. He visited the field in late January 1958 to examine some bulbs that were left in the field, but he only found

larvae of the lesser bulb fly, Eumerus strigatus (Fall.). His conclusion was that a third generation of onion maggots could not survive in Oregon. To substantiate his hypothesis (or so he thought), he performed a laboratory test in which he subjected second and third instar larvae to temperature conditions of 2-4°C. After 60 days only 10.3% of the third instars had survived. After 90 days all had died. (Note: Workman did not include a food source for them in this experiment.) Workman concluded that third generation onion maggot larvae cannot develop to the pupal stage.

It was not until Perron and LaFrance (LaFrance and Perron 1959, Perron and LaFrance 1961, Perron 1972) began their studies with the onion maggot in the 1950's that a life table approach was utilized and applied to the third generation. The first study reported on a three year field cage study where 100 adult flies (50 males and 50 females) were added to a cage as a pulse cohort. This was done for each of the three generations. Within the field cages, the third generation spanned August 10 through November 22, 1953 (104 days), August 9 through October 17, 1954 (64 days) and August 10 through October 14, 1955 (65 days). Other data showed that oviposition decreased whenever the temperature remained below 14°C; a mean of 24.3 eggs per female resulted over the generation for the three years, and the mean adult fly longevity was 66.6 days. The main conclusion was that of the three generations, the second generation was the most important when measuring population increase (in terms of pupa to pupa increase). These increases were 17.5X, 25.1X, and 10.5X respectively for the three generations. The result of the differential rates of growth were not due to existing mortality but to the proportion of diapause present in each generation (more about this will be mentioned later).

A study comparing the effect of soil type on the population dynamics of the onion maggot from 1955 to 1958 showed that over the four year period, first emergence of the third generation was from August 16 through August 27, with peak emergence occurring between the last week in August and the first week in September. Perron's last published study (Perron 1972) on the onion maggot involved a comparative study between the effect of bulb-type storage onions and green bunching onions on the population dynamics of the onion maggot. He stated that many larvae were forced to pupate before completing development (during the third generation). He also observed that thousands of small larvae were still feeding in November and December in bunching onions and estimated that there must have been tremendous mortality due to freezing temperatures.

Perron and his collegues gathered some important, though fractionated, data but this research never led them to look at the onion maggot biology after harvest. The only reference to a study of the onion maggot population dynamics after harvest is that of Hammond (1924) in Ottawa. He followed the onion maggot phenology past harvest in 1922 and 1923. In the first field season, oviposition by flies in the field continued until October 20; the greater number of third instar larvae failed to pupate by November 1. During the year of 1923, second generation oviposition occurred from July 20 through September 20, and the third generation females laid eggs from September 10 through October 17. Of 16,000 eggs collected in 1923, 2% were collected in May, 48% in June, 11% in July, 25% in August, 12% in September, and 2% in October. Hammond also reported on other species that were found in cull onions.

The lack of attention to the onion maggot's third generation is probably due to the onion harvest, the synchrony of third generation emergence, and the

dynamics of diapause induction, which until recently had not been fully understood. Armstrong (1924) and Hammond (1924) document the occurrence of diapause in the second generation of the onion maggot (81% and 87% respectively). Mann (1945) mentions the incidence of a low percentage of first generation pupae in the soil until the following year. Miles (1955) found in the laboratory that larvae reared at 12-18°C and maintained at that temperature induced diapause in pupae (85% induction rate at 18°C). She hypothesized on the appearance of a third generation of onion maggot flies: "the temperature during larval development of the second generation would determine the number of flies emerging for the third generation." Perron and LaFrance (1961) have reported mean diapause percentages of 6.3, 67.5 and 99.8 for the three generations of the onion maggot during the years of 1953 through 1955. LaFrance and Perron (1959) showed that soil temperature mediated by soil type produced frequencies of 20-29%, 65-91%, and 100% for the years 1956 through 1958 on organic soils and 2-8%, 89%, and 100% for the same period on sandy loam (three frequency classes refer to generations 1, 2 and 3 respectively). They believed that 21.1°C was the threshold temperature for larval development that would induce diapause. Many other authors have reported diapause frequencies from different parts of the world, and excellent synoposes have been given by Whitfield (1981), Ellington (1963), and Loosjes (1976).

Experiments performed by Whitfield (1981) to determine the proportion of pupal diapause in the first and second generation yielded similar results to what Ellington (1963) found in New York state. Ramakers (1973) and Kelderman (1972) determined the environmental factors inducing diapause in the pupae. Diapause induction is strongly age dependent (with regards to the third instar larvae). Short day length during the third instar induces diapause (Kelderman 1972), and low temperatures induce diapause in the first days of pupal development (Ramakers 1973). The interaction between photoperiod and temperature directs "a strong selection pressure in favor of a low percentage diapause at longer day lengths, provided the temperature is at least 18°C, and a high percentage diapause at shorter day lengths even if the temperature is high" (Loosjes 1976). The dynamics of diapause induction plays a role in creating a large third generation of onion flies one year and possibly a smaller generation the next (in certain locales, possibly marginal climates). This activity insures optimal conditions for the fly to increase either as a three generation strategy or a two generation strategy. The impact of diapause induction on the number of generations per year in a region has to be explored not only in context to the following generation of the onion maggot, but also as it relates to other organisms that utilize the same post-harvest niche.

The onion maggot is not the only insect that attacks or establishes in onions after harvest. Loosjes (1976) compiled a list of insects that were found in rotting onions. Eleven species of diptera and eleven species of Coleoptera were recorded. Among the more commonly found diptera in the Netherlands were Eumerus strigatus Fall., Hylemya platura (Rond.) seed corn maggot, and the onion maggot. Among what Loosjes termed "regular frequenters" were Lonchaeidae chorea (Fabr.), Fannia cannicularis L., Muscina assimilis Fall., and Ortarlis urticae L. Most beetles were predators of the family Staphylinidae. Diptera attacking Michigan onions have been documented (Merrill 1951, Merrill and Hutson 1953). Fifty-two species of diptera were collected in all. Of these, only 20 species were implicated in pre-harvest onion attack. Hylemya antiqua

was abundant in the autumn 42.6%. In decreasing order of incidence were: *Muscina assimilis* 12.5%, *Muscina stabulans* 8.4%, *Euxesta notata* 7.2%, *Eumerus* spp. 7.0%, *Scatopse fuscipes* 4.0% and *Fannia cannicularis* 3.5%. The other species were less than 2% represented in the mean proportion per collection. In sampling cull piles, the onion maggot was the most predominant. In older cull piles (after the spring), no onion maggot flies were found, but a variety of syrphid flies (including *E. strigatus*) and predators were found. Brooks (1951) documented fourteen species of diptera in onion; Diptera and Coleoptera most frequently visited onion bulbs after harvest. A mite species, *Rhizoglyphus echinopus* (Fumouze and Robin) is abundant on onion bulbs in storage and cull onions left in the field (McDaniel 1931). These accounts indicate that species diversity might be much greater after harvest, but there has been no documentation of any competitive interactions between species of arthropods found feeding on onion bulbs.

MATERIALS AND METHODS

STUDY AREA

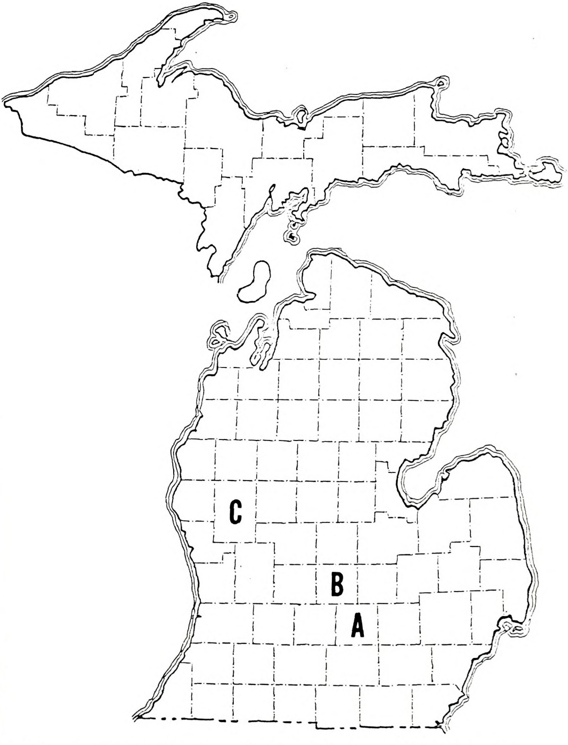
The research conducted during the third generation of the onion maggot was initiated on September 15, 1979, and was terminated towards the end of December, 1979. Geographically, three regions in the state served as study sites (Figure 1). Eleven fields were used for data collection: two fields in Eaton Rapids, Michigan; two fields in Laingsburg, Michigan; and seven fields in Grant, Michigan. Grant and Eaton Rapids are commercial onion growing areas. The Michigan State University Organic Soils Research Farm (MSU Muck Farm) in Laingsburg is strictly experimental. The fields at the Muck Farm and Eaton Rapids were coded with letters, and the fields in Grant were number coded according to a method by Whitfield (1981) and Carruthers (1981)--one difference being the code for field R is referred to as field 7 by Whitfield (1981). A more exact description of the location of these fields can be found in Whitfield (1981) and Carruthers (1981). The physical attributes and historical singularities of these fields formed a major part of the study; a brief summary of these are depicted in Table 1.

FALL ARTHROPOD POPULATION SAMPLING

The principal objective of the study was to quantify the numerical changes of onion infesting arthropod populations under different environmental conditions. Sampling was conducted by Whitfield (1981) and Carruthers (1981).

Life Table Method

A single-stage cluster sampling plan was the experimental design for this study (Cochran 1977). The sample universe was the three onion growing regions



gure 1. Geographic location of study sites for 1979 post harvest study A: Eaton Rapids-2 fields, B: MSU muckfarm-2 fields, C: Grant Swamp-7 fields.

Table 1A. Research field characteristics, Autumn 1978 in Grant.

Characteristics	R	1	2	3	4	5	6
Approx. Field Size (Hectares)[1]	1.8	14.4	3.2	3.3	6.0	12.7	2.8
Initial Cull Density[2]	344.8	840.4	18.4	28.2	628.9	11.0	12.8
Soil Type [3]	CM	CM	MF-CM	HM	HM	E	HM
N Border	I-Field 1	Onions	Carrots	R-Woodlot	I-Carrots	I-Onions	Carrots
S Border	Carrots	I-Field 0	I-Onions	I-Carrots	I-Onions	R-Meadow	I-Cow Pasture
E Border	Mint	Carrots	R-Field 1	I-Onions	Onions	Carrots	Carrots
W Border	R-Onions	R-Field 2	Woodlot	Carrots	I-Mint	I-Onions	R-Woodlot
Irrigation	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Insecticide Use	No Foliar 1/2 Soil	Yes	Yes	Yes	Yes	Yes	Yes
Cover Crop	No	**Rye**	Oats	No	Late rye	No	No
History	Onions 2 years in a row	Carrots year before	Carrots year before	?	?	Carrots year before	?

[1] fields were measured by pacing at least two sides for area computation

[2] based on 10, 9.2 meter^2 sample units

[3] for soil types see Mokma and Whiteside (1973)

I=irrigation ditch

R=road

Table 1B. Research field characteristics, Autumn 1978 in Eaton Rapids and Laingsburg.

Characteristics	Eaton Rapids		Laingsburg	
	K	R	R	P
Approx. Field Size (Hectares)[1]	10.0	3.6	1.8	0.2
Initial Cull Density[2]	131.8	14.0	134.2	9.8
Soil Type[3]	CM	CM	HM	HM
N Border	Field R	R-Meadow	I-Woodlot	R-Field O
S Border	Meadow	Field K	R-Field P	Woodlot
E Border	R-Onions	R-Cow Pasture	I-Meadow	I-Meadow
W Border	Woodlot	Woodlot	Woodlot-Meadow	I-Woodlot
Irrigation	No	No	No	Yes
Insecticide Use	No	Yes	No	Yes
Cover Crop	Late rye	Strip crop rye	Rye	No
History	Mixed veg. no sprays for 15 years	Onions 3 years in a row	Onions and wild flowers 2 years before	Carrots before

[1] fields were measured by pacing at least two sides for area computation
[2] based on 10,9.2 meters^2 sample units
[3] for soil types, see Mokma and Whiteside (1973)
I=irrigation ditch
R=road

discussed earlier, composed of eleven fields. The fields ranged from 0.2 to 14.4 hectares. Each field was divided into five strata from which random samples were regularly removed. The sample unit was a cluster of onions (each cluster consisted of the twenty nearest onions to a random point) (Cochran 1977). A stratification of the clusters was performed so that each strata in a field (total of five) received two clusters. Within each strata the origins for the clusters were selected randomly from a random number table (Cochran and Cox 1957, Steele and Torrie 1960). This was done by randomly selecting two coordinates (x and y). From the point of entry into the strata the two directions (perpendicular to one another) were paced off; the resultant vector was the origin for the cluster. The first cluster location served as the starting point from which the second cluster was located, as described above. Every onion within the cluster sample was checked for onion maggot life stages. Samples were taken at one week intervals. In the fall, the average developmental times were about a week; therefore, the construction of age-specific population curves was not severely affected (Helgesen and Haynes 1972). There was no previous data base to utilize for adjusting the standard sample error to 10% of the mean. The sample size was established purely on the limits set by time and labor availability. With three endividuals working, the sample size (N) was set at 10, 9.2 M^2 quadrats per field, thereby allowing the census of all 7 fields in Grant to be conducted in one day.

Cohort Method

The experimental design for establishing cohorts (egg sampling) in this study is labeled by Cochran (1977) as a simple, random, stratified sampling plan. Each field was subdivided into five equal subplots where cohorts were established. Initially three sample units were utilized, 0.83 sq m, 1.5 sq m, and 9.2 sq m. The most efficient unit was selected for the rest of the season (9.2 sq m). The sample size in this study was set at ten-9.2 sq m samples for a total sample size of 92 sq m per field. The fields were sampled once a week.

In this sampling plan, the type and number of onions were recorded per sample unit. Onions were categorized into five arbitrary classes: (1) whole, undamaged bulbs; (2) cut or crushed, but not rotted, bulbs; (3) rotting bulbs; (4) sprouting bulbs; and (5) tops (leaves of onions cut off and left in the field). Eggs found on bulbs were counted and recorded. The bulb was then moved four to five cm from the original location of the bulb. The depression left in the soil was gently scraped with a paintbrush or a pencil for a depth of approximately ten mm, and the eggs were collected. The eggs were transferred to fine mesh pouches (6.45 sq cm); a fine layer of muck soil was sprinkled over the pouch, and then the pouch was moved to the new location and laid under the original bulb.

A bulb with eggs was marked with a garden stake (30.5 cm) and an identification code. The bulb type, density and type of eggs (onion maggot, syrphid, or muscid) were recorded on a data sheet and the stake. For each sample unit that bulbs with eggs were found, a 1.2 m wooden lathe stake was pushed into the soil so that the same onions could be located again. The cohorts were separated into two groups one of which was not observed again until pupation was expected; 0.06 sq m nylon mesh swatches were dug in approximately 15 cm under the onions to catch the pupating larvae. It was hypothesized that this would facilitate pupae recovery. The second group of cohort individuals were visited every week and their progress recorded. With a few onions this meant careful dissections of the onion bulb (without trying to open the bulb too

much to the air) were made. If larvae had gone deep into the onion, which was unusual, the bulb was left and visited the next week. When pupation for the cohort was near, square sheets of nylon mesh were dug under the onions.

The cohort study initially was concerned only with documenting the change in numbers of onion maggot immature stages. After the first week of sampling, other arthropods infesting onions were included: adults and nymphs of the bulb mite Rhizoglyphus echinopus (F. and R.) were counted and recorded as one; eggs and larvae of Eumerus spp.; larvae of the black onion fly, Tritoxa flexa (Wiedemann); Muscid eggs, larvae, and pupae where possible; and immature stages of the seed corn maggot, Hylemya platura (Rond.), were looked for but not found. Identification was based on McDaniel (1931), Evans et al. (1961), and Hoffman (1979) for the bulb mite; Hodson (1927) for the lesser bulb fly, Eumerus spp.; Allen and Foote (1975) for the black onion fly; Fisher (1979, personal communication) for Muscid spp.; and Loosjes (1976) for H. platura pupae.

As microscopic observations were not realistic, a frequency distribution was used for determining size (see Discussion). Sampling efficiency was determined for eggs and pupae for three out of the four personnel in the study. Known quantities of these stages were buried in typical locations. Densities and environmental factors were varied while mock sampling was carried out. Sampling efficiencies were computed and correlated to sampling efforts during the season.

ADULT ONION MAGGOTS

Relative abundances of onion flies were determined by Whitfield (1981) through flight interception traps in the seven fields in Grant. Unfortunately,

there were no monitoring provisions in Eaton Rapids or Laingsburg. Adult longevity was studied using caged individuals in Grant and Eaton Rapids. These studies were initiated on September 19, 1979, and finished when it was no longer possible to collect adequate numbers of flies (late October). Thirty-one field cages were used in Field 1 in Grant and 10 cages in Field K in Eaton Rapids. The cages were set up in the field and field borders (25-6 respectively in Grant and 6-4 respectively in Eaton Rapids). Cage dimensions were 1 m in diameter at the base with a 1 m height. The cages were dug into the soil at a depth of ca. 15 cm, and crude lids of duct tape and nylon mesh screening were fitted on the tops.

Flies were initially caught in a vacuum sampler mounted on a tractor built by Carruthers (1981), but this method was abandoned and a sweepnet was used for collection. Three flies were put into each cage with an onion, and fly longevity was assessed daily. Fecundity was assessed on weekly. New flies were introduced at ca. 100 degree-day (DD) intervals. Infrequently some female flies that were not in the cages were dissected to estimate egg maturity (Theunissen 1976).

CULL ONION DYNAMICS

Cull Weight Loss and Rates of Population Change

A study of the rate of change in cull onions through time was conducted to determine the dynamics of cull transformations that impinged on the life system of the onion maggot. Two experiments were designed to measure average weight loss in soil type, cull type, cull location, and arthropod colonization. Data for the analysis of the change of numbers of culls were collected during the sampling efforts for life-stage density estimation (discussed earlier).

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The experiments were laid out in field 5 of the Grant Swamp Region. Field 5 was selected for its soil makeup. Approximately one-half of the field is of a Houghton-type muck soil while the other half is a Martisco soil classification (marl at the soil surface). The experimental units were collected the day the experiments were initiated from neighboring onion fields that had not yet been harvested. Weight loss was measured through repetitive sampling (repetitive means that the same experimental units were measured throughout the study). Each cull was weighed (g ± nearest 1/10 g) three times a sample period on a portable triple beam balance with the average weight used for analysis. An experimental unit (cull) found with an arthropod colonizer (except for experiment two) during these weighings was removed from the study.

The first experiment was actually two sub-experiments or trials evaluating two populations of culls through time. The first group was harvested on September 20, 1979 (Julian day 263). Sequential sampling periods were Julian days 271, 274, 276, 278, 281, 289, 315, and 347 (December 13, 1979). The second population was harvested on October 8, 1979 (Julian day 281) and were sampled on Julian days 289, 315, and 347. A three-way design was laid out with five experimental units per treatment combination. The variables were soil type (Houghton and Martisco, position with respect to the soil surface: 0 cm or on the soil surface and -2.5 cm below the surface) and cull type (whole, cut, crushed, or smashed, and cut top).

Experiment 2 looked at arthropod colonization of cut cull onions. Soil type (Houghton muck), position (0 cm.), and cull type (cut cull, ten per treatment) were held constant. The colonizers were the common arthropod species that feed on onions during the post-harvest season. These were the bulb mite, R.

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echinopus (F. and R.); the onion maggot, H. antiqua (Meig.); and the lesser bulb fly, Eumerus spp. A control was added from experiment 1. This was a valid procedure because the date of initiation and subsequent sampling dates were the same for the two experiments.

Cull Pile Survey

Six different cull piles in each of three locations within the Grant region were surveyed on November 20, 1979. One thousand onions from each pile were inspected for onion maggot life stages, and the distance of each pile from the border of the Grant swamp was measured.

Sprout Survey

By mid October, many fields in all three regions had sprouted culls. Frequent comparative sampling was carried out for immature life stages on prouts and other classes of onions. Sprouts with eggs were marked with garden takes, and the survival of the life stages was measured (see Cohort Study). Covariates, such as height and color of leaves, were recorded also. Data ollected from the life table study duplicated some of this effort.

Cover Crop Survey

In all three regions there were fields that had cover crops sown after arvest (see study site description, Table 1). A paired experimental design was et up to discover whether a cover crop influenced the population dynamics or e behavior of the onion maggot. Eggs on culls were sampled in both habitats roughout the fall. Fifty onions were sampled per habitat per sampling period, d onion maggot life stages were recorded. Field R (Eaton Rapids) was a rticularly useful field in the study because the rye crop had been sown in strips e study site description, Table 1).

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OVERWINTERING MORTALITY OF PUPAE

In November of 1979, an experiment was conducted to determine whether the habitat of the overwintering pupae would effect mortality. Eight treatment habitats were selected and replicated three times. Each replicate consisted of 225 pupae in nylon mesh packets with 75 pupae per packet. The habitats were: (1) sandy-mixture of muck soil, (2) rye grass cover crop, (3) clay or marly muck, (4) Houghton muck, (5) field border, (6) poorly drained field that flooded in the spring, (7) a simulated hardpan habitat, and (8) pupae within onion bulbs. Treatments 1 through 6 were buried at a depth of 10 cm. Treatment 7 consisted of a plastic-wrapped sheet rock surface with the pupal packets tacked onto the upper surface (packets were buried 2.5 cm below the surface). The onions in treatment 8 were not buried. In the spring before the the fields were plowed, the packets were recovered, and mortality was measured through emergence of adults in glass lamp globes in the laboratory at approximately 21°C. Another study designed to detect genetic population differences in regards to susceptibility to overwintering mortality, utilized the philosophy of a providence experiment (Haynes 1979, personal communication). Two hundred and fifty pupae (5 packets of 50) were transplanted from Grant to Eaton Rapids and buried at 10 cm depths along with the same number of pupae from Eaton Rapids (complete randomized design). Pupae from an Eaton Rapids population were likewise buried in Grant with pupae from a Grant population. All pupae were recovered in April before the fields were plowed. Mortality was assessed in the same manner as the overwintering habitat study.

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ENVIRONMENTAL MONITORING

Weather instrumentation was placed at all three regions (field K--Eaton Rapids; field R--Laingsburg; field R--Grant). Soil temperatures were recorded from soil depths of 2.5 cm, 7.5 cm, and 15 cm using continuous recording chart three-point soil thermographs. Air temperature and relative humidity were recorded continuously using hygrothermographs in Stevenson Weather Shelters approximately 1.5 m above the ground. Maximum and minimum daily temperatures were used to compute degree-days (Baskerville and Emin 1969). Daily precipitation data for the three areas was recorded at the nearest local airport within each region.

RESULTS AND DISCUSSION

DIAPAUSE INDUCTION

The number of flies emerging in the third generation depends on the eproduction and survival from the first two generations and the proportion of iapausing pupae in these generations. Ramaker (1973) developed a model of iapause induction based on laboratory data (Figure 2). Loosjes (1976) used the ean soil temperatures from ten years of field data to predict diapause duction. The validation data consisted of seven sets of pupal sampling data nly four complete sets). The expected percent diapause for the first and cond generation were: 10% and 75% for a photoperiod corresponding to the tronomical day length (sunrise to sunset) when third instar larvae were present, % and 86% for a photoperiod of astronomical day length minus one hour, and % and 94% for a photoperiod of astronomical day length minus two hours. osjes (1976) hypothesized that the larvae would not be able to sense photoiod within the onion except if the larva was near the bulb's outer surface. He

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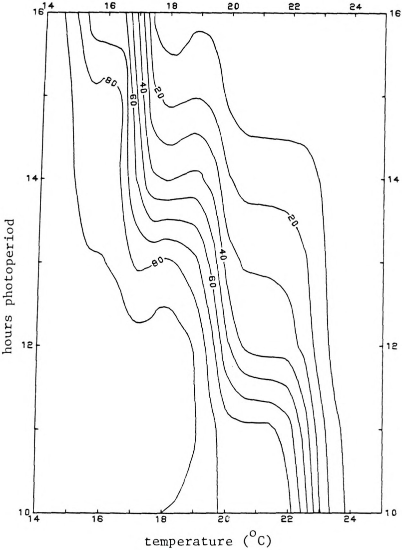

Figure 2. Percent diapause induction as a function of temperature and photoperiod--photoperiod expressed as hours of light per 24 hours.

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felt that this would make the larvae perceive shorter light periods than the biologically effective day length, which is the astronomical day length plus an additional half hour in the morning and evening. Loosjes (1976) does not include enough data to calculate a standard error for his prediction means, so it is difficult to interpret his results. The prediction is fairly close to the observed (21.9% and 84.6%, respectively, for first and second generation).

A rough validation of the model was performed on data sets from Michigan (Whitfield 1981) and Quebec (Perron and LaFrance 1961). Photoperiod data for Grant, Michigan (41° latitude), and St. Jean, Quebec (45.5°), was obtained from two sources, Sunset-Sunrise charts[1] and a computational formula slightly modified from a computer subroutine (Fulton 1978). Validation of the model with the Quebec data was done at the crudest of levels since temperatures were available only as mean values for the generation. The Michigan data had a complete temperature data set for the periods needed in the analysis. Peak third instar incidence was estimated in both generations from the DD requirements by Carruthers (1979, Table A2) with the aid of a biofix (Croft et al. 1976) from cumulative larval and pupal incidence (Whitfield 1981). Soil temperatures were measured at 3 cm in depth at the research weather station in Grant (Whitfield 1981, Appendix K). The data from Quebec did not have a sample size reported nor a standard error of the sample mean computed; therefore, it is not possible to determine the accuracy of the prediction.

Hypothetically, if the means are fairly representative of the population mean, the model's predictive capability is fairly accurate (7-25% in absolute percentage difference for second generation) for arriving at an estimate. The

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[1] Sunset-Sunrise charts, Nautical Almanac Office, U.S. Naval Observatory. C. G. Christie.

Table 2. Expected and observed diapause proportions.

		Proportion in Diapause					
		Generation 1			Generation 2		
Location	Year	Obs.	Exp. 1[1]	Exp. 2[2]	Obs.	Exp. 1[1]	Exp. 2[2]
Quebec	1953	0.0008	0.15	0.04	.677	0.75	0.60
Quebec	1954	0.1900	0.10	0.05	.900	0.80	0.65
Quebec	1955	0.0000	0.00	0.00	.430	0.70	0.50
Grant	1978	--	--	--	.036±.01	0.20	0.00
Grant	1979	0.0000	0.00	0.00	.058±.02	0.00	0.00

[1] Astronomical photoperiod

[2] Astronomical photoperiod minus one hour

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model appears to underestimate diapause from the Michigan populations (Table 2). Unfortunately, only low proportions of the pupae were induced into the diapause state in Michigan during 1978 and 1979. The model shows that cool soil temperatures and a late second generation induce a substantial proportion of the population to diapause.

Haynes (personal communication) hypothesized that there may be a tremendous selection pressure, due to heavy insecticide use, for the second generation pupae not to diapause and take advantage of an uncontaminated food resource. This seems conceivable in light of the onion maggot's genetic plasticity regarding pesticides (Carruthers 1979). A management strategy of cleaning up or burying the culls in the fall may reverse this action and push the the population back into two generations. The literature reporting on onion maggot population dynamics from the northern range of onion growing areas shows oscillating second to third generation incidence (Workman 1958, Ellington 1963, Perron and LaFrance 1961, and Armstrong 1924). Whether this is due to a dynamic process of diapause induction, pesticide pressure, a lack of research activity after harvest or all of these is unknown. These dynamics should be further evaluated since they could be important in deciding whether or not a post-harvest cull program need be implemented in a given year within a region.

MODEL FOR FIELD LEVEL INSTAR DETERMINATION

A major consideration at the start of the fall research effort was the development of a method enabling an observer to classify and record the occurrence of onion maggot larval stadia in the field. A method used in previous studies utilized determinations based on microscopic examination of the protho-

racic spiracles Brooks 1951). Whitfield (1981) adopted this procedure for developmental studies of the first two generations of the onion maggot. It was felt that the fall life table studies required a quick reference index that was reliable and accurate, but also versatile enough to use in the field under a variety of weather conditions and adaptable to different personnel skill levels. Most important, the technique was needed to assess development without harming the larvae.

A model for determining the three onion maggot larval instars was constructed from a data base of length and width measurements of a field population sampled in 1978. The larvae were measured in the contracted and the extended state. Only immature stages from mature green and dry bulbs were utilized to minimize spurious relationships due to host phenology that could add error to the frequency distribution of measurements. Data from two regions were included in the model, thereby, providing an index for differences in genetic populations. A micrometer was used to measure both length and width (basal cross-sectional diameter) (Table 3). These limits represent the variance due to measuring, as well as the variation between indivisuals. Standardizing body form (extended or contracted) minimizes measurement error (Table 3). These margins of error, however, are probably less than one might obtain when field-measuring live larvae. A standard body form probably could not be found in the field without killing the larvae in a preservative. Thus, measurements made for the data base were performed on a range of states (fully contracted to fully extended).

Determinations correlated to the measurements were based on the previ-ously mentioned technique of prothoracic spiracle examination. The data sets

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[2] Star
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le 3. Average precision of onion maggot immature life stage measurements.

	Standard error expressed as percent of mean[2]	
	Width	Length
	1.86	1.53
t instar	1.6	1.34
nd instar	1.22	0.55
d instar	1.33	.82
	0.72	0.56

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rce of immature onion maggot stages: Eaton Rapids; June, 1978.

ndard error of the mean was computed from 3 measurements from each 5 individuals.

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(measurements in millimeters) used for constructing the indices were summarized (Table 4). The choice of length or width as the variable for determinations could not be arrived at through comparing the coefficients of variation within larval stadia due to the overlap of the .95 confidence intervals. Therefore, another approach was used. Measurement data, either in the raw state or as a transformed variable, generally can be described by the normal distribution (Fisher 1938). This hypothesis was tested using the Kolmogorov-Smirnoff test and the Cramer-Von Mises test (Dimoff et al. 1980). The test statistics for these two nonparametric tests for goodness of fit are much less than the tabled values (Dimoff et al. 1980) at the p = .01 level. Therefore, there was no basis to reject the null hypothesis that the distributions were not significantly different from the theoretical normal distribution (Table 5). Based on the goodness of fit to the theoretical models, the proportion of overlap was calculated between the density functions for each larval stadium within each of the measurement criteria (length and width). These were compared, and the minimum overlap was used as the basis for the decision (Table 5). Therefore, the length character was chosen for identifying onion maggot larval instars. Metal standards made from nichrome ignition wire were used for field measurements (2.9 mm for separating first and second instars and 5.1 mm for distinguishing between second and third instars). Thirteen to 15% of the first and second larval instar populations (95% of expected populations) overlap one another (Table 5). Therefore, a small amount of error in determining first and second instar larvae (and to a lesser degree third instar larvae) will occur. The method for determinations was not modified and was used in the fall post-harvest study accepting the built-in error s a sacrifice for sampling more fields and onions within fields. (A better

Table 4. Summary of length and width measurements for the immature stages of the onion maggot.

measurements for the immature stages of the onion maggot.

		Length (mm.)							Width (mm.)						
Stage	Source	N	Min	Max	$\bar{x}$	SE	CV	2SD	N	Min	Max	$\bar{x}$	SE	CV	2SD
Egg	Grant	12	1.030	1.210	1.135	0.017	5.043	0.114	12	0.380	0.505	0.421	0.012	9.637	0.080
	Grant	25	1.015	1.270	1.170	0.014	5.870	0.138	25	0.310	0.632	0.462	0.015	16.221	0.148
	pooled	37	1.015	1.270	1.159	0.011	5.777±1.4	0.132	37	0.310	0.632	0.449	0.011	15.152±3.5	0.136
	weight	2	1.135	1.170	1.152	0.017	---	---	2	0.421	0.426	0.418	0.015	---	---
First instar	Grant	50	1.240	3.040	1.917	0.067	24.800	0.951	50	0.370	0.820	0.559	0.018	23.254	0.258
	Grant	20	1.020	2.970	1.746	0.108	27.797	0.970	20	0.350	0.950	0.598	0.037	28.351	0.338
	Grant	7	1.320	3.050	2.035	0.218	30.401	1.236	8	0.450	0.800	0.645	0.037	16.016	0.206
	Eaton Rapids	8	1.610	2.500	1.975	0.094	15.088	0.596	10	0.370	0.640	0.480	0.025	16.953	0.163
	Eaton Rapids	10	1.250	2.500	1.714	0.182	28.063	0.962	7	0.410	0.800	0.584	0.060	27.184	0.318
	Eaton Rapids	6	1.700	2.000	1.870	0.046	6.040	0.226	6	0.395	0.603	0.515	0.037	18.245	0.186
	Eaton Rapids	11	1.250	3.000	2.090	0.197	31.097	1.310	11	0.400	0.750	0.582	0.040	22.848	0.264
	pooled	112	1.020	3.050	1.908	0.046	25.352±3.5	0.967	112	0.350	0.950	0.569	0.013	23.67±3.3	0.269
	weight	7	1.714	2.090	1.894	0.053	---	---	7	0.480	0.645	0.566	0.021	---	---

Table 4. (cont.)

		Length (mm.)							Width (mm.)						
		N	Min	Max	$\bar{x}$	SE	CV	2SD	N	Min	Max	$\bar{x}$	SE	CV	2SD
Stage	Source														
Second instar	Grant	52	2.950	5.800	3.193	0.089	16.496	1.230	52	0.585	1.650	0.929	0.027	20.685	0.384
	Grant	30	2.600	4.955	3.393	0.095	15.294	1.038	30	0.705	1.700	0.935	0.034	20.034	0.374
	Eaton Rapids	20	2.950	5.155	3.838	0.145	16.885	1.296	20	0.685	1.250	0.914	0.056	27.637	0.504
	Eaton Rapids	33	2.950	4.500	3.887	0.104	15.338	1.191	33	0.600	1.600	0.885	0.031	19.343	0.342
	Eaton Rapids	11	2.800	5.315	3.622	0.148	13.556	1.201	11	0.550	1.100	0.867	0.044	17.017	0.290
	Eaton Rapids	30	2.715	5.800	3.446	0.109	17.416	1.261	30	0.670	1.570	0.925	0.034	20.260	0.374
	pooled	176	2.600	5.800	3.734	0.049	17.607±1.9	1.316	176	0.550	1.700	0.917	0.016	24.803±2.7	0.408
	weight	6	3.393	3.913	3.708	0.093	---	---	6	0.867	0.935	0.916	0.011	---	---
Third instar	Eaton Rapids	45	4.300	8.000	6290	0.135	14.343	1.806	45	1.000	2.100	1.636	0.043	17.670	0.578
	Eaton Rapids	55	4.355	8.400	6.511	0.130	14.815	1.928	55	0.950	2.010	1.603	0.031	14.327	0.458
	Grant	38	4.250	7.870	6.307	0.119	11.640	1.468	38	0.970	2.000	1.614	0.042	15.803	0.512
	pooled	138	4.250	8.400	6.403	0.076	13.977±1.7	1.790	138	0.950	2.100	1.624	0.021	15.280±1.85	0.496
	weight	3	6.290	6.511	6.383	0.071	---	---	3	1.603	1.636	1.617	0.011	---	---

Table 5. Indices for field determinations of larval stadia

Table 5. Indices for field determinations of larval stadia.

	Width				Length			
	index[1]	Kolmogorov Smirnov	Kramer Von-Mises	%[2] overlap	index[1]	Kolmogorov Smirnov	Kramer Von-Mises	%[2] overlap
First instar	u .838	0.125	0.090	25%	u 2.876	0.080	0.062	15%
Second instar	1 .509	0.080	0.042	64%	1 2.419	0.045	0.028	13%
	u 1.325			8%	u 5.049			0%
Third instar	1 1.128	0.120	0.085	12%	1 5.508	0.063	0.032	0%

[1] upper limit(u)=$\bar{x}$ + 2SD, lower limit(1)=$\bar{x}$ - 2SD.

[2] overlap of probability density functions computed using 2SD percentile as the end point of the distribution's tail.

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approach may be to calculate the sites of overlap for three standard deviation units and utilize the prothoracic spiracle technique on the population where there is uncertainty.) Another method would be to set the upper and lower limits (see Table 5) at 1.5-1.7 standard deviations to provide a better margin for error. Questionable individuals within the regions of overlap would be keyed out.

CULL ONION DYNAMICS

Onion harvests generate a food resource that can theoretically support large numbers of onion maggots (3000 g/m^2). Table 6 depicts regional estimates of cull production in the Grant Swamp for the years 1979 and 1980. Based on the 1980 statistics, which is a more reliable estimate since the sample size is more than three times that of 1979, the expected range of the number of cull onions available for attack in the Grant Swamp region on an average yearly basis (p=.95) is between 10,431,160 and 19,983,600 (based on 500 hectares of onions/year (Ellis 1980, personal communication)). Because harvesting practices vary little, I suspect that other onion growing regions in the state produce a similar initial density of culls per hectare. Therefore post-harvest cultural activities probably have the greatest impact on this food source. A few of these cultural practices will be discussed in the life table section as they directly affect onion maggot populaton dynamics.

The production, transformation, and attrition of cull onions in the fall post-harvest generation of the onion maggot was studied in a qualitative, descriptive manner from the perspective of numbers of culls and weight loss. (The term "cull" in this text refers to any onion bulb or onion plant part that has been left in the field after harvest.) The methodology was based on the hypothesis that

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able 6. Onions left in the field after harvest.[1]

	#/hectare ≥ ½[2]	#/hectare	kilogram/hectare
979[3]	13136.6±1583.5	--	528.0±72.9
980[4]	25341.6±3979.2	26696.2±4276.3	--

Based on September and October samples in Grant Swamp.

Only onion pieces 1.25 cm diameter or greater considered.

$\bar{x}$ ± SE based on 10 9.3m^2 sample units/field; fields=6.

$\bar{x}$ ± SE based on 20 9.3m^2 sample units/field; fields=21.

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culls possess characteristics that distinctly effect their environment. the population of parameters were not known specifically; therefore, six easily identifiable and distinct classes of culls or cull parts were defined and traced through time. These six classes were:

1) Whole culls--green or dried bulbs whose outer and inner integrity was not disturbed.
2) Cut culls--bulbs having a tear or gash penetrating through the outer dry scales and into the green epidermal tissue.
3) Crushed or smashed culls--culls with damage ranging from a water-soaked bruise to total obliteration of the bulb.
4) Rotted culls--bulbs having microbial-induced decay symptoms.
5) Sprouts--culls initiating root and leaf growth after the onion has been harvested (see discussion in Appendix A).
6) Tops--the excised leaf tissue from the neck-bulb interface left in the field after harvest.

Data collected from sampling cull onions to determine life-stage incidence (see discussion of sampling) was used for the descriptive analysis of numerical change through time within the three study sites. The first step in critically evaluating cull dynamics was to look at the change in estimated population densities through time using the first sampling date or date of harvest for each field as a reference point. The understanding of the post-harvest physiology of onion bulbs is exclusively related to the storage environment (Appendix A). The knowledge that might pertain to cull phenology is embraced in a biochemical ramework and not applicable to this study (Herner et al. 1975), thus chronologi-al time was used as an index. The sample number size for the 9.2 m^2 quadrat sa

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sample unit provided an average sampling precision of approximately 15-30% with regard to the standard error to mean ratio (see discussion on cull sampling). These limits allow for an analysis of the change through time, if not for each sampling interval at least between initial and final sampling dates. Figure 3 illustrates the average relationship between time from harvest in weeks and mean cull density for the fields in the three regions. Although the harvest date for each field was not the same, there are detectable trends.

A non-parametric test based on the sampling distribution of S (Ferguson 1965) was used for analyzing and describing the trends represented in Figure 3. The S distribution, as used in Kendalls Tau, is a symmetrical discrete distribution that approximates the normal distribution as N approaches infinity. The test statistics based on S are a corollary to the method of orthogonal polynomials in the analysis of variance, but can be applied to polytonic as well as monotonic functional relationships. Tests of significance can be applied to populations of continuous probability density functions by using the standard normal deviate of S, Z, where:

$$Z = \frac{\Sigma s}{\sigma \Sigma s} \quad \text{and} \quad \sigma^2 \Sigma s = N\sigma_S^2$$

and

$$\sigma_S^2 = \frac{1}{18} \left(K(K - 1)(2K + 5) - \sum_{i=1}^{M} t(t - 1)(2t + 5)\right)$$

K represents the different fields, t the number of M types, and Ss denotes S since each individual field with its inherent variation was used in the analysis as a multiway classification. Table 7 provides some interpretation of the data plotted in Figure 3. Each cull type exhibits a trend where the sum total of the


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whole

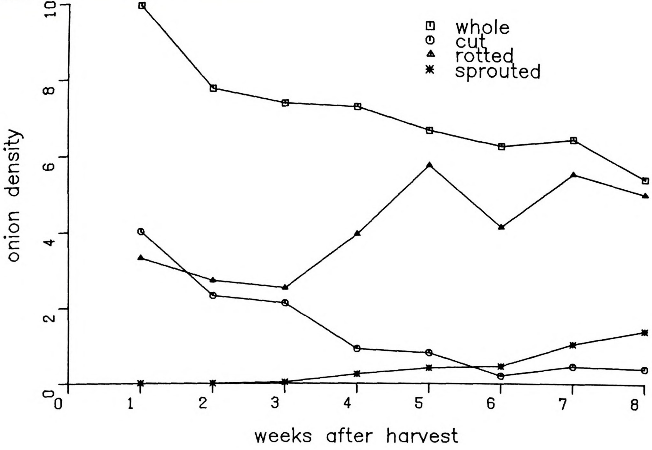

Figure 3. Relationship between onion cull types and time of harvest.

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Table 7. Nonparametric trend analysis for onion culls through time.

	Cull Type				
	Whole	Cut	Rotted	Sprouted	Total
ΣS	-78	-100	+64	+123	-16
Z^1	4.07	16.56	56.50	23.15	0.40

[1] Table Z is 2.03 at the .01 level, null hypothesis: a monotonic trend does not exist.

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culls remains fairly constant (Z=0.40). Based on the significance of Z (Table 7), the average cut cull tends to decrease in numbers at a higher rate than whole culls (ΣS = -78 and ΣS = -100, respectively). This decrease might be explained (1) by the cull's physiological response to damage (sprouting) or subsequent microbial invasion (rotting), and (2) because freshly damaged onions are more attractive to females for egg laying than undamaged bulbs (Carruthers 1979). The rotted culls increase through time (ΣS = +64) but the low relative correlation with a monotonic property suggests significantly more variation in the density estimates, a polytonic relationship, or both. An interesting relationship in Figure 3 is between weeks one and three. The decreasing rate of whole culls and cut culls is not synchronized with the increasing rate of rotted culls.

Unless the fields are synchronized at least initially on a chronological or pseudo-physiological time basis, events that are out of phase with each other may be obscured, thus interpretations of the trends may be incorrect. For example, sprout numbers show a positive correlation with time. The linearity of the response, however, is unexpected since one would hypothesize a time-delayed pulse initiated at harvest.

The physiological time base of cull dynamics could not be estimated. Therefore, the fields were grouped into two classes representing the two main dates that the research fields were harvested (Julian Days 254 and 268). The sample data was examined on the physiological time scale of the onion maggot with a biofix at 50% adult emergence (Whitfield 1981) or 1855 degree days (base 4.4°C). The fields harvested before emergence was completed had a mean harvest date of 15 degree days before 50% emergence. The first sampling date, however, was not until almost 40 degree days later. Figure 4 illustrates the

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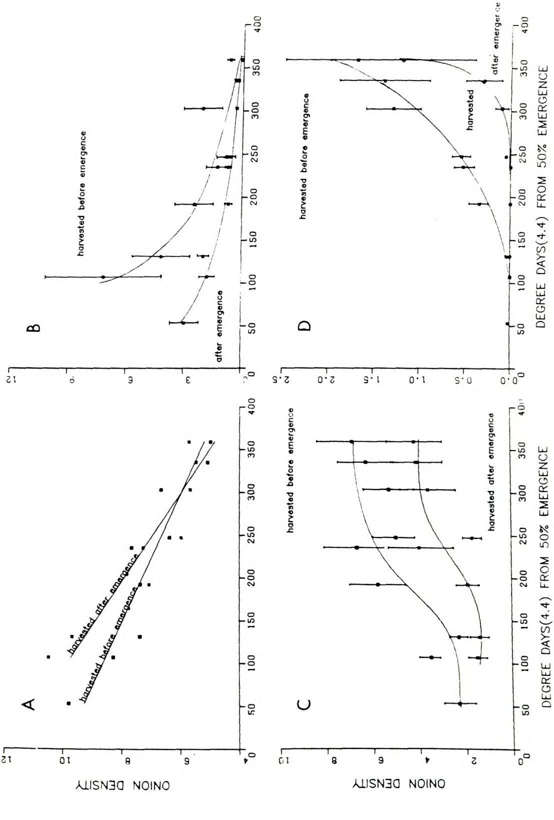
relationships between harvest times and cull type as would have been experienced by the onion maggot third generation. The mean duration of development from emergence to pupa was approximately 370 degree days (Carruthers 1979). The dashed line represents a hypothetical extrapolation to 50% emergence devoid of any confidence regions.

Date of harvest does not impact whole cull dynamics (Figure 4). Differences in whole cull numbers intitially sampled do not appear until 250 degree days, which corresponds with the mean first instar incidence. Whole cull numbers do not change dramatically through time after 250 degree days. I hypothesize that this may be because the infested culls are more attractive to ovipositing female flies or to the truncation of oviposition as a response to cool autumn weather (see Life Table Study).

The change in cut culls is more rapid (Figure 4). A decreasing slope with time suggests that these onions may be the first to be exploited by colonizers. The rate at which this happens could beneficially impact onion maggot survival. Rotted or infested culls provide an ideal food source and habitat for survival (see Life Table Study). Within 100 degree days after harvest, cut culls rot or are infested. Therefore, the physical process of harvesting may be a key to manipulating onion maggot survival as well as harvest timing.

The 107 degree day lag between the two populations of rotted culls continues until the end of the season when the two curves become one. Due to the sampling variance at the higher densities, it is difficult to tell whether the lag is real or an artifact and whether the associated slopes are changing at the same rate per degree day or whether there is a faster rate of change in the fields harvested after emergence. Logically, the slopes should be the same, and they

Figure 4. Change in onion cull density as a function of cull type and time of harvest in relation to adult onion maggot emergence (A = whole culls, B = cut culls, C = rotted culls, D = sprouted culls).


A
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ONION DENSITY
ONION DENSITY
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DEGREE DAYS(4.4) FROM 50% EMERGENCE
DEGREE DAYS(4.4) FROM 50% EMERGENCE
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should go to zero, since egg-laying causes an aggregated response that would not increase the rate of rotted cull production after random oviposition.

The data does not explain the transformation of cut culls to rotted culls. Cut culls have a high negative rate of change for the first 100 degree days after harvest (Figure 4c). Cut onions probably have to either stay as a cut bulb or start decaying. The data for rotted culls do not show an equally inverse geometric rate of increase. Instead, there is a lag in response. This cannot be explained since the sprouting onions were not detected until 150-200 degree days after harvest. Perhaps the sampling of low-level populations did not reflect the early season rates of change, since the distributions were more highly aggregated at first. Another possibility is that some cut bulbs calloused over and became whole culls.

The sprouts were the most attractive for oviposition and the best suited for population increase out of all the types of culls (see Life Table discussion).

In both groups of fields, sprouting began approximately 150 degree days after harvest. This response is probably more closely correlated than any of the other cull dynamics since the heat unit base for onions is 5.6° C (Bolgiano 1980). Using sprouts as a trap crop or forcing onion flies to oviposit on less desirable hosts could be a management tool. (Both onion maggot adult emergence and prout growth can be predicted.)

Weight loss of culls through time was the second component studied in elation to the population behavior of the onion maggot food source. A eliability analysis modeled the analysis since the experimental units from each ampling period we are the same (Mehrens et al. 1967) (Tables 8 and 9). A was sed to adjust the mean weight loss since the surface to volume ratio interacts

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Table 8. Repeated measures three-way anova results for weight loss, cohort II.[1]

Source	DF	SS	MS	F
S (soil type)	1	0.0159	0.0159	1.88 NS
L (location)	1	0.2168	0.2168	25.65 ***
C (cull type)	3	0.5417	0.1806	21.37 ***
SL	1	0.0064	0.0064	0.75 NS
SC	3	0.0208	0.0069	0.82 NS
LC	3	0.1651	0.0551	6.51 ***
SLC	3	0.0158	0.0053	0.62 NS
Covariate	1	6.6621	6.6621	788.51 ***
Error	63	0.5328	0.0085	
T (time)	3	0.7443	0.2481	112.57 ***
TS	3	0.0046	0.0015	0.69 NS
TL	3	0.0757	0.0252	11.45 ***
TC	9	1.1272	0.1253	56.83 ***
TSL	3	0.0123	0.0041	1.86 NS
TSC	9	0.0108	0.0012	0.54 NS
TLC	9	0.0688	0.0077	3.47 **
TSLC	9	0.0309	0.0034	1.56 NS
Error	192	0.4232	0.0022	

[1] Transformed data log (x+1)

** Significant at .01 level

*** Significant at .001 level

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Table **9.** Repeated measures three-way anova results for weight loss, cohort I[1].

Source	DF	SS	MS	F
S (soil type)	1	0.0299	0.0299	1.18 NS
L (location)	1	1.8301	1.8301	72.41 ***
C (cull type)	3	8.938	2.979	117.89 ***
SL	1	0.0001	0.0001	0.000 NS
SC	3	0.1209	0.0436	2.91 NS
LC	3	0.6181	0.2060	8.15 ***
SLC	3	0.0699	0.02330	0.92 NS
Covariate	1	25.3119	25.3119	1001.5 ***
Error	61	1.5417	0.0253	
T (time)	8	4.9621	0.6203	251.51 ***
TS	8	0.0200	0.0025	1.00 NS
TL	8	0.28368	0.0355	14.38 ***
TC	24	3.8009	0.1584	64.22 ***
TSL	8	0.0116	0.0013	0.56
TSC	24	0.1217	0.0051	2.04 NS
TLC	24	0.3378	0.0140	5.69 ***
TSLC	24	0.0415	0.0017	0.70 NS
Error	496	1.2232	0.0025	

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[1] Transformed data log (x+1)

** significant at .01 level

*** significant at .001 level

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with water loss. The adjusted means are plotted for both cohorts (Figure 5) to interpret the analysis of variance. Weight lost in the first cohort (Table 8) was a result of location (on the soil surface or 2.5 cm below), the type of cull, the interaction of location and cull type , time, and the interaction of time with these factors. This suggests that soil type (Houghton or Martisco) had little effect on weight loss. Cohort 2 (Table 8) responded similarly to the factors of location, cull type, and time. Tables B1 and B2 (Appendix B) show the results of the analysis on a per sample period basis. In both groups the interaction with time became less predominant through time. This suggests that most weight loss occurs soon after harvest except where culls are under the soil (Tables B1 and B2). The significance of this weight loss on the population dynamics of the onion maggot is unknown.

Data was collected on weight loss as affected by the bulb mite, *Rhizoglyphus echinopus* (F. and R.); the lesser bulb fly, *Eumerus* spp. (Fall.); and the onion maggot. The variance was analyzed through a log (x+1) transformation. Heteroscedasticity of the irregular type (Steele and Torrie 1960) was characterized by the onion maggot treatment possessing considerably more variability than the other three treatments with no apparent relation between means and variances. To make valid comparisons, the error mean square was subdivided into components so a weighted comparison of treatments could be made. Significant differences were not found between treatments of arthropod species (Table B3), although treatment interactions with time did exist. The variability between weight loss in culls colonized by onion maggots and that of the other treatments cannot be explained.

Cull type and location interactions through time may impact on onion maggot dynamics. It is hypothesized that the qualitative relationships will

ADJUSTED MEAN WEIGHT (GMS.)

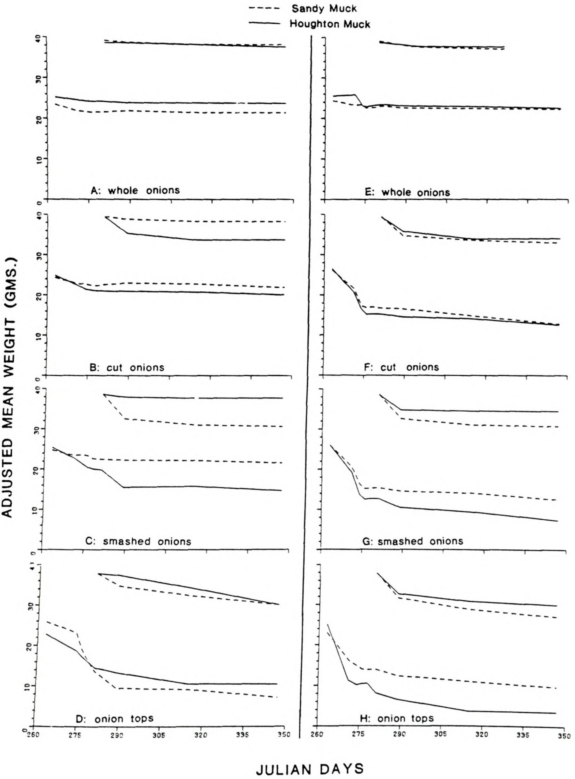

Figure 5. Mean adjusted cull weight loss through time (A-D: culls buried under the soil surface; E-H: culls left on top of soil surface.

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operate from season to season although the functional forms of these will be extremely dynamic especially right after harvest. Until more is known about water loss in onion culls and onion maggot population dynamics, future research efforts should be directed into cull transformation and the possible interactions between cull host and onion maggot synchronies.

CULL ONION SAMPLING

Sample Unit Size For Sampling Onion Culls

The efficiencies of three square sample units (0.84 m^2, 2.32 m^2 and 9.29 m^2) were estimated using a similar method as that of Helgesen and Haynes (1972). The relationship of the mean density of onions to sample standard deviation was approximated linearly. A sample size (n) for each sample unit was calculated for a mean of 2.0 onions/sample unit (a density within the range of all three regressions) by dividing the population variance (y^2) by the sample variance ($S\bar{x}^2$), where $S\bar{x}$ was fixed at 10% of the mean ($\bar{x}$):

$$N = y2/S\bar{x}2$$

In Table 10 the efficiency of the sample units is compared. The evaluation of the efficiencies should not be based on N converted to total square meters but on N, The majority of time taken to sample cull onion density was not as much a function of area of soil as it was moving from location to location and setting up the sampling quadrat (sample unit). In light of this, a sample unit of either 2.32 m^2 or 9.29 m^2 was equally efficient (slopes not significantly different at $P = .05$). The sample unit size of 9.29 m^2 was chosen for the remainder of the study.

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[2] N

Table 10. The relationship between the mean number of cull onions per sample unit and the sample standard deviation.

	Regression statistics[1]			
Sample unit size	N	b ± SE	r^2	N[2]
0.84 m^2	14	2.24 ± 0.15	.95	502
2.32 m^2	17	1.29 ± 0.16	.75	166
9.29 m^2	39	1.06 ± 0.07	.89	112

[1] Regressions forced through the origin.

[2] Number of samples which will allow a standard error ($s\bar{x}$) to be equal to or less than 10% of a mean of 2.0 onions/sample unit.

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Development Of A Sampling Plan For Cull Onions

Onions are not uniformly distributed within a field after harvest. Observations of harvest operations showed that the two major factors influencing cull distribution were initial onion distribution prior to harvest and the machinery and technique used during harvest. If these are constant from year to year, then the development of a standardized sampling plan for annual cull estimates should be feasible. These estimates can be used to determine total onion maggot production for the post-harvest season to estimate biomass for cost-benefit analysis regarding alternative uses for onion culls (Haynes et al. 1980).

The mathematical form of the spatial pattern of onions left in the field after harvest was derived from the 1979 data collected in Eaton Rapids and Grant, Michigan. The fields in the analysis (K, R, P, 1, 2, 3, 4, 5, 6) had not been culturally manipulated after harvest (disked, plowed, or harrowed), and all recorded cull types were pooled. Seven theoretical parent distributions: normal, logarithmic series, gamma, negative binomial, positive binomial, poisson, and exponential (algorithms developed by Dimoff 1979) were tested for goodness of fit to the sample frequency distributions. The basis of acceptance was derived from the results of the χ^2 test, Kolmogorov-Smirnov test, and the third moment test.

The three tests evaluate different criteria. The χ^2 test is based on the absolute differences between sample and theoretical frequency distribution. There has been debate as to the utility of the χ^2 test for "goodness of fit" determinations due to the test's sensitivity to chance irregularities in the data (Bliss and Fisher 1953). To minimize this effect, frequencies have been combined such that no expected values are less than 5 (Sokal and Rohlf 1969).

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Cochran (1954) believes this restriction weakens the sensitivity of the test and alters the alpha level. The third moment test measures the difference between the sample estimate of the third moment and the expected third moment (T). Agreement is accepted if the value of T differs from zero by less than its standard error. The third moment test is considered to be the most powerful test for "goodness of fit" (Anscombe 1950, Bliss and Fisher 1953, Bliss and Owen 1958, and Elliot 1973). The Kolmogorov-Smirnov test (a nonparametric test) is based on the absolute differences between the sample cumulative and the theoretical cumulative frequency distribution. It is an exact test and is believed to be more powerful than the χ^2 test, especially when the sample size is small (Conover 1971). A nice feature of the Kolmogorov-Smirnov test is that it enables a confidence band to be constructed about an unknown distribution function. I integrated the results of all of the tests, thereby averaging the effects of bias and various levels of power in any one individual test.

Despite the indication from the χ^2 test and the Kolmogorov-Smirnov test that there was good agreement between the observed data and the expected negative binomial frequencies (Table 11), the results of the more sensitive third moment test did not support this (only two of the nine fields were not significantly different from theoretical distribution). Evaluating the mechanics of the third moment test showed that it was not applicable in analyzing the spatial distribution of onion culls. The derivation of the third moment test is based on the assumption that an efficient estimate of K is not available for computing the expectation of the variance (Anscombe 1950). The estimate of K was arrived at using an interative algoritym, (Elliot 1973), to obtain the **maximum likelihood** estimate (algorithm programmed by Dimoff 1979). Both T and the variance of T (V(T)) are computed from a known value of K.

Table 11

Field	de
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able 11. Spatial distribution statistics of cull onions, 1979.

ield	density	s^2	$\hat{K}$	chi-square			K-S[3]
				Df[1]	Calculated	Tabled[2]	
1	15.87	96.80	3.93	3	1.014	7.82	.039
2	14.18	47.18	6.49	4	9.09	9.49	.076
3	17.14	114.70	5.66	2	3.30	5.99	.070
4	10.72	78.40	2.19	3	3.19	7.82	.069
5	12.51	59.38	4.34	3	7.17	7.82	.065
6	12.33	31.25	7.96	6	10.02	12.59	.042
P	7.91	19.26	6.77	3	1.81	7.82	.073
R	11.58	42.19	5.02	5	5.77	11.07	.059
K	23.81	473.08	2.01	3	0.31	7.82	.033

Degrees of freedom (no expected class values < 5)

$P = .05$

Kolmogorov-Smirnov test statistic, tabled value @ $P = .05$ and 8 degrees of freedom is .454

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$$T = \frac{\chi^3}{N} \quad - \sigma^2 \{\frac{2\sigma^2}{m} -1\}$$

T = sample third moment - expected third moment

where in the negative binomial distribution

$$\sigma^2 \simeq \bar{x} + \frac{\bar{x}^2}{\hat{K}}$$

$$V(T) = 2m(K + 1)p^2q^2\ (2(3 + 5p) + 3Kq)/N$$

where: m = arithmetic mean

K = estimate of K based on maximum likelihood estimate

$\chi^3 = \Sigma\, x^3 - 3\bar{x}\Sigma x^2 + 2\bar{x}^2\Sigma x$

p,q = expected proportions of binomial classes.

The problem is that the values of T and V(T) should be derived with independent estimates of K, otherwise the validity of V(T) is questionable (Bliss and Fisher 1953). Anscombe (1950) evaluated the efficiencies of the moment estimate of K, an estimate of K from the proportion of zeros, and the transformation method of estimating K. As these conditions (described by Anscombe 1950) were not met in the analysis of the cull onion data; therefore, the results of the third moment test (Elliot 1973) probably cannot be relied on as a basis for a decision. Table 11 shows the maximum likelihood estimates of K and the associated test statistics of the χ^2 test and the Kolmogorov-Smirnov test from which the acceptance of the negative binomial distribution as an adequate descriptive model was based.

Generality of a sampling scheme based on the negative binomial distribution can be achieved if the respective distributions have the same relative

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dispersion in terms of $\hat{K}$ A common K or stable K indicates that the level of clumping is a fairly constant characteristic of the populations being sampled. To justify the calculation of a common K, Elliot (1973) suggests that $\bar{x}$ vs. 1/K be plotted. A common K should be suspected only if no definite trend exists between $\bar{x}$ and 1/K (See Figure 6).

Several methods for estimating a common K have been described (Bliss and Owen 1958). The method chosen for this analysis utilizes a linear regression of y' on x' forced through the origin (0,0), where:

$x' = \bar{x}^2 - s^2/N$

$y' = s^2 - \bar{x}$

the resulting slope being the reciprocal of common K. The common K (3.460) for the 1979 data sets was tested for agreement to each individual field data set with the χ^2 test and Kolmogorov-Smirnov test ($p = .05$). (Table 12). There is no evidence to reject the negative binomial parent distribution with a common K of 3.460 as a model describing the spatial distribution of the sampled onions.

This model was validated using a randomly selected subset of data collected in Grant Township, Newaygo County, Michigan, 1980 (Ellis unpublished 1980). The model was applied to two groups of fields: (1) before cultural manipulations, and (2) after disking, plowing or harrowing. Since the sample sizes in the validation fields were smaller ($n = 20$), an additional goodness of fit test, the Cramer-von Mises test, was used as a decision criterion. The test is very discriminating when used with small sample sizes (Conover 1971) in rejecting the null hypothesis. The results of the validation are shown in Table 12. Only one field (#141) of the two groups did not fit the model at the 5% level

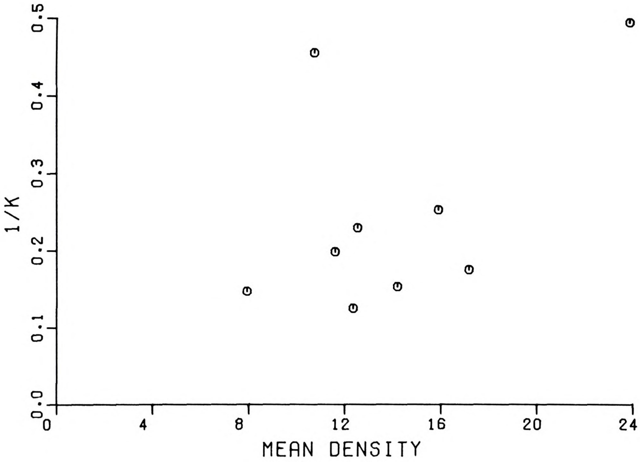

Figure 6. Reciprocal of the negative binomial parameter k as a function of the sample mean.

Table 12. Goodness of fit for a common K^d to cull distributions.

Kolmogorov-Smirnov	Cramer-von Mises[5]

Field	N	$\bar{x}$	Chi-square			Kolmogorov-Smirnov			Cramer-von Mises[5]
			Df	Calculated	Tabled[4]	Df	Calculated	Tabled[4]	
1979									
1	79	15.87	4	1.60	9.49	8	.0387	.410	
2	90	14.18	7	8.73	14.07	8	.0829	.410	
3	91	17.14	4	3.39	9.49	8	.0638	.410	
4	79	10.72	4	3.61	9.49	8	.0864	.410	
5	91	12.51	5	4.31	11.07	8	.0601	.410	
6	89	12.33	8	7.10	15.51	8	.0738	.410	
P	35	7.91	3	0.93	7.82	8	.0557	.410	
R	71	11.58	7	8.89	8.73	8	.0629	.410	
K	53	23.81	3	0.71	7.82	8	.0562	.410	
1980[2]									
142	20	30.10	4	3.57	9.49	5	.0949	.563	
141	20	80.15	4	9.89	9.49	5	.2183	.563	
127	20	16.45	3	2.50	7.82	5	.1768	.563	.389
61	20	25.80	4	.812	9.49	5	.0759	.563	.088

Table 12. (cont.)

	Chi-square			Kolmogorov-Smirnov			Cramer-von Mises[5]
	Df	Calculated	Tabled[4]	Df	Calculated	Tabled[4]	

Field	N	$\bar{x}$	Df	Calculated	Tabled[4]	Df	Calculated	Tabled[4]	
1980[2]									
77	20	7.15	4	1.94	9.49	5	.0797	.563	.097
92	20	26.50	4	2.09	9.49	5	.1629	.563	.175
106	20	21.80	5	8.53	11.07	6	.1843	.519	2.22
105	20	10.30	4	7.34	9.49	6	.1980	.519	.307
90	20	17.70	4	0.03	9.49	6	.1098	.519	.188
71	20	23.95	4	3.25	9.49	6	.1286	.519	.162
121	20	65.10	3	.568	7.82	6	.0775	.519	.092
79	20	16.20	4	2.10	9.49	6	.0945	.519	.138
85	20	54.30	4	3.05	9.49	6	.0848	.519	.412
1980[3]									
90	20	4.8	4	3.55	9.49	6	.2130	.519	.261
78	20	0.9	3	0.57	7.82	5	.0490	.563	.454
19	20	2.3	4	0.06	9.49	6	.0314	.519	.346
23	20	1.5	4	0.29	9.49	6	.0519	.519	.418
24	20	4.0	4	0.23	9.49	6	.0788	.519	.430

** Significant at $\alpha = .05$

[1] Kc = 3.460

[2] Fields not plowed or disked

[3] Fields plowed and disked

[4] $\alpha = .05$

[5] Tabled W(.95) = 0.461

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for two of the three tests. Whether the extremely high density of onions in the field (80.15 onions/9.29 m^2) was a factor is unknown. It does appear that fields with an average density (10-20 onions/9.29 m^2) are adequately described by the model, as are plowed and disked fields.

Using the negative binomial parent distribution with a common K of 3.460, a sampling scheme was constructed for determining the sample size necessary in estimating onion density for a given specified error term. The general formula outlined by Karandinos (1976) was used

$$n = \frac{Z^2_{\alpha/2}\left(\frac{1}{\bar{x}} + \frac{1}{Kc}\right)}{D^2}$$

where:

n = sample size

$Z_{\alpha/2}$ = upper $\alpha/2$ point of the standard normal distribution

$\bar{x}$ = arithmetic mean

Kc = common K

D = relative error of confidence limits.

Table 13 shows the number of square meter sample units necessary for estimating various mean densities at different specified error levels. No attempt was made to construct a regional sampling.

An interpretation of how to use the information depicted in Table 13 can best be conveyed via an example. Suppose that an extension agent needed to have an estimate of within field cull onion production, perhaps for approximating the overwintering onion maggot density. The agent would select a level of precision (expressed in terms of the confidence limit as a proportion of the mean or, more simply, the range of uncertainty one is willing to accept). If the

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le 13. Sample size based on cull distributions.

	confidence limit[1] as proportion of $\bar{x}$				
$\bar{x}$	.10	.20	.30	.40	.50
.5	881	220	98	55	35
1	481	120	53	30	19
5	161	40	18	10	6
10	121	30	13	8	5
15	105	26	12	7	4
20	101	25	11	6	4
25	97	24	11	6	4
50	89	22	10	6	4
α	81	20	9	5	3

ssuming a .95 probability level of error term for confidence limits.

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individual is satisfied to estimate a low cull density such as 5 culls/9.2 m^2 when the true mean could range from 6-4 culls/9.2 m^2 (.20 confidence level) then 40 sample of 9.2 m^2 per field would have to be taken. The critical decision is determining the upper bound of the cull density one is working with. If the agent decided on 40 sample units per field and ended up with an estimate of 1 cull/9.2 m^2 for a given field, the range for .40 (at a .95 level). This may not be of concern since the range would only be 0.6-1.4, whereas, a mean of 20 culls/9.2 m^2 is more affected by a shift in the confidence limit precision due to inadequate sample size.

EGG SAMPLING

Eggs were sampled by two different sampling plans during the fall of 1979. Age-specific density estimates were based on a twenty onion cluster sample unit. The following analysis of egg sampling is based on variances and cost structures associated with these fixed sample units and may be more energy intensive for a given precision level than one based on more appropriate sample units.

Both sampling schemes used a geographically stratified design (fields were apportioned into five equal sectors). Previous findings of the temporal and spatial distribution of adult flies during the growing season (Whitfield 1981, Carruthers 1981) initiated a preliminary study on existing ovipositional zones within a field. Three strata in fields 1 and 3 that were probably oviposition zones were: (1) strata with adjacent grassy borders, (2) strata adjacent to other onion fields, and (3) strata confined to the middle areas of the sampled fields. Results of an analysis of covariance (egg densities adjusted by onion densities)

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suggested that strata do not cause differences in egg density (Table 14). Nonetheless, the sample universe stratified partly to increase our knowledge of the post-harvest ecosystem. Optimal weights for strata were applied proportionately, thus yielding a self-weighting sample.

Only within field variation was analyzed concerning relative efficiency and optimal sample sizes (see Carruthers 1979 for discussion on damage sampling). The initial analysis of the sampling data (Tables 14 and 15) revealed that stratifying each sample field into five equal geographic sectors did not add precision to a simple randomized design. The mean square among strata (strata/field) was compared with the mean square error. Proportional stratification reduces variance over simple random sampling when the mean square among strata is larger than the mean square error (Cochran 1977). The mean square error was larger in 6 out of 7 sample dates for the quadrat sampling and greater than or equal to 5 out of 9 sample dates for the simple stage cluster sampling. Early sample dates for the cluster sampling showed a gain due to proportional stratification (degree days 1990-2081), but after the third sampling interval, the variance of the strata component was lower. Agricultural surveys where strata are based on geographic characters often show no gain (Jessen 1978). The possibility of a change in the strata variance should always be considered when sampling plans such as these are used between years and regions. The interactions of onion fly behavior, cull type, distribution, and weather may considerably influence egg distribution.

Initial analysis of the frequency distribution of the quadrat sampling data did not theoretically describe the spatial pattern of the eggs (see cull distribution section for methods of analysis). The overall mean to variance relationship

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Table 14. Results of analysis of covariance[1] in relation to egg density by strata.

Source of Variation	DF	Sum of Squares	Mean Square	F	Significance level
Field 1 Total	11	342.34			
Strata	3	85.45	28.49	.776	.543
Within	8	256.88	36.69		
Field 3 Total	11	65.55			
Strata	3	7.39	2.47	0.296	.826
Within	8	58.16	8.31		

[1] square root transform, Bartlett's test significance level: Field 1: P = .792 and Field 3: P = .135

ble 15. Results of nested analysis of covariance on mean numbers of eggs/9.26 M^2 in Grant, Michigan 1979.

Degree day ase 4.4°C)	Source of Variation	Degrees of Freedom	Adjusted[1] Sum of Squares	Adjusted[1] Mean Square
1934	Field	3	440.29	146.76
	Strata/Field	16	910.69	56.91
	Error	19	3148.59	165.72
1974	Field	5	23.95	4.79
	Strata/Field	24	226.81	9.45
	Error	29	372.04	12.83
1990	Field	5	559.96	111.99
	Strata/Field	24	1949.49	81.23
	Error	29	2571.58	91.84
2034	Field	5	4885.32	977.06
	Strata/Field	24	6663.19	277.63
	Error	29	4075.32	140.52
2100	Field	5	5724.27	1144.85
	Strata/Field	24	3797.08	158.21
	Error	29	6009.29	207.22
2110	Field	5	1144.67	228.94
	Strata/Field	24	2147.89	89.49
	Error	29	2910.81	100.37
2154	Field	5	18.31	3.66
	Strata/Field	24	219.82	9.16
	Error	29	288.64	9.95

[1] Adjusted by mean density of culls per quadrat

of the eggs through time indicated that the spatial distribution was contagious. The amount of aggregation (at least to the sample unit) was determined by quantifying the linear relationship between the log mean and log variance of eggs per unit area (Taylor 1961). Figure 7 shows the sampling data (slope = 1.91) as a poisson distributed (slope = 1.0) random variable. The sample variance for each sampling date was separated into its within and between field components using a one-way analysis of covariance (Table 15) to arrive at the mean-square error (within field variance) and the sum of squares of strata (field and error must be pooled and divided by the respective pooled degrees of freedom) (Harcourt and Binns 1980). This imposes a structure of randomized sampling where quadrats are widely distributed throughout the field. The mean-square error (MSw) of the analysis of covariance is an unbiased estimate of the within-field variance component ($\hat{S}_w^2$) corrected by cull density/quadrat (Jessen 1978). As $\hat{S}_w^2$ is dependent on the sample mean, a log-mean log-variance function was used to describe the relationship (Carruthers 1979). The estimated parameters for the relationship:

$$\log \sigma^2 = \log a + b \log \bar{x}$$

$$\sigma^2 = a\bar{x}^b$$

are shown in Table 16. The arithmetic mean (Carruthers 1979) was corrected to adjust for the biased regression estimate:

$$Y = \text{Antilog}\,(a + b \log x + 1.1513\ S^2)$$

where $\hat{S}2$ = residual mean square (Table 16). Thus, the adjusted relationship between the mean and the variance $\hat{S}_w^2$ is:

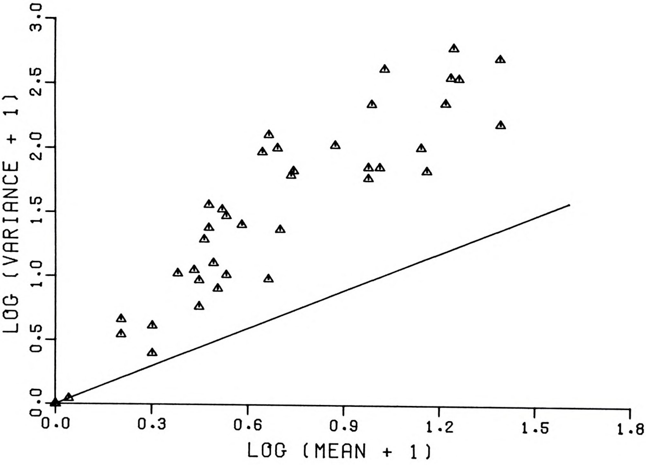

Figure 7. Log mean of variance relationship of quadrat egg sampling data (fitted line is poisson where b= 1).

able 16. Regression statistics for quadrat log mean-log $\hat{S}^2w$ relationship.

Source	Degrees of Freedom	Sum of Squares	Mean Square
egression	1	1.647	1.647
esidual	5	0.179	0.035
otal	6	1.827	

= 0.96 ± 0.07

= 1.35 ± 0.19

= .90

$$^{2}_{W} = 10.01\ \bar{x}^{1.35}$$

ssuming normality from the Central Limit Theorem (Steel and Torrie 1960), the ptimal number of samples per field can be estimated by substitution into the quation developed by Carruthers (1981). Therefore, within a region, the number samples taken per field (M) is:

$$= Z^2_{\alpha/2}\ (10.01\ \bar{\bar{x}}^{1.35})\ /\ NF(D\bar{\bar{x}})^2$$

here: $Z^2_{\alpha/2}$ = square of the one-tailed standard Z score (Karandinos 1976)

σ = probability of type 1 error (α),

NF = number of fields within a region, and

D = precision ($S\bar{x}/\bar{x}$).

the estimate of concern is eggs/onion, the coefficient of variation for both its can be adjusted to a common basis (eggs/onion) where the quadrat is a uster of varying size. Jessen (1978) found that the quadrat is only one-third to ree-fifths efficient as the cluster unit in estimating eggs/onion.

The relative precision of clustering was determined over the sample dates. lividual onion variance can be arrived at using Cochran (1978) and mean square ta (Table 17):

$$= \frac{(N - 1)\ \hat{S}^2_B + N\ (M - 1)\ \hat{S}^2_W}{NM - 1}$$

ere: $\hat{S}^2_B$ = an unbiased estimate of S^2 cluster,

$\hat{S}^2_W$ = an unbiased estimate of the error,

N = the number of clusters, and

M = the number of elements/cluster.

e 17. Results of nested analysis of variance on mean number of eggs/onion with single stage cluster sampling in Grant, Michigan 1979.

ree day e 4.4°c)	Source of Variation	Degrees of Freedom	Sum of Squares	Observed Mean Square
1990	Field	5	9.25	1.85
	Strata/Field	24	33.72	1.41
	Cluster/Strata	30	32.55	1.10
	Error	1140	979.80	0.86
2051	Field	5	147.71	29.54
	Strata/Field	24	262.32	10.93
	Cluster/Strata	30	222.60	7.42
	Error	1140	6956.50	6.10
2081	Field	5	428.35	85.67
	Strata/Field	24	375.90	15.67
	Cluster/Strata	30	417.28	13.91
	Error	1140	11159.95	9.79
2097	Field	5	131.55	26.31
	Strata/Field	24	206.18	8.59
	Cluster/Strata	30	367.30	12.24
	Error	1140	9918.70	8.71
2106	Field	5	1292.24	258.45
	Strata/Field	24	486.68	20.28
	Cluster/Strata	30	754.13	25.14
	Error	1140	32449.75	28.46
113	Field	5	102.84	258.45
	Strata/Field	24	71.78	2.99
	Cluster/Strata	30	166.95	5.56
	Error	1140	3514.10	3.08
134	Field	5	407.32	81.47
	Strata/Field	24	1894.34	78.93
	Cluster/Strata	30	2149.18	71.64
	Error	1140	1944.45	1.71
198	Field	5	4.18	0.84
	Strata/Field	24	7.60	0.32
	Cluster/Strata	30	11.40	0.38
	Error	1140	405.60	0.36
204	Field	5	0.11	0.02
	Strata/Field	24	1.02	0.04
	Cluster/Strata	30	0.98	0.03
	Error	1140	36.75	0.03

The relative variances for a fixed total sample size are shown in Table 18. On a straight precision basis, a cluster of twenty onions does not reduce the variance with sampling individual onions. This implies that within a cluster the onions are not similar to one another in terms of eggs laid. Thus it would be just as advantageous to sample random elements. The cost involved in selecting random locations makes it much more favorable, however, to sample clusters (C_0 = 3 man-minutes and C_{point} = 4 man-minutes).

As in the quadrat sampling, an underlying theoretical distribution could not be found that adequately described the dispersion of the eggs on onions through time. The overdispersion of the field counts is shown in Figure 8 (slope = 4.87). Again the strata variances were not large; therefore, a simple, randomized, single-stage cluster[1] sampling design was adopted. The contributions to the variance of the mean were estimated from a two-level nested analysis of variance for each sample date (Table 17: strata within field source of variation pooled with cluster source of variation to yield cluster within field source of variation). This essentially imposes on the data the structure of the cluster units well spread out over the sampled field. Presumably this should not effect the costs involved, as the cost of sampling random clusters within a geographically stratified field is equivalent to sampling random clusters throughout the whole field.

The estimate of variance for untransformed numbers of eggs per onion, considering the components of variance between and within clusters, is (Jessen 1978):

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[1] The terminology of single stage is used as suggested by Cochran (1977) where all the elements within the primary (cluster) are sampled as opposed to a 2-stage plan where the elements within the primary are a randomly selected subset of N total elements.

e 18. Relative precision of cluster sample to onion sample.

mple Degree (base 4.4°C)	Relative Variances for Fixed Sample Size		Relative Precision Cluster/Onion (%)
	Cluster	Onion	
1974	1.10	0.87	79.3
2034	7.42	6.17	83.2
2064	13.91	9.96	71.6
2080	12.24	8.89	72.6
2089	25.14	28.29	112.5
2097	5.56	3.20	57.5

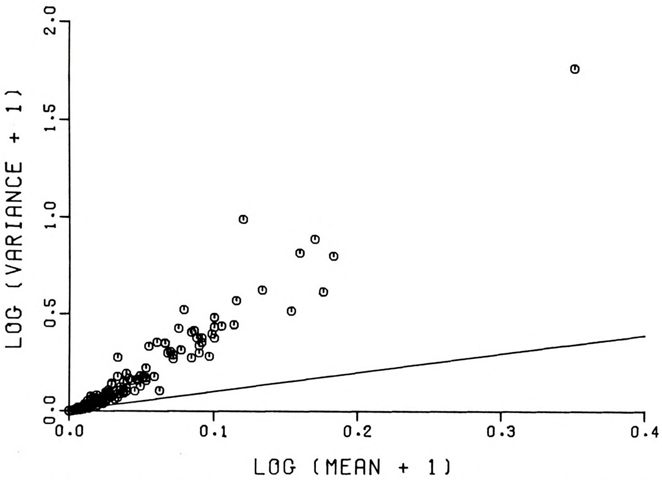


Figure 8. Log mean (eggs/onion) of variance relationship of cluster sampling data (fitted line is poisson where b = 1).

$$\text{AR}\;(\,\bar{\bar{x}}\,) = \frac{\hat{S}_W^2 + Mo\;\hat{S}_B^2}{nMo}$$

iere: $\hat{S}_W^2$ = variance within clusters

$\hat{S}_B^2$ = variance between clusters

n = elements per cluster, and

Mo = number of clusters per field.

The total cost (C_T) of sampling is defined as:

$$. = nC_B + nMoC_W$$

ere: C_B = cost of selecting a random cluster, and

C_W = cost of sampling an individual onion.

ilizing these equations, the optimal value for Mo (M(opt)) can be determined a fixed budget, C_T, and constant costs, C_W and C_B by:

$$\text{ppt)} \qquad = (C_B\,\hat{S}_W^2/C_W\,\hat{S}_B^2)^{1/2}$$

$$= [((C_B/C_W)\;/\;(1 - \sigma)]\}s))]^{1/2}$$

ere:$\sigma = \hat{S}_B^2/(\hat{S}_B^2 + \hat{S}_W^2)$

the intraclass correlation coefficient, σ (Jessen 1978) can be determined n the relationship:

$$= (MS_B - MS_E)/Mo$$

ere: MS_B = mean square of cluster/field (Table 20) and

MS_E = mean square error (Table 19).

able **19**. Regression statistics for log mean-log relationship $\hat{S}^2_w$ within clusters.

Source	Degrees of Freedom	Sum of Squares	Mean Square
egression	1	16.81	16.81
esidual	8	0.18	0.02
otal	9	17.00	

= 1.79 ± 0.05

= 1.43 ± 0.05

$^2 = 0.98$

Table **20**. Regression statistics for log mean-log $\hat{S}^2b$ $((MS_b - MS_w)/n)$ relationship between clusters.

Source	Degrees of Freedom	Sum of Squares	Mean Square
Regression	1	15.67	15.67
Residual	8	1.80	0.23
Total	9	17.47	

$a = -0.39 \pm 0.15$

$b = 1.38 \pm 0.17$

$r^2 = 0.90$

Table 21 shows the optimum number of clusters needed based on a total budget (C_T) of 100 man-minutes (average time alotted for 1979) per field, a C_B of 3.5 man-minutes and a C_w of 0.3 man-minutes. An optimal cluster size of 25 per field seems to be adequate for most of the season (except when densities drop off toward the end of the season). Based on a cluster size of 25, an optimal cluster unit size (n) can be determined for minimizing the variance at a set cost of 100 man-minutes per field by (as suggested by Cochran 1977):

$$N = C/(C_B + MoC_w)$$

which yields a value of 9. Therefore, the field should be sampled more intensively with respect to the numbers of clusters (Mo) and less intensively with respect to n.

To determine the precision of the estimate in the preceding case or to establish the optimum Mo to a desired confidence interval of width p% of the mean ($\bar{x}$) at a probability level of 100 (1 - σ) %, the variance of $\bar{x}$ must be computed as before and substituted into an equation discussed by Karandinos (1976) for values of field level densities and confidence limits of 10, 20 and 30% of the mean associated with a .95 level probability statement (Table 22).

Some additional factors that should be considered in constructing and implementing a sampling plan are the distribution of eggs in the soil with respect to those on the plant and the efficiency of detecting them, as well as, the temporal synchrony between cull transformations (see cull dynamics) and the oviposition function. Eggs, approximately 1-1.5 mm in length, are easily sampled when oviposited on the plant. Perron (1972) reported that 64% of the eggs laid

Table 21 . Optimal number of clustersper field[1]

Degree day base 4.4 °c	M(opt)	$\hat{S}^2x$	$\hat{S}^2b$
1990	16	0.86	0.04
2051	16	6.10	0.31
2081	16	9.79	0.50
2097	24	8.71	0.17
2106	25	28.46	0.64
2113	17	3.08	0.12
2198	35	0.36	0.001
2204	36	0.03	0.0005

[1] Total cost fixed at 100 man-minutes per field.

Table 22. Optimum values of M_o (number of clusters) for a given level of precision (N = 9).

	confidence limit[1] as percent of mean		
xeggs/onion	10	20	30
.1	237	59	26
.25	137	34	15
.5	91	23	10
.75	72	18	8
1.0	60	15	7
1.5	47	12	5
2.0	40	10	4

---

[1] $Z_{\alpha/2} = 1.96$

during the growing season were recovered from the soil. Sampling from three unharvested fields in the fall of 1979 produced a similar proportion (70 ± 3% (.95 C.I., N=1410)). Approximately 80% of the eggs recovered from harvested fields were oviposited in the soil (Figure 9). This proportion was fairly stable between the eleven fields. The sampling intervals suggested that soil type (within the range sampled) and soil moisture had no discernable effect. Fortunately, the eggs laid in the soil (after harvest) are usually placed between the cull-soil interface. Since most culls lie on the muck surface, recovery is not a great problem. A few, however, especially with sprouted onions, have been found to depths of 90 mm adjacent to the underground portions of the plant. Sampling eggs during and immediately after a rain was difficult because the muck soil could not be easily separated away from the eggs.

Halfway through the sampling program, a few trials were run to assess the impact of wet muck soil and egg density on the efficiency of recovery. Eggs were buried in known varying densities under whole onions 2-5 mm under the surface in aggregate, and each subject (three of the four people involved in the study) had one minute to find the eggs (Table 23). The sampling variation of the people probably would decrease as they gained experience. Contrary to the hypothesis, high egg density did not increase egg recovery. This might be due to the fact that the sample universe (area under the cull) was relatively small in comparison to the eggs. Soil moisture, however, did increase egg recovery. Therefore, eggs should be sampled during fairly constant conditions.

A complex set of factors that may impact on the estimation of egg density are the temporal interactions of cull dynamics (time of harvest and transformation of cull types) (see cull dynamics discussion), fly behavior, and the incidence

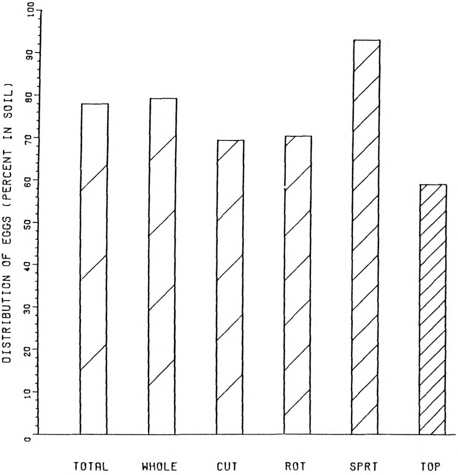


Figure 9. Proportion of eggs distributed in the soil during the third generation (n = 4952).

ble 23. Effect of soil moisture and egg density upon percent recovery[1] of buried eggs during one-minute trials (n=5).

	Soil Moisture					
	Dry			Wet		
	Egg Density			Egg Density		
mpler	1	5	10	1	5	10
1	80 ± 20	72 ± 10	80 ± 3	40 ± 24	56 ± 13	56 ± 8
2	80 ± 20	60 ± 11	72 ± 7	20 ± 20	60 ± 6	54 ± 7
3	80 ± 20	76 ± 7	82 ± 4	20 ± 20	48 ± 5	50 ± 9

mean percent recovery ± $S\bar{x}$ (n=5)

curve. As discussed earlier, culls are not static but undergo transposition and transformation within and between cull types. In reality, culls are not found in classes, but as a continuum. It is easier, however, to visualize the dynamics by assigning culls to categories. Thus, a distribution of culls (class types) always are present in a field as a function of harvest date, harvest technique, post-harvest cultural manipulations and meteorological factors. This phenomenon probably occurs at the regional level, where each field within a region represents an element (field level distribution of culls) that makes up the regional distribution of culls to a dispersing group of flies.

The true dynamics of oviposition is seen when fly behavior and physiological age of the population is overlaid on the cull dynamics. Shifts of egg laying behavior can occur when more attractive culls appear or disappear in a field. A more detailed discussion of these biologies are discussed in the oviposition chapter. An important relationship is that although 93% of the total onion density were whole onions and only 0.5% were sprouted onions, 34% and 31% of the total egg densities, respectively, were laid on these cull types (Table 24). Therefore, when sampling eggs, pay attention to the host resource in its entirety where techniques such as post-stratification (Jessen 1978) could prove invaluable in extracting efficient and precise density estimates from the sampling effort.

A MODEL FOR ESTIMATING THIRD INSTAR DENSITY IN THE FALL

A sampling scheme for estimating onion maggot egg density was presented in the preceding discussion. Precise estimates of age-specific larval densities could be obtained from a sample size using the larval count data collected in the 1979 cluster sampling effort. Precision might be possible using the sample sizes

Table 24 . Relationship[1] between incidence of culls and eggs for three post-harvest onion growing regions, 1979.

Cull Type	% of Total	% Culls with Egg(s)	$\bar{x}$ Eggs/Cull with Egg(s)	% of Total Eggs
Whole	92.4	0.6	5.8	44
Cut	1.8	10.0	4.0	8.8
Rot	3.9	7.5	5.6	22.7
Sprout	0.6	32.8	15.2	18.5
Top	1.3	9.3	7.5	6.0

[1] Based on 58,739 onions from eleven fields.

derived from the egg sampling analysis if the expected variances of field level larval densities were of the same magnitude or less than those associated with the egg population. This should be tenable unless sprouts with high densities of eggs are prevalent; thus, density dependent survival significantly increases variance (see Cohort study).

When estimating the overwintering pupal population of the Grant Swamp for the winter of 1979-1980 from third instar onion maggot densities, found that within a sampling interval the mean number of third instar larvae per infested bulb did not appreciably vary between fields. This relationship was strengthened when sprouted onions were excluded from the data (sprouted onions occurring usually in low frequency harbor high densities of maggots) and when the sample dates were corrected for the harvest date. (The coincidence of harvest and second and third generation female adults largely determine the initiated effective egg input on culls.)

Table 25 depicts the variation in the corrected sample date means as well as a regression analysis of the mean third instar density per infested bulb with the percentage of field level infestation (range: 0-18%). None of the slopes for the various sample dates were significantly different from zero. The standard errors ranged from 10-50% (higher standard errors in the early season) indicating that these levels were fairly constant between the sampled fields within each sample date. Based on the assumption that this relationship characterized third generation population dynamics, I hypothesized that a predictive model utilizing degree days combined with sampling the density of infested onions would approximate of third instar density, thus pupal density. Since the population is truncated with the onset of constant subzero temperatures, peak instar incidence was a boundary for the first version of the model.

Table 25. The relationship between the mean number of third instar onion maggots/bulb and the percentage of infested onions (Grant Region).

			Regression Statistics		
Degree day	Mean[1]	SE	b	SE(b)	P(b=0)[2]
1974	.87	.31	-.07	.26	.78
2034	.17	.08	-.01	.06	.87
2064	.20	.12	-.02	.03	.45
2080	.18	.07	-.02	.04	.67
2089	.79	.21	-.06	.09	.56
2096	.72	.09	-.02	.04	.62
2117	1.09	.20	-.07	.08	.42
2180	1.62	.21	-.01	.05	.79
2186	2.17	.31	-.02	.10	.86
2210	2.09	.20	-.05	.08	.56

[1] Mean number of third instar onion maggots/bulb

[2] based on T test

The choice of a mathematical model in describing a relationship can be based either on the theory of the underlying mechanism or on a purely statistical framework associated with minimizing error. From a biological or mechanistic point of view, incidence curves for a single life stage generally form a normal distribution or some transformation such as the logarithmic series (Southwood 1978). This can be explained, partly, by the individual variation in behavioral and physiological processes. As the main objective was to construct a model with predictive capabilities, a more statistical approach was pursued.

A popular criterion for selecting models for linear or linearizable curvilinear relationships is the statistic r^2, which measures the proportion of total variation about the mean, y, explained by linear regression. Some other statistics are the residual root mean square (rrs) and the total squared error (Cp). The residual root mean square measures the scatter or deviations of the observed values around those calculated by the fitted equation. When no bias is present, it estimates the standard deviation of y. The total squared error more commonly used in multiple regression applications (Daniel and Wood 1971) measures the sum of the squared biases plus the squared random errors in y at all n data points.

Draper and Smith (1966) discuss the use of statistics for accepting the adequacy of a model in terms of "fit." After screening several linear and nonlinear models based on these statistics and ending up with five adequately fitting equations, it became clear that the criteria should not be solely a function of "goodness of fit." If the decision to accept a model was based on these statistics, only the relationship of the fit to the n data points would be evaluated, not the potential for estimation. Therefore, the optimum model for

"goodness of fit" may not be the best predictor. Based on this philosophy, an alternative criterion was the mean square predictive error (Allen 1971, Dimoff 1979). The mean square predictive error (MSPE) was calculated in the following analysis as:

$$\mathrm{MSPE} = 1/N \sum_{i=1}^{N} Y_i - f(X_i \mid X_i, X_2 \ldots X_{i-1}, X_{i+1}, \ldots X_n)^2$$

where:

Y_i = observed values,

$f(X_i)$ = functional relationship based on the subset of data points.

The relationship between "goodness of fit" (represented as the residual sum of squares) and the stability of estimation (MSPE) are shown in Figure 10. The residual sum of squares was not related to good prediction and estimation. The mean square predictive error for five of the best fitting models is depicted in Figure 11. Using both criteria as a basis for a decision as to which model to use, the asymptotic model of the form $A - B\,(e^{-cx})$ was chosen.

Having selected the model, it was thought best that the independent variable in the model not be absolute degree days, as time synchrony of events will differ from year to year and region to region. Thus, degree days for the onset of egg laying in the third generation or the first appearance of third instar larvae was used. The initial or minimum egg laying in the fall was approximately 1886 degree days, base 4.4°C (3350, base 40°F). Based on the calculated developmental requirement in degree days from egg through the second instar, 317 + 16 (Mean + 2SE) degree days (Carruthers 1979), the first appearance of third instars was estimated. This index was considered conservative enough and also flexible enough that a starting point for estimation could be predicted from egg sampling data and then confirmed with the first recovered third instar.

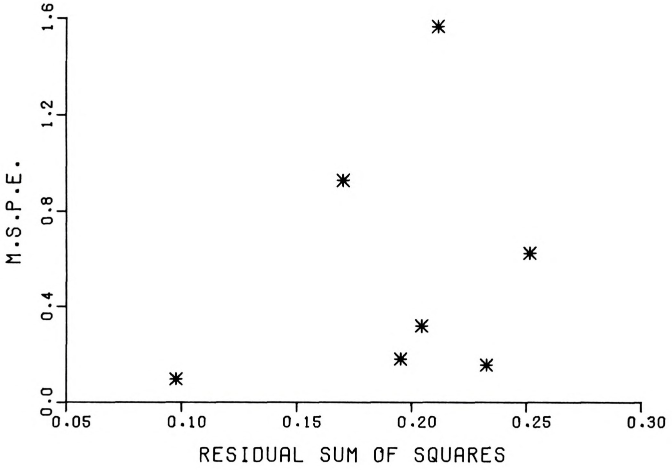


Figure 10. Relationship between residual sum of squares and mean square predictive error.

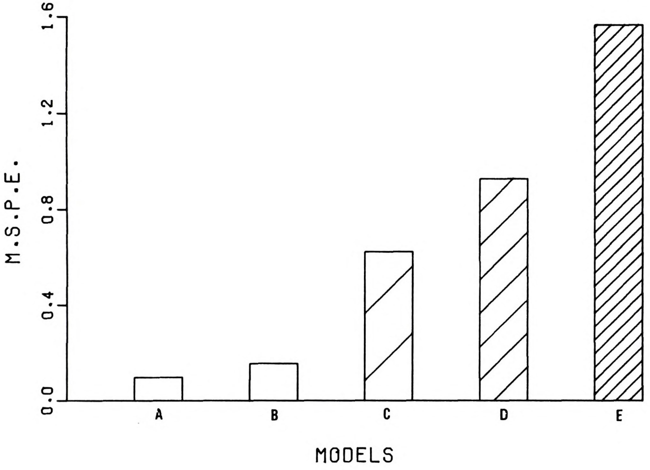


Figure 11. The mean square predictive error for various model forms exhibiting adequate fit (small RSS). A = A-(Be^{-cx}), B = 1/($a+be^{-x}$), C = A+BX, D = A+B/X, E = probit log.

The model was validated, ($y = 2.7899 - 3.4559 (e^{-.006x})$, with an independent data set from Eaton Rapidsand two sample estimates from Grant (Figure 12). The model may be used to predict overwintering pupal populations although more extensive validation must be conducted.

ONION MAGGOT POST-HARVEST BIOLOGY

Adult Onion Maggot Survival

Methods for estimating the absolute density of onion maggot adults have not been developed as of yet, although Whitfield (1981) estimated the field-level relative abundance of flies with flight interception traps. A measure of mortality can be derived from this index if one corrects for the weather dependent variation in activity (Whitfield 1981) and if immigration and emigration within the study area is insignificant. Another approach to estimating mortality is through cage studies, although one has to be cautious in interpreting these results since modifying the environment in the cage will probably affect the survival distribution relative to actual field response. To minimize this bias, I used a sequential series of cages and made comparisons between series. This approach also corrected for the bias within the tail of any one survival distribution (Gross and Clark 1975).

Data on the survival of a field population (adjusted trap captures: Whitfield 1981, Figure 27A) were used to evaluate the trends in the cage relationships. Julian day 260 was the base point for accumulating degree days ($4.4^{o}C$) for the analysis since, presumably, 100% of the third generation emergence had occurred by that time (Whitfield 1981, Figure 13B). Therefore, subsequent changes in trap capture should not be due to new additions in the population.

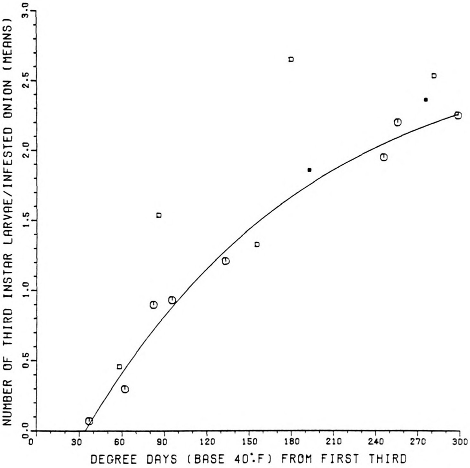


Figure 12. Model for the prediction of third instar incidence, independent data sets: ■ - 1980 Grant, Michigan (Nolling and Ellis), □ - 1979 Eaton Rapids, Michigan (Drummond).

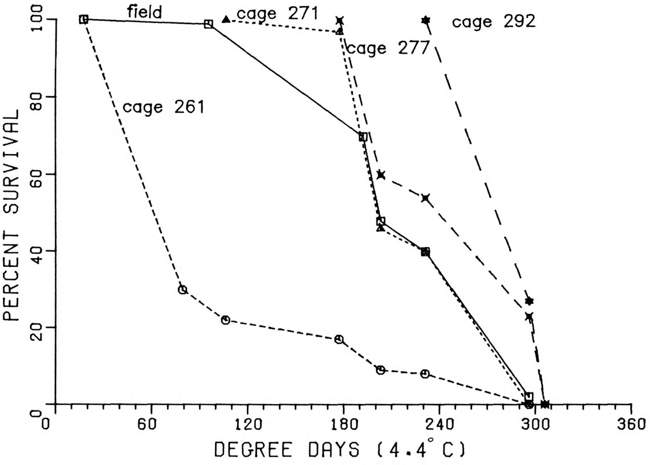


Figure 13. Relationship between adult onion maggot survival and physiological time from 100% emergence for both cage and field results.

The high initial rate of mortality in the first series (julian day 261) (Figure 13) was unexpected. Short of any mortality factors introduced during the set up of the trial, and comparing the survival curve to the field population ($X^2_{(4)}$= 49.18, P < .001), I hypothesized that the flies introduced into the first series were mostly the tail end of the second generation. The first two intervals (17^0D -110^0D from julian day 261) exhibit a high incidence of mortality; however, from the third interval on, similar mortality was seen among all of the cage studies, possibly representing the proportion of third generation flies within the sample. The series initiated on julian day 271 (September 28th) conformed to the survival distribution of the field data (starting on ^{o}Day 120, based on Desu's algorithm $X^2_{(4)}$ = 0.78, P < .90, Hull and Nie 1980).

An empirical feel for the data was attained by plotting the instantaneous death rate or hazard function associated with degree days. The hazard function, $\lambda(^oD)$ (Gross and Clark 1975) is the probability that an individual dies in the interval ^{o}Dj-(^{o}D; + Δ ^{o}D) given it has survived to ^{o}Dj. A linear relationship (Y=.1 + .002x, r^2=.88, T(H_o · B = 1)=2.7, P=.22) showed that survival was probably a function of degree days or aging. With third generation adults, however, there may be years that a constant hazard rate indicative of a negative exponential distribution is a better descriptor. This suggests a Poisson death process where an individual is subject to stochastic events causing death in contrast to an aging or age dependent process. The survival curves (field and cage 271, 277, and 292) of the 1979 third generation support the contention that mortality was age dependent, as the average degree day (4.4^{o}C) lifespan of the onion maggot, 185 ^{o}Days (Whitfield 1981), was associated with the median survival time (see Figure 13).

The fall of 1979 was unusually mild with average temperatures ranging from 10°C-16°C (with only four days in September and October having minimum temperatures below 0°C) until November when the minimum temperatures frequently fell below 0°C. Therefore, the 1979 season probably represented an optimum time span for colonization of culls by the onion maggot relative to the average post-harvest season.

Oviposition

Whitfield (1981) calculated the relative abundance of flies caught within the borders of seven research fields in Grant during the 1979 post-harvest season. To determine whether any relationship existed between estimated fly abundance and egg density, two estimates of total egg production (TEP) were computed for the research fields using a modified computer algorithm by Lampert (1981) where:

$$TEP = \sum_{i=1}^{n-1} [(\frac{D_{ij} + D_{i,\,jr}}{2}) (DD_{j+1} - DD_j) \div 50.0 \text{ DD}$$

and TEP = total production,

DD_j = accumulated degree days on the jth date,

D_{ij} = density of the ith stage on the jth sample date,

50.0 DD = developmental time of the onion maggot egg stage.

Redundancy of density estimates due to frequency of sampling was corrected by the onion maggot egg stage developmental time (Helgesen and Haynes 1972, Whitfield 1981, Groden 1982). Table 26 summarizes the relationship between relative abundance of the flies and total egg production based on two sampling frames, 9.2 m^2 and 20 onions (see egg sampling). A linear

Table 26. The relationship between the relative abundance[1] of onion flies within a field and the incidence of eggs[2].

Field	Relative fly Abundance	Eggs per 9.2 m^2	
		Estimate[3] 1	Estimate 2
R	787.9	34.2	24.2
1	534.8	43.9	45.6
2	237.9	6.08	6.7
3	712.9	45.6	49.8
4	315.2	8.10	10.5
5	343.6	43.0	9.7
6	699.2	70.8	54.7

[1] Estimates of relative abundance taken from Whitfield (1982, Table 8).

[2] Total third generation egg production (TEP).

[3] Converted from eggs/200 onions to eggs/9.2 m^2 based on total $\bar{x}$ cull density within each field.

regression analysis was used to examine the relationship between the two estimates (Sokal and Rholf 1969).

Only fields 2, 3, 5, and 6 were used, as fields 1 and 4 received different cultural practices (cover crop, continual harrowing and disking) and field R was never harvested. Both estimates of egg density per field were utilized (Pearson's correlation coefficient between the two was +.77 (H_o (r=0), P=.04) and two regression lines resulting from each egg density estimate did not differ in relation to .95 confidence boundaries about each line). The resulting relationship (Figure 14) was significant ($Y=3.5 + 0.7X$, $r^2=.48$, H_o (B=0), T=2.45, P=0.053). This was the first time a relationship between onion fly numbers and egg density has been found.

Although only 48% of the variation in egg density was attributed to numbers of adult flies, the relationship suggested that a reduction in flies during the third generation would impact egg input in a field. This is important for management. If third generation fly numbers can be reduced either during the post-harvest season or during previous generations, then egg density should be reduced. Over the range of abundance that was investigated, a 50% reduction in flies should result in a 53% reduction in eggs. Interfield migration was believed to be a predominant feature of onion fly biology within the post-harvest period.

During the fall, flies may be heavily concentrated in fields being harvested and, to a lesser extent in fields either previously harvested or yet to be harvested (T. Ellis, personal communication, Michigan State University). This behavior would influence any post-harvest management strategy using insecticides aimed at reducing the population level of adult onion maggots. If the attraction of harvested fields is beyond the immediate field border, then perhaps

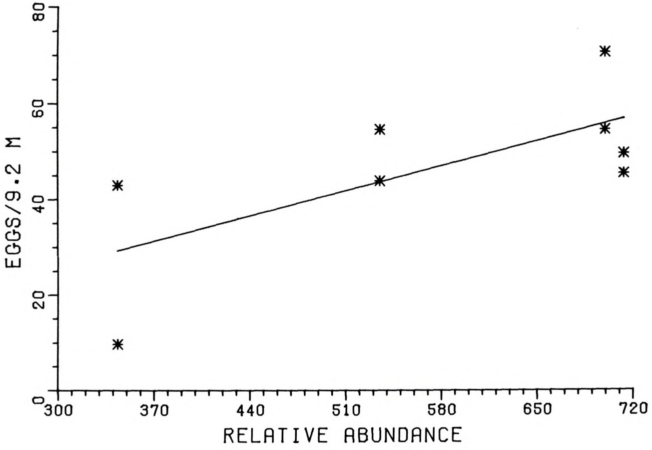


Figure 14. Relationship between relative abundance and egg input for four fields (two estimates/field) in Grant, post-harvest.

a few "trap" fields could be harvested before the rest of the region, thus concentrating most of the population where an efficient pesticide could be applied. If the insecticide were applied at 100% emergence, only one application would be necessary. Another strategy would involve following each grower's harvest schedule and applying an insecticide in each harvested field during peak oviposition. both strategies would have to be well coordinated with every grower in a region cooperating.

Migration as a factor influencing egg production within a field was included in the relationship between relative abundance and egg density since activity (within field and between field) was integrated with density as an index of relative abundance. Other factors that were not considered in the functional description of egg input were density of total culls within a field and the proportional composition of cull types (see cull dynamics).

Two years of post-harvest data (1979-1980 and 1980-1981 suggest no correlation between mean cull density within a field ($9.2m^2$) and the proportion of total culls with eggs. Total egg production per unit area and mean cull density was also inconclusively correlated. Cull type did appear, however, to influence the spatial dynamics of egg density.

Table 27 summarizes the effect of cull type on the resulting proportion of culls within a class (whole, cut, rotted, sprouted) that had eggs on them. Cross tabulation revealed that the ratios of cull types with eggs to the population distribution of cull types differed significantly ($\chi^2_{(4)} = 3127.2$, tabled value = 14.9 at $\alpha = .05$) when compared to an expected distribution based on an equal probability of selection or choice of cull types by females (meaning that all cull types with equal probability within a field). Similar preferences exist with

Table 27. Relative attractiveness of various cull types[1] as reflected by oviposition.

			Relative Attractiveness	
Cull type	observed	expected[2]	to whole	to sprout
whole	353	707	-	-
cut	102	14	16x	.3x
rotted	164	30	12x	.2x
sprout	87	4	51x	-
top	60	9	15x	.3x

[1] pooled over all fields samples, harvested and unharvested.

[2] based on assumption of no preference with cull type distribution of 54979:2343:352:710 respectively.

oviposition during the growing season when onion flies are presented large dry bulbs, large green bulbs, and small green bulbs in various states (infested, rotted, and unblemished) (Carruthers 1979). Anemotaxis plays a significant role in fly responses to onion host versus a non-onion host plant location (Dindonis and Miller 1980). The role of onion volatiles where non-point source emission is most likely the rule and not the exception is unclear. However, Harris (1982) found that visual cues mimicking a leaf add to the attractiveness of a treatment even when volatiles are present. This may explain the ranking of unblemished whole bulbs, injured or infested bulbs, and sprouts in an increasing order of "attractiveness."

Differences in the mean number of eggs per cull type and eggs per infested cull type were influenced by cull type (Friedman's two-way, fields as blocks, $\chi^2_{(4)} = 9.87$, $P < .04$, and $\chi^2_{(4)} = 8.0$, $P < .1$ for infested culls and total culls, respectively). Multiple comparison tests (Hollander and Wolfe 1973, see Table 28) were used to base inferences about cull types.

Sprouts appeared to possess a significantly greater mean number of eggs per plant than any of the other three bulb type culls (TAble 28). Thus, it appears that not only are sprouts more attractive to female flies but they may also induce flies to lay more eggs.

The average relationship between the total proportion of eggs per cull type and the proportion of cull types within the eleven fields is shown in Table 28. Total egg incidence (18.5%) was associated with only 0.6% of the total food resource; whereas, 44% of the eggs were associated with whole culls, or 92.4% of the cull density. Thus it appears that sprouts are important to the post-harvest generation. When interpreting the significance of this relationship, the temporal

Table 28. Number of onion maggot eggs per cull and infested culls as a function of cull type.

Cull Type	Eggs/Cull Type[1]	Eggs/Infested Cull Type	Percent of Total Culls	Percent of Total Eggs
Whole	.16 ± .05^{b}[3]	5.8 ± 0.8^{ab}	92.4	44
Cut	.44 ± .10^{b}	4.0 ± 0.7^{b}	1.8	8.8
Rotted	.51 ± .14^{ab}	5.6 ± 1.0^{ab}	3.9	22.7
Sprout	5.4 ± 2.2^{c}	15.2 ± 4.3^{c}	0.6	18.5
Top	4.3 ± 3.3^{ac}	7.5 ± 3.6^{ac}	1.3	6.0

[1] $\bar{x} \pm S\bar{x}$ (N = 11 fields)

[2] $\bar{x} \pm S\bar{x}$ (N = 11 fields), only culls infested with onion maggot life stages included in the estimate.

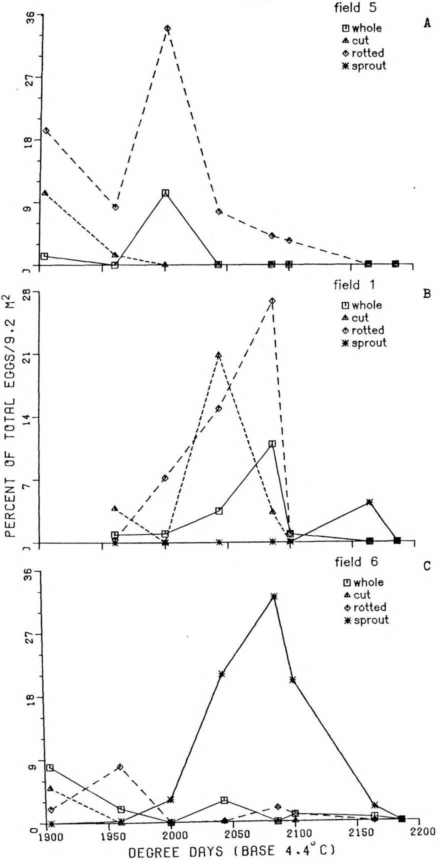
[3] Mean rankings (not shown) followed by the same letter are not significantly different at $\alpha = .10$ (where $1R_i - R_j, 1 \geq q\ (\alpha,\kappa,\infty) [\frac{n(\kappa)(\kappa+1)}{12}]^{\frac{1}{2}}$), Hollander and Wolfe (1973).

dynamics between sprout emergence and oviposition must also be studied. Sprouts were shown to lag in emergence until well after they had been plowed under (see cull dynamics); therefore, the spatial and temporal effects of sprouts on the onion maggot post-harvest population is most likely due to the synchrony between fly emergence and harvest (both temporally and spatially within a region).

The dynamics of oviposition in response to cull composition within a field are depicted in Figure 15 (total cull density was similar among fields). Figure 15A shows a mean total cull density of 14.4 culls/9.2m^2. Figure 15b shows a mean total cull density of 16.0 culls/9.2m^2. Figure 15c shows a mean total cull density of 12.5 culls/9.2 m^2. Without sprouts (Figure 15A), rotted culls received most of the eggs, followed by cut culls. Whole culls were attractive during peak oviposition, although not as highly as rotted culls (1:3). As the season progressed, rotted culls tended to receive most of the eggs. For most of the post-harvest season, scenarios 1 and 2 were similar except for cut onions (Figure 15A and 15B), which were attractive to females. This was expected because field 1 was harvested on julian day 265 (^{O}Day 1946) and the density of freshly cut onions was very high.

When sprouts appeared at the end of the fall, all oviposition shifted onto them. This indicates how powerful sprouts can be at concentrating a local population of flies. Oviposition, however, might have been occurring at a level (Figure 15A) that could not be detected. Another explanation is that the flies were responding to a "super-normal oviposition stimulant" (Drummond et al. 1982) (Figure 15A, 2154 ^{O}Days) on other not as "attractive" cull types. When sprouts were present during most of oviposition, (Figure 15C) the sprouts acted as a "sink" for most of the eggs being laid.

Figure 15. Effect of cull type on the temporal and spatial distribution of oviposition.


field 5
A
whole
cut
rotted
sprout
0
9
18
27
36
field 1
B
whole
cut
rotted
sprout
0
7
14
21
28
PERCENT OF TOTAL EGGS/9.2 M^2
field 6
C
whole
cut
rotted
sprout
0
9
18
27
36
1900
1950
2000
2050
2100
2150
2200
DEGREE DAYS (BASE 4.4°C)

These three senarios indicate the tremendous potential that sprouts could have as a management tool. If the attractiveness of sprouts could be determined, and if we could control when they emerged, management strategies could be possible. Plowing under small strips of culls on the field borders, resulting in a synchronized appearance of gravid females and emerging sprouts, could be the basis of a trap crop concentrating all of the flies and immature stages of the onion maggot along the field borders where predation and parasitism could be maximized (Groden 1982).

The height and pigment of sprout leaves were measured (hgt. in mm above the ground, rank assessment = dark or light pigment) and associated egg density per plant was recorded October 2 (n=50) and October 5 (n=50). Both height and leaf color markedly varied within a field during the fall of 1979. An investigation was conducted to determine whether height or plant condition (age x physiological condition expressed possibly as pigment) affected oviposition. Linear correlation analysis (r= +.02, P=.88; r= +.15, P=.29) revealed no significant correlation between height (range = 6.4mm - 279.4 mm) and eggs/plant. Hue intensity within the range exhibited by the sprouts surveyed did not affect differential egg input (Mann-Whitney U test, z= -.25, P=.80). Thus, sprout appearance did not affect oviposition.

In sampling eggs by the quadrat method, records were kept throughout the season for all eleven fields and cull types within those fields as to distribution of eggs relative to cull and soil (Figure 16). Except for the onion leaves cut off from the bulbs and left in the field, the percent of eggs recovered from the soil relative to the cull was approximately 70%, 90% sprouted onions (sprt). Table 29 shows the egg distribution summary broken down by harvested and unharvested

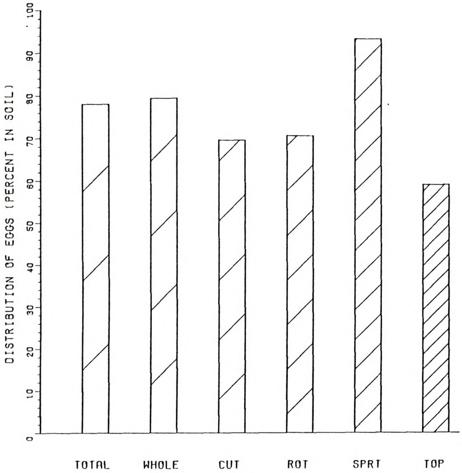


Figure 16. Proportion of eggs laid in soil for various cull types (pooled over all fields).

le 29. Relationship between cull type and egg distribution.

	Cull type				
	Whole	Cut	Rotted	Sprout	Top
vested Fields(11)[1]					
Soil	80.6±2.8[2]	63.1±9.9	69.4±5.8	84.3±9.1	41.5±2.38
Plant	19.9±2.8	35.1±10.0	30.6±5.8	15.7±9.1	58.5±2.38
arvested Fields(4)					
Soil	70.7±6.5	-	60.7±1.9	-	-
Plant	29.3±6.5	-	39.3±1.9	-	-
led					
Soil	79.3±1.7[3]	69.4±4.8	70.4±2.8	93.2±1.7	59.1±5.8
Plant	20.7±1.6	30.6±4.7	29.6±2.8	6.8±1.7	40.9±5.8
n	2115	346	1018	817	276

= number of fields in sample.

± $S\bar{x}$

.95 confidence limits (normal approximation)

fields. The variation from field to field was considerable, but the true mean of eggs in the soil between all fields on all cull types (except for the tops) was at least 50% (.95 confidence intervals). Observations on oviposition on tops revealed that after the tops started to dehydrate, two to three days after cutting, the probability of finding eggs placed within the soil increased. Perron (1972) found that 68% of all eggs laid by the first two generations of the onion maggot were in the soil. No trend was seen in egg placement for cull type, field, or sampling date.

Across all fields, sampling dates, and cull types (137 observations with oviposition occurring), 114 represented more than 50% of the eggs placed in the soil, 2 were equal for soil and cull, and in only 21 were 50% of the eggs placed on the culls. Of these 21 there was no correlation to sample date (i.e. weather conditions) or field.

Since this relationship was so strong in all three regions, a management strategy might be successfully implemented based on separating the onion maggot from its host. Culls left in the fields after harvest were the major link between the third generation in the fall and the following season's spring generation. Plowing under the culls may be one answer. Another approach may be to use the oviposition behavior of the fly to soil distribution of the eggs. Laboratory studies (Appendix F) showed that the migration distance and detection radius of first instar larvae is very limited (2.5 cm); therefore, if culls could be moved 5-10 cm from the eggs with a rock rake or a chain harrow every 50 ^{o}Days (4.4^{o}C), a 60-80% mortality factor could be induced. Monitoring first egg laying or maturation of adult females would be needed as a biofix to initiate the management strategy. I found that eggs placed on cull parts were not dislodged

easily unless the egg has been wxposed to very dry conditions for a few days. This strategy could be integrated with parasitoid management (Groden 1982).

Cover crops, usually grain or grass, are commonly planted after harvest, particularly on the lighter soils. Cover crops and sprouts were the only green plant life found in the onion fields during 1979 (with the exception of a few occasional purslane plants, Portulaca oleracea L.). Field 1, within the Grant Swamp, was sown in a cover crop after harvest resulting in dense rye grass during oviposition. The proportion of infested culls (with eggs) in this field was much lower than neighboring fields (R,2). There were other fields in 1979 sown to a cover crop, but the rye or oats usually came up too late to evaluate any impact resulting in reduced oviposition.

The commercial field in Eaton Rapids (field R) was sown in a cover crop early enough in the season so that by October 21st the plantings were well established. The field was planted in strips of rye grass and fallow (strips approximately 12.2 m wide each). Five random strips from each of the two treatment conditions were sampled (20 culls per plot) three times during the fall. A randomized block model (time as a blocking variable) was used for the covariance (cull density) analysis. Sprouts located within the strips not planted in rye grass received significantly more eggs (Table 30) than the other treatment combinations (Duncan's multiple range test at α=.10). Thus, a cover crop may reduce oviposition on culls. More work needs to be done to evaluate the density and height of planting needed to evoke this response and whether the mechanism of such an inhibition is due to a chemical or a structural phenomenon. Certainly, cover cropping being a good soil conservation technique would integrate well as a management strategy aimed at preventing egg laying.

		Rye Cover Strips(n=5)			No Cover Strips(n=5)		
Sample Date	$\bar{x}$ rye hgt.	$\bar{x}$ sprouts/ $9.2m^2$	$\bar{x}$ eggs/ sprout[1]	$\bar{x}$ eggs/ other culls[1]	$\bar{x}$ sprouts/ $9.2m^2$	$\bar{x}$ eggs/ sprout[1]	$\bar{x}$ eggs/ other culls[1]
October 21	not measured	0.2±.2	.7±.4	.1±.1	0.2±.2	3.2±1.3	.2±.09
October 28	13.9 cm.	0.6±.4	.3±.2	.02±.01	0.8±.4	4.9±1.2	.26±.07
November 5	19.1 cm.	0.4±.2	.7±.6	.06±.06	1.2±.4	0.9±.4	.23±.08
Average[3]			$.57^a$	$.06^a$		3.0^b	$.23^a$

[1] n = 10 culls/strip, 5 strips per sampling date, $\bar{x} \pm S\bar{x}$

[2] n = 5, $\bar{x} \pm S\bar{x}$

[3] Means followed by the same letter are not significantly different at $\alpha = .05$ (Duncan's Multiple range) test

Cull Pile Survey

After harvest onions may be found in cull piles. Usually these piles are close to the packing sheds and storage facilities involved in preparing the onions for market. Onion flies have been seen emerging from cull piles in the early spring (A. Wells 1979, personal communication) although sampling conducted by Carruthers and Whitfield (unpublished) in the spring did not find that cull piles contributed to the population buildup of the onion maggot.

A sample survey of three cull pile locations within varying distances from onion fields was conducted on November 8, 1979 (Table 31). The farther the cull pile was from the onion fields, the fewer the onion maggot pupae were recovered. The number of pupae recovered did not show any possible role of cull piles in the regional population dynamics of the onion maggot. Furthermore, it was unknown whether the pupae collected from the onion cull piles came from storage, from the fields, or from migrating flies.

Occurrence of the Immature Stages of the Fall Generation

The third generation onion maggots experience a very different environment than the first and second generations. The onion is more heterogeneous in the fall, and pesticides are not a key mortality factor. Other differences in the environment are decreased average temperature to a below developmental threshold level and increased predator and parasite activity after harvest (Groden 1982). Three percent of the second generation (summer) pupae diapause in Michigan (Whitfield 1981). Therefore, unless environmental conditions are favorable in the fall, a 97% reduction in spring emergence is possible. The potential population increase, however, is large, because if only 4% of the eggs

ble 31. Results of fall cull pile sampling.

Location	Distance from Nearest Onion field	Percent[2] Infested Culls	Size of Pile[3] L x W x H(M)
ink' Pasture(36)[1]	1.39 km.		
		0.2	3.1 x 3.0 x 0.3
		0.4	3.1 x 5.9 x 0.2
		0.2	4.4 x 3.2 x 0.4
		0.9	10.3 x 1.9 x 0.4
		0	2.2 x 2.8 x 0.3
		0.4	2.7 x 2.4 x 0.4
k Brothers(105)	4.5 km.		
		0.2	4.7 x 3.7 x 0.8
		0	5.2 x 8.5 x 1.0
		0.1	4.0 x 8.2 x 0.7
		0.1	4.0 x 8.2 x 0.7
		0	2.8 x 3.2 x 0.4
		0	3.7 x 3.8 x 0.5
ower's Coop(1)	8.1 km.		
		0	one large pile
		0	8.8 x 3.8 x 1.1
		0	
		0	
		0	
		0	

---

umber of distinct piles at locale.

ased on 1,000 culls per subsample

f onions are not badly degraded an estimate of the number of onions in .5 m was 277, based on one trial.

oviposited after harvest survive (based on estimates of fecundity by Ellington 1963) then a two order of magnitude increase in density can occur. Figure 16 shows the cummulative oviposition trend plotted on a degree day basis (base = 4.4°C). Oviposition covered the entire fall (not shown) beginning in the middle of September until November 11th. Figures 18-22 depict the population trends of the immature stages with egg laying incidence. The stages overlap with the physiological time scale of the onion maggot. The incidence curves show the relative proportion of each of the life stages comapred with one another throughout the season. Mortality was high between the egg stage and establishment of first instar larvae. Field 4 was an exception to this, although no explanation can be offered. A cohort study could not be conducted in field 4, as it was the only field in Grant that received intensive soil disturbance (harrowing, disking, and dragging) frequently throughout the fall.

Once the larvae became established, the prospect for survival to the third instar was quite high (Figure 23). A life table analysis was used to interpret the dynamics in the age specific frequency count data (Southwood 1978, Helgesen and Haynes 1969, Lampert 1980). The summarized incidence and survival indices are shown in Table 32. The two fields that received proposed management options (field 4) and an early cover crop planting (field 2) had the lowest egg input per cull. The use of such indices in describing real world phenomenon has to be questioned for the post-harvest generation of the onion maggot. The proper approach in conducting field life table studies is to design complementary cohort studies from which the underlying survival distribution can be derived and applied to the frequency count data. This was performed during the fall study but, unfortunately for the early part of the season sampling was not carried out

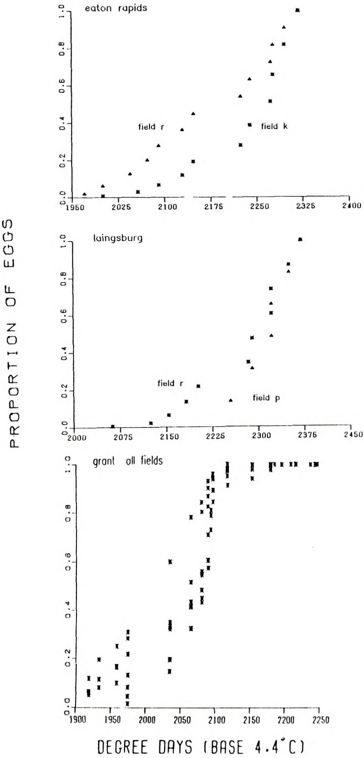


Figure 17. Cumulative oviposition for the fall of 1979.

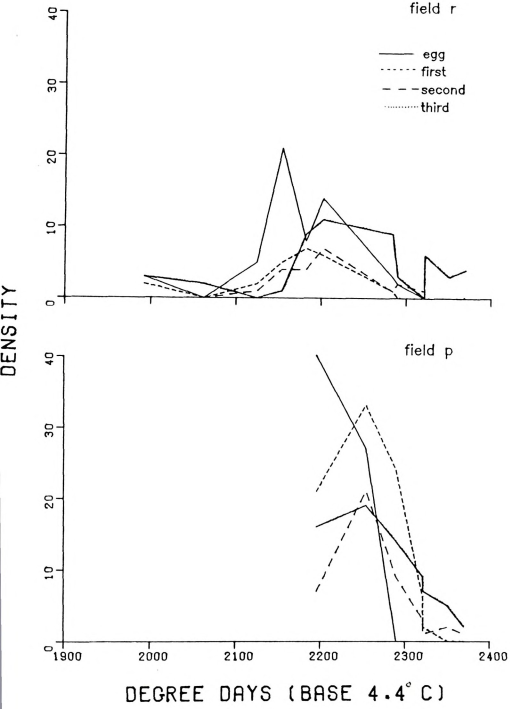


Figure 18. Immature incidence during the fall of 1979, Laingsburg (count/200 onions).

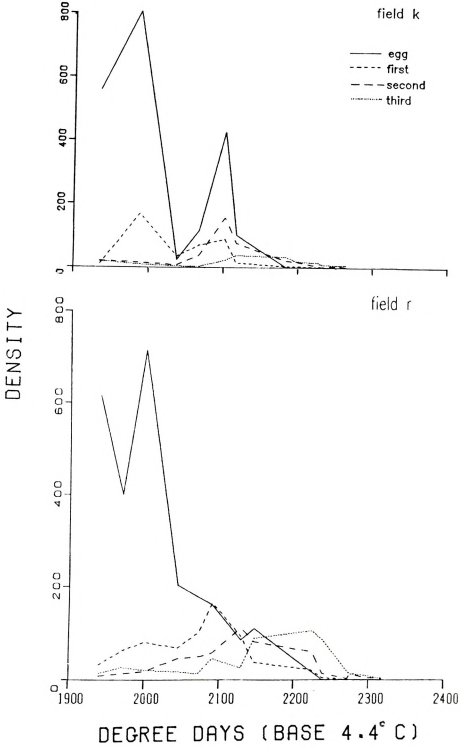
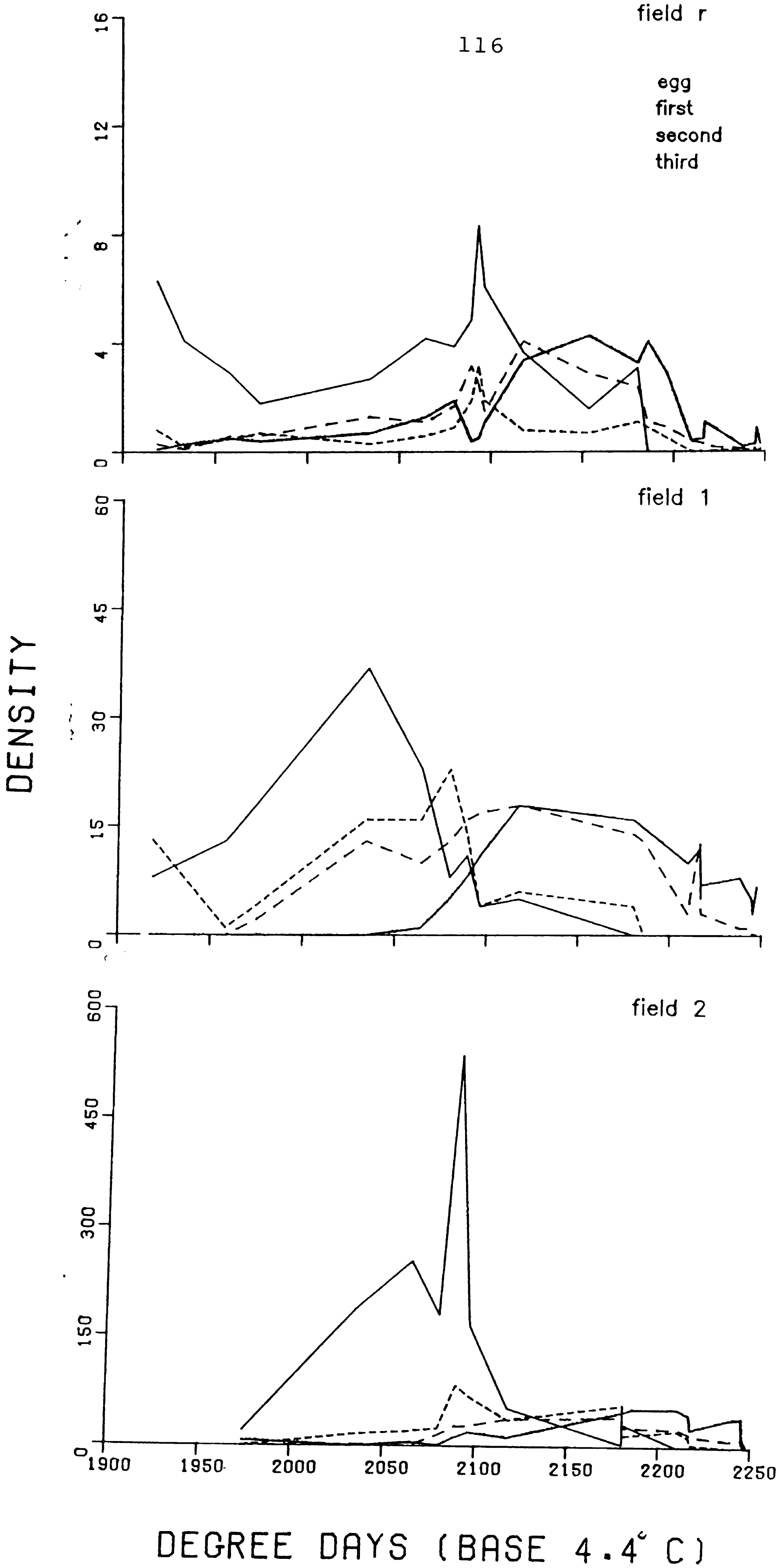


Figure 19. Immature incidence during the fall of 1979, Eaton Rapids (count/200 onions).

Figure 20. Immature incidence during the fall of 1979, Grant (fields R, 1, and 2, count/200 onions).


field r
egg
first
second
third
16
12
8
4
0
field 1
60
45
30
15
0
field 2
600
450
300
150
0
DENSITY
1900
1950
2000
2050
2100
2150
2200
2250
DEGREE DAYS (BASE 4.4° C)

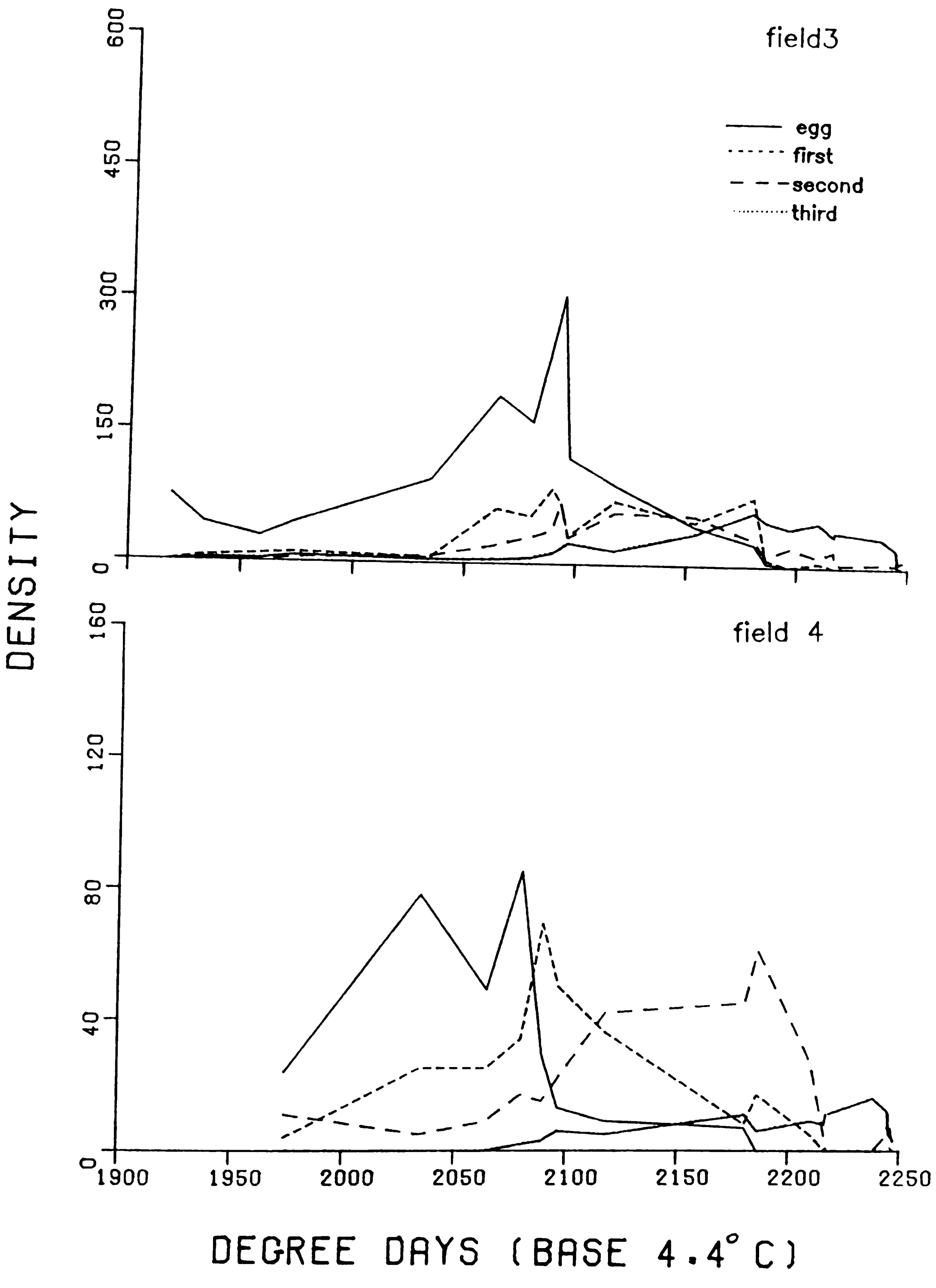


Figure 21. Immature incidence during the fall of 1979, Grant (fields 3 and 4, count/200 onions).

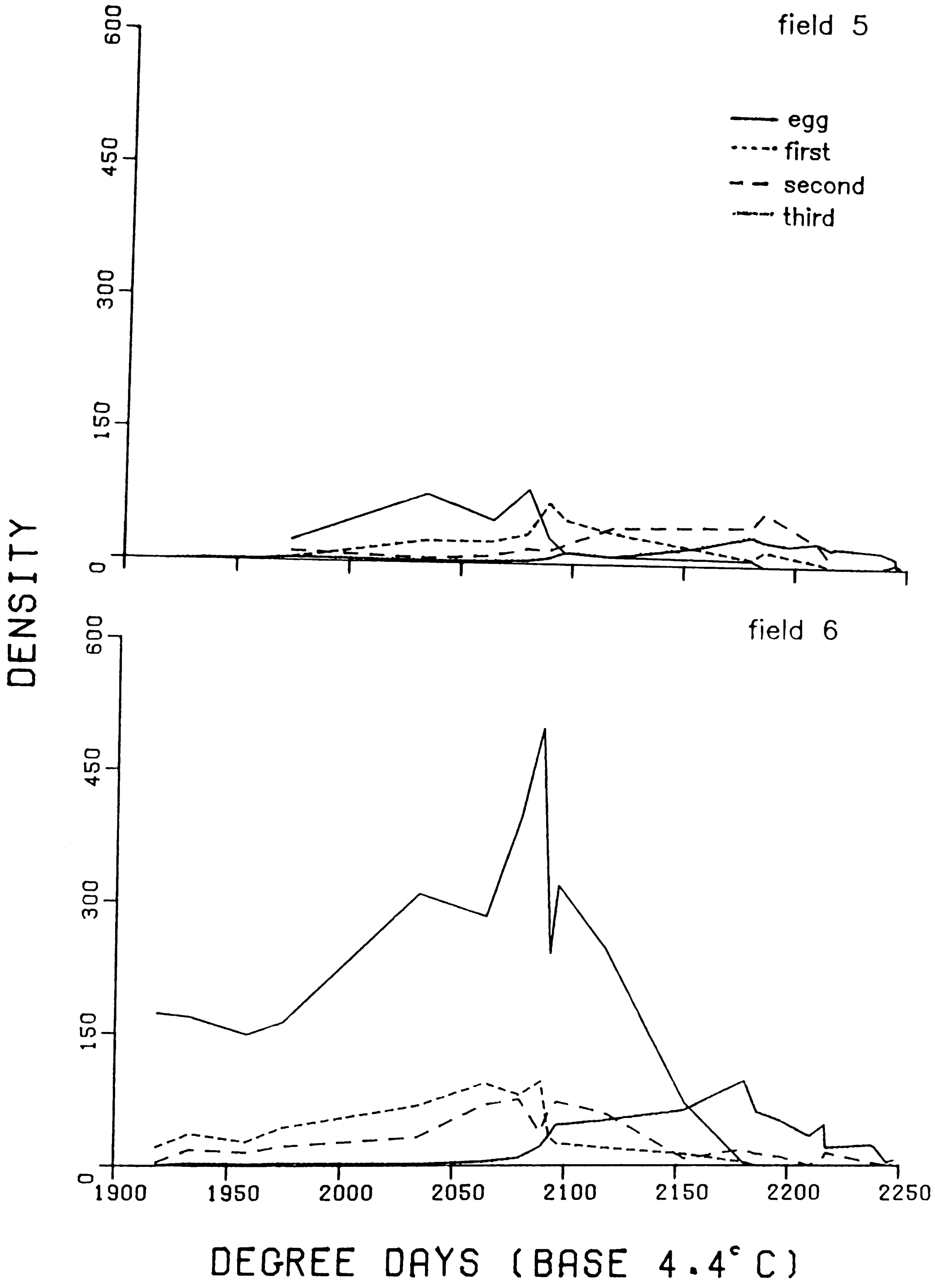


Figure 22. Immature incidence during the fall of 1979, Grant (fields 5 and 6, count/200 onions).

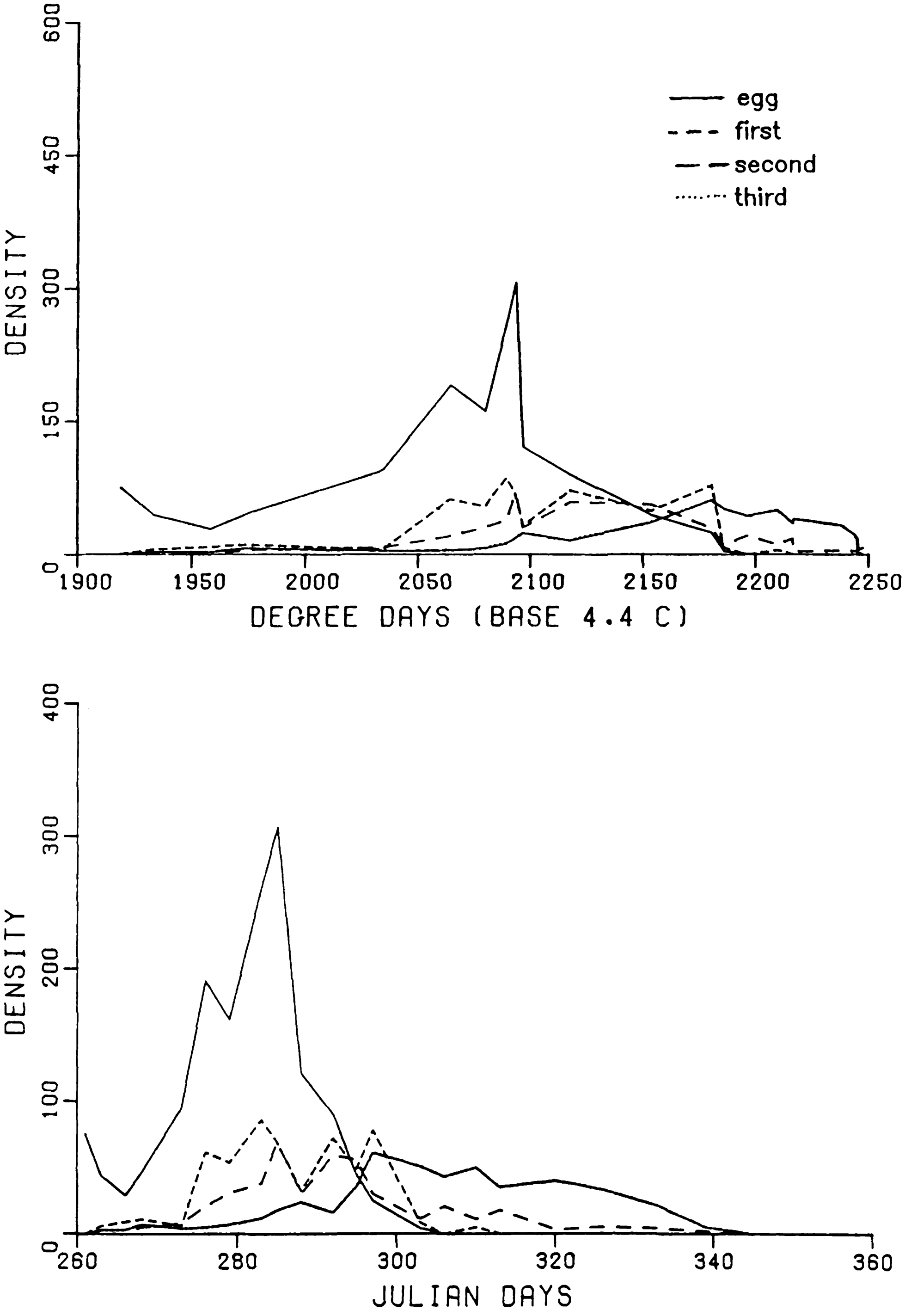


Figure 23. Comparison of immature incidence plotted on a physiological time scale (^{o}Days) and a chronological time scale (julian days), field 3 (Grant).

Table 32. Total production (TP) and survival (S) of eggs and larvae per cull during the post-harvest season, 1979.

Location	Field	Cull density	Egg TP	Egg S	First Instar TP	First Instar S	Second Instar TP	Second Instar S	Third Instar TP
Grant									
	R	339.0	0.08	13	.01	50	0.005	60	0.003
	1	15.7	0.38	58	.22	77	0.17	41	0.07
	2	16.2	2.70	36	.96	28	0.27	59	0.16
	3	19.7	2.27	66	1.49	48	0.72	15	0.11
	4	10.2	0.74	103	0.76	45	0.34	13	0.04
	5[1]	14.4	2.90	48	1.40	51	0.72	15	0.11
	6	12.5	5.20	29	1.50	24	0.36	17	0.06
Eaton Rapids									
	R[2]	10.2	7.20	38	2.70	33	0.89	44	0.39
	K	66.9	6.70	27	1.84	29	0.54	24	0.13
Laingsburg									
	R	129.3	0.20	55	0.11	36	0.04	130	0.05
	P[3]	6.7	0.24	110	0.27	33	0.09	67	0.06

---

[1] Represents only non-marl 20 acre section of field.

[2] Only non-cover crop areas of field.

[3] First sample date at harvest, October 17, 1979.

often enough to evaluate within stage survival as a function of the physiological age of the egg or larva. Total survival estimates could only be obtained through time (Table 33). Despite the variation between regions, a relationship was seen between survival and oviposition.

A characteristic of the fall generation that could not be brought out in a frequency count analysis was the likelihood of larval survival as a function of the time of year. Survival estimates derived from the cohort study were used to analyze the effect of this relationship. I found that once a first instar was established, the probability that it would develop to a third instar was quite high (Table 34) until the second week in October. Onion maggot mortality in the larval stage due to freezing was found. The larvae look bloated and were fully extended. The cadaver, for a few days after possessed a brownish tint, markedly different from the gray-white appearance of many other dead larvae found within the sampling periods. Field observations revealed that onion maggot larvae had a high tolerance to below freezing conditions. This could be from behavioral adaptations (Appendix E). In the Laingsburg region (Table 35) cold-related mortality increased as the season progressed. Of the larvae found dead from freezing, all were second or third instars (in equal proportion). This may be due to the difficulty in detecting dead first instars. From accumulated degree day ($4.4^{\circ}C$) data, very little development occurred at this time, yet larvae had pupated. I wondered whether stress due to cold temperatures could stimulate premature pupation. An analysis of this would be complex.

Casagrande and Haynes (1976) developed a model relating mortality of adult cereal leaf beetles, Oulema melanopus L., to the duration and severity of continuous cold exposures. They showed that tolerance to below threshold

Table 33. Cohort survival[1] (egg-pupa) during the fall generation

	Grant								Eaton Rapids			Laingsburg	
Cohort	R	1	2	3	4	5	6	Cohort	R	K	Cohort	R	P
261	8.7	10.9	-	-	-	19.6	4.3	264	-	7.9	270	1.9	
267	5.8	6.7	3.4	6.8	-	6.7	0	269	5.3	5.5	276	20.0	
275	3.8	7.9	15.3	10.5	-	-	5.3	277	5.1	2.7	284	7.1	
282	11	7.8	4.5	3.9	9.4	7.3	5.7	283	-	5.3	292	6.8	8.2
291	4.1	4.0	1.5	0	-	-	1.1	288	1.7	1.9	297	0	0
296	0	-	0	0	-	-	0	295	0	0	304	0	0
312	0	-	0	0	-	-	0	301	-	0			

---

[1] percent survival, - = No data available

Table 34. Likelihood of larval survival to the third instar given that it is an established first instar.

Cohort	N	Proportion of firsts that survived to Third Instar
Week 3 September	189	.47
Week 4 September	209	.37
Week 1 October	386	.41
Week 2 October	527	.25
Week 3 October	176	.24
Week 4 October	85	0
Week 1 November	35	0

Table 35. Percent mortality due to freezing, Laingsburg 1979.

Date	N	Onions	Percent Mortality due to Freezing	Accmm °Day
November 10	99	44	6.6	2321.5
November 17	72	36	0	2321.8
November 24	52	36	26.2	2356.3
December 3	19	16	5.2	2361.5
December 11	17	15	52.9	2364.9

temperatures decreased as the season progressed and that periods of recovery between chilling treatments is a dynamic process determined by the temperature from which the beetles recovered, the duration of the recovery period, and the temperature during the recovery period. Raske (1975) found that spring mortality in the larval stage of tent caterpillars is a function of temperature and time exposed to the critical temperatures. Therefore, to understand the fall population dynamics of the onion maggot, physiological response (mortality and pupation) must be studied.

Within all three regions, an average of 57.6 $^{\circ}$Days accumulated between November 2 and December 31. The soil surface was frozen on several occasions starting November 5th and was frozen to 7.5 cm in depth by December 11th. Based on the theoretical mean degree day requirements for the composite of all the immature stages (337.2 base = 4.4°C, Carruthers 1979) and using the Grant population as an example, I hypothesized that eggs laid after 50% of the total cummulative oviposition ($\bar{x}$ $^{\circ}$Day=2002) occurred would not pupate until $^{\circ}$Day 2237 (November 23). Since it is difficult to detect the cummulative egg incidence (Figures 18-22), the cumulative proportion of egg input was linearized by probit transformation. Least-squares regression analysis was performed to more easily determine the proportion of total egg input per $^{\circ}$Day (Table 36).

The distribution of egg laying between fields within each region was fairly uniform (no significant differences in slope), although differences in the intercepts occurred suggesting that extraneous factors such as adult behavioral activity differences, cull type interactions, harvest date differences, and sampling error contributed to the variations in oviposition between fields. Mean third generation emergence between the years 1978-1980 were not too different ($\bar{x}$ $\pm$

Table 36. Probit regression statistics for onion maggot oviposition for the Fall of 1979.

		Regression Statistics					
Region	Field	Intercept[1]	Slope[1]	r^2	.10P	.5P[2]	Standard Deviation
Grant							
	R	-34.82±.17	0.019±.002	.88	1964	2022	52.6
	1	-33.74±.15	0.019±.001	.92		2000	51.6
	2	-47.29±.15	0.025±.002	.93		2061	40.0
	3	-38.01±.14	0.021±.001	.93		2035	47.3
	4	-46.76±.13	0.025±.002	.95		2036	39.3
	5	-44.60±.12	0.024±.001	.95		2050	41.3
	6	-36.87±.13	0.021±.001	.93		2023	48.3
	2,3,56[3]	-37.42±.07	0.021±.007	.92		2020	47.6
	All	-39.06±.07	0.022±.007	.90		2002	45.5
Eaton Rapids							
	R	-19.96±.08	0.013±.001	.96		1977	79.2
	K	-24.30±.23	0.015±.002	.85		1982	67.6
	R,K	-22.12±.12	0.014±.001	.89		1981	71.4
Laingsburg							
	R	-36.49±.23	0.019±.002	.91		2183	52.6
	P	-36.56±.39	0.019±.007	.59		2187	52.6
	R,P	-37.98±.19	0.029±.002	.87		2180	50.0

---

[1] statistic ± $s_{\bar{x}}$

[2] Degree day at which 50% of oviposition occurred (base 4.4°C from April 1, 1979.

[3] Similar harvest dates and cultural practices.

SE = 1840 ± 44, Whitfield 1981). However, this was probably not true for oviposition as it is a function of behavioral activity and physiological development. Of interest was the relationship between cummulative egg laying, resulting generation survival, and time. As mentioned previously, the 1979 post-harvest season represented an optimum period for third generation success (relative to the average fall). The cohort study (Table 33) suggested that individual eggs laid after julian day 291 (October 18 ^{o}day 2110) had little chance of surviving to the pupal stage. This point in the egg input density function equals one standard deviation from the mean. Figure 24 graphically depicts this automatic mortality as the maximum attainable survival given the fall temperature trends within Grant.

On October 2, 1979, approximately three acres of white onions were harvested in field K in Eaton Rapids. The onions were planted on June 10, 1979 and were not mature by early October. Since the onions were destined for immediate fresh market sale, the farmer cut the leaves off at the top of the bulb with a rotary cutting bar and harvested the onions without curing them. This is an unusual practice as it is generally thought that such harvesting will leave the onions susceptible to gray mold infection (Botrytis allii Munn).

The resulting impact on the behavior and survival of the onion maggots (Table 37) showed that the cut tops ($\bar{x}$ cut tops/9.2 m^2=7.2) served as an oviposition "sink" where 76% of the eggs found on onion cull parts on julian day 277 were associated with cut tops. Subsequent oviposition on the dried residue of the remaining tops was high 24 days later. No survival occurred on the cut tops, although eggs hatched and first instar larvae became established. The leaves rapidly dessicated, such that 18 days after the production of the cut tops

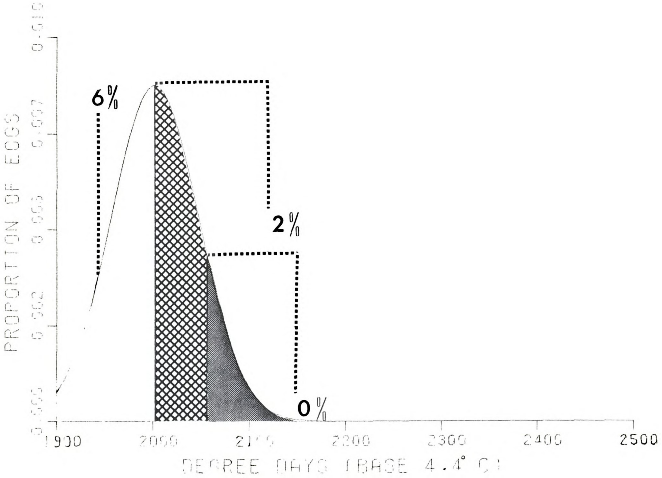


Figure 24. The effect of the seasonal occurrence of oviposition on survival to the pupal stage.

Table 37. Estimated survival[1] of OM immatures on cut tops[2], Eaton Rapids, 1979.

Cohort[3]	Percentage of Total Eggs Laid on Tops	Percent Survival on Tops	Percent Survival on Culls
277	76.0 (N = 417)	0	11.3
283	33.0 (N = 92)	0	8.1
288	37.8 (N = 314)	0	9.3
295	3.7 (N = 54)	0	1.9
301	27.0 (N = 97)	0	0

[1] Survival to pupation.

[2] Produced on julian day 275.

[3] Julian day cohorts were established.

almost all were shriveled dry tissue. Thus, this unusual production practice became a major mortality factor in the fall population of the onion flies.

Planting small plots of late onions within fields along the borders might inflict mortality on the onion maggot and at the same time provide a food source for predators. Frequent new cuttings of tops would be a highly attractive oviposition source throughout the post-harvest season. Also, cut tops from the previous year's volunteer culls in the spring might be used as a trap crop, as the need to find a method to kill the onion maggots infesting the trap crop would not be necessary. Long rows of culls planted in a furrow could be utilized as a cut top crop throughout the growing season.

Competition for the Cull Resource

Three other species were found during the post-harvest season infesting cull onions. Two of the species were identified as the lesser bulb fly, Eumerus spp. (Diptera: Syrphidae), and the bulb mite, Rhizoglyphus echinopus (F. and R.) (Sarcoptiforma: Acaridae). Two species of lesser bulb flies in Michigan are commonly associated with onions (Merrill and Hutson 1953) Eumerus strigatus (Fall.) and E. tuberculatus (Rond.). E. strigatus is the predominant species in America (McDaniel 1931). Both have identical life histories and can only be identified from each other in the adult stage (Hodson 1927). A positive identification was never made on the third species (Diptera), although the one fly that emerged from a pupa collected in the fall was a member of the family Muscidae.

Table 38 shows the densities per cull (percent culls infested in the case of R. echinopus) found during the fall of 1979 in Grant. R. echinopus was the only

Table 38. Population trends of arthropod colonizers of culls in Grant other than the onion maggot.

Sample Date	Eumerus spp./cull	Muscid sp./cull	Percent of[1] total culls infested by *R. echinopus*
September 19 (N = 450)	.148	.55	3.1
September 27 (N = 1200)	-[3]	-	2.0
October 12 (N = 140)[2]	.10	.002	1.9
October 19 (N = 140)[2]	.18	.04	2.1
October 24 (N = 140)[2]	.26	.36	4.2
October 30 (N = 140)[2]	.21	.06	-

[1] Even though *Rhizoglypus echinopus* are easily seen with the naked eye, densities per cull were too high to accurately count within the time available and so just a presence or absence rating was utilized.

[2] based on a sample of 140 infested culls and so density per cull were estimated by multiplying these indices by the proportion of infested culls of total culls at that point in time.

[3] Not counted.

species other than H. antiqua found in culls in Eaton Rapids. The proportion of culls infested with this mite were one tenth of one percent. In Laingsburg, only Eumerus spp. used the culls as a food resource, other than the onion maggot. Of all the culls sampled through the fall, only three larvae were found in two onions (November 5th and 10th). Less abundant insect colonizers of culls found in Grant were adults and immatures of the family Nitidulidae (Coleoptera), an occasional Lepidoptera larva, other unidentified syrphid larvae, and larvae and adults of the ottitid, Tritoxa flexa (Wied.). Seed corn maggots, Hylemya platura (Rond.) did not colonize culls during 1979.

The effect of Eumerus spp. and R. echinopus on weight loss of culls was discussed earlier. The incidence of the two species in storage facilities is discussed in Appendix A. These species competing with the onion maggot for food resources may affect the population dynamics. The syrphid and muscid maggot larvae may be alternative hosts for parasites and predators during the post-harvest season, although this was not true for Aphaereta pallipes (Say) (Groden 1982).

Direct competition for cull onions between the lesser bulb fly and other species was probably more the rule than the exception, despite the large number of culls available. Hodson (1927) stated that although females oviposit on healthy uninfested bulbs, they prefer damaged and degrading tissue. Larval displacement of H. antiqua by the lesser bulb fly could occur although bulbs infested with both Eumerus spp. and H. antiqua were seldom observed. This may have been due to the low density of the lesser bulb fly (see Table 38) or to onion maggot mortality from competition.

The larvae of E. strigatus usually the overwintering stage (a small number overwinter as pupae). In Michigan adult flies do not emerge until the following

June. While onions are attacked by the lesser bulb fly during the growing season (Wilcox 1926) usually the incidence of damage is low, possibly because larvae do not migrate from one bulb to another when the food resource is exhausted; therefore, many of the larvae perish in the spring (Broadbent 1925).

R. echinopus was often associated with the lesser bulb fly (24.4% of the bulbs infested with R. echinopus were also colonized by the lesser bulb fly). This is probably partly from the "hypopus" stage after the second nymphal molt which is generally produced in response to a stressing environment (usually wet sticky conditions). The stage is endowed with suckers or claspers for grasping insects. Thus, the lesser bulb fly and the onion maggot may be major vehicles in distributing the bulb mite (McDaniel 1931, Garman 1937, and Baker and Wharton 1952). Large populations of R. echinopus, resultingfrom post-harvest activities, could damage onions the following spring. Also, mites carried by other insects to new onions may be the most significant vector relationship of bulb rot fungi and bacteria infesting bulb crops.

Unidentified muscid larvae were associated with onion maggot larval cadavers in the fall. Eight cases (cull onions found with both onion maggot immature stages and muscid immature stages) were followed on a regular basis throughout the fall (Table 29). In each at least one dead onion maggot larva was found by the end of the observation period (November 11, 1979). This was highly significant in suggesting predation or competition resulting in death. Only three other muscid species have been associated with damaged onions in Michigan besides Hylemya spp.: Muscina assimilis (Fall.), Muscina stabulans (Fall.), and Fannia cannicularis (L.), two of which (Muscina spp.) are carnivorous in the larval stadia (Merrill and Hutson 1953). Perhaps one or both of the Muscina spp. were

Table 39. Culls occupied by onion maggot larvae and other species that were marked and followed through time.

Cull	Number of unidentified Muscid immatures	Number of *Eumerus* spp. immatures	Number of surviving onion maggots	Number of dead onion maggots observed
1	7	0	0	1
2	9	0	0	3
3	14	0	0	3
4	11	0	0	3
5	7	0	2	1
6	21	14	0	3
7	16	0	1	2
8	6	0	0	1

present during the post-harvest season resulting in direct mortality of the onion maggot larvae.

The Pupal Stage

The vertical distribution of overwintering onion maggot pupae was estimated by sifting through soil directly beneath 200 infested bulbs (November 2 and November 5, 1979) in Grant and Eaton Rapids. Soil was taken from within a 15 cm radius of the onion to a depth of 27.5 cm. The resulting distribution (Table 40) did not resemble that found by Carruthers (1979) in August of 1977 ($\chi^2_{(4)} = 1996.2$, $p < .005$). Some discrepancy might be attributed to only sampling soil within a 15 cm radius of the infested bulbs. Carruthers (1979) found that when sampling from 0-15 cm, only 90% of the population is accounted for. A functional relationship might exist between horizontal and vertical distance; if so, a bias would have been introduced into the data. Two deviations from the summer distribution that would not be expected from too small a sampling unit were the large percentage of pupae found within 2.5 cm of the soil surface and the number of pupae (28%) found below a 15 cm depth from which none were retrieved in the summer. Whether the vertical distribution of pupae is a dynamic process affecting both summer and fall generations (possibly due to the abiotic environment: soil temperature, air temperature, or photoperiod soil moisture) from year to year or whether these distributions are stable genetic characteristics of the generations is unknown.

Pupae collected in the fall were markedly different in size. Records on field origin, third instar larval density per bulb (where applicable), and cull type were kept for each pupa. Pupal volume, estimated from length and width measurements (to the nearest one hundredth of a millimeter), where:

Table 40. The vertical distribution of onion maggot pupae in the fall of 1979 in comparison to that of the summer 1977.

Soil Depth (cm.)	Percent of Total Population	
	Summer 1977[1]	Fall 1979[2]
0 - 2.5	1	8
2.5 - 5.0	24	2
5.0 - 7.5	50.3	15
7.5 - 10.0	17	9
10.0 - 12.5	7	32
12.5 - 15.0	0.7	6
15.0 - 17.5	0	9
17.5 - 20.0	0	6
20.0 - 22.5	0	9
22.5 - 25.0	0	2
25.0 - 27.5	0	2
27.5 - 30.0	0	0

[1] Data acquired from Carruthers (1979, Figure 7), N = 329.

[2] N = 159.

$$V = \frac{4\ell\pi\,(\tfrac{1}{2}x)^2}{3}$$

was used as a criteria for assessing the variation. A two way analysis of covariance was used to isolate factors influencing pupal volume.

Neither field nor cull type were found to be significant (Table 41), although third instar density (covariate) had a common slope among treatments and was found to be significant ($F_{1,181}$ = 9.98, p < .005). The relationship between density and pupal volume (Y = 25.2 - .119x) only explained 6% of the variation, however. An analysis of variance revealed significant differences ($F_{4,35}$ = 1.48, P = .23) when the data were pooled into five classes from low to high densities. This may indicate a trend toward reduced pupal volume at high densities (Figure 25).

One data set of summer pupal sizes was available for comparing the mean fall pupal size. Two hundred pupae were randomly selected from both the summer and fall data sets in groups of twenty. A t-test was performed to determine whether the means came from two different populations. The result was that the two means (summer: 32.1 ± 0.6 ($S\bar{x}$), fall: 25.1 ± 0.7 ($S\bar{x}$) were significantly different (T_{18} = -7.59, P < .001). The variances were also suspected of representing different populations, as the summer pupal variance was 16.8 ± 4.5 (.95 confidence interval) and the fall pupal volume variance was 44.6 ± 15.2.

One reason for these differences might be abiotic environmental stress during the fall. Temperatures often dropped below 4.4°C (hypothetical threshold for development) during late October and in November. How this affected larval development and the subsequent timing of pupation (stressed early third instar larvae pupate early, Sleesman and Gui 1931, Ellington 1963) is not known. Unfortunately pupae collected in the fall were not assessed for survival and were

Table 41. Pupal volume in relation to field of origin, cull type, and third instar density.

Field	Pupal volume (MM^3)[1]
Grant	
R	24.5 ± 0.8
6	20.4 ± 1.2
5	24.9 ± 0.9
4	22.7 ± 0.8
Eaton Rapids	
K	23.8 ± 1.7
Cull type	
Whole	25.8 ± 1.1
Cut	23.6 ± 0.8
Rotted	24.4 ± 0.9
Sprout	23.9 ± 1.1
Density Class	
1 - 5	24.06 ± 1.5
5 - 10	23.6 ± 1.7
10 - 15	26.2 ± 1.7
20 - 30	20.4 ± 2.2
40 - 50	19.3 ± 3.6

[1] $\bar{x} \pm s\bar{x}$ (N = 186)

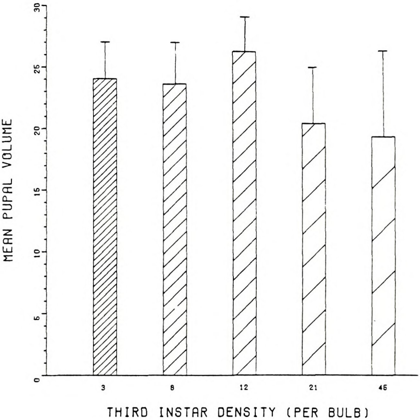


Figure 25. Relationship between third instar density/cull and mean pupal volume.

not examined for the presence of parasitism by Aphaereta pallipes Say (Groden 1982 personal communication).

Third instar larvae parasitized by A. pallipes often are smaller in size on pupation. This factor alone may be the underlying cause of the difference in pupal size as parasitism by A. pallipes is usually not found in the onion maggot until after harvest (Groden 1982).

Results of studies on the survival of overwintering pupae during the winter of 1978 - 1979 (Table 42) yielded an average survival (pooled over all treatments and regions) of 80.5% ± 1.7% ($S\bar{x}$). Analyses of variance provided no criteria to suspect differences in survival due to habitat types, regional environments, or genetic predisposition. The survival of the pupae in 1978 compares well to the findings of Whitfield (1981) who studied overwintering pupal survival during 1978 and 1979 over a variety of different soil depths (0-23 cm) and locations (87.8% ± 0.9). These results suggest that the winter hardiness of the onion maggot is great and that the potential to manipulate abiotic environmental conditions to adversely affect the population is low.

SUMMARY

The construction of a data base concerning the population dynamics of the post-harvest generation of Hylemya antiqua in Michigan has been initiated. While by no means being comprehensive, it offers a perspective into possible key factors that could impact the post-harvest generation of the onion maggot. The future holds promise for an agroecosystem design and management philosophy based on integrating cull dynamics with parasite management (Carruthers 1981, Groden 1982), trap crops, and a keen understanding of the temporal and spatial dynamics of the onion maggot (Whitfield 1981).

Table 42. Overwintering survival of onion maggot pupae placed in different habitats and in various locations, 1979.

Habitat[1]	Overwintering Pupal Survival
Sandy muck soil	81.0 ± 8.8
Clay muck soil	73.6 ± 13.7
Field border	71.3 ± 11.1
Rye Cover Crop	71.0 ± 4.2
Muck control	83.3 ± 2.6
Simulated hardpan[2]	82.0 ± 8.9
Flooded muck soil[3]	82.3 ± 1.6
Within onions[4]	78.6 ± 3.7
Snow fence[5]	88.3 ± 7.6
Providence Study[6]	
Grant Pupae Buried at Eaton Rapids	81.2 ± 6.3
Eaton Rapids Pupae Buried at Eaton Rapids	80.8 ± 4.3
Grant Pupae Buried at Grant	91.6 ± 3.2
Eaton Rapids Pupae Buried at Grant	81.2 ± 4.5

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[1] $\bar{x} \pm 5\bar{x}$ based on 3 replicates of 75 pupae each.

[2] Nylon packets of pupae buried 2.5 cm. below the soil surface resting upon plastic wrapped sheet rock.

[3] Pupae buried in a field (#6) that historically has had a drainage problem, pupae were under the water for most of the winter.

[4] Pupae placed within bulbs and set onto soil surface.

[5] Pupae buried on southeastern side of a 3.5 M. length of lathe snow fencing.

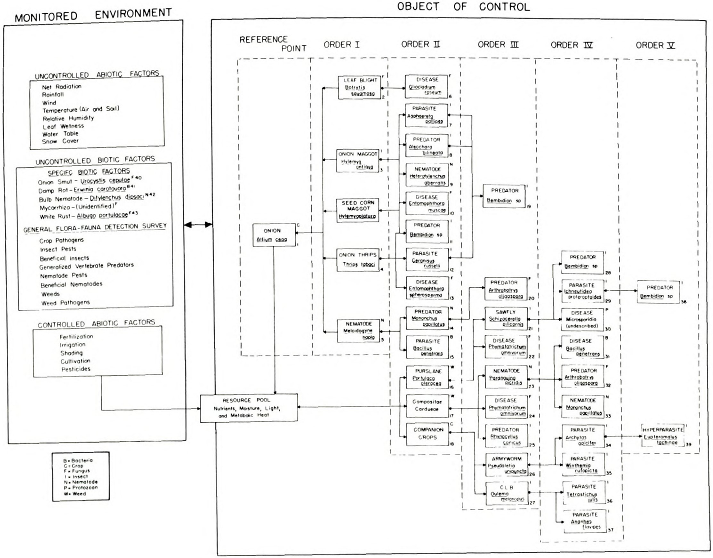
[6] $\bar{x} \pm 5\bar{x}$ based on 5 replicates of 50 pupae each.

Figure 26 depicts the conceptualized structure of the various interacting levels of the within season agroecosystem (footnote sources appear in Appendix G). More specific microcosm dissections of these levels can be found for the onion maggot as the object of control (Whitfield 1981), *Entomopthora muscae* (Cohn) as the object of control (Carruthers 1981), *Aleochara bilineata* (Gyll.) and *Aphaereta pallipes* Say as the objects of control (Groden 1982), the onion plant as the object of control (Pet and Bolgiano, unpublished), and the mycorrhizal fungi associated with the onion as the object of control (Bolgiano, 1982). Many of the interactions represented in the within season conceptualizations are probably main features within the post-harvest dynamics as well. This research suggests that there are many levels of interactions not found within the confines of the growing season that predominate in the fall.

Results from sampling culls and categorizing cull onions into arbitrary classes indicated that culls were not static entities, but have their own characteristic rates of change and potentials for transformation into other cull types (whole, cut, rotted, and sprouted). Experiments designed to evaluate weight loss showed that some cull types, such as whole culls, experience little weight loss throughout the season. This occurs within the first few days. Other cull types, such as cut tops, lose a large proportion of the original biomass. Burying culls under the soil surface decreased the rate of these trends. The soil type, however, made no difference. Thus, it appears that not only the time of harvest, but also the method of harvest affects the cull composition in the field by the time oviposition commences in the third generation.

Regression analysis of the relative abundance of third generation flies and oviposition on culls (expressed as total egg production per unit area) explained

Figure 26. Conceptualization of the onion agroecosystem showing levels of interaction within the object of control (Haynes *et al*. 1980).


MONITORED ENVIRONMENT
UNCONTROLLED ABIOTIC FACTORS
Net Radiation
Rainfall
Wind
Temperature (Air and Soil)
Relative Humidity
Leaf Wetness
Water Table
Snow Cover
UNCONTROLLED BIOTIC FACTORS
SPECIFC BIOTIC FACTORS
Onion Smut – Urocystis cepulae F40
Damp Rot – Erwinia carotouora B41
Bulb Nematode – Ditylenchus dipsaci N42
Mycorrhiza – (Unidentified) F
White Rust – Albugo portulacae F43
GENERAL FLORA-FAUNA DETECTION SURVEY
Crop Pathogens
Insect Pests
Beneficial Insects
Generalized Vertebrate Predators
Nematode Pests
Beneficial Nematodes
Weeds
Weed Pathogens
CONTROLLED ABIOTIC FACTORS
Fertilization
Irrigation
Shading
Cultivation
Pesticides
B = Bacteria
C = Crop
F = Fungus
I = Insect
N = Nematode
P = Protozoan
W = Weed
OBJECT OF CONTROL
REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
ORDER V
ONION Allium cepa C 1
RESOURCE POOL Nutrients, Moisture, Light, and Metabolic Heat
LEAF BLIGHT Botrytis squamosa F 2
ONION MAGGOT Hylemya antiqua I 3
SEED CORN MAGGOT Hylemya platura I
ONION THRIPS Thrips tabaci I 4
NEMATODE Meloidogyne hapla N 5
DISEASE Gliocladium roseum F 6
PARASITE Aphaereta pallipes I 7
PREDATOR Aleochara bilineata I 8
NEMATODE Heterotylenchus aberrans N 9
DISEASE Entomophthora muscae F 10
PREDATOR Bembidion sp I 11
PARASITE Ceranisus russelli I 12
DISEASE Entomophthora spherosperma F 13
PREDATOR Mononchus papillatus N 14
PARASITE Bacillus penetrans B 15
PURSLANE Portulaca oleracea W 16
Compositae Carduege W 17
COMPANION CROPS C 18
PREDATOR Bembidion sp I 19
PREDATOR Arthrobotrys oligospora F 20
SAWFLY Schizocerella pilicornis I 21
DISEASE Phymatotrichum omnivorum F 22
NEMATODE Paranguina picridis N 23
DISEASE Phymatotrichum omnivorum F 24
PREDATOR Rhynocyllus conicus I 25
ARMYWORM Pseudaletia unipuncta I 26
CLB Oulema melanopus I 27
PREDATOR Bembidion sp I 28
PARASITE Ichneutidea proteroptoides I 29
DISEASE Microsporidia (undescribed) P 30
DISEASE Bacillus penetrans B 31
PREDATOR Arthrobotrys oligospora F 32
NEMATODE Mononchus papillatus N 33
PARASITE Archytas apicifer I 34
PARASITE Winthemia rufopicta I 35
PARASITE Tetrastichus julis I 36
PARASITE Anaphes flavipes I 37
PREDATOR Bembidion sp I 38
HYPERPARASITE Eupteromalus tachinae I 39

48% of the variance in egg incidence. An association such as this indicates that a pest management strategy for the fall could be aimed at adults. This implies that reducing the number of flies will decrease egg density. The behavior of fly migration with harvest should be investigated if a management strategy utilizing insecticides after harvest is needed.

Egg deposition per cull was shown to be a function of cull type both temporally and spatially. The degree of attraction of gravid females to culls were sprouts, cut tops, cut, rotted, and whole onions. The temporal distribution of sprouts was a major component in the resulting preference regarding oviposition on other cull types. Based on egg incidence data, sprouts may represent a super-normal oviposition stimulus in conditions where the lack of activity precludes any oviposition on other cull types. Egg distribution with respect to placement in the soil was relatively constant across all cull types, field types, regions, and days.

Data obtained from two methods of sampling for establishing a life table data base were used to develop sampling plans for culls, eggs, and third instar larvae. Optimal sample sizes for cull density estimation were based on the negative binomial distribution with a common Kc. Two schemes were developed for egg sampling. A single stage randomized design, utilizing a unit area of 9.2 m^2 as the sample unit size, was compared to a two-stage cluster sampling design that was less labor intensive. Third instar larval sampling was based on the finding that density of third instars per infested cull (not including sprouts) was a constant within a sampling interval; therefore, a rough estimate of density could be obtained by approximating the proportion of onion maggot infested culls within a field, thereby decreasing the time involved when estimating larval density on a regional level.

Survival analysis of the fall population revealed that mortality between the egg stage and first instar establishment was the major proportion of mortality within the immature stages. It was also found that early in the fall (September to mid-October) the probability of first instar surviving to the third instar stage was relatively constant, but decreased as the season progressed. Survival generally was effected by time of the post-harvest period. Eggs laid prior to 50% cumulative oviposition (^{o} Day 2002) were more likely to survive to the pupal stage compared to those laid between 50% and one standard deviation away from the mean. Eggs oviposited during the last 30% of the cumulative egg input did not survive. This is especially significant if viewed from the premise that the 1979 post-harvest generation was an optimal autumn for third generation survival and development relative to the average year. A culturally induced key mortality factor was the production of cut tops which were very attractive to females laying eggs but did not allow larvae to complete development due to the rapid rate of leaf dessication.

The vertical distribution of pupae within the soil was different from the summer. Overwintering pupae survival was uniformly high over a variety of natural and artificial conditions. There were no apparent differences in survival due to the region in which the onion maggot populations were studied.

Onion maggots were not the only arthropods infesting culls after harvest. The bulb mite, R. echinopus, the lesser bulb flies, Eumerus spp., and an undetermined muscid were all present in fairly high numbers in Grant, but not the two other regions. The muscid larvae might cause mortality in the onion maggot.

All of these components and linkages affecting the population dynamics of the third generation of the onion maggot contribute to an overall frameork of

the ecology of the onion agroecosystem. Figure 27 represents my perspectives and hypotheses formulated while studying the post-harvest generation of the onion maggot.

CONCLUSIONS

The following are recommendations for further study of post-harvest population dynamics. If culls are to be managed after harvest and possibly during the next spring, a knowledge of the plant dynamics is necessary. The effect of cultural practices, as well as abiotic factors, needs to be investigated as to the nature and degree of association they have with sprout production both temporally and spatially. Critical in understanding the population dynamics of the onion maggot after harvest is knowing the relationship between air temperature and oviposition. This complex endeavor may involve both the physiology of maturation (temperature dependent rate and thermal threshold) and the thermal threshold for oviposition behavior. Predicting overwintering pupal density depends on the unique circumstances associated with the development and survival of the third generation immature stages and their exposue to subdevelopmental threshold temperatures. The study of these components, based on current knowledge, should enable modeling efforts to play a role in designing long-term management strategies.

Alternatives to scheduled insecticide applications during the growing season are techniques based on post-harvest onion maggot biology: (1) a post-harvest insecticide program aimed at the adults; (2) use of trap crops, the production and manipulation of sprout onion culls and cut top culls directed at the female fly's oviposition behavior; (3) early harvesting combined with planting

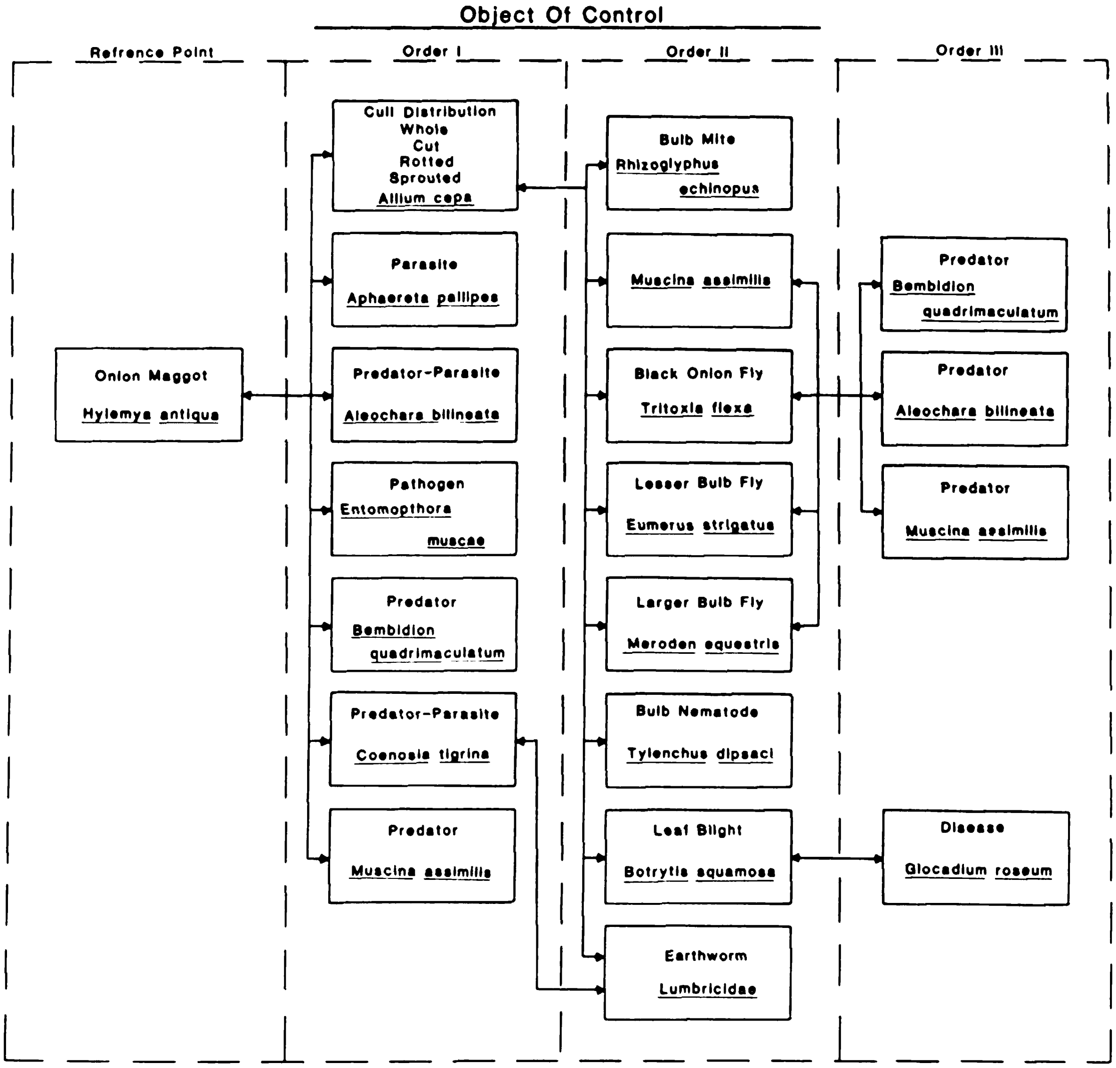


Figure 27. Conceptualization of the post-harvest onion agroecosystem showing levels of interaction with the object of control.

a rye cover crop to interfere with oviposition via host finding; and (4) well-timed (peak oviposition) displacement of surface cull onions with a harrow aimed at separating hatching eggs from their food resource (culls). The most promising is the post-harvest spray program. The advantages of such a program are that it would be independent of activities during the growing season and would integrate well with a variety of management approaches. A major consideration associated with implementing such a strategy is the degree of attractiveness of a freshly harvested field. Studies should be designed to determine what size of planting has to be harveted (as a trap crop) to attract a large proportion of the adult post-harvest generation. Timing must be synchronized between harvest (spray application and 100% adult emergence if the goal is for only one application to be made.

A perhaps obvious element in this strategy, but possibly not an easy one to implement, is the use of an effective insecticide (the onion maggot has developed resistance or tolerance to most of the chemical compounds used to combat it (Carruthers 1979)). Utilizing a program based on a fall insecticide application will pose a challenge in preserving important mortality factors that have carry-over potential to the spring generation such as disease organisms (Carruthers 1981) and predators and parasitoids (Groden 1982). Strip spraying may be helpful. More work needs to be started where this thesis has left off for an effective "cull management" program to be implemented.

What appears to be critical in understanding the population dynamics of the onion maggot in the fall is the relationship between weather conditions (mainly temperature and soil moisture) and the behavior and physiology of female flies and the survival and development of the immatures. With regard to temperature

both long periods of subthreshold in conjunction with sub-zero temperatures should be a primary goal inorder to determine total production for the following spring.

The last statement that I would like to make pertains to the research findings of all the investigators to date in the onion project at Michigan State University. Based on a philosophy of agroecosystem design with respect to parasitoid and disease management along with potentials for trap crops, and cull manipulations I am convinced that the onion maggot population within a region can be successfully kept in check without the use of any chemicals. Integration of such specific design options as increasing incidence of Entomopthora muscae infection within the adult population by strip cropping onion fields with habitats that concentrate the spatial occurrence the diseased flies and healthy flies (Carruthers 1981), or providing alternate host to increase predator and parasitoid populations (Groden 1982). These strategies can also be integrated into a full management program in which sprouts can be concentrated near field borders so as to provide a high density food source for predators or parasites as well as localize the adult populations inorder to increase disease incidence. Other culls can be displaced every 50 degree days causing first instar mortality. More work needs to be done for effective implementation of these options but this should not be beyond the scope of the near future.

APPENDIX A

HARVEST AND STORAGE STUDIES

HARVEST AND STORAGE STUDIES

INTRODUCTION

The period beginning with onion harvest and ending with planting has received little attention since the development of the modern controlled atmosphere storage facility. The exceptions have been research conducted on plant breeding and post-harvest physiology as it pertains to sprouting and dehydration (Rickels et al. 1975, Herner et al. 1975, Lorenz and Hoyle 1952, Boyd and Davis 1953). Pathogen biology has also been studied (but not as recently) on the organisms that cause the symptoms of the diseases neck-rot and basal-rot (Vaughn et al. 1961, Boyd and Davis 1953, Hoyle 1948, Newhall et al. 1959, Walker 1937, Munn 1917). Arthropod problems are not well documented in the scientific literature, and little information is available on the interactions that many of these cultural and environmental (abiotic and biotic) factors may possess.

Studies were initiated from the time bulbs were cut and lifted until the last Michigan storage onions were marketed in spring the following year. An attempt was made to elucidate any dynamic interactions or management options that may have existed in the harvest and post-harvest season of onion production.

The following studies were performed from August 1978-February 1980 in Grant, Michigan: (1) pinhole damage study, (2) storage dynamics of maggot infested onions, (3) estimation of cull production, and (4) assessment of factors leading to cull production and their relationships amongst one another. These studies were carried out at different times and locales and will be discussed independently.

PINHOLE DAMAGE STUDY

Introduction

In 1978, a new form of onion maggot damage was found in mature bulbs while sampling onion maggot injury levels in Grant, Michigan (Gary Whitfield 1978), and Eaton Rapids, Michigan. A considerable proportion of the onions (up to 23%, N=1,000) in some fields had small cavities in the bottom surface of the onion. These holes were usually within a few millimeters of the bulb-root interface. The hypothesis was that this damage was from third instar onion maggot larvae as they migrated from dehydrating rotted onions to mature bulbs. A study was initiated to find the cause of the damage and to assess its consequences.

Materials and Methods

Further sampling and observations were made on onion fields in different phases of harvest in Eaton Rapids in 1978. In the laboratory, large bulb onions were populated with second and third instar larvae (determinations based on Brooks 1951) and checked periodically for feeding scars. Onions damaged in this manner were brought back to the laboratory, and the diameter and depth of the holes were measured with a pair of micrometer calipers. To determine whether these "pinholes" had any other ramifications besides unsightly cosmetic value, an experiment was designed to test their stability in cold storage. Six plastic-mesh onion bags from the Michigan Onion Growers' Cooperative in Grant, Michigan, were filled with 100 pinhole onions each. Three bags were tagged with plastic marker tape and incorporated into the middle of a bulk storage facility (Mr. Jerry Plaisier's facility, Grant, Michigan). The other three bags were tagged and put in storage crates with other onions packed around them (Mr. Plakmeyer's storage facility, Grant, Michigan). The experiment was initiated on September 22, 1978, and terminated when the contents of the mesh bags were checked on January 4, 1979.

Results and Discussion

Observations of onions in the field before and after harvest supported the hypothesis that the pinhole damage was from late instar onion maggot larvae attempting to become established in mature bulbs. Many bulbs were found with large larvae adjacent to the bulbs with damage, as well as half way inside the bulb within the pinhole. Early instars were never found in association with this damage. Undamaged onion bulbs brought into the laboratory and subjected to third instar onion maggot larvae possessed the distinctive pinhole only when the 1-3 larvae per onion and the muck the bulb was set on was dry. Large numbers of larvae and a wet substrate yielded the more typical late season onion maggot damage found in subterranean bulbs. This phenomenon is probably keyed into a time synchrony between harvest (cutting and lifting of the bulbs along with the amount of time the bulbs are left in the field) and the occurrence of the second generation third instar larvae.

Based on onions sampled in Grant and Eaton Rapidsthe average depth of these pinholes was 3.06 mm (N=202, S.D.=1.31), and the average cross-sectional diameter was 2.14 mm (N=202, S.D.=0.9). The number of pinholes per onion ranged from 1-8 with an average of 1.8 per onion (N=202).

The storage experiment showed no evidence that pinhole damage in itself initiates storage decay or soft rots under typical storage conditions (no rot was

found in any of the bagged pinhole onions at the end of the study). As of 1979 most onion growers in Michigan were unaware of the damage. The storage survey revealed that little if any of the onions culled that year were selected for this reason. Based on the findings, no management options during the harvest period are needed to prevent pinhole damage.

STORAGE OF MAGGOT INFESTED ONIONS

Introduction

At the same time that the pinhole damage was being investigated, some entomological researchers and onion growers (Wells 1978) were concerned that maggots infesting onions during harvest threatened undamaged onions in storage. This concern initiated a harvest cover spray of parathion.--well documented cultural practice in Canada (McEwen 1978). To determine the fate of harvested, infested onions, an experiment was set up on September 22, 1978.

Materials and Methods

Six plastic-mesh onion bags from the Michigan Onion Growers' Cooperative in Grant, Michigan, were filled with 100 onions each, 10% were infested with groups of onion maggot larvae of varying age-structure. Three bags were tagged with plastic marker tape and incorporated into the middle of a bulk storage facility (Mr. Jerry Plaisier's facility, Grant, Michigan). The other three bags were tagged and put in storage crates with other onions packed around them (Mr. Plakmeyer's facility, Grant, Michigan). The experiment began September 22, 1978, and terminated when the contents of the mesh bags were checked on January 4, 1979.

Results and Discussion

The bags of onions with 10% maggot infested onions showed no new damage. This does not mean that onion maggots will not move from infested bulbs to undamaged bulbs but perhaps indicates that conditions must be more conducive for this to occur than was found in the storage environments. Concerning abiotic conditions, it was hypothesized that the first few days of bulk curing before the water has been evaporated out of the outside epithelial layers of the onion is the time when maggots may become established in new bulbs.

The onion maggot dynamics involved in this process depend on the host or food source. In greenhouse experiments conducted later (see discussion in larval migration section), onions that reached a state of "undesirability" stimulated third instar onion maggot larvae to search of a new host. Thus, this factor may be responsible for new damage in storage. If this is true, providing and instituting a management procedure for infested onions is unnecessary (except possibly culling infested onions prior to putting onions into storage). These migratory stimulating onions are so few at any time during harvest that a significant increase in onion maggot damage would probably not happen in storage.

ESTIMATES OF CULL PRODUCTION

Introduction

A survey of onions coming out of storage was conducted at several pack-out or sorting sheds in Grant, Michigan during the 1978-1979 and the 1979-1980 onion marketing season. One of the aims of this study was to arrive at some point estimates for the proportion of onions being culled out. The amount of

onions culled at the sorting shed, along with the 400-500 pounds of onions per acre left in the field and the 20% of the total harvested crop that are dumped (Finkbinder 1979 and Espie 1981) due to increasing competition from long distance markets all might be an economic advantage. Another reason for investigating cull production stems from the problem in Grant, Michigan, in 1979 and 1980 when culled onions buried in the earth polluted ground water.

Materials and Methods

Two methods were used to estimate the proportion of culls produced. The first method consisted of weighing whole loads before sorting and then subtracting the number of bagged onions after packing. Tractor trailer trucks carrying onions from the storage units to the sorting sheds were weighed on a truck scale in downtown Grant, Michigan. The onions were then taken to the sorting shed where they were unloaded and packed. The trucks were then weighed while empty. The weight of packed onions was computed by counting the number of bags, and this was subtracted from the total weight of the truck minus the empty truck weight. An estimate of culls from a load of onions was then computed. The computation was performed seven times over the two year study.

The other method involved taking five repetitive counts, for one minute each, of the onions on the cull conveyer ramp and the packout ramp that moved parallel and at the same rate as the preceeding one (Figure A1). Two persons were needed for this as the counts were taken simultaneously.

Results and Discussion

The seven weigh-ins (Table A1) show that culling operations produced between 8 and 17.4% culls during the 1978-1979 period and between 7 and 26%

Figure A1. Generalized schematic of the physical layout of an onion packing shed.

CODE	
***	path of onions culled
— —	path of onions not culled
B	boiler onions (< 1-1/2")
BR	brushes (scrape dirt of onions)
C	culling stations (variable number active at any one time)
D	cull disposal
J	jumbo onions (> 3")
M	automatic bagging machines
P	boxing stations
R	rollers (sort out jumbos)
S	state inspectors station
SL	slates (sort boilers)
ST	conveyer belts for culling and sorting #2's
2	grade #2 onions
3	3-5 pound bags packed
5	50 pound bags packed

out

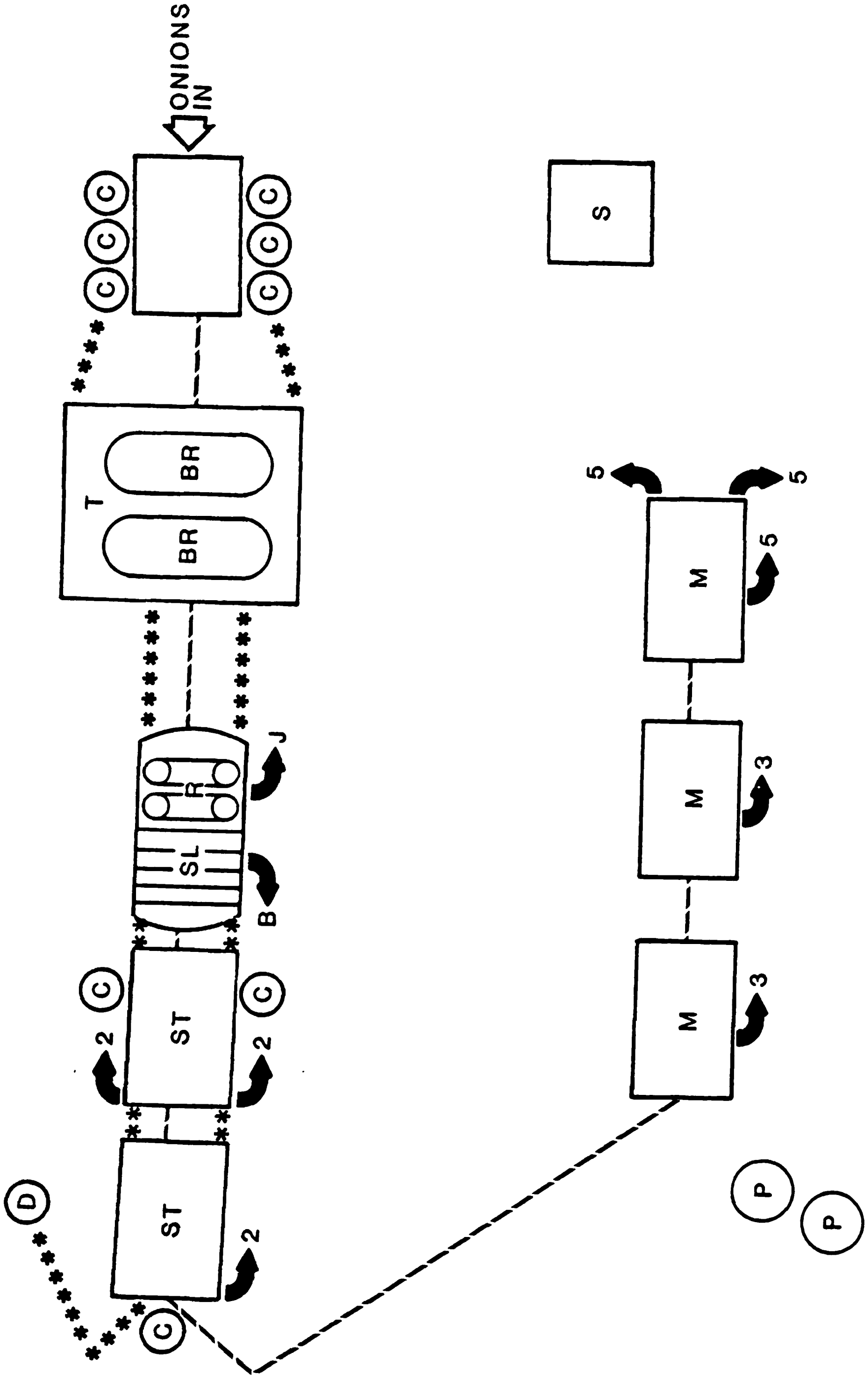


Table A1. Cull production for 1978-1979 and 1979-1980.

Truck Weigh-in					Line Count			
Date	Pounds In	Pounds Out	Pounds Culled	Percent Culled	Date	$\bar{x}$ Number Packed/Minute	$\bar{x}$ Number Culled/Minute	Percent Culled
3/15/79	45,560	38,300	7,260	15.9	11/10/79	249.0	35.0	12.3
3/17/79	41,070	37,950	3,120	8.2	12/6/79*	284.5	79.3	21.8
3/17/79	42,870	35,400	7,470	17.4	2/28/80	121.4	55.2	31.2
11/7/79	43,550	40,501	3,049	7.2				
11/7/79	34,840	30,659	4,181	12.4				
12/6/79*	44,950	33,263	11,687	26.0				
12/6/79	39,830	31,864	7,966	20.1				

*indicates estimates from same load of onions

culls for the 1979-1980 period. The proportion of culls calculated from line counts were performed only for the 1979-1980 season. The second method was based on numbers of onions, not pounds as was the first method. These two methods should have estimated the same value as long as the load did not have too many minimum size onions. The December 6 cull production for truck number 1 and the line counts are estimations of cull production from the same load. The estimates in proportion are quite similar (26% vs. 22%).

The proportion of onions ending up as culls was a marketing phenomenon independent quality. The Michigan Onion Growers' Cooperative, which operated LIKE the other sorting sheds, put more personnel on the culling stations as the season progressed (Finkbinder 1979). This is reflected somewhat in Table A1. The reasons for this are (see Sorting Shed Survey) the loss of quality through time and the appearance of competing long distance markets (Texas and the west).

SORTING SHED SURVEY

Introduction

There is a lack of documentation in the scientific literature of losses incurred in the storage of onions. Potential problems are mentioned (Riekels et al 1975; and Herner et al. 1975) and how to minimize losses (Herner et al. 1975, Lorenz it al. 1952, Boyd et al. 1953, Hoyle 1948, Vaughn et al. 1961). Estimates of storage losses from plant pathogens are available: Iowa--15% loss due to bulb rot, Fusarium sp. (Davis and Hendersen 1937); New York and Massachusetts--7-50% losses due to neck-rot (Munn 1917); and a national average of 2-10% losses due to neck rot (Vaughn et al. 1961). Arthropod-induced losses have not been

well documented (Bulb Mite, *Rhizoglyphus echinopus* L.; Onion Maggot, *Hylemya antiqua* (Meig.); Black Onion Fly, *Tritoxa flexa* (Wied.); and Lesser Bulb Fly, *Eumerus strigatus* (Fall.), nor have losses due to sunscald, waterstain, mechanical damage, peeling and any other cultural, varietal, and abiotic factors. These maladies however, are the basis of an onion grading system.

The aim of this storage study was to determine the definition of a population of culls produced at the sorting shed and, perhaps, learn something about the dynamics of onion storage.

Materials and Methods

The storage cull survey was conducted at three packing sheds in Grant, Michigan (see Figure A1 for a generalized diagram of the physical layout of a packing shed). The packing sheds in this study were the Michigan Onion Growers' Cooperative, Plaisier Brothers' Packing House, and Dyke Brothers' Packing House. Eighteen loads of onions were sampled in the 1978-1979 season and eight different loads in 1979-1980. These loads were grown in four geographical regions in Michigan: Grant (23 loads), Clarksville (1 load), Jackson (1 load) and Hudsonville (1 load).

Onions were randomly sampled by picking the fourth digit from a randomly selected phone number (N) in the Newaygo area phone book (Michigan Bell Telephone Company) and spotting an onion on the cull conveyor belt, then selecting the N^{th} onion away from that onion. The sample size was a function of the number of people working on the project that day and the duration of the packing process (most packing was performed in the mornings; onions were not packed every morning). The sample sizes ranged from 116-1582 during the first year and 72-196 the second year.

A crop history including grower origin, harvest date, curing method, storage dates, cultivar, storage method, and weather records for the locale where the crop was grown; was compiled (not all growers had this information since different fields of onions might be mixed during storage). The information helped determine how growers handled their crop after harvest and served as a control or covariate in analysis.

The onions were examined for the presence or absence of twenty-one storage disorders. A few were numerically classified (example: number of onion maggot life stages per onion). The presence of disease was verified and classified by Dr. M. Lacy, Department of Botany and Plant Pathology, Michigan State University. The categories of storage disorders were as follows:

1. Mechanical Damage: a bruise resulting in water soaked tissue where disease symptoms are not visible, or a cut or slice penetrating deeper than the outside dry scales.
2. Discolor: a green pigment in the outside scales of the onion generally resulting from immaturity at harvest or exposure to direct sunlight prior to storage.
3. Sprout: a breaking of dormancy and an issuing forth of true leaves, commonly associated with high relative humidity and damage to the bulb. The potential to sprout in storage is a variety characteristic, although it generally occurs in any variety given enough time and optimum conditions.
4. Thick skin: outside scales of the onion break away from the bulb and dry and toughen forming a thick, leathery, loose skin around the onion.

5. Peeler: peeling or cracking of outer dry scales to the point where green tissue is exposed. The green tissue is not cut but when the bulb is rubbed, the outer scales come off easily.
6. Spindle: onions looks like a cigar. This is not to be confused with the typical globe shape that many of the varieties grown in Michigan take on. Excessive planting density or addition of nitrogen fertilizer at the time of bulb initiation can cause this.
7. Soft: this condition is more arbitrary than the above imperfections. The criterion is the lack of sufficient density such that when a person culling onions applies pressure with their fingers or thumb, the tissue of the onion collapses (should not be confused with water soak damage). Because the culling operation depends on visual signs and only a small proportion of onions are handled, culling for this condition is probably less efficient than other ones. The low grade density onions are more probably a result of storage than handling conditions (Johnson 1979).
8. Thick neck: improperly cured onions, immaturity at harvest, or untimely nitrogen fertilizer may create a condition where the neck remains green.
9. Multiple center: generally a genetically determined phenomenon although it can result from damage to a young plant (Fobes 1979). The onion possesses two or more meristematic tissue origins from which true leaves arise.
10. Water stain: when onion bulbs have been cut and lifted, they are susceptible to a variety of blemishes, one of which is staining due to

moist soil in contact with the bulb. The stain resulting is a black, sooty waterline around bulb where the contact was made.

11. Sun scorch: differentiated from discolor by the tissue exposed to the sun. Discolor is a response to freshly lifted onions exposed to an unshielded intense sun, while sun scorch is a condition resulting from cured onions being exposed to intense sunlight. The stain is a copper-bronze pigmentation in the outer scales.
12. Miscellaneous stains: other stains and odd pigmentations on onions.
13. Neck-rot: a disease symptom commonly incited by *Botrytis allii* Munn (Walker and Lindegren 1924) although can also be due to infection by *Botrytis byssoidea* Walker or *Botrytis squamosa* Walker. The disease is most commonly found on bulbs after harvest. The infection usually takes place through neck tissue (Walker and Tims 1932). Afflicted scalessoften and look water-soaked. Mycelium generally is found in the older diseased tissue, and as it increases, a dense, grayish mycelial mat often develops on the surface of the scales (Munn 1917). In older decayed tissue, sclerotia appear first as whitish compact masses of myceliumthat darken with age. Eventually, the sclerotia resemble hard, black, kernel-like entities varying from 1-5 mm in length (Walker and Tims 1932). They usually form on the outer surface of the scale or are slightly imbedded in the diseased host tissue.
14. Basal-rot: also known as Fusarium-rot, is incited by *Fusarium* spp. organisms. These organisms are referred to as "wound organisms" (Davis and Henderson 1937) in that a wound in the plant is necessary for these pathogens to enter and become established. This organism

can invade the plant any time during the growing season (temperature-dependent response), but the infection that occurs shortly before harvest time becomes a storage problem. The bulbs become soft, and when they are cut, a semi-watery decay is found. The rot progresses slowly and advances from the base of the scales upward (Walker 1937).

15. Purple blotch: a disease of leaves, seed stems, and bulbs caused by a fungus (Alternaria porri (Ell.) Cif.). The symptoms usually result from infection during harvest. The fungus enters through the neck (Walker 1937). The decay is at first semi-watery and is especially conspicuous due to the red-purple pigment secreted by the parasite (Walker 1937). Affected tissue is deep yellow, but turns to a wine red. With time, the decaying area turns dark brown to black; eventually the tissue dessicates, and the diseased scales become dry and papery.
16. Onion Maggot: Hylemya antiqua (Meig.) only onions with a remnant of an onion maggot life-stage present (eggs, larvae, pupae) were classified in this category. The same held true for Bulb Mite and Lesser Bulb Fly.
17. Bulb Mite: Rhizoglyphus ecinopus (F. and R.)
18. Lesser Bulb Fly: Eumerus spp.
19. Small: onions less than 2.5-3.8 cm do not meet U.S. grade No. 1 specifications, and when a demand for "boiler" onions was not present, these onions were culled.
20. Jumbo: onions greater than 8.8 cm do not meet U.S. grade No. 1 specifications, and when a demand for "Jumbo" onions was not present, they were culled.

21. New roots: new root growth initiated in response to sprouting, injury, or relative humidity (Fobes 1979).

Results and Discussion

The culling process is partially regulated by a dual lower-limit quality standard: No. 1 grade onion. Two sets of criteria exist for the determination of this quality standard: a local state guideline and a federal benchmark. The USDA No. 1 grade onion is determined by both standards and tolerances (Bridgeford 1979).

Standards:

1. minimum size = 3.8 cm diameter (all varieties);
2. 40-60% in any one lot should be 5 cm in diameter or larger (yellow and red varieties), 30% in any one lot should be 5 cm in diameter or larger (white varieties);
3. not more than 15% can be greater than 2-1/2" in diameter;
4. all onions in a lot must be the same variety; and
5. all onions in a lot must be mature.

Tolerances:

1. not more than 10% should be damaged by peeling;
2. not more than 5% should be damaged by multiple centers, sprouting, bruising, maggot damage, bulb stalk nematode, or thick necks; and
3. not more than 2% should be affected by decay or wet sunscald.

The state criteria comply with the federal standards but adjust tolerances (Johnson 1979). State inspectors in Michigan select three pound bags off the line for testing. Michigan tolerances for three to five pound bags are set at three

times the federal levels. Fifty pound bags are allowed two times the federal tolerances (Johnson 1979). Texas markets its onions on one half the tolerance levels of Michigan. Growers in Texas are in a different time frame and compete in a different market.

The hypothesis for this study was that the dynamic component of the culling process was a function of the Michigan growers' production (quantity and quality). The production statistics for the Michigan onion crop over the last nine years (Table A2) have remained relatively constant with fluctuations of 15% per year. (A non-directional test based on Kendall's S sampling distribution (Ferguson 1965) showed no evidence at $p = .05$ level for accepting the hypothesis that a monotonic trend exists.) However, in the last nine years, the percentage of crop buried at the end of the marketing season has increased (Figure A2) ($p = .05$, $Z = 2.22$). With sales tracking production (the proportion of the crop sold by January 1 has been relatively constant over the last nine years), neither Michigan nor New York production is probably not a main component in the culling process (this component is approximately responsible for 15% (Table A1) of the total culls over the last two years, or 2.4%). (New York shares the Michigan market.) Michigan sales are truncated after January 1. Texas onions have gained in the storage onion market over the last decade. In 1979, the members of the Michigan Onion Growers' Cooperative had to dump the remainder of their crop by March 30 (estimated at 20% of total production). As a result, the cooperative's packing house closed for the year and bought Texas onions for their customers (Finkbiner 1979).

A preliminary analysis of the storage survey data (Table A3) shows that when the samples were pooled within years, the frequencies of class damage that

Table A2. Onion production in Michigan 1972-1980.[1]

Year	Harvest[2]	Sales[2]	Percent Sold by January 1	Percent Not Sold
1972	2,144	1,980	66.2	7.7
1973	2,046	1,800	62.7	12.1
1974	2,139	1,917	62.1	10.4
1975	1,768	1,440	63.5	18.6
1976	2,166	1,960	62.0	9.5
1977	2,272	1,820	63.2	19.9
1978	2,686	2,250	55.1	16.3
1979	2,686	2,240	57.6	16.7
1980	1,800	1,400	62.1	22.3
$\bar{x}$	2,189	1,867	62.3	14.7

[1] data taken from Espie (1980)

[2] each unit = 1,000 cwt.

Table A3. Distribution of damage classes among culled onions.

	1978-1979(N=7,335)		1979-1980(N=932)	
Class	Percent[1]	±Conf. Limits[2]	Percent[1]	±Conf. Limits[2]
Mechanical	14.3	0.8	11.0	2.1
Peeler	38.1	1.1	43.9	3.2
Thick skin	8.8	0.6	8.5	1.8
Thick neck	2.1	0.3	3.7	1.2
Multiple	2.3	0.3	3.1	1.2
New roots	1.4	0.2	1.2	0.7
Sprout	3.3	0.4	5.2	1.3
Soft	12.3	0.7	12.8	2.2
Spindle	13.1	0.8	10.4	1.9
Small	11.2	0.7	11.0	2.1
Jumbo	2.2	0.3	3.1	1.2
Discolor	14.7	0.8	8.2	1.7
Miscellaneous stain	6.6	0.5	8.1	1.7
Water stain	20.9	0.9	7.5	1.7
Sun scorch	7.5	0.5	3.8	1.2
Basal-rot	2.5	0.3	1.7	0.8
Neck-rot	2.5	0.3	5.2	1.3
Purple blotch	0.6	0.1	0.0	
Onion maggot	6.0	0.5	3.3	1.2
Black onion fly	0.007	0.03	0.0	
Bulb mite	0.2	0.1	0.2	0.3

[1] classes are not mutually exclusive, 1 onion can be in many classes

[2] normal approximation, .95 confidence coefficient

changed the most between the two years were discolor, water stain, and sunscorch, and to a lesser degree sprouting, neck-rot, and onion maggot. This pattern shows that production-related damage tends to be constant unless there are major technological changes.

Cluster analyses were used to describe the structure of the data set. The first step in the analysis was to explore the structure of the storage survey from the context of the growers. The growers were organized into natural groupings as determined by the respective frequency distributions of the damage classes. These were then compared to descriptions of the growers' loads (method of curing, method of storage, variety of onion, harvest date, and packing date). An agglomerative average linkage hierarchical clustering procedure (Colgan 1978, Ch. 5) was used. Clusters were formed sequentially based on their similarity until one cluster contained all the growers.

The criterion of similarity used the average Euclidian (square root of the sums of squares) distance between the values of the variables for two growers. The data values were standardized to Z-scores and weighted to the respective sample sizes. A tree depicting the outcome of the analysis is shown in Figure A3. By visually examining the tree, a number of groupings or clusters can be defined. In Figure A3, at an intergroup distance of slightly more than four, a large cluster joins all the growers. An intergroup distance of three serves as a merging point for two distinct clusters, 5-21 and 13, 14, 3. The large cluster (5-21) represents the loads sampled before January 1. The rest of the growers (sampled after January 1) tend to be less closely correlated. This may be because early in the storage season most of the classes can be discerned and many classes on one sampling unit can be detected. After onions have been

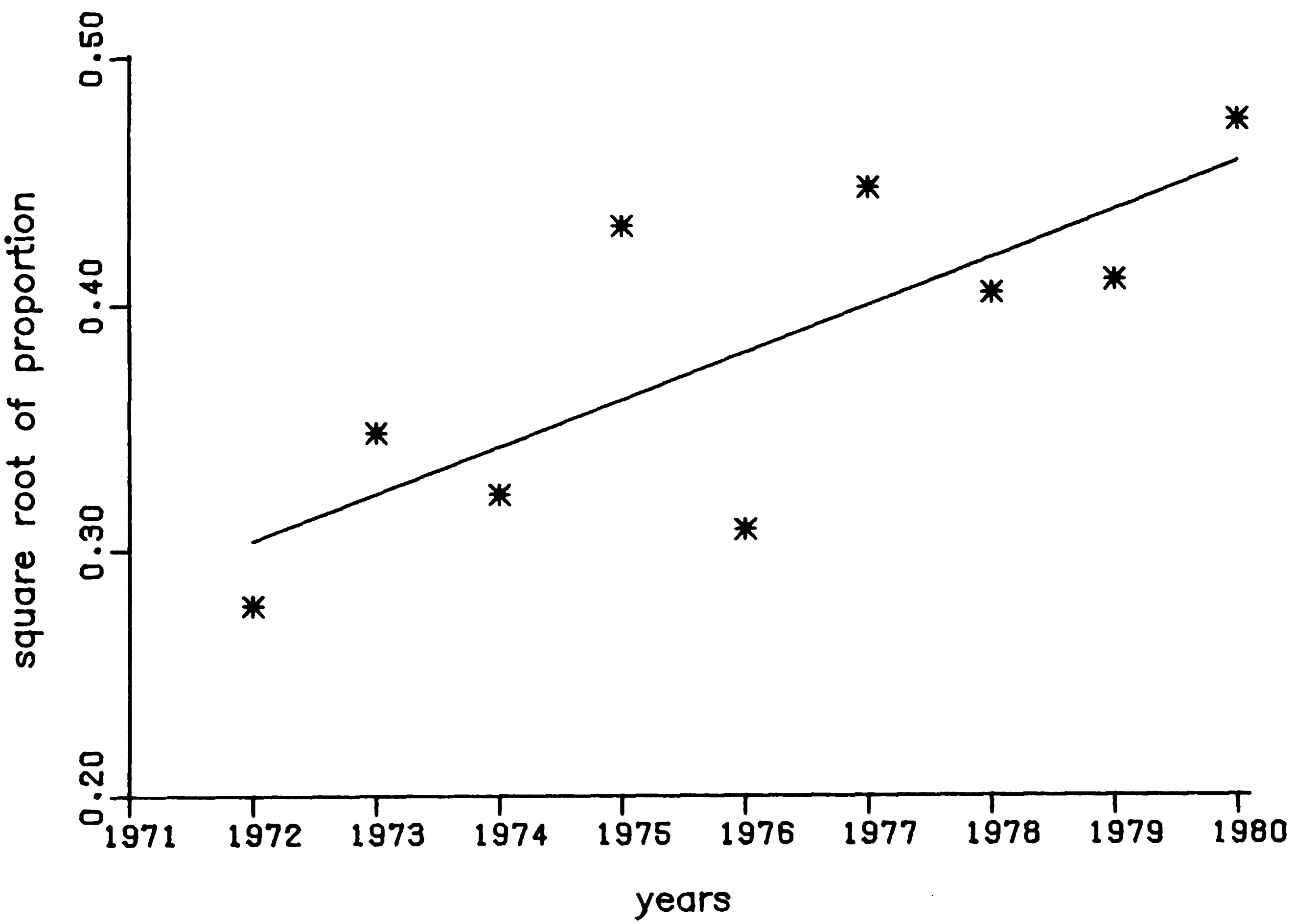


Figure A2. Proportion (square root transform) of Michigan onion crop buried at the end of the marketing season for the years, 1972-1980.

stored for five to six months, sprouting and rots may disguise other symptoms. The other parameters used for comparison (method of curing, method of storage, variety of onion, and harvest date) did not appear to correlate with any of the clusters.

The early season storage groups (5-21) were used in a second cluster analysis where the structure of the relationship between damage classes was of interest. Again an agglomerative average linkage hierarchical clustering procedure was used, but this time the similarity index used was the arc-cosine of the correlation coefficient between variables and all other variables (Anderberg 1973) (see Figure 4A for results). Definitions of the damage class abbreviations are as follows: MD-mechanical damage, SPR-sprouted onion, TN-thick neck, NEW-new adventitious roots, BO-black onion fly, SPI-spindle onion, SM-small onion, MC-miscolor, PE-peeler, SO-soft onion, WS-water stain, NR-neck rot, TH-thick skin, OM-onion maggot, MU-multiple center, JU-jumbo onion, BR-basal rot, ST-miscellaneous stains, SS-sunscald, and PB-purple blotch. Detailed descriptions of each of these storage problems can be found on pages 185-189. Three distinct clusters can be seen in the tree (Figure A4): mechanical damage--small onions (MD-SM), miscolor and onion maggot (MC-OM), and multiple centers and basal rot (MU-BR).

Onion maggot damage and neck-rot were the main factors studied. These are found in cluster two (Figure A4). Onion maggot is the most dissimilar member of the cluster (merged last) and is probably equally likely to be associated with cluster three (two and three form a cluster in the next step). The variables tested for relationship to onion maggot incidence were water stain (cluster 2) and basal rot (cluster 3). Doane (1953) reported an association

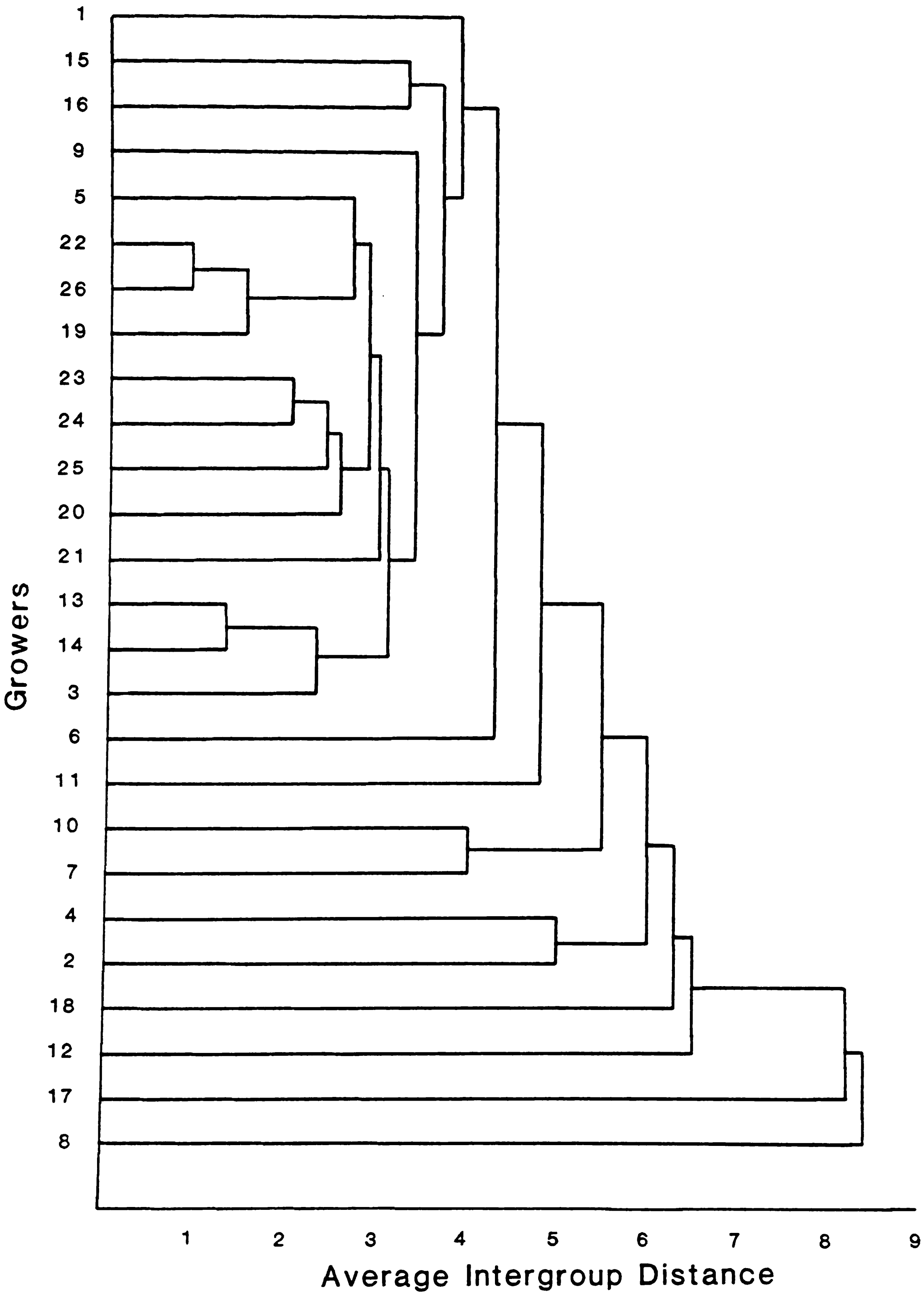


Figure A3. Dendogram derived from a hierarchial cluster analysis depicting the relationships between onion growers based on storage surveys.

between Fusarium sp. basal-rot and onion maggot incidence. It has also been stated that in order for Fusarium sp. to become established within the onion plant, injury must have occurred in advance (Davis and Henderson 1937). A linear correlation analysis was performed between these two variables and a positive relationship (r = +.61, p = .08) was found to exist. Workman (1958) surveyed twenty sets of weather data along with the associated onion maggot incidence and found that summers of above average rainfall were quite often associated with high levels of onion maggot damage. I had found previously that survival of onion maggot eggs and first instar larvae was increased in irrigated treatments over non-irrigated treatments (Haynes et al. 1979). To see if water stain, a result of fall environmental conditions, could be used as an indicator for onion maggot damage, a partial correlation analysis was performed. This was done in order to take into account the possibility of soft onions or neck-rot acting to mask the relationship. A simple linear model yielded a good correlation (r = +.6315, p = .09), but when a partial correlation was performed in order to remove the effects of neck-rot and soft onions, it showed a stronger relationship (r = .813, p = .03). Thus, water stain is seen to account for 62% of the variance in onion maggot storage infestations during 1978-1979.

A similar analysis was performed with variables associated with neck-rot symptoms. A partial correlation in this case did not reveal any masking properties from the damage classes: soft onions, peeling, thick neck, sprouting, and thick skin. Approximately (r = +.869, p = .005) 77% of the variance of neck-rot in the early-season storage is associated with water stain. It is very surprising that thick neck is not more strongly associated with neck-rot (r = +.16, p = .18). In experimental results thick neck is one of the major factors (besides

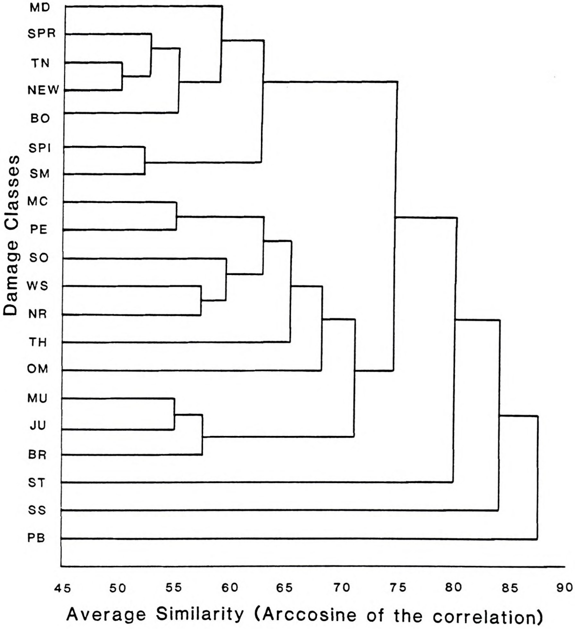


Figure A4. Dendogram derived from a hierarchial cluster analysis depicting the relationships between storage damage problems.

variety) mentioned as a cause of high incidence of neck-rot (Munn 1917, Newhall et al. 1959, Walker and Tims 1932, and Vaughn et al. 1961). Whether variety had an important role to play in terms of interactions with the relationship between thick neck and neck-rot is unknown.

APPENDIX B

CULL WEIGHT LOSS ANALYSIS

Table B1. Repeated measures through time, three-way ANOVA results cohort I.[1]

Source	DF	SS	MS	F	
Time 2	1	3.8284	3.8284	378.22	***
TS	1	.0224	.0224	2.213	NS
TL	1	.0390	.0390	3.85	*
TC	3	3.0917	1.0315	101.81	***
TSL	1	.0000	.0000	.00	NS
TSC	3	.0919	.0306	3.03	*
TLC	3	.1229	.0409	4.05	*
TSLC	3	.0089	.0029	.29	NS
Error	62	.6276	.0101		
Time 3	1	1.0745	1.0745	295.71	***
TS	1	.0018	.0018	.6206	NS
TL	1	.0772	.0772	21.47	***
TC	3	.5601	.1867	51.90	***
TSL	1	.0007	.0007	.02	NS
TSC	3	.0045	.0015	.50	NS
TLC	3	.0841	.0281	9.38	***
TSLC	3	.0030	.0010	.34	NS
Error	62	.18537	.0029		
Time 4	1	.0231	.0231	7.71	**
TS	1	.0004	.0004	.14	NS
TL	1	.1206	.1206	40.32	***
TC	3	.0765	.0255	8.53	***
TSL	1	.001	.0001	.02	NS
TSC	3	.0045	.0015	.50	NS
TLC	3	.0841	.0281	9.38	***
TSLC	3	.0031	.0011	.34	NS
Error	62	.1854	.0029		

Table B1. (cont.)

Source	DF	SS	MS	F	
Time 5	1	.0130	.0130	13.13	***
TS	1	.00145	.00145	1.46	NS
TL	1	.0175	.0175	17.69	***
TC	3	.0246	.0082	8.27	***
TSL	1	.0006	.0006	.63	NS
TSC	3	.0148	.0049	5.00	NS
TLC	3	.0443	.0147	14.93	***
TSLC	3	.0012	.0004	.41	NS
Error	62	.0614	.0009		
Time 6	1	.0118	.0118	12.70	***
TS	1	.0018	.0018	1.93	NS
TL	1	.0011	.0011	1.15	NS
TC	3	.0040	.0013	1.44	NS
TSL	1	.0035	.0035	3.79	*
TSC	3	.0030	.0010	1.10	NS
TLC	3	.0376	.0125	13.49	***
TSLC	3	.0062	.0021	2.22	NS
Error	62	.0576	.0009		
Time 7	1	.0098	.0098	14.46	***
TS	1	.0005	.0005	.74	NS
TL	1	.0233	.0233	34.19	***
TC	3	.0432	.0144	21.11	***
TSL	1	.0021	.0021	3.00	NS
TSC	3	.0061	.0020	2.96	NS
TLC	3	.0078	.0026	3.8	*
TSLC	3	.0037	.0012	1.8	NS
Error	62	.0423	.0007		

Table B1. (cont.)

Source	DF	SS	MS	F	
Time 8	1	.0012	.0012	3.91	*
TS	1	.0006	.0006	1.96	NS
TL	1	.0048	.0048	15.82	***
TC	3	.0002	.00006	.20	NS
TSL	1	.0002	.0002	.56	NS
TSC	3	.0038	.00127	4.14	NS
TLC	3	.0018	.0006	2.02	NS
TSLC	3	.0047	.0016	5.07	*
Error	62	.0190	.0003		
Time 9	1	.0003	.0003	2.45	NS
TS	1	.0000	.0000	.00	NS
TL	1	.0001	.0001	1.12	NS
TC	3	.0008	.0003	2.31	NS
TSL	1	.0001	.0001	1.21	NS
TSC	3	.0006	.0002	1.68	NS
TLC	3	.0001	.0000	.42	NS
TSLC	3	.0001	.0000	.20	NS
Error	62	.0069	.0001	.00	NS

[1] Transformed data; log(x+1)
*significant at .05 level
**significant at .01 level
***significant at .001 level

where:
T=time
S=soil type
C=cull type
L=location with respect to soil surface

Table B2. Repeated measures through time, three-way ANOVA results cohort II.[1]

Source	DF	SS	MS	F	
Time 2	1	.5862	.5862	170.1	***
TS	1	.0004	.0004	.1	NS
TL	1	.0138	.0138	4.0	*
TC	3	.9804	.3268	94.8	***
TSL	1	.0111	.0111	3.2	NS
TSC	3	.0035	.0011	.3	NS
TLC	3	.0083	.0027	.8	NS
TSLC	3	.0097	.0032	.9	NS
Error	64	.2205	.0034		
Time 3	1	.1580	.1580	89.0	***
TS	1	.0039	.0039	2.2	NS
TL	1	.0585	.0585	32.9	***
TC	3	.1435	.0478	26.9	***
TSL	1	.0001	.0001	.0	NS
TSC	3	.0072	.0024	1.3	NS
TLC	3	.0577	.0192	10.8	***
TSLC	3	.0126	.0042	2.4	NS
Error	64	.1136	.0017		
Time 4	1	.0000	.0000	.0	NS
TS	1	.0002	.0001	.1	NS
TL	1	.0033	.0033	2.3	NS
TC	3	.0033	.0011	.7	NS
TSL	1	.0010	.0010	.7	NS
TSC	3	.0001	.0000	.0	NS
TLC	3	.0027	.0009	.6	NS
TSLC	3	.0084	.0028	2.0	NS
Error	64	.0890	.0013		

[1] Transformed data; log(x+1)
*significant at .05 level
**significant at .01 level
***significant at .001 level

where
T=time
S=soil type
C=cull type
L=location with respect to soil surface

Table B3. Weight loss and arthropod colonizers ANOVA with irregular heteroscedasticity.

Source	DF	SS	MS	F	
A	3	.1904	.0635	4.03	**
Covariate	1	7.3635	7.3635	524.56	***
Error	6	.5011	.0139		
A	6	1.7243	.2874	198.43	***
A Time	18	.0702	.0039	2.69	**
Error	222	.3215	.0014		
Comparison					
Control with bulb mite and lesser bulbfly		3.193	3.193	3.107	NS
Onion maggot with others		1.514	1.514	0.72	NS

**significant at the .01 level
***significant at the .001 level

A=arthropod colonizers

APPENDIX C

RELATIVE ABUNDANCE OF CARABIDS AND OTHER GENERAL PREDATORS ASSOCIATED WITH THE MICHIGAN ONION AGROECOSYSTEM

INTRODUCTION

There has been very little research conducted on the ecology of general predators of _Hylemya antiqua_ in onion production. Kastner (1930) observed that swallow species (Hirundindidae) prey upon onion flies and Loosjes (1976) recorded seven species of birds that were seen frequently feeding on onion flies, although his contention was that birds play an insignificant role in reducing the onion maggot population. Even the common toad, _Bufo bufo_ L. is a supposed predator of the onion maggot (Loosjes 1976). Arthropods that prey on onion maggot are represented mainly by the Coleoptera (Perron 1972 and Loosjes 1976), although two species of Diptera have been reported as being voracious predators of the onion fly, _Coenosia tigrina_ L. in Canada (Perron et al 1956), and _Scatophaga stercoraria_ (L.) in Holland (Loosjes 1976). Loosjes (1976) makes mention of seven species of carabids that were found to be predators of onion maggot eggs in the laboratory (see Table C1) determined by labelling the eggs with a radioactive isotope. No evaluation of their impact in the field was pursued. A more comprehensive study was undertaken by Perron (1972) in Quebec. A survey of the arthropod predators captured in both organic soil and clay soil onion production areas was made. Seventy-eight percent of the predators were Coleoptera, 26 species belonging to the family Carabidae (see Table C1). Perron (1972) compared the relative abundance of predators in onion production areas of muck and clay soils and found ten times as many predators and parasites in muck as opposed to clay soil. Despite this he felt that first generation onion maggot eggs escape mortality due to predation since predator populations did not start to build up until late June after the majority of first generation eggs had hatched and, therefore, dismissed predators as being important as far as having an impact upon the population dynamics of the onion maggot.

Table C1. Known carabid and staphylinid species associated with onion or cabbage ecosystems.

Predator Species	Location[1]					
	Onion Fields			*Brassica* Fields		
	H	Q	M	B	E	O
<u>Carabidae</u>						
Abacidus permundus			✓			
Abax ater (de Vill.)					✓	
Acupalpus carus (Lec.)						✓
Agonoderus comma (F.)		✓	✓			
A. lecontei (F.)			✓			✓
Agonum sp.						✓
A. carbo Lec.		✓	✓			
A. dorsale (Pont.)	✓				✓	
A. mulleri (Hbst.)						
A. placidum Say		✓				
Acupalpus carus (Lec.)						✓
Amara sp.			✓	✓		✓
A. aenea (DeG.)					✓	
A. avida Say		✓	✓			
A. apricaria (Payk.)					✓	
A. communis (Pz.)					✓	
A. eurynota (Pz.)					✓	
A. familiaris (Duff.)					✓	
A. fallax Lec.						✓
A. littoralis Lec.			✓			
A. ovata (F.)					✓	
A. plebeia (Gyll.)					✓	
A. similata (Gyll.)					✓	
Anisodactylus baltimorensis (Say)		✓				
A. binotatus				✓		
A. discoideus (Dej.)		✓				
A. sanctaecrucis (F.)		✓	✓			
Asaphidion flavipes	✓					
Bembidion sp.			✓	✓		✓
B. biguttatum (F.)					✓	
B. decipiens Dej.		✓				
B. gilvipes Sturm.					✓	
B. lampros (Hbst.)				✓	✓	
B. lampros s. *properans* Steph.					✓	
B. lunulatum (Geoff.)					✓	
B. mimus Hayw.		✓	✓			
B. nitidum (Kby.)						✓
B. normannum Dej.					✓	
B. obscurellum				✓		
B. obtusum Ser.					✓	
B. quadrimaculatum L.		✓	✓	✓	✓	✓
B. rupestre (L.)					✓	

Table C1, continued

Predator Species	Location[1]					
	Onion Fields			*Brassica* Fields		
	H	Q	M	B	E	O
B. ustulatum (L.)	✓				✓	
B. versicolor Lec.		✓	✓			
Bradytus latior (Kby.)						✓
Calathus fuscipes	✓			✓		
C. melanocephalus	✓					
Carabus gradulatus	✓			✓		
C. nemoralis				✓		
Celia gibba (Lec.)						✓
Chlaenius sericeus Forst.		✓				
Clivinia bipustulata			✓			
C. fossor (L.)		✓	✓	✓	✓	
C. impressifrons (Lec.)			✓			
Dysidius mutus (Say)		✓				
Feronia anthracina (Ill.)					✓	
F. cuprea (L.)					✓	
F. diligens Sturm.					✓	
F. macra (Marsh.)					✓	
F. madida (F.)					✓	
F. melanaria (Ill.)					✓	
F. nigra (Sch.)					✓	
F. nigrita (F.)					✓	
F. strenua (Pz.)					✓	
Harpalus spp.			✓			✓
H. aeneus (F.)				✓	✓	
H. affinis Schr.		✓	✓			✓
H. caliginosus (Fab.)						✓
H. compar Lec.		✓				
H. erraticus Say						✓
H. pensylvanicus DeG.		✓	✓			✓
H. pubescens	✓					
H. rufipes (DeG.)					✓	
H. viridiaeneus Beauv.						✓
Leiocnemus avida (Say)		✓				
Metabletus americanus (Dej.)		✓				
Nebria brevicollis (F.)					✓	
N. gullenhali (Schoen.)					✓	
N. livida (L.)					✓	
Notiophilus palustris (Duff.)					✓	
N. biguttatus (F.)					✓	
N. substriatus Wat.					✓	
Patrobus atrorufus (Stroem.)					✓	
P. longicornis (Say)		✓				
Poecilus chalates Say		✓				✓
P. lucublandus Say		✓				✓
Pseudamphasia sericea (Harr.)		✓				
Pterostichus lucublandus (Say)		✓	✓			

Table C1, continued

Predator Species	Location[1]					
	Onion Fields			*Brassica* Fields		
	H	Q	M	B	E	O
P. vulgaris				✓		
Tachyura incurva (Say)		✓				✓
Trachypachus holmbergi				✓		
Trechus quadristriatus (Sch.)	✓				✓	
T. obtusus Erichs.					✓	
Triplectrus rusticus (Say)						✓
Staphylinidae						
Aleochara sp.			✓		✓	
A. bilineata (Gyll.)		✓	✓	✓	✓	✓
A. bipustulata (L.)					✓	
Chiloporata sp.					✓	
Cordalia sp.					✓	
Dinarea angustula	✓					
Gyrohypnus hamatus (Say)		✓				✓
Homolata sp.					✓	
Leptacinus sp.					✓	
Medan sp.					✓	
Megalinus linearis				✓		
Micropeplus sp.					✓	
Ocypus aenocephalus				✓		
Oxypoda sp.					✓	
Oxytelus sp.		✓			✓	✓
O. rugosus (F.)	✓				✓	
Philanthrus sp.					✓	
P. concinnus				✓		
P. fuscipennis				✓		
P. varius				✓		
Staphylinus sp.					✓	
Tachyporus sp.		✓			✓	
T. hypnorum (F.)					✓	

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[1] H = Holland (Loosjes 1976), Q = Quebec (Perron 1972), M = Michigan (Haynes et al. 1979), B = British Columbia (Finnlayson and Campbell 1976), E = England (Hughes 1959, Davies 1963, and Coaker 1965), O = Ontario (Wishart et al. 1956).

[2] Not a reliable determination.

Unfortunately none of these studies explored the biology or ecology of the predators as they interact with the onion agroecosystem or attempted to evaluate the impact they have on the onion maggot population. There has been a considerable amount of research in a similar ecosystem pertaining to predators of the cabbage maggot, Hylemya brassicae (Bouche'). Treherne (1916) was the first investigator to provide data to show that carabids observed in cabbage fields, attack cabbage maggot eggs. His evidence was, however, obtained in the laboratory and though it showed that these beetles are potential destroyers of eggs, there was no direct evidence that they were important in the field. Not until 1956 did Wishart (Wishart et al. 1956) show that predation by ground beetles may result in the destruction of large numbers of cabbage maggot eggs and concluded that carabids are more important as predators than staphylinids. Hughes (1959), Hughes and Salter (1959), Hughes and Mitchell (1960), and Coaker and Williams (1963) concluded that predation accounted for over 90% of cabbage maggot egg losses in the field. Coaker and Williams (1963) found that although carabids are important egg predators, staphylinids were more effective. Continued research by Coaker (1965), using barriers of hay to restrict the movement of adult carabids into and out of plots of brassica crops, showed that the survival of immature stages of H. brassicae was inversely related to the numbers of predatory carabids present. It was calculated that the adult carabids were responsible for 33% of the total egg mortality. Utilization of carabids in pest management has generally been thought to be impractical. An interesting experiment by Wyman et al. (1976) revealed that seed corn beetles, Agonoderus lencontei Chandoir and A. comma (F.), predators of the cabbage maggot could be managed (densities manipulated) by attracting adults into rutabaga and radish plots with black light. Damage to lit plots was lower than that in unlit plots.

The predator studies during 1978 and 1979 were preliminary in nature with the aim of describing the effect of various characteristics of habitat typical to an organic soil ecosystem in different stages of evolution, on the relative activity and numbers of predators. Included in this approach was the attempt to elucidate some of the biology of the predators, evaluate predator potential, and devise a method for estimating absolute density over different habitat types. Pitfall trapping by several methods was the predominant technique utilized in the study along with soil sampling and controlled experimentation in the greenhouse.

MATERIALS AND METHODS

Studies were conducted in three onion growing regions in Michigan (see Fall Study: Study Sites) during the growing seasons of 1978 and 1979. In 1978 a predator survey was initiated at the Michigan State University Organic Soils Research Farm in Laingsburg, Clinton County. Pitfall traps were used to census the predator populations (trapping began June 10) in and around a 4.5 acre field that had been planted in onions the previous year although no maintenance was carried out and the field was soon colonized by weeds. Prior to this the field had been undergoing old field succession for approximately fifteen years. Eight habitats were sampled to assess the effect of environment on the relative abundance of potential onion maggot predators. Three of the habitats bordered the main study field, these being: a mixed grass field border, a pine tree wind break border, and a chemically intensive 1/4 acre onion plot (separated from the main study site by an unpaved road and wire fence). Five habitats layed out in a non-randomized block design (four blocks) consisted of two onion plantings

(Downy Yellow Globe, single row, three rows in a bed) one in which weeds were allowed to recolonize (among them: nut sedge (Cyperus esculentus L.), sowthistle (Sonchus oleraceus L.), lambsquarters (Chenopodium album L.), green foxtail (Setaria viridis L.), large crabgrass (Digitaria sanguinalis L.), ladysthumb (Polygonum persicaria), and redroot pigweed (Amaranthus retroflexus)). The other onion planting was hand weeded throughout the duration of the study. There were three companion plantings with onions, one of radish (scarlet globe), rye grass (cultivar unknown), and oats (cultivar unknown). Twenty-four unbaited pitfall traps (10 cm x 10 cm. x 12.5 cm. food grade plastic containers without preservative fluid) per habitat for a total of 192 traps were emptied and reset (traps not rerandomized within plots), with soil pushed up over the lip, on a daily basis. Arthropods captured each day were pooled within treatment habitats and preserved in ethylene glycol. The study was terminated September 15, 1978. Insects were identified to the family level only, except for some of the Carabidae which were determined to the generic and the species level. Determinations were made by Mr. Bob Ward and Joe Mahar at Michigan State University (Department of Entomology) and by Dr. T. L. Erwin at the U.S. Nation Museum, Washington, D.C.

In 1979 five studies regarding carabids in muck soil ecosystems were conducted. These were designed to: measure migration into and out of an onion field by carabids; evaluate the potential of some of the more common carabids as predators of the onion maggot; gauge the impact of weeds on carabid larval populations in onion plots; compare relative numbers of carabids, by open grid pitfall trapping in three different onion production systems; and compare predator complexes within three non-commercial muck soil habitats by the technique of enclosure or extinction plot trapping.

Three Michigan onion production systems: a chemically intensive commercial field in Grant, an energy intensive non-chemical commercial field in Eaton Rapids, and a low energy non-chemcial noncommercial field at the Michigan State University Organic Soils Research Farm in Laingsburg were surveyed for predators on a weekly basis. The field in Grant was divided into two habitats that were sampled, an area that had soil granular insecticide (Dyfonate) incorporated under the onion row at the time of planting and an area that did not. Open plots with 9 pitfall traps (the same as those used in the 1978 study) arranged in a 3 m. x 3 m. grid were set out in Laingsburg on April 18th, in Grant on June 2nd, and in Eaton Rapids on June 9th. Starting September 15th six more fields were surveyed in this manner in Grant (1-6), one other in Eaton Rapids (R), and another in Laingsburg (P) (see Fall Study: Study Site). The study was terminated December 13th.

Aluminum enclosure pens (1.8 m. x 1.8 m. x 0.46 m.) 3.2 m^2 were used to compare absolute density estimates of predators in three mucksoil habitats at the Organic Soils Research Farm. These areas were representative of three phases of evolution (one man-made) in an organic soil ecosystem: a poplar forest, a meadow, and an onion field (no pesticide input). Four pens were randomly assigned (with the toss of a ball) to each habitat and dug in 15 cm. below the soil surface. Every pen had nine pitfall traps within it set flush to the soil surface with three internal drift fences (0.6 m. in length) set in place. Traps were emptied on a weekly basis from June 4th to July 2nd. Integrity of the pens were inspected and maintained at every sample date.

Movement of carabids between the onion field and the field borders was assessed by the use of directional pitfall traps. Four traps were placed towards

the interior of the field (2 facing north-south, and 2 facing east-west) and four traps were placed in parallel along the field borders. The traps were 0.9 meters in length and approximately 3.25 cm. in width except at the ends where the width approached 0 cm. The traps were made from aluminum sheet metal and had a wall in the middle running lengthwise so that the direction of approach could be determined. Experiments were only run a few times during the year (June 7, June 15, and June 27).

The effect of vegetation in cultivated areas upon the incidence of onion plant damage due to the onion maggot and associated carabid populations was studied (June 21 and June 23) at the Organic Soils Research Farm. Twelve (1.2 m. x 1.2 m.) plots in a weed free onion planting and twelve plots in a weed colonized onion planting were sampled both with pitfall traps (one/plot) and soil samples (30 cm. x 30 cm. x 7.5 cm., 3/plot) for carabid adults and immatures. Vegetative cover was assessed by determining species dry weights/plot and total leaf area per plant species (licor leaf area meter).

A greenhouse study was performed to identify potential onion maggot predators. Carabids used in experiments were collected live from pitfall traps and then put in food grade plastic quart containers along with 2.5 cm. of moist muck soil (1 carabid/container) and transported to a greenhouse at the Pesticide Research Center, Michigan State University. The first preliminary experiment tested individuals of eight species of ground beetles. Two third instar onion maggot larvae were introduced into each of three containers for each species and five onion maggot eggs were introduced into each of three containers (three individuals) in a completely randomized design. Twenty-four hours later the remaining eggs and larvae were counted. Another study based on the results of

the first experiment, tested ten individuals from each of five species of carabids set up in a similar manner as before except that twenty onion maggot eggs (field collected) were introduced into every container in a completely randomized design. Two species were evaluated in regards to larval predation with 10 larvae within each onion bulb. Onion bulbs were set in 10 cm. of soil in each container and ten individuals from each species were tested (see Table C7). Results were determined after forty-eight hours from the onset of the two experiments.

RESULTS AND DISCUSSION

The number of arthropod predator species associated with habitats supporting onion maggot or cabbage maggot populations is quite large (Treherne 1916, Hughes and Mitchell 1960, Davies 1963, Coaker 1965, Perron 1972, Finlayson and Campbell 1976, Loosjes 1976, and Haynes et al. 1979). Table C1 lists the species of Carabidae and Staphylinidae that have been collected in agroecosystems. Information as to the relative abundance of these predators in various crop production regions, especially as it relates to cultural practices is lacking (Finlayson and Campbell 1976, and Finlayson et al. 1980). Results from pitfall trap collections in Michigan onion fields are summarized in Tables C2 and C3. Unfortunately the arthropods from each of nine traps within each field were pooled upon collection and therefore an estimate of a variance for each mean trap capture per sample date could not be computed. The assumption was made that since the unit of habitat being surveyed was similar in soil type and vegetation and collections were made during the same time intervals then differences in trap catch would reflect arthropod densities since activity would be similar between sample areas. Hypothesis testing based on probability theory

Table C2. Mean pitfall trap captures[1] per sample date in three onion-growing regions during the 1979 growing season and post-harvest.

	Carabinae							Other Coleoptera			Arachnida	
	Agonoderus spp.	*Anisodactylus sanctaecrucis*	*Bembidion quadrimaculatum*	*Amara* spp.	*Abacidus* sp.	*Clivinia impressifrons*	*Pterostichus* sp.	*Cicindelidae*	*Staphylinidae*	*Coccinelidae*	*Araneida*	*Phalangida*
June-August												
Grant (22)[2]												
Research:												
Dyfonate	2.9	1.1	0.9	0.03	0.4	0.1	0.04	0.1	1.3	0.5	0.4	1.5
No Dyfonate	1.6	0.8	0.8	0.03	0.7	0.1	0	0.2	0.8	0.4	0.4	2.5
Eaton Rapids (15)												
Organic Commercial	10.9	8.3	6.8	0.4	4.8	1.5	2.5	0.05	1.9	0	6.6	1.6
Laingsburg (15)												
Research:												
No pesticide	11.8	28.4	2.1	0.5	3.4	2.6	2.7	1.0	9.2	0.7	10.9	2.4
September-December												
Grant (15)												
Research:												
No Dyfonate	0.2	0.3	0.4	0.05	0.15	0.15	0	0	0.6	0	0	0
Commercial 1	0	0.08	0.05	0.05	0	0.05	0	0	0.2	0	0	0
Commercial 2	0	0.2	0	0	0.05	0	0	0	0.3	0	0	0
Commercial 3	0	0	0	0.05	0.05	0.1	0	0	0.1	0	0	0

Table C2, continued

	Carabinae							Other Coleoptera			Arachnida	
	Agnoderus spp.	*Anisodactylus sanctaecrucis*	*Bembidion quadrimaculatum*	*Amara spp.*	*Abacidus sp.*	*Clivinia impressifrons*	*Pterostichus sp.*	*Cicindelidae*	*Staphylinidae*	*Coccinelidae*	*Ananeida*	*Phalangida*
Commercial 4	0.05	0.05	0	0	0	0.05	0	0	0	0	0	0
Commercial 5	0	0.1	0.05	0.05	0.05	0	0	0	0	0	0	0
Commercial 6	0	0	0	0	0	0	0	0	0.3	0	0	0
<u>Eaton Rapids (13)</u>												
Organic Comm'l	2.0	3.0	1.5	0.3	1.3	0.3	0.06	0	0.9	0.9	6.6	0.8
Conventional Commercial	1.4	0.4	0.5	0.08	1.0	0.5	0.06	0	0.3	0.2	2.1	0.2
<u>Laingsburg (10)</u>												
Research:												
No pesticide	10.1	13.9	1.1	0.3	0.2	1.7	1.9	0.6	2.6	0.3	1.1	1.5
Pesticide	1.1	0.2	0.2	0	0.2	0	0.2	0	0	0	0	0.2

[1] 9 traps per field

[2] ( ) = number of sample dates

Table C3. Pitfall trap captures[1] in three neighboring research onion fields, Laingsburg, 1979.

	Carabinae						Other Coleoptera		Arachnida		
	Agnoderus spp.	*Anisodactylus sanctaecrucis*	*Bembidion quadrimaculatum*	*Amara spp.*	*Pterostichus sp*	*Clivinia impressifrons*	*Cicindelidae*	*Staphylinidae*	*Coccinelidae*	*Ananeida*	*Phalangida*
June:											
Non-pesticide	19.2	15.0	3.5	0.8	4.0	3.0	0	8.3	1.7	26.2	5.6
Insecticide & Herbicide[2]	7.2	4.0	0.4	0.2	0.8	0.6	0	1.0	0.4	0.8	0
Insecticide (stubble-mulch)[3]	7.0	5.2	0.6	0.6	0.8	0.4	0.2	0.4	0	1.2	0
July:											
Non-pesticide	10.5	46.3	1.5	0.5	4.3	2.8	1.0	13.4	0	4.5	1.2
Insecticide & Herbicide	1.3	5.3	0.7	0.2	0.7	0.5	0.2	1.0	0	0	0.3
Insecticide (stubble-mulch)	0.5	4.0	0	0.2	0.3	0.7	0.4	0.3	0	0.4	0

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[1] Mean catch per sample date based on 9 traps per field, collected bi-weekly.

[2] Dyfonate at planting and parathion applied to foliage when first damage appeared, June 11, 1979, glyphosate was used previous fall.

[3] Dyfonate at planting and parathion applied to foliage when first damage appeared, June 11, 1979.

or theoretical distributions can not be performed due to the nature of the way in which the data was collected and so inferences were drawn based on an arbitrary criteria. This being that differences in trap capture had to be of the order of one or more magnitudes to be judged significant. This does not allow for an objective framework for the basis of decision making but it at least provides a basis from which hypotheses can be formulated for more detailed future studies. Relative abundance of arthropods in three onion growing regions in Michigan (all fields without intensive insecticide use) appear not to differ in areas free of pesticides during the growing season (see Table C2, June-July). Table C3 summarizes the trap captures in a paired comparison between fields receiving insecticides and a field that did not (MSU Organic Soils Research Farm). The results suggest that early in the season (first foliar insecticide application was not applied until June 11th) little difference in the densities of arthropods existed (except possibly for the Araenida where there was a 22-23 fold difference) in the three fields. Later in the growing season (July) differences in the range of one order of magnitude resulted for Agonoderus spp., Anisodactylus sanctaecrucis, the Staphylinidae, and the Araenida. Table C4 shows an even greater difference in relative abundance between carabid species trapped in a pesticide free onion field compared to an onion field receiving frequent applications of insecticide. A similar study conducted after harvest in all three onion growing regions did not provide the evidence to suspect a difference in arthropod population densities as a result of insecticide applications. This may suggest that dispersal from surrounding areas by many of these predators is quite rapid. Mitchell (1963) found that the main factor affecting the abundance of carabids in cabbage plots was their presence in surrounding fields. The

Table C4. Pitfall trap captures[1] in eight muck soil habitats, 1978.

Habitat	Total Trap Captures (June - September) / Sample Date (N = 90)													
	Agnoderus spp.	*Amara* spp.	*Anisodactylis sanctaecrucis*	*Bembidion quadramaculatum*	*Clivinia impressifrons*	*Pterostichus* spp.	Other *Carabidae*	*Staphylinidae*	*Coccinelidae*	*Elateridae*	*Arachnida*		*Diplopoda*	*Chilopoda*
											Araneida	*Phalangida*		
Radish & Onions	95.5	2.7	89.4	0.4	3.7	2.5	9.2	7.1	0.3	0.2	2.0	1.1	0.2	0.01
Rye grass & Onions	83.9	3.3	82.7	0.4	2.8	2.4	9.8	9.4	0.3	0.2	2.6	0.4	0.3	0.04
Onions	71.5	1.6	107.4	0.5	2.9	2.4	7.7	6.9	0.1	0.3	4.1	0.6	0.2	0
Oats & Onions	79.5	1.6	101.0	0.4	2.6	0.9	7.3	4.9	0.1	0.4	2.5	1.3	0.2	0.04
Onions[2]	69.7	1.8	89.5	0.3	4.2	1.6	9.3	6.4	0.1	0.1	2.5	0.5	0.1	0.03
Pine border	0.3	0.03	4.7	0.1	0.2	0.1	3.2	1.7	0	0.1	0.8	0.4	0.6	0.01
Onions & Pesticides	2.9	0	1.8	0.1	0.2	1.1	0.9	0	0	0.01	0.03	0	0	0
Grass border	17.8	0.3	17.4	0.1	2.8	0.3	4.8	0.8	0.1	0.3	0.2	0.1	0	0

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[1] Based on 24 traps per treatment habitat.

[2] Only plots that were kept weed-free (hand-weeded) throughout entire study period.

measurement of carabid movement across onion field borders (Table C4) shows that depending on the species the exchange rate of individuals into and out of fields could result in the recolonization of a field depleted of predators by insecticides. Based on research findings regarding the effect of various insecticides on the carabid and staphylinid predators of the cabbage maggot, many of which are found in the onion agroecosystem, it seems reasonable to hypothesize that lower densities of beetles found in onion fields receiving insecticide applications in comparison to those not receiving any are due to the detrimental effects of the insecticides. Harris et al. (1972) found that carabids are especially susceptible to applications of fensulfothion, ten times more than to chlorfenvinphos for *Agonoderus comma* (F.) and one hundred times more for *Bembidion quadrimaculatum* (L.). Other workers that have studied the effects of insecticides on carabids have found a wide range of toxicity to different insecticides depending on the host. Finlayson et al. (1980) showed that *Bembidion lampros* Herbst, a major egg predator in the cabbage agroecosystem in Europe and Canada, was tolerant to chlorfenvinphos, moderately susceptible to carbofuran and isofenphos, and very susceptible to terbufos. *Pterostichus chalcites* Say is very susceptible to carbofuran and terbufos sprays (Hsin et al. 1979) while carbofuran granules (at recommended field rates) cause low beetle (*P. chalates*) mortality (Gholson et al. 1978). Tomlin (1975), using topical application, found that chlorfenvinphos was fairly inocuous to carabid larvae although it had a wide range of effects upon adult carabids. These findings along with those of Critchley (1972) who found that mortality in carabids due to organophosphorous compounds and soil fumigants was inversely related to the size of the beetle, suggest that while onion fields may not become devoid of

carabid predators (from intensive use of insecticides) species compositions might certainly be altered.

A preference for a particular habitat has also been shown to be responsible for the relative abundance and distribution of carabids in agricultural environments (Finlayson and Campbell 1976). Table C4 presents the results of data collected by open plot pitfall trapping in eight habital types. Differences in relative abundance among the species and groups of arthropods listed in relation to the less stable, annually disrupted habitats (radish and onions, rye grass and onions, onions, oats and onion, hand weeded onions, and onions receiving applications of pesiticides) appear to be markedly present only between the onion plot receiving pesticides and the other plots. Although weeds were the dominant vegetation by late July of 1978 the plantings within the individual treatment plots were kept sufficiently clear of weeds to maintain integrity of the treatments, although movement between blocks could have been severely limited by the weed growth. Despite this problem of the plots changing through time, comparisons between the more stable habitats that changed little over the course of the summer (grass border and pine border) and the rapidly colonized habitats are of interest in that this is a common spatial phenomenon within newly acquired agricultural land in the muck soil agroecosystem. The pine border habitat exhibited very low carabid abundance in relation to the less stable habitats although the other groups of arthropods appeared to be present in similar levels of abundance. The grass habitat appeared to lack only the spiders on a consistent basis relative to the disturbed habitats. These results agree with those of Finlayson and Campbell (1976) who conducted a comparative pitfall trap study in three habitats: brassica plots, adjacent fallow plots, and grass plots.

They found that on the average species distribution and relative abundance were similar in brassica and fallow plots, with reference to carabids, but that abundance was lower in grass plots (although the reverse was true for most species of staphylinids trapped). In Iowa, Esau and Peters (1975) found that Agonoderus spp., Anisodactylus sanctaecrucis, Bembidion quadrimaculatum and Pterostichus chalcites (all common predators in the muck agroecosystem) were most frequently collected in disturbed habitats in comparison to fencerows and prairies.

One has to be cautious when interpreting the data obtained from pitfall traps. The main disadvantage of these traps is that catches depend upon the density of the population being sampled and the activity of individuals within the region. Not only does weather influence the amount of carabid locomotor activity (Briggs 1961), but other factors such as ground vegetation impeding carabid movement, and the differential susceptibility of species to trapping (Greenslade 1964). Pitfall trap size, shape, and composition also have been found to effect trap capture (Luff 1975). The advantages of pitfall traps are that they are inexpensive, simple, and they can provide large amounts of data where few animals will be found by absolute methods. Relative trapping methods such as pitfall trapping do provide good estimates of insect activity and are thus useful in tracking the phenology of a population.

Figures C1 and C2 depict two years worth of trap data from three study sites for four carabid species found in Michigan onion fields. The slender seed corn beetle, Clivinia impressifrons Leconte (Figure C1) appears to have two generations of adults per year (overwinter as adults) or one larval generation per year. This agrees well with the findings of Pausch and Pausch (1980). They

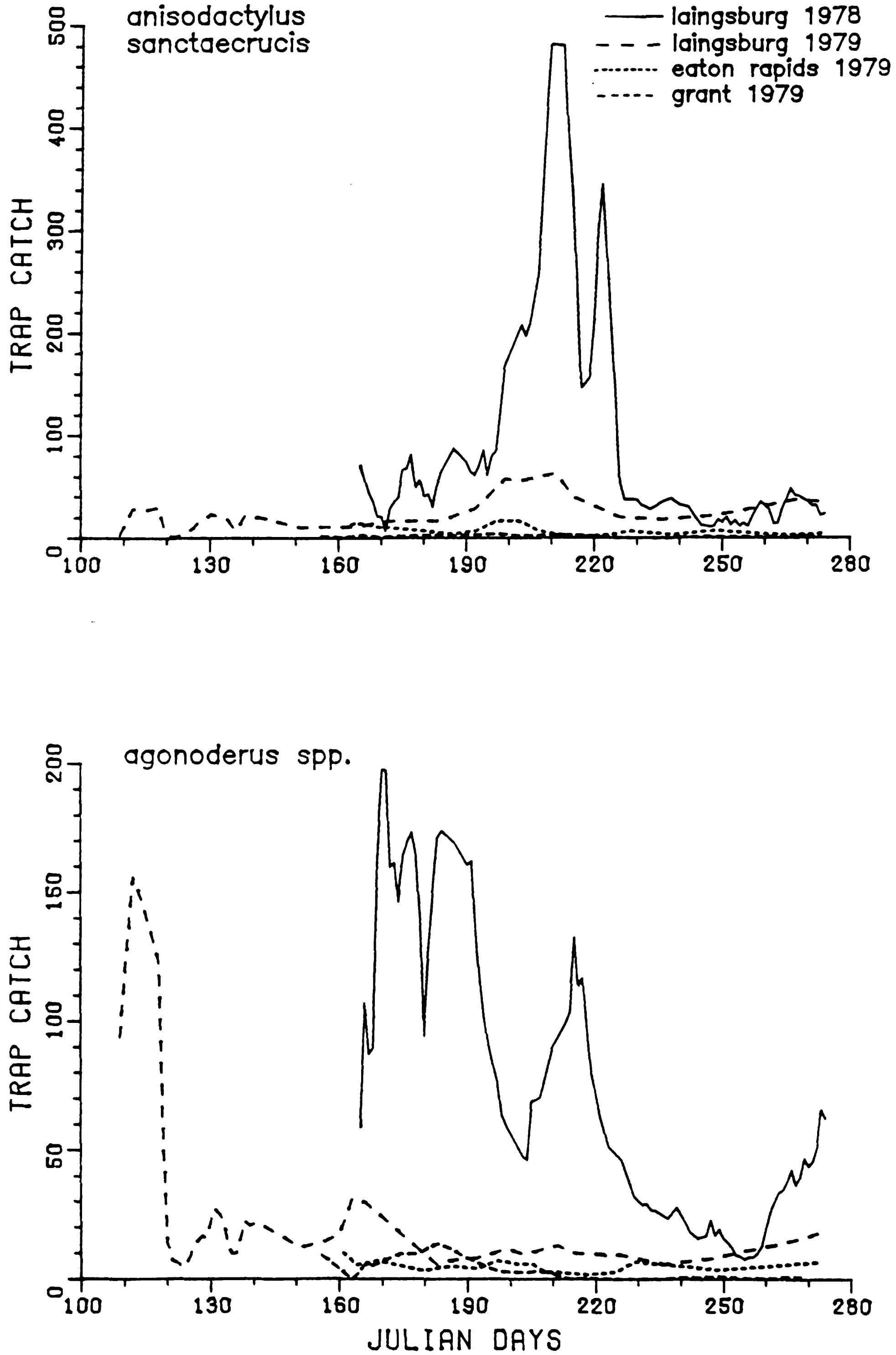

Figure C1. Seasonal trap catch of two carabid species in onion fields, 1978-1979 (three point running average).

discovered that the spring peak activity occurred between the middle of June and the middle of July. The seedcorn beetles, Agonoderus comma (F.) and Agonoderus lencontei Chaudoir, were not distinguished as two different species. Both have very similar biologies and can only be taxonomically separated by the relative shape of the penis sac armature (Lindroth 1968). Kirk (1975) found that in South Dakota A. comma exhibited two peak adult activities, one in June and one in September. Three peak adult activities were found to be characteristic of Agonoderus spp. (seedcorn beetles) in Wisconsin (Wyman et al. 1976). The data plotted in Figure C1 tends to support Wyman's findings, for peak activities in Michigan. Three peak adult activities also appear to be the case for Anisodactylus sanctaecrucis (Figure C2) although no supporting evidence from the literature could be found. The activity response of Bembidion quadrimaculatum L. is not clear. This may be due to the low level population densities during 1978 and 1979. Perron (1972) suggests that B. quadrimaculatum is not a viable biocontrol agent since it doesn't appear in onion fields in Quebec until late June. In Michigan I have caught B. quadrimaculatum in April which suggests that it overwinters as an adult and so most likely possesses two adult generations a year.

Southwood (1978) reviews the use of relative trapping procedures for obtaining reliable absolute density estimates. He describes two basic approaches, one involves correction of the data by calibrating trap catches for various senarios with absolute densities (for each given species), the other derives an estimate of density from the rate by which trapping reduces the sizes of successive samples (removal trapping). Unless a model for correcting species specific trap data is available, removal trapping is the most promising. The

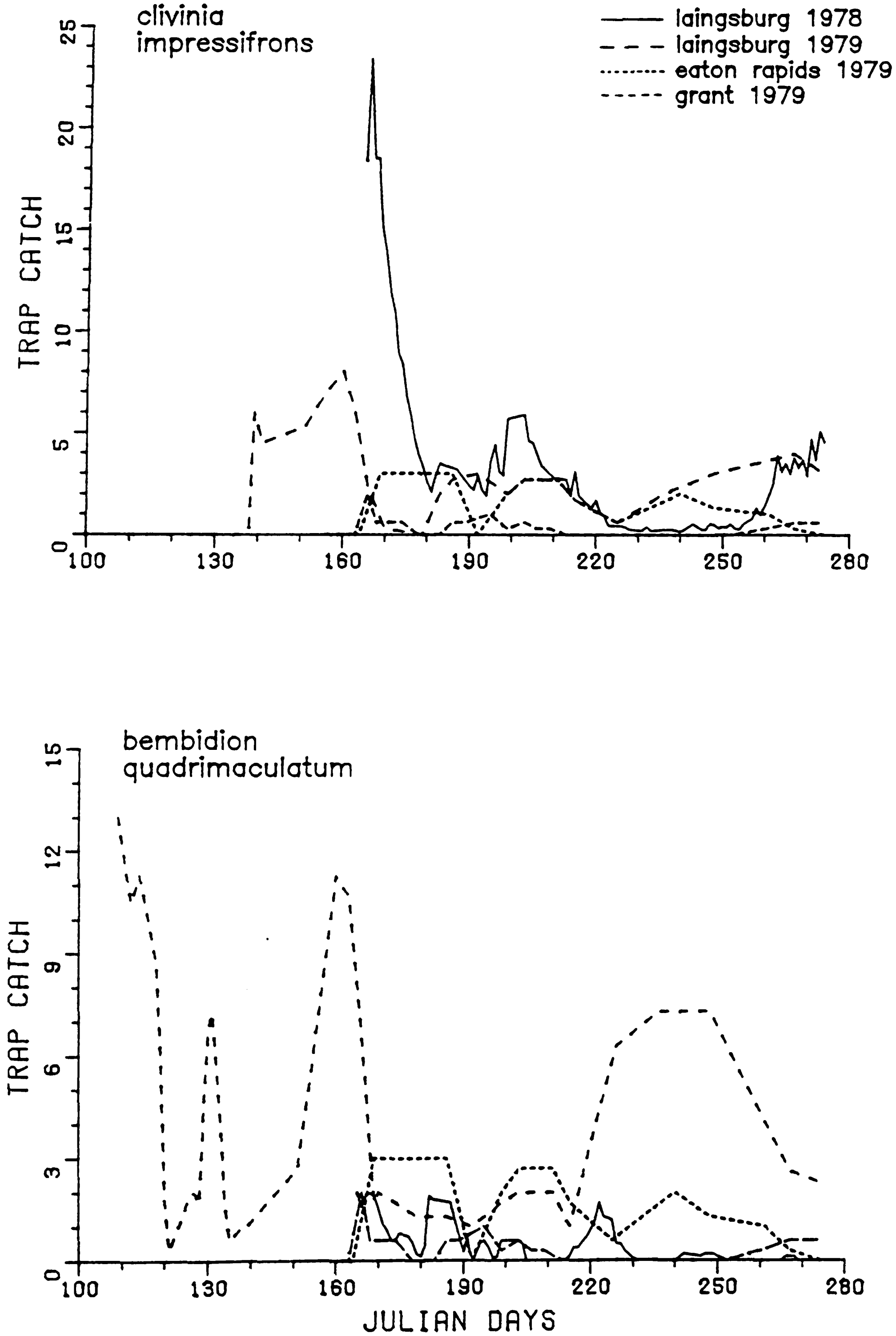

Figure C2. Seasonal trap catch of two carabid species in onion fields, 1978-1979 (three point running average).

three principle methods to the analysis of removal trapping data (regression method, time-unity, and the maximum likelihood method) are all based on the assumption that the rate at which trap captures fall off will be directly related to the size of the total population. The techniques are very sensitive to changes in population levels other than that due to trapping and require a stable population during the trapping interval (i.e. no migration, natality or mortality within the trapping area). Activity changes, being a major component of pitfall trap data, also effect the reliability of removal trapping in open plot situations. These limitations were responsible in part for the adoption of a modified removal trapping method, extinction plot trapping (Mispagel and Sleeper 1982). This approach utilizes barrier plots from which all the individuals within the plots are trapped to extinction. This method is also sensitive to mortality and natality during the trapping period. Increased trapping efficiency can be realized with the inclusion of internal drift fences. This technique also allows better estimates of relative differences between habitats than open pitfall trapping since (activity per day becomes less important in the analysis of the data since more emphasis is placed on total catch at the time of extinction). Table C5 summarizes the absolute density estimates of several groups of arthropods (present in May) from three diverse muck soil habitats. The three common carabid predators found in unsprayed onion fields (*Agonoderus* spp., *Clivinia impressifrons*, and *Anisodactylus sanctaecrucis* are not present in high densities within the two neighboring habitats.The meadow and forest areas sampled had high densities of spiders, harvestman, millipedes, centipedes, and sowbugs, as well as a different complex of carabid species.

Table C5. Density (per 3.2 m^2) of arthropods[1] trapped in three muck soil habitats, Laingsburg (May-June, 1979).

	Extinction Plots		
	Onion Field	Meadow	Poplar Forest
Carabidae:			
Agnoderus spp.	158.3 ± 8.8	1.0 ± 0.7	0
Anisodactylus sanctaecrucis	78.0 ± 7.1	0	0
Bembidion quadrimaculatum	1.5 ± 0.6	0.8 ± 0.5	0
Amara spp.	0.3 ± 0.3	0.3 ± 0.3	0
Abacidus sp.	0	0.8 ± 0.5	0.3 ± 0.3
Clivinia impressifrons	11.5 ± 7.5	0	0
Pterostichus spp.	0	0.8 ± 0.5	0
Other carabinae	9.0 ± 0.6	10.5 ± 2.2	15.6 ± 3.1
Cicindellinae	2.0 ± 0.9	0	0
Staphylinidae	10.8 ± 2.0	7.5 ± 1.3	7.0 ± 1.3
Araneida	2.0 ± 1.2	44.5 ± 6.5	22.5 ± 5.2
Phalangida	1.0 ± 0.6	2.8 ± 1.3	2.0 ± 0.7
Diplopoda	0	46.5 ± 10.5	31.5 ± 9.9
Chilopoda	0	4.8 ± 2.2	12.0 ± 1.7
Isopoda	0	48.5 ± 9.4	58.3 ± 12.6

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[1] Mean ± S.E. (N = 4).

Only one independent estimate of density is available for evaluating the extinction plot method. Agonoderus spp. females excavate small 1 cm. diameter tunnels during the end of May and beginning of June in which copulation takes place (many pairs in copulation were found inside the tunnels) and oviposition occurs. In sampling five one meter square plots the number of tunnels were recorded per unit area and the number of beetles inside each tunnel was counted. An average of 20.6 ± 2.5 (SE) tunnels per square meter was found with approximately 1.2 female beetles/tunnel (not many males were present in the tunnels at the time of sampling). If one assumes a 50:50 sex ratio (unknown) then a crude approximation of the number of Agonoderus spp. per 3.2 m^2 is between 119.8 and 196.6 beetles/3.2 m^2. This estimate is within the realm of that derived from the extinction plot trapping (158.6 ± 8.8). Zippin's maximum likelihood method (Southwood 1978) which has been considered to provide the most accurate absolute density estimate (among the three methods) was utilized for comparison with the values shown in Table C5. The results were very inconsistent, in the case of Agonoderus spp. Zippin's method yielded a value 323% that of the extinction plot density estimate, but only 10% and 5% differences were realized with respect to Anisodactylus sanctaecrucis and elaterid (not reported in Table C5) estimates. The discrepancies in density estimates from the two methods may be due to the extreme sensitivity of Zippin's method to variation in activity through time which can be a function of weather conditions or circadian rhythms. Sixty to seventy-five percent of the Agonderus spp. population may be active at night, where as, B. quadrimaculatum activity appears to be much more uniformily distributed throughout the day (Table C6).

Table C6. Percent of total trap capture within a day for four carabids.[1]

	Time of Collection (h)						
	1500	1800	2100	2400	400	900	1200
Agnoderus spp.							
May 7 (31)[2]	3.2	3.2	6.5	40	35	12.1	0
May 8 (54)	14.8	1.8	9.2	14.8	50	9.4	0
June 9 (34)	0	26.5	14.7	26.5	26.5	2.9	12
Anisodactylis sanctaecrucis							
May 7 (45)	20	6.7	4.4	35.6	20	2.2	11.1
May 8 (66)	22.2	6.3	14.3	38.1	9.5	3.2	6.4
June 9 (36)	0	16.7	14.7	26.5	47.2	11.1	5.1
Bembidion quadrimaculatum							
May 7 (21)	14.3	14.3	9.5	28.5	9.5	19	4.9
May 8 (21)	23.8	9.5	4.7	38.1	14.3	9.6	0
June 9 (8)	100	0	0	0	0	0	0

[1] Trapping conducted at the MSU Organic Soils Farm in 1979.

[2] Total catch

As was seen previously, extremes in habitat effect the relative abundance and distribution of some of the more common carabids within the onion agroecosystem. The results of an experiment designed to further investigate and quantify the relationship between weed density within an onion field and carabid abundance showed that while there was no evidence to suspect a change in density of carabids with a change in weed density (measured in dry weight and leaf area). However, the presence or absence of weeds colonizing an onion field may have a direct or indirect impact on larval carabid density ($\bar{x}$ larvae/.006m^3 soil in weeds = 1.41 and 0.16 in weeded onion plots, F=2.15, p=.04). There was no reason to suspect that this was true with carabid adults (F=0.7, p=0.47) although densities of carabid adults were based on open plot pitfall trap captures which do not directly reflect population density. Table C7 summarizes the results of this study (Table C8 tabulates the results on a per plot basis). It can be seen that the onion plant damage appears to be less in the weedy plots in relation to the hand-weeded plots. Regression analysis was utilized to determine the relationships between weed dry weight per unit area and onion maggot induced plant damage, and weed leaf area and damage. Dry weight did not explain a significant proportion of the variation in plant damage, but leaf area contributed to 30% (R^2=.301, Y=10.3-.002x) of the variation in damage (H_0: B=0, T=-2.2, P=.05). When weediness was looked at in a more qualitative manner (i.e. the presence or absence of weeds) a difference was found to exist in onion damage due to onion maggot (T=-4.6, P=.001). Unfortunately eggs were not sampled and so it is not known whether this phenomenon was due to the predation of eggs and larvae by carabids or other predators, differential oviposition, or the interaction of both of these. There is evidence to suggest that it is equally likely that either of these

Table C7. Carabid densities in weedy vs. non-weedy onion plots.

Onion Planting	$\overline{x}$ % damage[1]	$\overline{x}$ weed leaf area (cm^2)	$\overline{x}$ weed dry wt.(g)	$\overline{x}$ carabid larvae/ soil sample	$\overline{x}$ adult carabid/pit-fall trap/day
weeded	13.8 ± 5.3[2]	0	0	0.16 ± 0.3	1.6 ± 0.9
non-weeded	2.2 ± 2.0	143.8	32.6	1.41 ± 1.3	1.2 ± 0.7

[1] N = 12 plots/treatment

[2] .95 confidence intervals

Table C8. Onion damage in weedy vs. non-weedy plots.

						species leaf area (cm^2) / plot						
Plot	Percent Damage	Adult Carabids[1]		Total Weed Dry Wt.	Total Leaf area(cm^2)	*Digitaria sanguinalis*	*Amaranthus retroflexus*	*Sonchus arvensis*	*Agropyron repens*	*Cyperus esculentus*	*Sonchus oleraceus*	*Polygonum persicaria*
12	5.2	2.0	5	13.3	2186.9	1536.1	56.4	32.6	561.8			
18	2.5	0.7	1	3.4	672	295.3		334.2		42.43		
15	6.4	0.3	1	1.9	135.7	105.6					30.1	
13	8.1	3.2	6	1.5	87.1	63						24.3
24	3.0	0.2	0	0.7	22.1	22.1	22.1					
16	0	2.0	1	6.1	604.1	554.8	49.3					
23	0	3.5	0	3.1	224.9	162.3					62.6	
1	1.0	0.2	0	10.1	829.5	201.1			48.9			579.6
8	0	1.1	1	30.8	5101.5	1001.7		488.3			3611.5	
21	0	4.0	1	14.5	1557.9	1557.9						
10	0	0	0	224.1	3539.6	3185		354.6				
3	0	0.4	1	81.2	4974.3	127.3		1895.3		71.4	2862.8	17.5

Table C8, continued

Plot	Percent Damage	Adult Carabids	Immature Carabids
2	2.0	0.6	1
4	25.1	1.5	0
5	10.0	1.8	0
6	6.5	0.3	0
7	14.2	0.5	0
9	17.5	0.9	0
11	20.1	1.0	0
14	30.3	0.2	0
17	11.1	1.0	0
19	15.8	0.9	0
20	6.0	3.8	0
22	8.4	2.7	1

could have been responsible. Harris (1982) has found in the laboratory that the female onion fly utilizes visual cues as well as olfactory cues in locating hosts for oviposition. Thus, it might be hypothesized that a substantial density of weeds within an onion field may mask the host (onion) from the searching female fly. On the other hand, there is also ample evidence (within the cabbage agroecosystem) that predation has a pronounced effect upon egg survival of *Hylemya brassicae*, Wyman et al. (1976) cite many documented cases of this.

The role of predation on the population dynamics of the onion maggot was never directly evaluated. Laboratory studies were conducted inorder to identify species of carabids that showed potential as biological control agents. Preliminary studies (Haynes et al. 1979) produced five promising species that were subjected to further tests. Table C9 shows the results of these "no choice" experiments. *B. quadrimaculatum* appears to be the most promising egg and larval predator. Due to the lack of replication conclusions as to the potential of *Agonoderus* spp. or *Anisodactylus sanctaecrucis* could not be made, although field evaluations of *Agonoderus* spp. associated with the cabbage agroecosystem have indicated them as significant factors in reducing damage (Wyman et al. 1976). A rate of consumption is not available for the slender seedcorn beetle, however, Pausch and Pausch (1980) reported a preference for house fly , *Musca domestica* L., eggs and larvae that was high in comparison to other alternative food choices.

Summary and Conclusions

The heterogeneous environment within the onion agroecosystem, both in and outside the onion field may have an affect on the distribution, density, and

Table **C9**. Onion maggot egg and larva consumption by seven species of carabids associated with the onion agroecosystem.

Species	$\bar{x}$ eggs consumed	$\bar{x}$ larvae killed[2]
Abacidus permundus	1.5 ± .43	0.9 ± 0.4
Bembidion quadrimaculatum	8.1 ± 1.6	1.6 ± 0.5
Microlestes sp.	3.3 ± 1.0	N.T.[3]
Agnoderus spp.	5.3[4] ± 0.7	N.T.
Anisodactylus sanctaecrucis	9.0[4] ± 1.6	N.T
Clivinia impressifrons[5]	+++	+++

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[1] $\bar{x}$ ± SE of missing eggs / 48 hrs / individual, (N = 10)

[2] $\bar{x}$ SE of dead third instar larvae in an onion bulb (N = 10)

[3] not tested

[4] N = 3

[5] Show high level of feeding activity (Pausch and Pausch 1980).

species complexes of predators. Carabids that are probable predators of the onion maggot appear to have "preferred" habitats (as measured by relative abundance) that are disturbed environments. Movement from these habitats into onion fields is a frequent occurrence (Table C10). Chemically treated onion fields support low densities of carabids during the growing season although if source populations are relatively close by recolonization of these areas may happen fairly rapidly. Weeds within an onion field have been shown to have an effect upon the resulting damage due to onion maggot. This may be due to disruption of the searching behavior of the onion fly or due to ovipositional preference of female carabids.

The preliminary nature of this study was not aimed at proving or disproving any one hypothesis but was orientated towards establishing a data base upon which suggestive trends might be elucidated and new hypotheses formulated for more intensive studies concerned with evaluating the role of predators in the onion agroecosystem. When integrating the results from this study the importance of the habitat comes forth as a central theme. Based upon what has been learned it would be unwise to isolate (from a research perspective) the carabid inside the confines of an onion field for evaluation without taking into account the source of local populations moving into and out of the onion field. Perhaps islands of disrupted entropic habitats could act as dispersal sites within large muck soil production areas from which predator numbers could eminate despite of or in place of the intensive use of chemicals.

Table **C10**. Movement of Carabids with respect to the field border.

Species	Mean Number Trapped								
	Within Field			Between Field-Entering			Between Field-Leaving		
	June 7	June 15	June 27	June 7	June 15	June 27	June 7	June 15	June 27
B. quadrimaculatum	1.3±0.5	2.0±0.9	0.8±0.5	0.8±0.5	0.5±0.2	0.3±0.3	0.3±0.3	0.5±0.2	0
C. impressifrons	3.3±0.9	2.5±1.0	1.8±0.9	1.5±0.7	1.5±0.7	2.0±1.1	2.5±1.0	1.5±0.7	1.8±0.9
A. sanctaecrucis	10.5±2.4	5.8±1.2	15.3±4.2	4.5±1.3	1.5±0.7	2.5±0.9	0	3.3±1.5	1.5±0.7
Agonoderus	13.5±1.5	4.3±1.3	20.3±1.5	4.5±2.9	1.8±1.2	9.5±3.4	0	2.3±0.8	4.3±1.3

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[1] Number captured/trap side/0.9M, N = 4 traps.

APPENDIX D

ABUNDANCE OF EARTHWORMS IN THE ONION AGROECOSYSTEM

INTRODUCTION

The adult tiger fly[1], *Coenosia tigrina* (F.), has been reported as an important predator of the adult onion maggot (LeRoux and Perron 1960). Carruthers (1981) shows evidence that insecticide usage in Michigan onion growing regions may have a considerable impact on the adult tiger fly's spatial distribution. A comprehensive review of the literature by Groden (1982) suggests that the biology of the larval stage of the tiger fly may be a key determinant in relation to the distribution of the species in muck soil regions.

The feeding habits of the larval stage have not been fully elucidated. It has been hypothesized that the larvae derive their nourishment from decaying organic matter in the soil (LeRoux and Perron 1960) despite the contradictory laboratory findings that larval survival on decaying vegetation was extremely low (Perron et al. 1956). Yahnke and George (1972) observed *C. tigrina* larvae preying on earthworms (species: *Eisenia rosea* (Savigny)) under field conditions. A further laboratory investigation showed that the host must be alive for the survival of the larval stage until pupation. Adopting the hypothesis that earthworms play a critical role in the interaction between *C. tigrina* and *H. antigua*, a survey in a few select onion growing regions in Michigan was initiated for the purposes of determining whether earthworms are present within the onion agroecosystem and also to indirectly measure the impact of intensive agrochemical use on earthworm abundance.

The important role that earthworms play in most agroecosystems is discussed in detail by Edwards and Lofty (1972). Some of the benefits that have

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[1] Diptera (Anthomyiidae)

been documented are the cycling of organic matter, increase of soil fertility through the output of mineralized nitrogen, turning over the soil, and the increase of drainage. A review of the literature did not make it apparent that a similar relationship exists in the muck soil agroecosystem. In fact, Kuhnelt (1961) states that one of the major abiotic factors influencing the distribution and abundance of the Lumbricidae is the hydrogen ion concentration of the soil, and that one is unlikely to find large populations of earthworms in acid soils. Allee et al. (1930) states that most earthworm species "prefer" a pH of about 7. A classification of Lumbricidae based on their distribution in relation to soil acidity developed by Satchell (1955) has shown that even acid intolerant species are found in a range of soil pH's of 4.8-7.0. No mention, however, is made in relation to the abundance of these species under acid conditions. Muck soils cultivated for onion production are rarely below a pH of 5.0 (Lucas 1955), thus, from a species presence or absence perspective mucksoil agroecosystems may differ little from upland soil ecosystems. An excellent review of the effect of soil pH on earthworms is presented by Edwards and Lofty (1972), and although general statements as to the effect of acid soils on earthworms are made, no quantitative assessment of these dynamics is discussed.

The most common techniques for estimating earthworm population densities are hand sorting, soil washing, electricution, chemical poisoning and heat extraction. Several workers have compared the relative efficiency of extracting earthworms from soil by two or more of these methods. Svendson (1955) and Raw (1959) reported that hand sorting was much more efficient than using potassium permanganate and other chemical agents. Despite the disadvantage of hand sorting being more time consuming than many of the other techniques, the

proportion of medium to large size earthworms recovered by hand sorting is quite often .90 or higher (Nelson and Satchell 1962). Optimal sample sizes have been determined for a few sample units. Edwards and Lofty (1972) report that a fairly precise estimate of density of medium sized species can be arrived at by taking 16 sample units of an area of 0.063 m^2 taken to a depth of 20 cm.

MATERIALS AND METHODS

The fields selected for the study sites were located in Laingsburg, Grant, and Eaton Rapids (Michigan). In each of the three regions at least one field representative of a chemically intensive onion production system (six fields in Grant) and one representing a system with no pesticide input were incorporated into the design (see study site description in fall dynamics section for further details). The earthworm survey was conducted at two times of the year during 1979, in mid-July (July 11th-July 18th) and after harvest (October 20th-November 4th). The sampling procedure utilized in July consisted of taking ten randomly selected sample units 1647 cm^3 in soil volume (par-aide turf cutter) between onion rows. The method of hand-sorting was used for the extraction of Lumbricids from each soil sample. After harvest, the sampling method was changed to 15 quadrat samples (9.26 m^2 to a depth of 15 cm) per field, stratified such that one-third of the randomly selected samples were from areas of low cull density, one-third were from areas of medium cull density, and one-third were from areas of high cull density relative to the specific field level density of culls. During both survey periods each field within a region was sampled on the same day so as to minimize the effect of day-to-day fluctuations in weather conditions on the vertical earthworm distribution (see Edwards and Lofty 1972, Chapter 5 for detailed discussion).

RESULTS AND DISCUSSION

The species sampled in this study were all of the family Lumbricidae as determined from Edwards and Lofty (1972). Earthworms were not identified to the species level, although preliminary investigations to the generic level suggested that more than 80% of the individuals were of the genus Eisenia (taxonomic keys utilized were found in Edwards and Lofty 1972). A classification of the Michigan earthworm fauna by Murchie (1956) suggests that it is likely that the predominant species in Michigan muck agroecosystems might be <u>Eisenia rosea</u> (Savigny). There is discrepancy in the literature as to the correct genus that this species belongs to as the European specialists prefer to include it as a member of the genus Allolobophora (disagreement being as to whether the cross-section of the coelom is trapazoidal in appearance). Interestingly enough it is <u>E. rosea</u> that was first found as a host for the larval stage of <u>C. tigrina</u> (Yahnke and George 1972).

An inspection of the data collected during the July sampling period suggests that a trend might exist in which fields without pesticide contamination have higher earthworm densities than fields that had pesticides applied throughout the season; however, upon analysis of the data no supportive evidence of this hypothesis exists (Laingsburg region, x^2 = 1.00, significance = .317; Grant region, x^2 = 3.804, significance = .703; and the Eaton Rapids region, x^2 = 1.00, significance = .317 (based on Friedman's two-way analysis of ranks)). The data (Table D1) reflects the low population levels inherent in all fields sampled. Since the sampling effort is representative of a single moment in time (latter half of July), it is not clear from these results whether the muck agroecosystem is a suboptimal environment and generally devoid of earthworms irrespective of

Table D1. Estimated earthworm densities[1] in three onion growing regions in Michigan during July, 1979.

Region	Field	Soil pH[2]	Sampling Date[3]			
			July 11	July 13	July 16	July 18
Laingsburg						
	Pesticide (P)	5.7	.1±.32	.1±.32	0	.2±.63
	Non-pesticide (0)	5.5	.3±.48	.1±.32	0	.5±.97
Eaton Rapids						
	Pesticide (R)	-	0	0	.1±.32	0
	Non-pesticide (K)	-	.2±.63	.1±.32	.1±.32	0
Grant						
	Pesticide (1)	5.7±.4	0	.1±.32	0	0
	Pesticide (2)	-	0	0	0	0
	Pesticide (3)	5.6±1.0	.1±.32	.2±.63	.1±.32	0
	Pesticide (4)	-	.1±.32	0	.3±.48	0
	Pesticide (5)	7.1±.7	0	0	.4±.70	0
	Pesticide (6)	6.3±.1.0	0	0	.1±.32	0
	Non-pesticide (R)	5.9±.64	.1±.32	0	.3±.48	0

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[1] Only adult or juvenile stages detectable by hand-sorting.

[2] Soil pH data obtained from Nick Bolgiano, Department of Botany and Plant Pathology, Michigan State University ($\bar{x}$ ± SD, N = 3).

[3] $\bar{x}$ ± SD, N = 10.

agricultural practices or whether these data are due to seasonal variation in the activity of Eisenia rosea and other similarly behaving species of Lumbricids. Murchie (1958) found that E. rosea in southern Michigan were at relatively low numbers (in reference to the upper soil strata) during late July and August compared with densities detected in the spring and fall of 1952. Similar results obtained from researchers in Europe (Edwards and Lofty 1972) have shown that the densities of some earthworm populations exhibit dramatic seasonal variation, and that high soil temperatures (>21°c) along with low levels of soil moisture (>25%) may be factors responsible for such vertical migrations. If dynamics such as these are characteristic of the muck agroecosystem, it is conceivable that muck soils with their propensity to exhibit high soil temperatures and low moisture levels particularly near the surface (throughout a large part of the growing season) may be providing a spatial separation of C. tigrina and its hosts thereby resulting in regulation of the tiger fly population or at least confining the larval stage of the population outside of the muck agroecosystem.

The fall earthworm survey was initiated in a response to the high surface densities (relative to the July survey) of earthworms found in onion fields toward the end of October, 1979. The results of the survey (based on data in Table D2) in which fields that hadn't received pesticides during the growing season and those that had (within each of three regions) were compared, suggest that in two of the three regions (Eaton Rapids and Laingsburg) earthworm densities were higher in fields that didn't receive pesticides than fields that did (Table D3). Pesticides, in certain circumstances, have been demonstrated to cause mortality to earthworms. There has not been sufficient evidence from research findings to suggest that herbicides directly effect earthworm populations in this manner

Table D2. Estimated earthworm densities in three onion growing regions in Michigan during the fall of 1979.

Region	Field	Sampling Date	Cull Density[2]	Earthworm Density[3]	Nearest Cull[4]
Laingsburg	P	Oct. 18	5	0	-
	P	Oct. 18	0	0	-
	P	Oct. 18	3	0	-
	P	Oct. 18	4	0	-
	P	Oct. 18	1	0	-
	P	Oct. 18	2	0	-
	P	Oct. 18	0	0	-
	P	Oct. 18	6	0	-
	P	Oct. 18	2	0	-
	P	Oct. 18	4	0	-
	P	Oct. 18	5	0	-
	P	Oct. 18	7	0	-
	P	Oct. 18	0	0	-
	P	Oct. 18	1	0	-
	P	Oct. 18	4	0	-
	R	Oct. 18	63	2	3.5 + 2.1
	R	Oct. 18	8	0	-
	R	Oct. 18	79	0	-
	R	Oct. 18	15	0	-
	R	Oct. 18	29	1	3.0
	R	Oct. 18	4	0	-
	R	Oct. 18	79	4	2.5 ± 1.3
	R	Oct. 18	14	0	-
	R	Oct. 18	7	0	-
	R	Oct. 18	6	1	2.0
	R	Oct. 18	19	0	-
	R	Oct. 18	4	4	4.8 ± 3.1
	R	Oct. 18	84	0	-
	R	Oct. 18	13	0	-
	R	Oct. 18	11	0	-
	P	Nov. 2	5	0	-
	P	Nov. 2	3	0	-
	P	Nov. 2	0	0	-
	P	Nov. 2	0	0	-
	P	Nov. 2	1	0	-
	P	Nov. 2	3	0	-
	P	Nov. 2	2	0	-
	P	Nov. 2	0	0	-
	P	Nov. 2	1	0	-
	P	Nov. 2	4	0	-
	P	Nov. 2	7	0	-
	P	Nov. 2	0	0	-
	P	Nov. 2	1	0	-
	P	Nov. 2	0	0	-
	P	Nov. 2	0	0	-
	R	Nov. 2	3	0	-

Table D2.

Region	Field	Sampling Date	Cull Density[2]	Earthworm Density[3]	Nearest Cull[4]
	R	Nov. 2	4	0	-
	R	Nov. 2	2	0	-
	R	Nov. 2	1	0	-
	R	Nov. 2	4	0	-
	R	Nov. 2	11	0	-
	R	Nov. 2	17	0	-
	R	Nov. 2	24	1	0.8
	R	Nov. 2	8	0	-
	R	Nov. 2	15	1	1.0
	R	Nov. 2	85	0	-
	R	Nov. 2	94	1	2.0
	R	Nov. 2	72	2	2.1 + .85
	R	Nov. 2	103	0	-
	R	Nov. 2	69	1	0.5
Grant	GR	Nov. 5	3	0	-
	GR	Nov. 5	1	0	-
	GR	Nov. 5	0	0	-
	GR	Nov. 5	4	0	-
	GR	Nov. 5	5	0	-
	GR	Nov. 5	53	1	0.0
	GR	Nov. 5	27	0	-
	GR	Nov. 5	34	0	-
	GR	Nov. 5	19	0	-
	GR	Nov. 5	22	0	-
	GR	Nov. 5	109	0	-
	GR	Nov. 5	137	2	0.0
	GR	Nov. 5	118	0	-
	GR	Nov. 5	152	0	-
	GR	Nov. 5	121	0	-
	G1	Nov. 5	0	0	-
	G1	Nov. 5	0	0	-
	G1	Nov. 5	3	0	-
	G1	Nov. 5	4	0	-
	G1	Nov. 5	14	0	-
	G1	Nov. 5	19	0	-
	G1	Nov. 5	27	0	-
	G1	Nov. 5	38	0	-
	G1	Nov. 5	29	0	-
	G1	Nov. 5	54	0	-
	G1	Nov. 5	72	0	-
	G1	Nov. 5	68	0	-
	G1	Nov. 5	71	0	-
	G1	Nov. 5	50	0	-
	G1	Nov. 5	47	0	-

Table D2.

Region	Field	Sampling Date	Cull Density^2	Earthworm Density^3	Nearest Cull^4
	G3	Nov. 5	6	0	-
	G3	Nov. 5	4	0	-
	G3	Nov. 5	3	0	-
	G3	Nov. 5	8	0	-
	G3	Nov. 5	2	0	-
	G3	Nov. 5	11	0	-
	G3	Nov. 5	19	0	-
	G3	Nov. 5	22	0	-
	G3	Nov. 5	15	0	-
	G3	Nov. 5	19	0	-
	G3	Nov. 5	39	0	-
	G3	Nov. 5	42	0	-
	G3	Nov. 5	27	0	-
	G3	Nov. 5	52	0	-
	G3	Nov. 5	61	0	-
	Border-G1	Nov. 5	-	3	-
	Border-G1	Nov. 5	-	0	-
	Border-G1	Nov. 5	-	7	-
	Border-G3	Nov. 5	-	1	-
	Border-G3	Nov. 5	-	0	-
	Border-G3	Nov. 5	-	4	-
Eaton Rapids	K	Oct. 21	4	0	-
	K	Oct. 21	5	0	-
	K	Oct. 21	5	0	-
	K	Oct. 21	6	0	-
	K	Oct. 21	3	0	-
	K	Oct. 21	11	1	0.0
	K	Oct. 21	15	2	1 ± 0
	K	Oct. 21	13	1	0
	K	Oct. 21	12	0	-
	K	Oct. 21	9	0	-
	K	Oct. 21	60	3	1.7 ± 1.2
	K	Oct. 21	56	4	1 ± 1.4
	K	Oct. 21	111	11	0.3 ± 0.5
	K	Oct. 21	93	11	1.0 ± 1.4
	K	Oct. 21	82	27	.82 ± 1.3
	K	Nov. 4	1	0	-
	K	Nov. 4	3	0	-
	K	Nov. 4	0	0	-
	K	Nov. 4	4	1	2
	K	Nov. 4	6	0	-
	K	Nov. 4	8	0	-
	K	Nov. 4	11	2	0.5 ± 0.7
	K	Nov. 4	19	3	0

Table D2.

Region	Field	Sampling Date	Cull Density[2]	Earthworm Density[3]	Nearest Cull[4]
	K	Nov. 4	12	0	-
	K	Nov. 4	13	4	0
	K	Nov. 4	71	5	1 ± 1
	K	Nov. 4	34	3	0
	K	Nov. 4	46	6	0.2 ± .4
	K	Nov. 4	35	14	.07 ± 0.3
	K	Nov. 4	53	2	0.5 ± 0.7
	R	Oct. 21	1	0	-
	R	Oct. 21	4	0	-
	R	Oct. 21	5	0	-
	R	Oct. 21	3	0	-
	R	Oct. 21	4	0	-
	R	Oct. 21	7	0	-
	R	Oct. 21	9	1	0.0
	R	Oct. 21	9	0	-
	R	Oct. 21	13	0	-
	R	Oct. 21	17	0	-
	R	Oct. 21	24	0	-
	R	Oct. 21	28	0	-
	R	Oct. 21	26	0	-
	R	Oct. 21	25	0	-
	R	Oct. 21	29	0	-
	R	Nov. 4	1	0	-
	R	Nov. 4	2	0	-
	R	Nov. 4	1	0	-
	R	Nov. 4	4	0	-
	R	Nov. 4	0	0	-
	R	Nov. 4	12	0	-
	R	Nov. 4	16	0	-
	R	Nov. 4	9	0	-
	R	Nov. 4	11	0	-
	R	Nov. 4	15	0	-
	R	Nov. 4	29	0	-
	R	Nov. 4	34	0	-
	R	Nov. 4	39	0	-
	R	Nov. 4	24	0	-

---

[1] Definition of field codes: Laingsburg, P = onions grown under typical commercial methodology, R = no pesticide input; Grant, G1 and G3 = onions grown under typical commercial methodology, GR = no pesticide input, Border = grassy border between field and irrigation ditch; Eaton Rapids, R = onions grown under typical commercial methodology, K = no pesticide input.

[2,3] Density expressed in terms of culls per 9.26 m^2.

[4] Mean distance of earthworms to nearest cull (cm).

Table D3. Summarized results of fall earthworm survey, 1979.

Region	Field[1]	Mean Earthworm Density		χ^2	Significance[2]
		October	November		
Eaton Rapids				2.10	.10
	K	4.00	2.67		
	R	0.07	0.00		
Grant				2.40	.16
	GR	0.20	-		
	G1	0.00	-		
	G3	0.00	-		
Laingsburg				2.10	.10
	R	0.80	0.40		
	P	0.00	0.00		

---

[1] Fields without pesticide treatment = K (Eaton Rapids), GR (Grant), R (Laingsburg); all others received pesticides during the growing season.

[2] based on Friedman's two-way analysis of ranks

(except for the triazine compounds) although it has been hypothesized (Edwards and Lofty 1972) that herbicides may still play a major role in reducing population densities by killing the vegetation that serves as the earthworms food source. The fungicides, in general, have not been considered deleterious to earthworm populations although one class of these, the copper fungicides, have proven to be extremely lethal to earthworms (Edwards and Lofty 1972, and Stringer and Lyons 1974). There have been many studies of the effects of insecticides on earthworms, many of which are reviewed by Edwards and Lofty (1972). Some insecticides such as aldrin, dieldrin, and BHC (all chlorinated hydrocarbons) have little effect on earthworms as far as direct mortality is concerned, whereas chlordane is extremely toxic to earthworms. The effect of organophosphate insecticides, the basis for onion maggot control in Michigan, is also dependent upon the particular chemical in question. Azinphosmethyl and carbofuran have not been shown to effect earthworms whereas Diazinon®, Dyfonate®, and Dursban® (all common soil insecticides used for the control of onion maggot) have slight deleterious effects on earthworm populations (Edwards and Lofty 1972). Parathion and malathion (two commonly used foliar insecticides used to control adults of the onion maggot) have been reported as being toxic to earthworms (Hopkins and Kirk 1957).

Despite these findings, it cannot be presumed that the higher densities of earthworms sampled in the fall of 1979 were due solely to the nonpesticide history of these fields. Both fields (K in Eaton Rapids and R in Laingsburg) relied upon mechanical cultivation as a means for weed control. It is generally agreed upon that cultivation does not cause a decrease in earthworm numbers, and some researchers have documented a greater number and biomass of

earthworms in the soil the more the soil is cultivated (Edwards and Lofty 1972). Loosening of the soil along with the tremendous regenerative powers of earthworms have been the reasons given for this. Cropping design from year to year has a dramatic effect on earthworm populations. The more often row crops are grown, the greater the decline of earthworms in comparison to continuous plantings of legumes or grains (Edwards and Lofty 1972). Hopp (1946) found that continuous row cropping resulted in a 50% decrease in earthworm numbers in comparison to row crops planted every second year and an 80% decrease when compared to row crops planted only every third year. Fields K and R were the only fields not subjected to annual row cropping, field K by way of stubble-mulch farming (where crop residues of soybeans from the year before were tilled and used as a seed bed for onions the following year) and field R (Laingsburg) being in old field succession two years previous to the 1979 sowing of onions. The cropping histories of both these fields consisted of leaving a considerable amount of vegetation covering the soil surface (weeds in the case of field R and soybean residues in the case of field K). The findings of Hopp (1946) showed that an insulating layer such as this during the winter in the northern United States reduced earthworm mortality. The most important factor influencing earthworm populations that is reflected by cropping designs is the amount of organic matter in the soil available for food (Satchell 1955). It has been demonstrated (Edwards and Lofty 1972) that exhaustive cropping without adding organic matter decreases earthworm populations to a very low level. Thus, it is not possible to attribute high levels of earthworms in muck soils to the lack of pesticide use, cultural techniques, or crop rotation alone.

Results from the fall survey also suggested that the spatial distribution of onion culls within a field effects the spatial distribution or aggregation of earthworms in the muck agroecosystem. The relationship between cull density and earthworm density in field K for both the October and November sampling dates is shown in Figure D1. Correlation analysis for both dates respectively yielded correlation coefficients of +.77 (n=15) and +.55 (n=15). Since the sampling variation in "r" is quite large for small sample sizes, homogeneity of the correlation coefficients was tested through the use of the inverse tangent transformation (Steel and Torrie 1960). The correlation coefficients were not found to be significantly different (z=.98, m.s.α=.05, df=30). A pooled estimate of the association (r = +.72 ± .12, p=.001) indicated that there is sufficient evidence to suspect a positive relationship between onion cull density and earthworm density (basd on a per area unit of 9.2 m^2). It would appear from this that earthworms in muck soils can migrate at a fairly fast rate, greater than the 10 m per year estimate given by (Edwards and Lofty 1972) for earthworms in a grassland ecosystem. There is little experimental evidence to suggest that factors other than soil moisture cause aggregations, although it has been observed that <u>Dendrobaena octaedra</u> and <u>Lubricus rubellus</u> were significantly aggregated beneath dung pats in the spring (Edwards and Lofty 1972). Depending on the affinity that earthworms have for onions and the maximum distance of migration, it may be possible to manipulate the density of culls in such a manner that predation and survival of the tiger fly is increased. Many unknown factors would have to be elucidated before this could be more practically considered. I feel the results of the earthworm survey have provided evidence that such dynamics may exist given that the tiger fly is linked to the earthworm as suggested by Yahnke and George (1972).

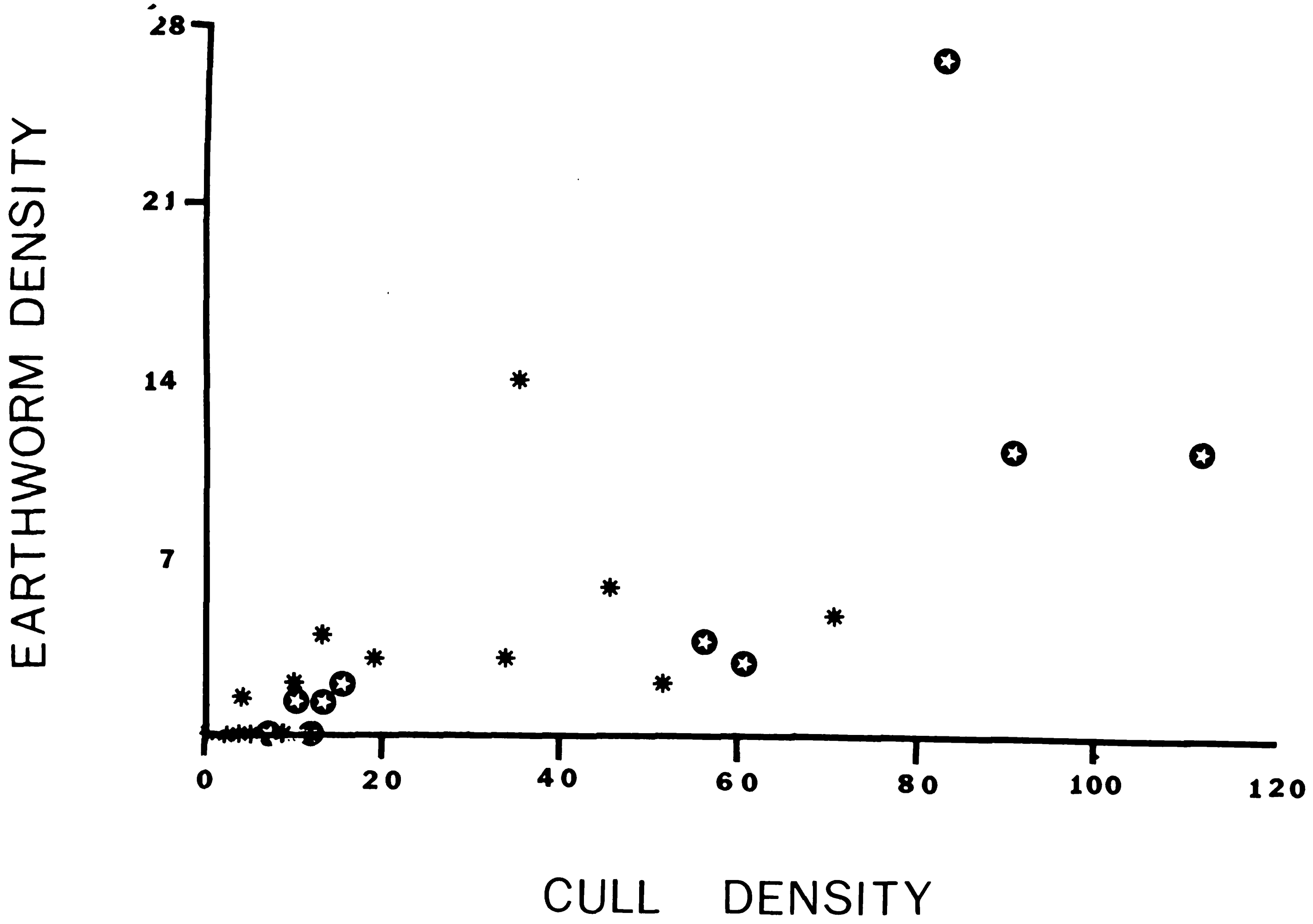


Figure D1. Relationship between cull density and earthworm density (9.26 M^2)
✱ = November 4, ✪ = October 21.

APPENDIX E

A SIMULATION MODEL OF THE ONION MAGGOT SUBSYSTEM

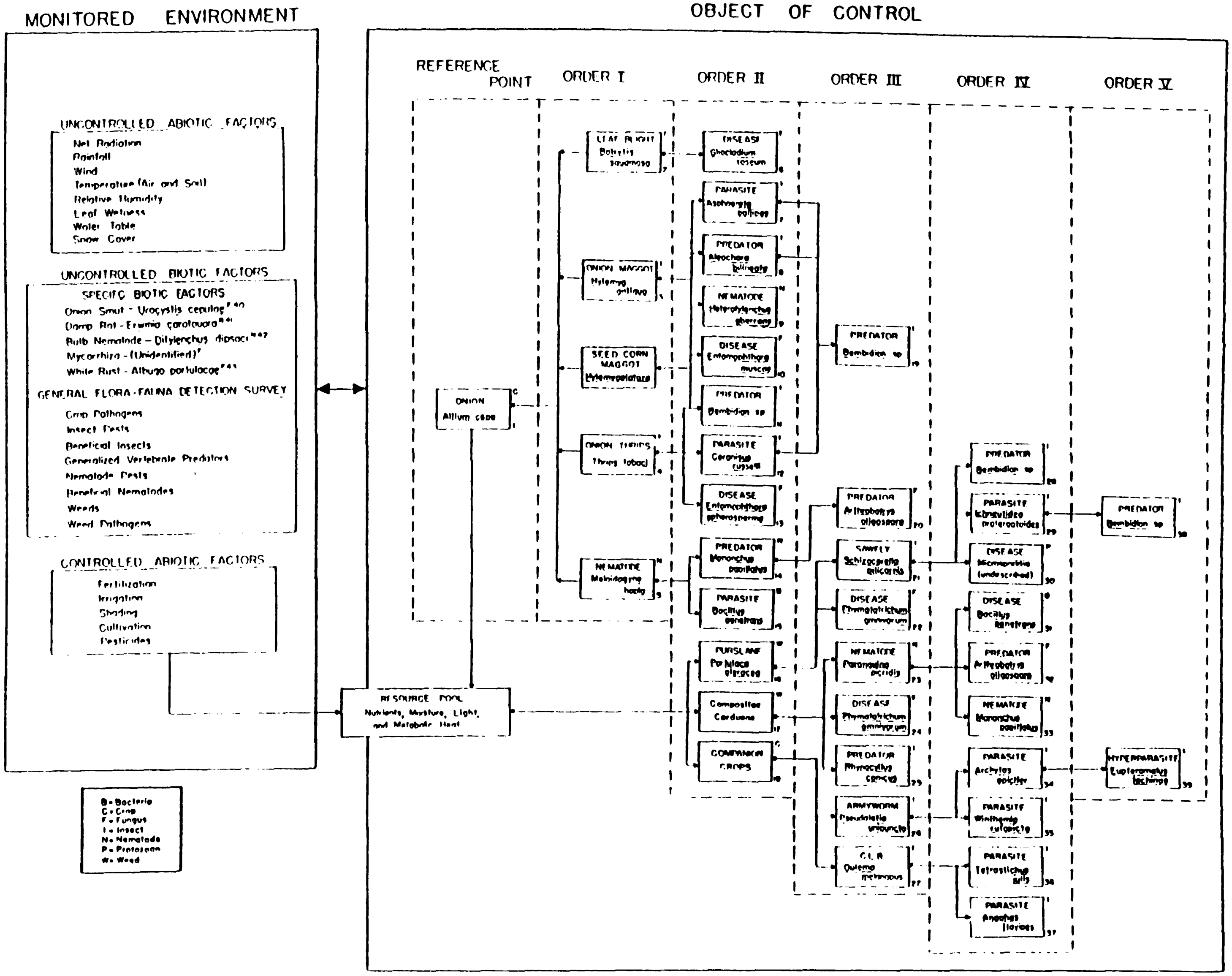
Introduction

The lack of ecological consideration in the onion agroecosystem pest control program initiated the development of a submodel of the onion ecosystem. Due to an insufficient data base, it is not possible to construct a complete model for the onion agroecosystem (Figure E1). Consequently, a sub-component of the whole conceptualized system was chosen to be modeled. This sub-component consists of the onion maggot, the onion plant and a braconid parasitoid of the onion maggot. This sub-component was chosen because a thorough understanding of it was necessary for management alternatives to be explored.

The onion maggot is the major insect pest of cultivated onions in the temperate zone (Drake 1923). It was first described by Meigen in 1826 as Hylemya antiqua. Various aspects of some of the more important biology concerning the onion maggot have been reviewed by several authors: Lintner (1882), Eyer (1922), Baker and Stewart (1927), Kastner (1929), Mann (1945), Doane (1953), Tozloski (1954), Workman (1958), Ellington (1963) and Loosjes (1976).

The onion maggot, its parasitoid and the onion bulb form the biological variables of the model. Abiotic variables of the model are soil and foliar pesticides, weather and time. These variables were used to construct a model that would show the maturity distribution of the organism at any point in time. As a corollary of this, it should show the damage to onions that occurs given various abiotic and biotic conditions. The model was constructed so that the effects of various control strategies could be evaluated without changing the model structure. It is also imperative that it be possible to couple models of the other components of the system (presently in preparation) to this model without

Figure E1. Conceptualization of the onion agroecosystem showing levels of interaction within the object of control (Haynes et al. 1980).


MONITORED ENVIRONMENT
UNCONTROLLED ABIOTIC FACTORS
Net Radiation
Rainfall
Wind
Temperature (Air and Soil)
Relative Humidity
Leaf Wetness
Water Table
Snow Cover
UNCONTROLLED BIOTIC FACTORS
SPECIFC BIOTIC FACTORS
Onion Smut - Urocystis cepulae F 40
Damp Rot - Erwinia carotovora B 41
Bulb Nematode - Ditylenchus dipsaci N 42
Mycorrhiza - (Unidentified) F
White Rust - Albugo portulacae F 43
GENERAL FLORA-FAUNA DETECTION SURVEY
Crop Pathogens
Insect Pests
Beneficial Insects
Generalized Vertebrate Predators
Nematode Pests
Beneficial Nematodes
Weeds
Weed Pathogens
CONTROLLED ABIOTIC FACTORS
Fertilization
Irrigation
Shading
Cultivation
Pesticides
B = Bacteria
C = Crop
F = Fungus
I = Insect
N = Nematode
P = Protozoan
W = Weed
OBJECT OF CONTROL
REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
ORDER V
ONION Allium cepa C 1
RESOURCE POOL Nutrients, Moisture, Light, and Metabolic Heat
LEAF BLIGHT Botrytis squamosa F 2
ONION MAGGOT Hylemya antiqua I 3
SEED CORN MAGGOT Hylemya platura
ONION THRIPS Thrips tabaci I 4
NEMATODE Meloidogyne hapla N 5
DISEASE Gliocladium roseum F 6
PARASITE Aphaereta pallipes I 7
PREDATOR Aleochara bilineata I 8
NEMATODE Heterotylenchus aberrans N 9
DISEASE Entomophthora muscae F 10
PREDATOR Bembidion sp I 11
PARASITE Ceranisus russelli I 12
DISEASE Entomophthora sphaerosperma F 13
PREDATOR Mononchus papillatus N 14
PARASITE Bacillus penetrans B 15
PURSLANE Portulaca oleracea W 16
Compositae Carduus W 17
COMPANION CROPS C 18
PREDATOR Bembidion sp I 19
PREDATOR Arthrobotrys oligospora F 20
SAWFLY Schizocerella pilicornis I 21
DISEASE Plasmodiophora? Trichothecium? omnivorum F 22
NEMATODE Paranagrolaimus? acridis N 23
DISEASE Phymatotrichum omnivorum F 24
PREDATOR Rhynocoris? cinctus I 25
ARMYWORM Pseudaletia unipuncta I 26
C.L.B. Oulema melanopus I 27
PREDATOR Bembidion sp I 28
PARASITE Ichneumonidae? pteromaloides I 29
DISEASE Micrococcus? (undescribed) P 30
DISEASE Bacillus penetrans B 31
PREDATOR Arthrobotrys oligospora F 32
NEMATODE Mononchus papillatus N 33
PARASITE Archytas apicifer I 34
PARASITE Winthemia rufopicta I 35
PARASITE Tetrastichus julis I 36
PARASITE Anaphes flavipes I 37
PREDATOR Bembidion sp I 38
HYPERPARASITE Eupteromalus leguminis I 39

major revision. This model has also become a research tool, directing attention to parameters that must be estimated in the field to understand the population dynamics of the onion maggot.

The Model

The conceptualized model was formulated by the author, Dr. Gary Whitfield and J. Valenti (Department of Computer Science) (Fig. E2). The has controllable inputs are: weather (three different weather sets from lansing, Ludington and Houghton, MI), parasitism (Aphaereta pallipes Say), planting density, type of pesticide, frequency of pesticide use, initial date of application of pesticide, and spring density of onion maggot pupae. The outputs of the model are yield (amount per acre), net profit and the number of inidividuals in each age class (for each organism). The model was judged a success if good correspondence between output and field observations occurred.

In formulating the model, a one-acre field of onions was considered. It was thought that the size of the field would have no bearing on the dynamic interactions that were taken into account by the model. With minor modification, any sized field could be implemented into the model structure. This assumption was based on two restraints that were built into the model. First, no immigration or emigration would take place with the onion maggot or the parasitoid component (closed system). Second, onion bulb growth would be based on a static regression model that would result in uniform growth for all onions. These restraints enabled the model to elucidate the interactions independent of the size of fields. The economic section of the model was a static submodel in that the cost of labor and materials, as well as marketability of the crop,

Figure E2. Functional diagram of the life system of the onion maggot (S=spacing of onions, D=dead onion plants, P=mortality due to pesticides, E=eggs, A=parasitism, N=natural mortality). A, submodel of the onion, pesticide, and economics components; B, submodel of the dynamics of the onion maggot population; C, submodel of the dynamics of the parasitoid population.

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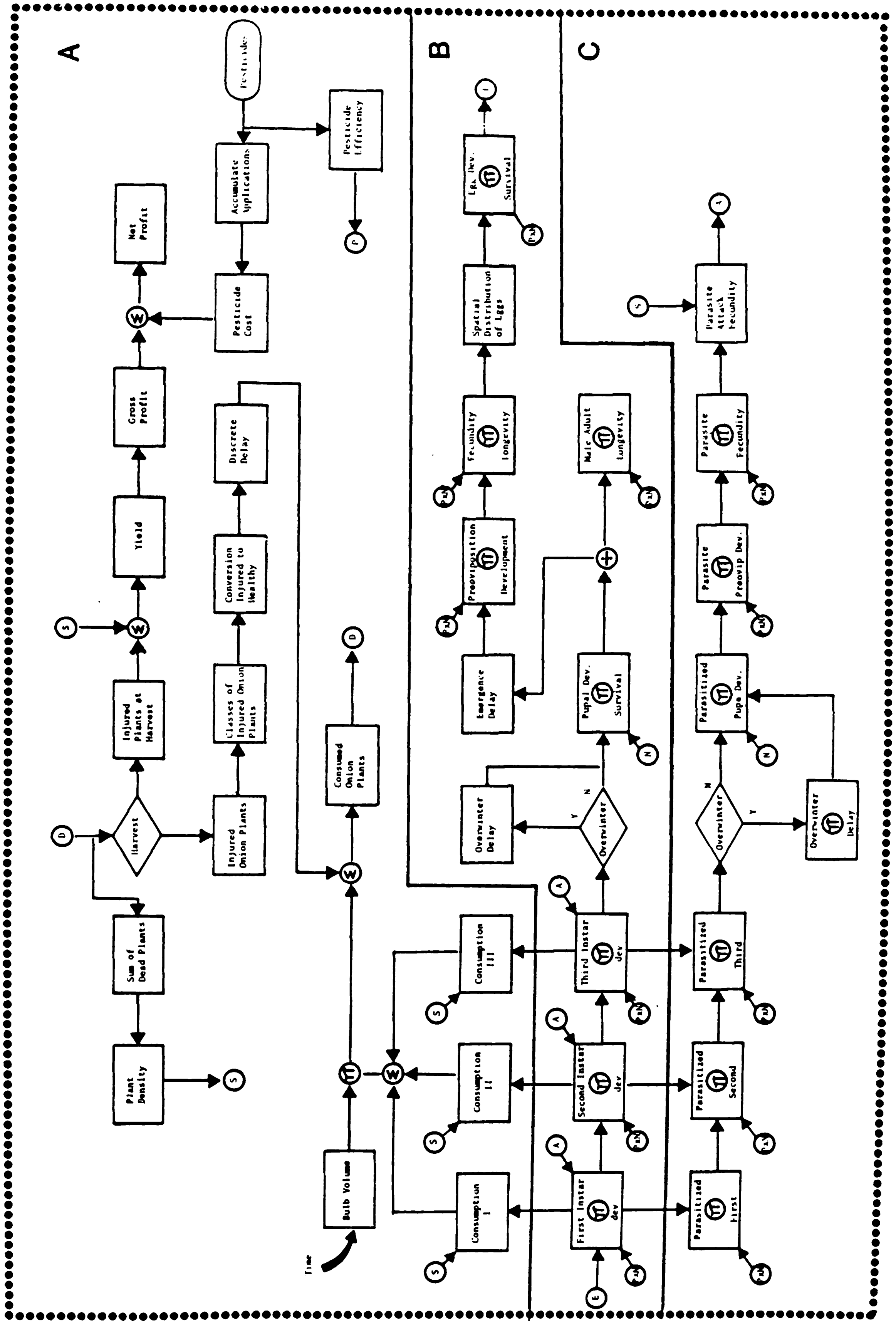

remained constant through time. This was not detrimental to the performance of the model since it provided a standard measure where comparisons between simulation runs could be made quickly. A dynamic model, although being more realistic, may not be as useful in analyzing the population dynamics of the various organisms.

The complex relationships between various abiotic parameters and pesticide breakdown prevented construction of a model in the time frame available. Instead, it was assumed that data on average half-life tendencies of certain pesticides approximated most pesticide behavior over a wide range of weather conditions (Matsumura, personal communication, Department of Entomology, Michigan State University, February 1975; Wells, personal communication, Department of Entomology, Michigan State University, December 1977). A number of restrictions or assumptions were incorporated into the model components concerning the population dynamics of the onion maggot and parasitoid. Assumptions that applied to all the organisms were: (a) mortality was not age-specific in each age class, but was distributed uniformly; (b) the reaction to temperature of all life stages was instantaneous; (c) there were no after effects in the temperature reaction; and (d) development was temperature dependent. No age-specific mortality was assumed because no pertinent information on this topic was found in the literature. It was felt that the best approach was to treat mortality uniformly across the life stage until research dictated differently. Presently, the three assumptions (b-d) in relation to temperature effects on development form a basis of most insect population dynamics models (Rabinge', personal communication, Agriculture Institute, Wageningen, Netherlands, January 1978; Fulton 1978). More specifically, the data of Ellington (1963) and

Salkeld (1959) tend to suggest that these temperature relationships hold true for the onion maggot and A. pallipes.

Temperature was the environmental input that had the most widely distributed effects in this model. It was used to drive a number of functions that affect adult emergence, oviposition, survival and length of stay in a life stage. Temperature data available from the National Weather Service is in the form of daily maximums and minimums. The time sequence of the model was in tenths of days, each tenth or 2.4 hours representing a DT (Δ t). In order to calculate an average temperature for each DT, we assumed that temperature changes within a day are sinusoidal with the maximum and minimum twelve hours apart (Fulton 1978).

$$\text{Average air temperature} = \text{Min} + !(\text{Max}-\text{Min})/2l + !(\text{Max}-\text{Min})/2l * !\cos(2.4\ \text{DT})l$$

These calculated temperature values, when used to determine degree-day accumulations, produce errors that are insignificant when looked at over an entire season (Baskerville and Emin 1969). Heat units or degree-days were used to synchronize emergence, to place gravid onion maggot females in the corect fecundity class, to regulate the numbers of onion maggot pupae going into diapause, and to evaluate the model's performance (by comparing observed simulation results with field data).

$$\text{Degree days} = F(t) = \text{Max}\ !0, T(t)-T_0 l\ \text{V}T(t)$$

where: $T(t)$ = temperature at time t

T_0 = threshold temperature

and heat accumulation in degree days, TDD, is

$$\text{TDD} = \int_0^x F(t)\,dt$$

where x represents the mean number of calendar days required to complete development in a life stage.

For some calculations, soil temperature (ST) was required (egg, larval and pupal development) and this was obtained through use of a regression equation, using air temperature (Vail, personal communication, Department of Entomology, Michigan State University, 1977).

$$ST = 16.41966 + .750848 * \text{average air temperature}$$

The main structure of the model could be viewed as a union of three free-body components. These components represent the onion-pesticide-economics submodel (Figure E2A), the onion maggot population dynamics submodel (Figure E2B), and the parasitoid submodel (Figure E2C). The component approach was felt to be an ideal method for constructing a model of a smaller subsystem so that the model can be expanded by interfacing more components without drastic model restructuring. Table look-up functions (Llewellyn 1965) were used in all three components for linear interpolations between data points in each entry and linear extrapolations below and above the minimum and maximum values for each data set. The function approximation by linear interpolation is given by Manetsch and Park (1977) as being:

$$FNL (X) = DVAL (I) + [(XD - (I-1) * DX) (DVAL (I+1) - DVAL (I))] / DX$$

where: FNL is the desired approximation to the function,

DVAL is an array that represents values of the function F(•) at N+1 intervals of independent variables,

XD is the difference between (X-XS) (difference between independent value X and its smallest value XS).

The density of onions per acre available for consumption by the onion maggot is a function of within-row spacing, specified by the user.

$$NO = 22366 \times 12/SPC$$

where: NO = number of onions per acre,

SPC = spacing of onions (in inches) within a double-row bed.

Onion consumption by each larval stage was determined at the end of every ten DTs (one day). Consumption rates were based on data by Workman (1958) and scaled according to the larval instars involved. Consumption by all instars was then summed and subtracted from the number of onions left in the field, given the size of the onion bulb at that time.

The relationship between larval consumption (volume of onion consumed) and bulb diameter (Figure E3) is as follows:

First instar consumption = $.196\ e^{-.95 \times BD}$

Second instar consumption = $.4\ e^{-.85 \times BD}$

Third instar consumption = $6.75\ e^{-1.0 \times BD}$

where: BD = bulb diameter (Bird 1976).

It was assumed that all available onions in the field were the same size at any one point in time and bulb volume was obtained from use of table look-up function for any date specified (Figure E4, Bird 1976).

bulb volume = $.0002\ e^{(.09 \times \text{days after seeding})}$

The number of consumed onions (NK) was determined by subtracting total onion volume consumed by all instars from available onion volume (bulb volume x number of onions per acre). From this, the number of damaged onions was determined (Loosjes, 1976):

$$ND = 1.9 \times NK$$

where: ND = number of damaged onions per day,

NK = number of killed onions per day.

Figure E3. Relationship between bulb diameter and consumption (represents migration and feeding rate).

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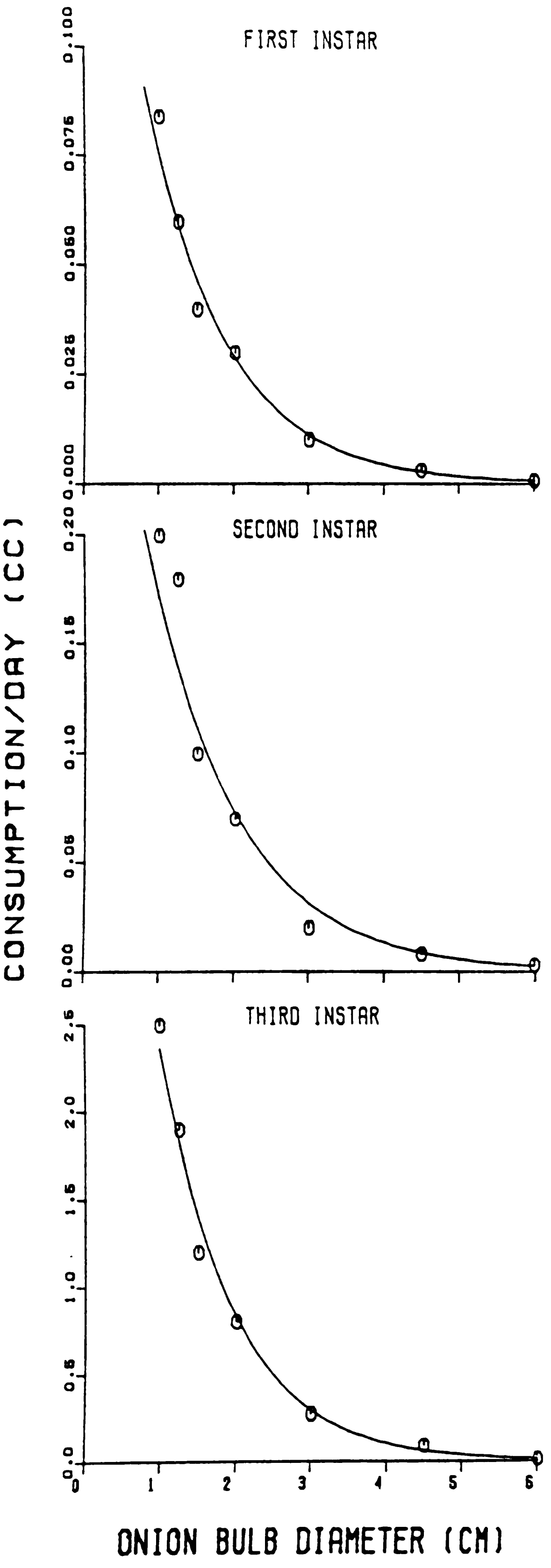
FIRST INSTAR
SECOND INSTAR
THIRD INSTAR
CONSUMPTION/DAY (CC)
0.000
0.025
0.050
0.075
0.100
0.00
0.05
0.10
0.15
0.20
0.0
0.5
1.0
1.5
2.0
2.5
0
1
2
3
4
5
6
ONION BULB DIAMETER (CM)

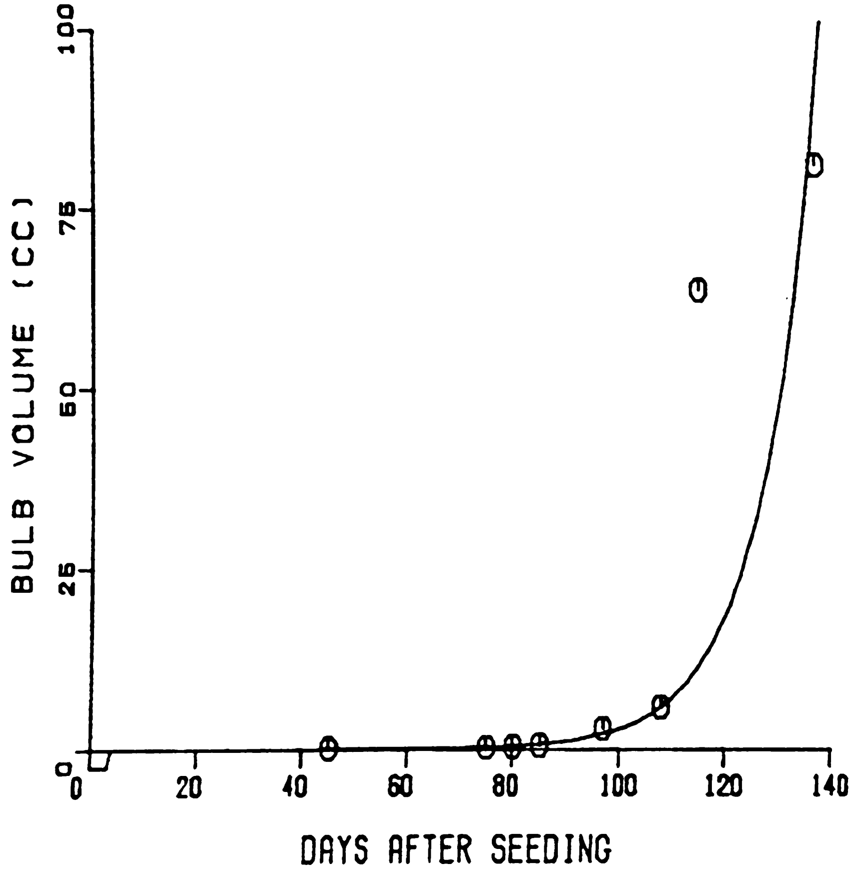

Figure E4. Onion bulb volume as a function of time since planting.

Damaged onions were assigned a percent damage according to a negative exponential equation where 50% of the damaged onions (ND) were assumed to be 90% consumed.

$$NO = NO + (ND \times .5) \times .1, .2, .3, .4, .5, .6, .7, .8, .9.$$

This gave a damage distribution of 9 classes of partial onion consumption. Remaining onion volume within these classes was available for consumption the next day. The percent of volume not consumed was converted back to healthy onions, based on the assumption that the onion maggot larva usually migrates only when the onion has been consumed (Rabinge' 1976). Calculation of this number of damaged onions is necessary as an input for the economic subcomponent.

Furrow and foliar insecticide applications were available management options. An in-furrow application that results in 98% mortality on all larval stages (A. Wells, 1979) can be made at planting time. A foliar spray directed at the adult onion maggot may also be applied at various times during the season. Depending on the particular spray chosen, the mortality factor of adult onion maggots and A. pallipes follows an exponential decay curve with a half-life of 1, 2 or 4 days (Matsumura, personal communication, Department of Entomology, Michigan State University, February 1978).

$$PMORT = 1.0 - .96 * EXP ((-CPDAY) * (.69314/FREQ))$$

where: PMORT = mortality due to insecticide spray,

CPDAY = number of days between sprays,

FREQ = residual effectiveness of spray applied

(Malathion - 1 day, Parathion - 2 days, Diazinon - 3 days).

At harvest the total number of onions remaining in the field (NO) was converted to 100 pound quantities (440 onions per cwt) and multiplied by the market price (\$6.00) to give a gross profit for the end of the growing season. The net profit was obtained by deducting the costs of any pesticides used and the fixed costs of production, estimated to be \$1200.00, from the gross profit.

$$NETP = ((NO/440) * 6.0) - (CF + CS)) - 1200.$$

where: NETP = net profit,

NO = number of healthy onions remaining in field,

CF = cost of a furrow insecticide,

CS = cost of foliar insecticide.

Viewing a population of organisms as they undergo development, one finds that the developmental period is distributed over time. That is, for the aggregate flows, individual entities have different lag times so that while entities may enter the process at the same point in time, the output flow will be distributed over time. This is usually due to genetic differences among individuals and varying microclimatic conditions. A method of modeling this type of aggregative behavior can be performed by the use of time-varying distributed delays (Manetsch and Park 1977). Simulating development with the various mortalities taken into account, a modified version of the Manetsch and Park (1977) routine was used (Fulton 1978).

The basic assumption in using time-varying distributed delays to simulate insect development is that the rate at which the aggregate passes through a particular stage is distributed with a specific mean and associated variance. Depending on the characteristics of the particular process in which the distributed delay model is used, the parameters D and K are chosen where D is the

mean lag time (D = D(t), the mean of the probability density function describing the transit times of the population passing through the process) and K is the order of the delay specifying a member of the "Erlang" family of density functions used to distribute the transit times of the individuals of the population. The Erlang density function is given by:

$$f(\tau) = !D(t)/kl^{k} (\tau)^{(k-1)} \exp !-k\tau/D(t)l \; / \; (k-1)½$$

where: τ = lag time.

The mean and variance of the random variable τ are, respectively:

$$\mu_{\tau}^{2} = D(t)^{2}/k$$

As k approaches infinity, for a given value of D, the distribution degenerates to a normal distribution with mean D and zero variance (i.e., a discrete delay of length D).

One important property of this delay model is that it does not conserve flow--that is, a proportion of the entities that enter the delay will be lost along the process. The storage, Q_i, or the number of entities in each stage of the delay, and at any time t, is:

(1) $Q_i(t) = !D(t)/kl \; R_i(t), \quad i = 1, \ldots, k$

where: R_i = rate out of the ith stage,

D = mean delay time,

k = the order of the delay process.

The rate of change of Q_i is the net flow into the ith stage:

(2) $!dQ_i(t)/dtl = R_{i+1}(t) - R_i(t) - L_i(t), \quad i = 1, \ldots, k$

where: R_{k+1} = RIN, the rate into the delay (Fig. 7),

L_i = storage loss rate from the ith stage.

(3) $L_i(t) = PLR(T) * Q_i(t)$

and PLR is a mortality constant or a function of time, thus there results a proportional loss rate for the storage in the whole delay.

So from (1), (2) and (3),

(4) $!dQ_i(t)l \,/\, dt = (1/k)\,(D(t) * !dR_i(t)l \,/\, dt + R_i(t) * !dD(t)l \,/\, dt)$

Upon rearrangement of terms, a first-order differential equation modeling the i^{th} stage of a k^{th}-order delay with storage losses and variable delay time becomes:

(5) $R_{i+1}(t) = !D(t)/dt * !dR_i(t)/dtl + !1+(1/k) * (dD(t))/k * PLR(t) * R_i(t)$

This can be solved numerically using Euler's integration approximation and taking

$$!dD(t)/dt \simeq !D\,(t+DT) - D(t)l \,/\, DT$$

by (6) $R_i(t) \simeq R_i(t-DT) + DT \simeq !k/D(t-DT)l * !R_{i+1}(t-DT) - R_i(t-DT) *$
$(1 + DD(t-DT) + (D(t-DT))/k * PLR\,(t-DT))l$

where: $DD(t-DT) = 1/k * !D(t) - D(t-DT)l \,/\, DT$

and DT is the integration step size and the simulation time increment.

In the light of modeling a continuous process as opposed to a discrete one, the assumption is made that temperature-dependent mortalities operated continuously. This implies that:

$Pt = Po\ e^{at}$

where: t = time,

a = instantaneous survival

Po = initial population,

Pt = population at time t.

Fulton (1978) developed the idea of instantaneous survival being a linear, exponential relationship with temperature. This idea enabled mortalities to be implemented in the delay technique.

In trying to apply a survival function over the entire life stage, a complication arose since the time spent within the stage was also a function of temperature. The interaction was eliminated by using the instantaneous survival rate as the proportional loss rate.

$Pt + DT = Pt\ e^{PLR}$

where: $PLR = a + b * \text{temperature}$

The instantaneous survival rate was used to compute half-lives of the individuals under the existing temperature regime. By setting $Pt/Po = e^{at} = 1/2$, the half-life became $t = -(\ln 2/a)$ is the half-life. This half-life represents a median survival time.

The following relationships between instantaneous survival and temperature were used in the model (depicted in Figure E5):

egg survival = .16 - .03 temperature ($r^2 = .828$, $p < .002$),

first instar survival = 1. - .02 temperature ($r^2 = .973$, $p < .05$),

second instar survival = .5 - .01 temperature ($r^2 = .883$, $p < .01$),

third instar survival = .11 - .002 temperature ($r^2 = .989$, $p < .005$),

The onion maggot component was responsible for simulating the passage of individuals through the various age classes, the effects of different mortality factors, and supplying the other components with numbers of onion maggots in various age classes. Two important assumptions were made: (a) density-dependent relationships did not operate in the onion maggot system, and (b) all female adults were mated and fertilized. These assumptions were made purely in response to possessing insufficient data in order to model the interactions. The time-varying, distributed delays that yield the rates at which aggregates are moving through the age classes were dependent on the mean developmental

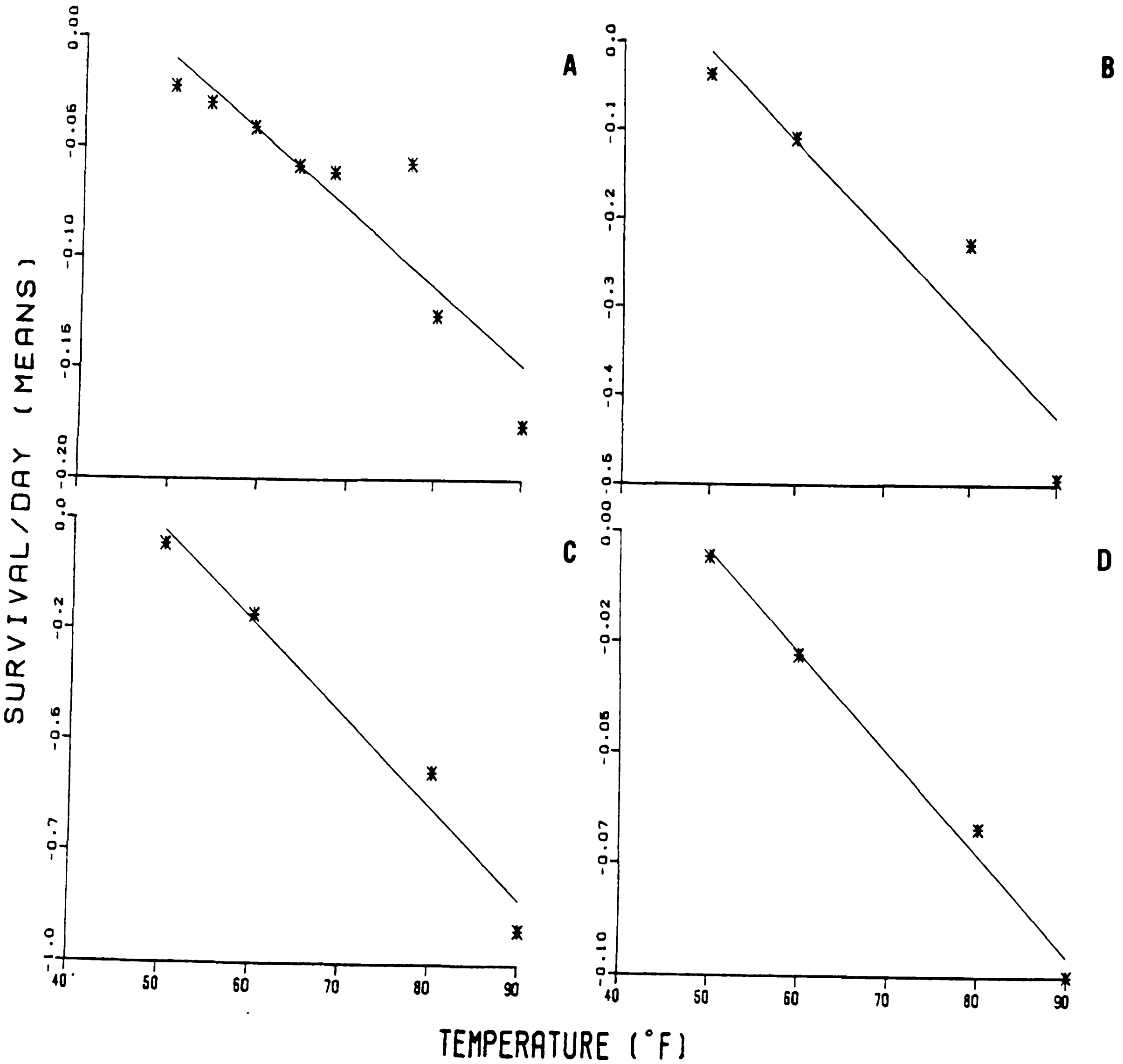

Figure E5. Instantaneous survival rate as a function of constant temperature (°F), A = egg stage, B = first instar, C = second instar, and D = third instar.

times. The onion maggot component for the most part was executed on a per-DT basis. The mortality acting within the larval stages, adult male stage, preovipositional adult stage, mature female adult stage, and egg stage was a product of the "natural" temperature-dependent mortality and the mortality due to pesticides. These were assumed to be independent events. The pupal mortality depended solely on soil temperature. The overwintering delay represented the number that entered diapause. The subroutine "diapause" converted pupae to diapausing pupae, depending on degree-day accumulations. The three generations were tracked by accumulating degree-days. Ten, 67 and 100% of the pupae were put into diapause from each generation, respectively (Perron 1972). The constant proportion was used to "black-box" the diapause process since deterministic data dependent on temperature and day length was inconclusive and contradictory.

Degree-days were also used to place mature females into fecundity classes. The number of eggs oviposited by a gravid female was tied to the temperature regime that the individual was exposed to during preoviposition (Loosjes 1976). The approximate length of the preovipositional period for onion maggot is 120 degree-days. This was calculated by averaging the temperatures of those past days that were involved in accumulating 120 degree-days.

TOTAL = TOTAL + !2.0 * MAXTEMP (I) + MINTEMP (I)1 + !MINTEMP (I+1)1/4.0

where: TOTAL = sum of average daily temperatures of preovipositional period (120 degree days).

Five fecundity delays were used at 50¼, 60¼, 70¼, 80¼ and 90¼F. If a group of females underwent preovipositional development between 45¼ and 55¼F, they were put into delay 50¼F. Similarly, if an aggregate of females were exposed to

an average temperature of 74¼F during preovipositional development, they were put into delay 70¼F, etc.

$$\mathrm{BIN} = (.5 + \mathrm{TOTAL}/S/10.0) - 4$$

where: BIN = developmental class (1, 2, 3, 4 or 5, corresponding to classes of 50¼, 60¼, 70¼, 80¼ and 90¼ developmental delays)

S = number of days for preovipositional period.

Each day the total number of females remaining in each delay would oviposit an average number of eggs for their fecundity class.

$$\mathrm{NUMEGG} = \sum_{i=1}^{5} \mathrm{NROLEF(I)} * \mathrm{NT}$$

where: I = developmental class 1 through 5,

NT = .75, 2.5, 4.0, .5 or 0, corresponding to developmental class,

NROLEF(I) = number of ovipositing onion maggot females in each developmental class (I),

NUMEGG = total number of eggs oviposited per day.

The spatial distribution of the eggs was derived from data of Perron (1972) who gave probabilities for eggs found in the soil and on the plant (65% in the soil).

The parasitoid component involved a structure (use of delays for the various life stages) similar to the onion maggot component. The parasite attack model was a modified version of Griffith and Holling (1969).

$$\mathrm{ANHA} = \mathrm{ANO} * !!1-(1+A*\mathrm{TAG}*P)1/(\mathrm{ANO}*\mathrm{AK})1 - \mathrm{AK}$$

where: ANHA = total number of hosts attacked during DT,

ANO = prey density,

A = number of attacks per unit time,

TAG = total time available for generating attacks,

P = parasitoid density,

AK = dispersion coefficient, "k" of negative binomial (parasite).

The model used the number of available hosts, along with the number of adult parasitoids, to generate a percent parasitism.

PATT = ANHA/(ANO*2.0/SPC) * .1

RESULTS AND DISCUSSION

It was essential to show that the model adequately met known features of onion maggot biology before any parameters could be varied for effects. These features included:

1) The onion maggot has three overlapping generations per season in Michigan.
2) The development of the life stages are temperature controlled and peaks of adult emergence may be predicted through degree-day accumulations.
3) The maximum damage to onions usually occurs early in the season when bulbs are small.

Figure E6A shows how the model adequately simulated the first two of these conditions. Given an initial population of 1000 pupae per acre, three, non-overlapping, generations were simulated due to the relatively short time spent in preoviposition. The peaks of these curves represent maximum adult emergence and occur at degree-day accumulations of 500, 2200 and 3500 for the East Lansing, Michigan, weather data of 1977. These values agree with those of Eckenrode et al. (1975) who reported a thermal unit accumulation of 712, 1899 and 3157 for the first, second and third broods, respectively.

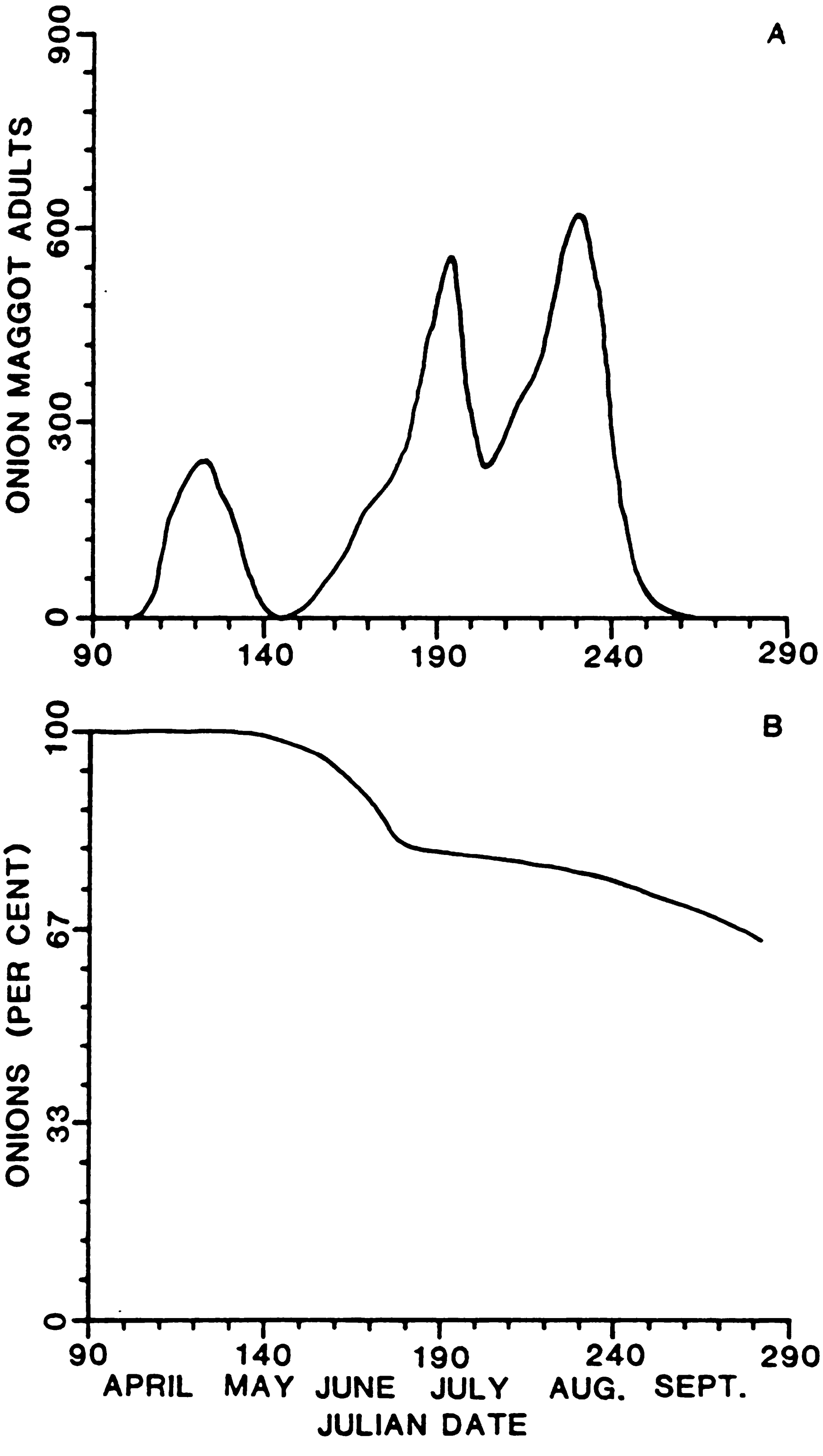

Figure E6. Simulation with an initial overwintering population of 1000 OM pupae per acre. A, number of adults in preovipositionary classes; B, percent of onions not damaged by maggots over time.

The third condition was also simulated, as illustrated by plotting the percent of onions left in the field versus the number of days in the growing season (Figure E6B). Early in the season, damage increased as total numbers of larvae increased. Damage then tended to level off even though the larval population continued to increase in the latter part of the season. The response was due to the increase in onion bulb size, which resulted in greater tolerance to larval feeding.

Given that the model simulated onion maggot development and consumption correctly, three simulations were made to analyze:

1) the effect of a parasitoid on onion maggot densities and onion yield,
2) the effect of foliar sprays on onion maggot, parasitoid densities and onion yield, and
3) the importance of the timing of the first foliar spray.

For the first run, an initial population of 1000 pupae and 500 parasitized pupae per acre were used. There were three distinct peaks of reproducing parasite populations (Figure E7A) that were closely synchronized with the preoviposition peaks of the previous run (Figure E6A).

The parasitoid population decreased during the second and third generation of preoviposition onion maggots, from peaks of 515 to 220 and from 610 to 200 over the previous run (Figure E7B). The first generation was not affected. As a result of the decrease in the onion maggot population later in the season, late damage to onions was less. This simulation resulted in a net profit of $298.00 per acre, as opposed to $9.00 without parasitoids.

In the second analysis, a spray of malathion was applied on day 50, and every 40 days thereafter, to an initial population of 10,000 pupae and 2000

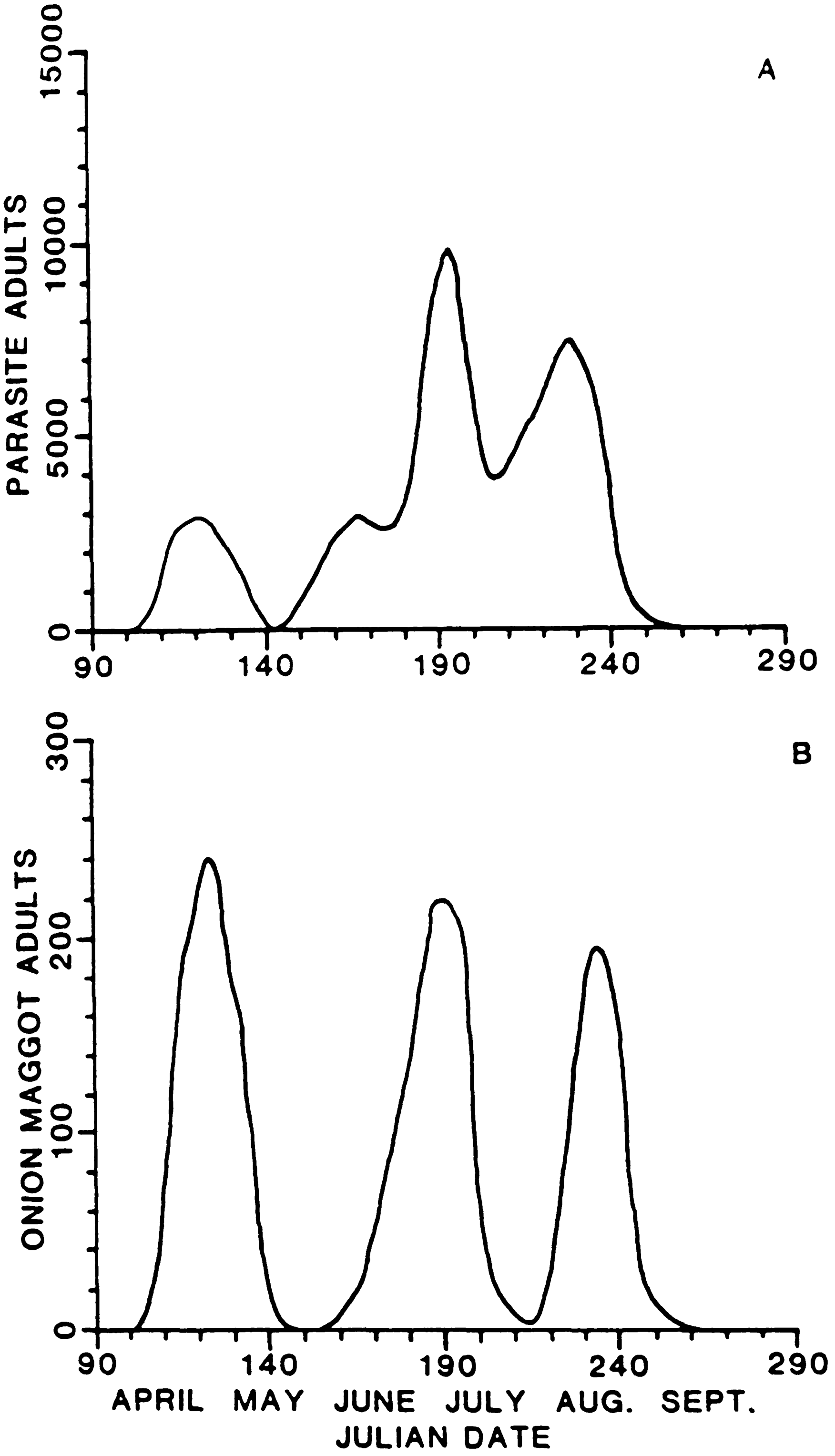

Figure E7. Simulation with an initial overwintering population of 1500 pupae of which 500 are parasitized. A, number of adult parasitoids; B, number of OM adults in preovipositionary classes.

parasitized pupae per acre. Day 50 was picked for the first spray date to coincide with the end of the first preoviposition peak of the onion maggot, so that the resultant reproducing adult population would be sprayed at an optimum time. By spraying every 40 days thereafter, each successive generation of reproducing adults would also be sprayed at an optimum time. Onion maggot densities decreased considerably (Figure E8A). The first generation of reproducing parasitoids, however, had already reached a peak at day 50 and the malathion spray had little effect on the first generation adults (Figure E8B). The second generation of parasitoids was reduced a little by the residual effect of the day 50 spray, but again was not greatly reduced by the next spray at day 90, since the population had already peaked. The $172.18 net profit was low due to larval feeding early in the season. The number of parasitized, diapausing pupae, however, was high at the end of the season compared to onion maggot densities and could be expected to have an important effect the following year.

The third analysis investigated whether the timing of the first spray was critical to onion maggot and parasitoid populations. A spray of malathion was applied on day 80, and every 40 days thereafter, to an initial population of 10,000 onion maggot pupae and 2000 parasitized pupae per acre. The first spray was applied after the build-up of reproducing onion maggots. As a result, the second generation of onion maggots was not decreased as much as it was in the previous run, and onion maggot densities remained higher late in the season (Figure E9A).

The reproducing parasitoid population, however, was not reduced by the first spray until halfway through their second generation (Figure E9B). The parasitoid population remained high to the end of the season. Although the high parasitoid population would reduce numbers of onion maggots the next year, the outcome for the current year was a net loss of $1100.00 per acre.

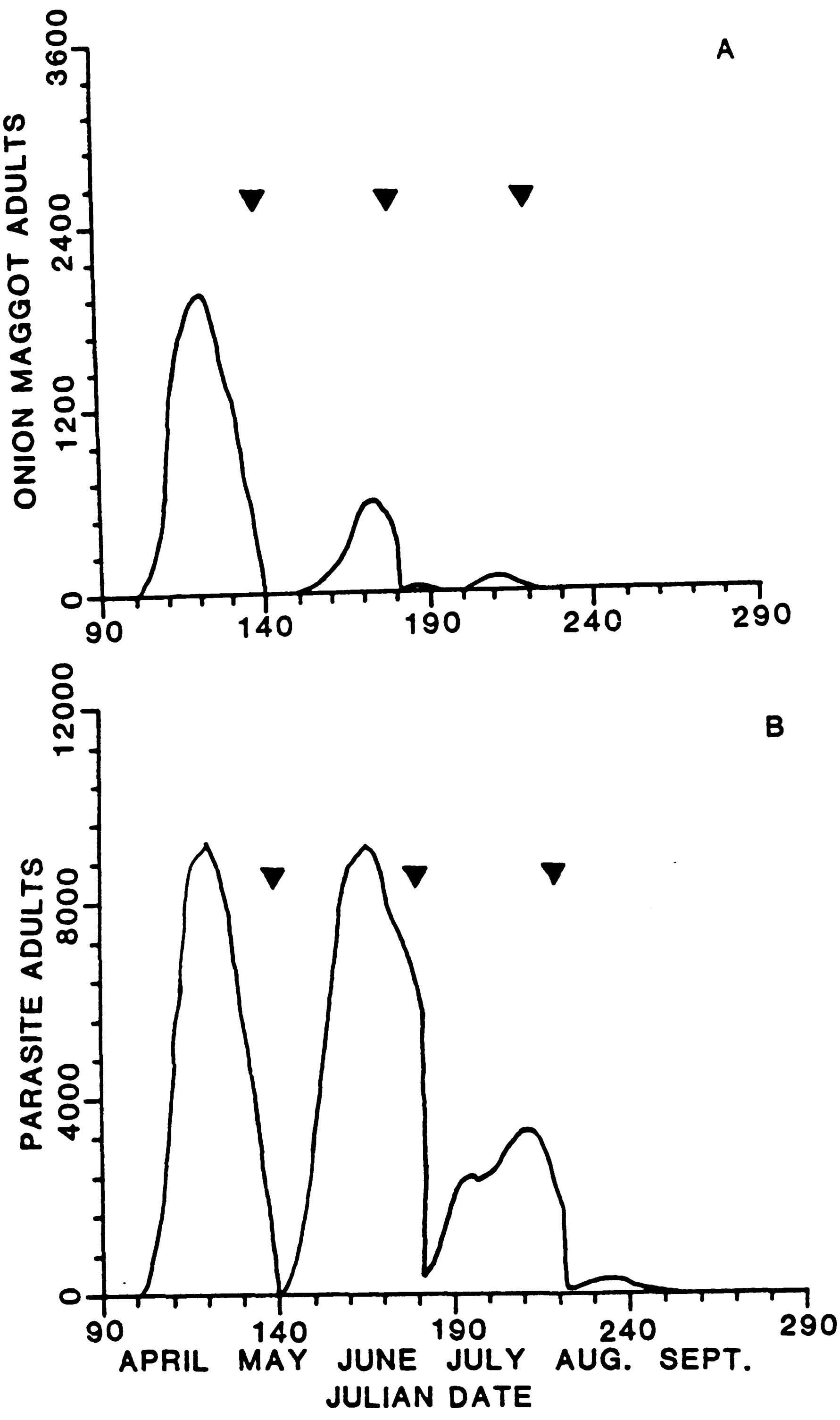

Figure E8. Simulation with an initial overwintering population of 12,000 OM pupae of which 2000 were parasitized. A foliar spray of malathion was applied at day 140, and every 40 days thereafter (▼=spray date). A, number of OM adults in preovipositionary classes; B, number of adult parasitoids.

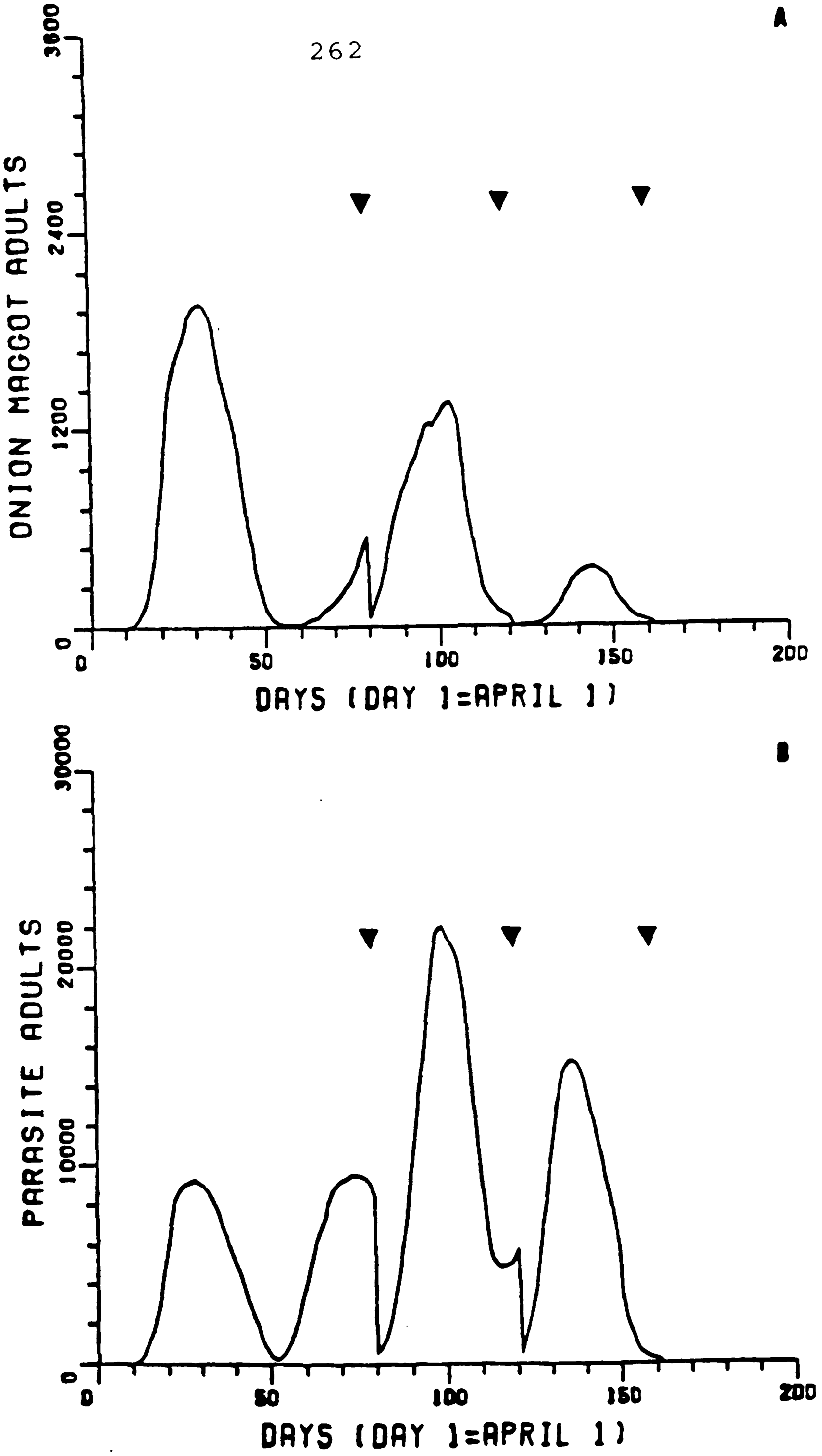

Figure E9. Simulation run with an initial overwintering onion maggot population of 12,000 pupae of which 2000 are parasitized. A foliar spray of malathion was applied at day 80 and every 40 days thereafter (▼ = spray date).

Validation of the onion maggot submodel has been undertaken by Whitfield (1981). He found that first generation emergence of onion maggot adults was predicted quite well by the model when modified to integrate actualfield soil and air temperatures. Predicted second and third generation onion maggot adult emergence was found to lag several days behind observed emergence. Carruthers (1981) corrected for these discrepancies by adding a submodel of E. muscae infection. The phenology of immature stages predicted by the model did not track the field observations well (Whitfield 1981) except for the pupal stage. Timing of peak first generation incidence coincided nicely but predicted second generation phenology lagged behind the observed incidence. Whitfield (1981) hypothesizes that this may be due to the use of an inaccurate developmental base temperature. Another major source of error could be the instantaneous survival rates which were derived from laboratory growth chamber studies. The assumption made in treating mortality in this manner is that death is the result of acquiring a fixed number of mortality units (synonymous with modeling the developmental process by summing heat units), which may not be an adequate methodology if stress is a reversible process.

CONCLUSION

The model adequately simulates the development of the life stages of the onion maggot and is sensitive to changes in biotic and abiotic parameters. It has revealed interesting information and relationships about onion maggot population dynamics as well as the effect of carefully timed insecticide sprays to avoid parasitoid mortality and the effect of onion bulb size on damage estimates early in the season. At the same time, it has presented areas where more information

is needed, such as migration, damage distributions and density-dependent effects.

The model does not satisfactorily portray migration by the onion maggot larvae from plant to plant, nor migration or emigration by the adult. An ongoing research project at Michigan State University will provide the data to include these components at a later date. At present, the model represents a relatively small closed system and, as such, is limited.

The damage distribution assumed in the model was random, although data suggest a clumped distribution, especially later in the season (Carruthers, personal communication, Department of Entomology, Michigan State University, 1978). Damage distribution can affect consumption rates, survivorship and parasitism. As a result, a damage distribution component is essential to the perfection of the model.

It was also assumed that there are no density-dependent effects. No information is available on density-dependent features at this time, however, such effects, if present, would undoubtedly influence all areas of the model.

Further work on the sub-components of the onion ecosystem, presently in progress, will eventually lead to an overall model that can be used in a pest management approach to pest control.

The model was coded in Fortran IV and designed specifically to be run on the Michigan State University CDC 6500 computer system. A listing of the code is available upon request.

ACKNOWLEDGMENTS

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Table E. 1

```
      PROGRAM MAGGOT(INPUT,OUTPUT,TAPE60=INPUT,TAPE61=OUTPUT,TAPE1,TAPE
     +8,TAPE3,TAPE5)
*  COMPUTER SIMULATION MODEL FOR THE ONION MAGGOT, HYLEMYA ANTIQUA
*     (MEIGEN).  THIS MODEL IS A MODIFIED VERSION OF A MODEL ORIGINALLY
*     PREPARED BY FRANK DRUMMOND, JOHN VALENTI, AND GARY WHITFIELD IN
*     SYSTEM SCIENCE 843.  THE MAIN PROGRAM (MAGGOT) CALLS A NUMBER OF
*     FUNCTIONS AND SUBROUTINES, AND A CONTINUOUS TIME MODEL IS
*     APPROXIMATED USING A DISCRETE APPROACH.  THE SIMULATION UTILIZES
*     PREVIOUSLY PUBLISHED DATA FROM MANY SOURCES TO DRIVE A CHAIN OF
*     TIME VARYING DELAYS WITH ATTRITION.  POPULATION DENSITIES AND
*     INSECTICIDE USE AND TIMING CAN BE MANIPULATED.  AIR AND SOIL
*     TEMPERATURE DATA CAN BE INPUT DIRECTLY.
*
*   MAIN PROGRAM MAGGOT
*   GLOSSARY
*
*      AFL=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR ADULT FEMALE
*      APEST=FOLIAR PESTICIDE (1=MALATHION, 2=PARATHION,3=DIAZINON)
*      ARGE=(DATA) TEMPERATURE ARGUMENT FOR EGG DEVELOPMENT
*      ARGES=(DATA) TEMPERATUR ARGUMENT FOR EGG SURVIVAL
*      ARGL1=(DATA) TEMPERATURE ARGUMENT FOR FIRST INSTAR DEVELOPMENT
*      ARGPF=(DATA) TEMPERATURE ARGUMENT FOR PUPAL DEVELOPMENT
*      ARGPS=(DATA) TEMPERATURE ARGUMENT FOR PUPAL SURVIVAL
*      ARGSL1=(DATA) TEMPERATURE ARGUMENT FPR FIRST INSTAR DEVELOPMENT
*      BIN=EGG CLASS (1-5)
*      DDTOT=DEGREE DAY TOTAL (AIR)
*      DEADM=NUMBER OF DEAD ADULT MALES
*      DEAD1=NUMBER OF DEAD ADULT FEMALES OF CLASS 1
*      DEAD2=NUMBER OF DEAD ADULT FEMALES OF CLASS 2
*      DEAD3=NUMBER OF DEAD ADULT FEMALES OF CLASS 3
*      DEAD4=NUMBER OF DEAD ADULT FEMALES OF CLASS 4
*      DEAD5=NUMBER OF DEAD ADULT FEMALES OF CLASS 5
*      DEGDAYS=DEGREE DAYS (AIR)
*      DEGG=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR EGGS
*      DELAFL=DEVELOPMENT TIME OF REPRODUCING FEMALES
*      DELEA=DEVELOPMENT TIME OF EGGS (AIR)
*      DELEAS=DEVELOPMENT TIMES OF EGGS (SOIL)
*      DELL1=DEVELOPMENT TIME OF FIRST INSTAR
*      DELL2=DEVELOPMENT TIME OF SECOND INSTAR
*      DELL3=DEVELOPMENT TIME OF THIRD INSTAR
*      DELMLG=DEVELOPMENT TIME OF ADULT MALES
*      DELMP=DEVELOPMENT TIME OF MALE PUPAE
*      DELPOP=DEVELOPMENT TIME OF PRE-OVIP FEMALES
*      DELPPF=DEVELOPMENT TIME OF FEMALE PUPAE
*      DELPOPP=PREVIOUS DELPOP
*      DL1=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR FIRST INSTAR
*      DL2=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR SECOND INSTAR
*      DL3=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR THIRD INSTAR
*      DM=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR MALE ADULTS
*      DPF=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR FEMALE PUPAE
*      DPM=(DATA) DEVELOPMENTAL TIME ARGUMENT FOR MALE PUPAE
*      DT=TIME INCREMENT (DELTA T)
*      EGGP=EGGS ON PLANT
*      EGGS=EGGS IN SOIL
*      FL3=THIRD INSTARS (FEMALES)
*      FP=FEMALE PUPAE
*      FPEST=FURROW INSECTICIDE (0=NONE, 1=DYFONATE, 2=ETHION)
*      FPS=SURVIVAL VALUE FOR FEMALE PUPAE
*      FREQ=FREQUENCY OF SPRAY APPLICATION
*      IDAY=(JULIAN DATE-90)
*      IPOP=NUMBER OF PRE-OVIP ADULTS
*      KEA=K FOR EGGS
*      KFL=K FOR REPRODUCING ADULTS
*      KPP=K FOR PUPAE
*      KL1=K FOR FIRST INSTAR
*      KL2=K FOR SECIND INSTAR
*      KL3=K FOR THIRD INSTAR
*      KM=K FOR MALE ADULTS
*      KP=K FOR PRE-OVIP ADULTS
*      L1=TOTAL NUMBER OF FIRST INSTAR
*      L1A=NUMBER OF FIRST INSTAR ON PLANT
*      L1S=NUMBER OF FIRST INSTAR IN SIOL
*      L2=NUMBER OF SECOND INSTAR
*      L3=NUMBER OF THIRD INSTAR
*      MA=NUMBER OF MALE ADULTS
*      MAXTEMP=MAXIMUM DAILY TEMPERATURE
*      MINTEMP=MINIMUM DAILY TEMPERATURE
*      MLG=SURVIVAL VALUE FOR ADULT MALES
*      ML3=MALES THIRD INSTAR LAVAE
*      MP=NUMBER OF MALE PUPAE
*      NEGGA=TOTAL STORAGE OF EGGS (AIR)
*      NEGGS=TOTAL STORAGE OF EGGS (SOIL)
*      NFL3=TOTAL STORAGE FEMALE THIRD INSTAR
*      NFP=TOTAL STORAGE OF FEMALE PUPAE
*      NL1=TOTAL STORAGE OF FIRST INSTAR
*      NL2=TOTAL STORAGE OF SECOND INSTAR
*      NL3=TOTAL STORAGE OF THIRD INSTAR
*      NML=TOTAL STORAGE OF MALE ADULTS
*      NML3=TOTAL STORAGE OF MALE THIRD INSTAR
*      NMP=TOTAL STORAGE OF MALE PUPAE
```

Table E. 1 continued

```
*       NPOP=TOTAL STORAGE OF PRE-OVIP ADULTS
*       NROLEF=TOTAL STORAGE OF REPRODUCING ADULTS
*       NROLEF1=STORAGE OF REPRODUCING ADULTS (CLASS 1)
*       NROLEF2=STORAGE OF REPRODUCING ADULTS (CLASS 2)
*       NROLEF3=STORAGE OF REPRODUCING ADULTS (CLASS 3)
*       NROLEF4=STORAGE OF REPRODUCING ADULTS (CLASS 4)
*       NROLEF5=STORAGE OF REPRODUCING ADULTS (CLASS 5)
*       NUMEGG1=STORAGE OF EGGS (CLASS 1)
*       NUMEGG2=STORAGE OF EGGS (CLASS 2)
*       NUMEGG3=STORAGE OF EGGS (CLASS 3)
*       NUMEGG4=STORAGE OF EGGS (CLASS 4)
*       NUMEGG5=STORAGE OF EGGS (CLASS 5)
*       PE=RATE OF ADULT EMERGENCE
*       PMORT=MORTALITY DUE TO PESTICIDE (FURROW)
*       PMORTD=EXPONENTIAL DECAY OF PMORT
*       PMORTE=MORTALITY DUE TO PESTICIDE (FOLIAR)
*       PMORTED=EXPONENTIAL DECAY OF PMORTE
*       POP=DEVELOPMENT VALUE FOR PRE-OVIP ADULTS
*       RAM1=RATE OF REPRODUCING ADULTS (CLASS 1)
*       RAM2=RATE OF REPRODUCING ADULTS (CLASS 2)
*       RAM3=RATE OF REPRODUCING ADULTS (CLASS 3)
*       RAM4=RATE OF REPRODUCING ADULTS (CLASS 4)
*       RAM5=RATE OF REPRODUCING ADULTS (CLASS 5)
*       RE=RATE OF EGGS (SOIL)
*       REA=RATE OF EGGS (AIR)
*       RFP=RATE OF FEMALE PUPAE
*       RLM3=RATE OF MALE THIRD INSTAR
*       RL1=RATE OF FIRST INSTAR
*       RL2=RATE OF SECIND INSTAR
*       RL3=RATE OF FEMALE THIRD INSTAR
*       RMA=RATE OF MALE ADULTS
*       RMP=RATE OF MALE PUPAE
*       RO=NUMBER OF REPRODUCING ADULTS
*       RPOP=RATE OF PRE-OVIP ADULTS
*       SEGG=SURVIVAL VALUE FOR EGGS
*       SL1=SURVIVAL VALUE FOR FIRST INSTAR
*       SL2=SURVIVAL VALUE FOR SECOND INSTAR
*       SL3-SURVIVAL VALUE FOR THIRD INSTAR
*       ST=SOIL TEMP (PER DT)
*       STEMP=SOIL TEMP (PER 2 HOURS)
*       SUMFP=TOTAL FEMALE PUPAE
*       SUMLT=TOTAL LARVAE
*       SUML1=TOTAL FIRST INSTAR
*       SUML2=TOTAL SECOND INSTAR
*       SUML3=TOTAL THIRD INSTAR
*       SUMMAPP=TOTAL MALE PUPAE
*       SUMNML=TOTAL MALE ADULTS
*       SUMNPO=TOTAL PRE-OVIP ADULTS
*       SUMNRO=TOTAL OF ADULTS IN CLASSES 1-5
*       SUMOM=TOTAL FEMALE ADULTS
*       SUMRO=TOTAL REPRODUCING ADULTS
*       SUREGAD=INSTANTANEOUS SURVIVAL OF EGGS (AIR)
*       SUREGGA=SURVIVAL OF EGGS (AIR)
*       SUREGGD=INSTANTANEOUS SURVIVAL OF EGGS (SOIL)
*       SUREGGS=SURVIVAL OF EGGS (SOIL)
*       SURFLD=SURVIVAL OF REPRODUCING FEMALES
*       SURFPS=SURVIVAL OF FEMALE PUPARE
*       SURFPSD=INSTANTANEOUS SURVIVAL OF FEMALE PUPAE
*       SURL1=SURVIVAL OF FIRST INSTAR
*       SURL1D=INSTANTANEOUS SURVIVAL OF FIRST INSTAR
*       SURL2=SURVIVAL OF SECOND INSTAR
*       SURL2D=INSTANTANEOUS SURVIVAL OF SECOND INSTAR
*       SURL3=SURVIVAL OF THIRD INSTAR
*       SURL3D=INSTANTANEOUS SURVIVAL OF THIRD INSTAR.
*       SURMLD=SURVIVAL OF MALES
*       SURPOPD=SURVIVAL OF PRE-OVIP FEMALES
*       T=TEMP PER DT (AIR)
*       TOMP=NUMBER IF STARTING PUPAE
*       TOTEGG=TOTAL EGGS (AIR AND SOIL)
*       TOTPUP=TOTAL PUPAE (MALE AND FEMALE)
*       TPOP=TOTAL ADULTS (MALE AND FEMALE)
*       TPP=TOTAL STORAGE OF PUPAE (MALE AND FEMALE)
*
*               COMMON BLOCKS
*
      COMMON/PESTS/PDAY,PMORTE,A,APEST,FREQ,MFREQ
      COMMON /WEATHER/DEGDAYS(300),MAXTEMP(300),MINTEMP(300)
*
*                TYPE DECLARATIONS FOR MAIN PROGRAM
*
      TYPE REAL NROLEF,IPOP,NPOP,NFP,MA,MP
      TYPE REAL NMP,NFL3,ML3,NML3,L3,L2,L1,NL3,NL2
      TYPE REAL NL1,L1S,L1A,NEGGSS,NEGGA
      TYPE REAL NROLEF1,NROLEF2,NROLEF3,NROLEF4,NROLEF5
      TYPE REAL NML,NUMEGG1,NUMEGG2
      TYPE REAL NUMEGG3,NUMEGG5,NUMEGG4
      TYPE REAL MLG
      TYPE INTEGER BIN,PDAY,DDTOT
      TYPE INTEGER DEGDAYS
      TYPE REAL MAXTEMP,MINTEMP,MFREQ
```

Table E. 1 continued

```
      TYPE INTEGER TOMP,FPEST,APEST,FREQ
*
*               DIMENSION STATEMENTS FOR MAIN PROGRAM
*
      DIMENSION DEGG(7)
      DIMENSION DPF(7)
      DIMENSION SEGG(8)
      DIMENSION SL1(4)
      DIMENSION SL2(4)
      DIMENSION SL3(4)
      DIMENSION AM(5),
      DIMENSION RAM1(10),RAM2(10),RAM3(10),RAM4(10),RAM5(10)
      DIMENSION AFL(6)
      DIMENSION DPM(7)
      DIMENSION RMA(10)
      DIMENSION POP(5)
      DIMENSION MLG(5)
      DIMENSION DL1(7)
      DIMENSION ARGE(7)
      DIMENSION ARGL1(7)
      DIMENSION ARGPF(7)
      DIMENSION FPS(5)
      DIMENSION ARGPS(5)
      DIMENSION ARGES(8)
      DIMENSION ARGSL1(4)
      DIMENSION RL3(10),RL2(10),RL1(10)
      DIMENSION RFP(20)
      DIMENSION RMP(20)
      DIMENSION RLM3(10)
      DIMENSION RE(10)
      DIMENSION REA(10)
      DIMENSION RPOP(10)
      DIMENSION STEMP(13)
      DIMENSION IVAL(1)
      DIMENSION IREADIN(1)
      DIMENSION DL2(5)
      DIMENSION DL3(5)
*
*               DATA STATEMENTS FOR MAIN PROGRAM
*
      DATA DL2/7.6,5.0,3.0,2.5,3.0/
      DATA DL1/7.1,4.3,3.5,2.5,2.2,1.6,1.7/
      DATA DEGG/10.0,7.0,5.6,4.0,3.2,2.4,2.6/
      DATA DL3/27.8,14.3,8.6,7.6,8.6/
      DATA DPF/50.0,33.0,25.0,20.0,17.0,12.0,13.0/
      DATA SEGG/-0.023,-0.031,-0.042,-0.059,-0.062,-0.058,
     + -0.12634,-0.176/
      DATA SL1/-0.0607,-0.2157,-0.5727,-0.92262/
      DATA SL2/-0.0378,-0.1124,-0.23104,-0.49515/
      DATA SL3/-0.0058,-0.0280,-0.0672,-0.10948/
      DATA DPM/47.0,30.0,22.0,17.0,14.0,9.0,10.0/
      DATA AFL/112.,55.,35.,22.,16.,10./
      DATA POP/22.0,10.0,7.0,5.0,3.0/
      DATA MLG/72.8,35.75,22.75,14.3,3.9/
      DATA ARGE/50.,55.,59.,64.,68.,77.,85./
      DATA ARGL1/50.,55.,59.,64.,68.,77.,85./
      DATA FPS/-.007,-.007,-.006,
     +  -.007,-.02/
      DATA ARGPS/50.0,60.0,70.0,84.0,90.0/
      DATA ARGPF/50.,55.,59.,64.,68.,77.,83./
      DATA ARGES/50.,54.,59.,63.5,68.,77.,80.,90./
      DATA ARGSL1/50.0,60.0,80.0,90.0/
*
*               INITIALIZE VARIOUS VARIABLES
*
      DM=DET=0.0
      DELPPF=DELPAFL=DELPPOP=1.0
      DELPMP=1.0
      DELPMLG=1.0
      A=0.0
      PDAY=0
      K5=214
      FREQ=1
      DDTOT=0
      K=10
      IPOP=0.0
      RO=0.0
      EGGSS=NEGGSS=EGGA=L1=L2=L3=0.0
      NL1=0.0
      NL2=0.0
      AM(1)=AM(2)=AM(3)=AM(4)=AM(5)=0.0
      NL3=0.0
      MA=0.0
      NPOP=FP=0.0
      FL3=NFL3=ML3=NML3=NML=0.0
      IDAY=0
      BIN=5
      MP=0.0
      NEGGA=0.0
      NMP=0.0
```

Table E. 1 continued

```
      NFP=0.0
      KL3=10
      KL2=10
      KL1=10
      KEA=10
      KFP=20
      KP=KM=KFL=10
      PMORT=1.0
      FPEST=APEST=0
      NROLEF1=NROLEF2=NROLEF3=NROLEF4=NROLEF5=0.0
      NROLEF=0.0
      SUMFP=SUMNRO=SUML1=SUML2=SUML3=0.0
      SUMNPO=0.0
      LX=0
      SUMMAP=0.0
      SUMNML=0.0
      SUMRO=0.0
      EGG=0.0
      DT=.1
      ZI=DT*24.
      DELPL3=1.
      DELPL2=1.
      DELPL1=1.
      DELPEA=1.
      DELPES=1.
      L=0
*
*           LOOP TO INITIALIZE ARRAYS
*
      DO 13 J=1,K
          RL3(J)=0.0
          RL2(J)=0.0
          RL1(J)=0.0
          RE(J)=0.0
      RAM1(J)=0.0
      RAM2(J)=0.0
      RAM3(J)=0.0
      RAM4(J)=0.0
      RAM5(J)=0.0
      RMP(J)=0.0
      RMA(J)=0.0
          RPOP(J)=0.0
          RFP(J)=0.0
          RMP(J)=0.0
          RLM3(J)=0.0
      REA(J)=0.0
13    CONTINUE
      DO 112 J=11,20
      RFP(J)=0.0
      RMP(J)=0.0
112   CONTINUE
*
*   INPUT  SECTION...
*
*             FIRST THE WEATHER DATA
*
      DO 33 J=1,214
      READ(1,2500)MAXTEMP(J),MINTEMP(J)
      CALL DEGDAY(MAXTEMP(J),MINTEMP(J),39.0,IHEAT)
      DEGDAYS(J)=IHEAT
33    CONTINUE
2500  FORMAT(14X,F3.0,5X,F3.0)
*
*             AND THE RESULTS OF THE PREVIOUS RUN
*
      WRITE(61,1100)
1100  FORMAT(* ONION MAGGOT DENSITIES FROM PREVIOUS RUN$*)
      CALL INPUTER(IREADIN,2)
      TOMP=IREADIN(1)
      WRITE(61,1500)
1500  FORMAT(* INPUT FURROW PESTICIDE -- 0=NONE,1=DYFONATE,*
     +*2=ETHION*)
      CALL INPUTER(IREADIN,2)
      FPEST=IREADIN(1)
      WRITE(61,1600)
1600  FORMAT(* ENTER FOLIAR PESTICIDE CODE */* 0=NONE,*
     +*1=MALATHION,2=PARATHION,3=DIAZINON*)
      CALL INPUTER(IREADIN,2)
      APEST=IREADIN(1)
      IF(APEST.LE.0)GO TO 1651
      WRITE(61,1700)
1700  FORMAT(* ENTER FREQUENCY OF APPLICATION(DAYS)$*)
      CALL INPUTER(IREADIN,2)
      FREQ=IREADIN(1)
      WRITE(61,1650)
1650  FORMAT(* FIRST DAY FOR SPRAY APPLICATION= *)
      CALL INPUTER(IREADIN,2)
      KS=IREADIN(1)
1651  CONTINUE
*
```

Table E. 1 continued

```
*    FIRST CALCULATIONS
*
      PMORTE=1.0
      IF(FPEST.GT.0) PMORT=.07
      IF(APEST.EQ.1)MFREQ=1.0
      IF(APEST.EQ.2)MFREQ=2.0
      MP=FLOAT(TOMP)*5.0
      FP=FLOAT(TOMP)*5.0
      IF(APEST.EQ.3)MFREQ=3.0
*
*
*     OUTER LOOP FOR EACH DAY BEGINS HERE
9     CONTINUE
      PE=0.0
      HTIME=0.
      CALL SSTEMP(STEMP,LX)
      LX=1
      IDAY=IDAY+1
      DDTOT=DDTOT+DEGDAYS(IDAY)
      IF(APEST.EQ.0)GO TO 97
      IF(IDAY.LT.KS)GO TO 97
96    CALL SPRAY
97    CONTINUE
*
*         INNER LOOP FOR EACH DT BEGINS HERE
*
      DO 11 M=1,K
      CALL TEMCAL(MAXTEMP(IDAY),MINTEMP(IDAY),M,T)
      HTIME=HTIME+ZI
      ST=TABEXE(STEMP,0.,2.,12,HTIME)
      DELEA=TABEX(DEGG,ARGE,T,6)
      DELES=TABEX(DEGG,ARGE,ST,6)
      DELL1=TABEX(DL1,ARGL1,ST,6)
      DELL2=TABEXE(DL2,50.0,10.0,4,ST)
      DELMP=TABEX(DPM,ARGPF,ST,6)
      IF(ST.LE.40.)DELMP=100.
      DELL3=TABEXE(DL3,50.0,10.0,4,ST)
      DELPF=TABEX(DPF,ARGPF,ST,6)
      IF(ST.LE.40.)DELPF=100.
      DELPOP=TABEXE(POP,50.0,10.0,4,T)
      IF(DELPOP.LT.1.0)DELPOP=10.0
      DELAFL=TABEXE(AFL,50.0,10.0,5,T)
      IF(DELAFL.LT.1.0)DELAFL=10.0
      DELMLG=TABEXE(MLG,50.0,10.0,4,T)
      IF(DELMLG.LT.1.0)DELMLG=10.0
      SUREGGA=TABEX(SEGG,ARGES,T,7)
      SUREGGS=TABEX(SEGG,ARGES,ST,7)
      SURL1=TABEX(SL1,ARGSL1,ST,3)
      SURL2=TABEX(SL2,ARGSL1,ST,3)
      SURL3=TABEX(SL3,ARGSL1,ST,3)
      SUREGAD=AMIN1(EXP(SUREGGA*DT),1.)
      SURFPS=TABEX(FPS,ARGPS,ST,4)
      SUREGGD=AMIN1(EXP(SUREGGS*DT),1.)
      PMORTD=0.997185*PMORT**0.09549
      IF(FPEST.EQ.0)PMORTD=1.0
      PMORTED=0.997185*PMORTE**0.09549
      SURL1D=AMIN1(EXP(SURL1*DT)*PMORTD**(1.0/DELL1),1.)
      SURL2D=AMIN1(EXP(SURL2*DT)*PMORTD**(1.0/DELL2),1.)
      SURL3D=AMIN1(EXP(SURL3*DT)*PMORTD**(1.0/DELL3),1.)
      SURFPSD=AMIN1(EXP(SURFPS*DT),1.)
      IF(APEST.EQ.0)PMORTED=1.0
C    SURFLD=ADULT MORTALITY
      SURFLD=PMORTED
      SURMLD=PMORTED
      SURPOPD=PMORTED
      DEAD1=DELLVF(AM(1),RAM1,NROLEF1,SURFLD,DELAFL,DELPAFL,DT,KFL)
      DEAD2=DELLVF(AM(2),RAM2,NROLEF2,SURFLD,DELAFL,DELPAFL,DT,KFL)
      DEAD3=DELLVF(AM(3),RAM3,NROLEF3,SURFLD,DELAFL,DELPAFL,DT,KFL)
      DEAD4=DELLVF(AM(4),RAM4,NROLEF4,SURFLD,DELAFL,DELPAFL,DT,KFL)
      DEAD5=DELLVF(AM(5),RAM5,NROLEF5,SURFLD,DELAFL,DELPAFL,DT,KFL)
      DEADT=DEAD1+DEAD2+DEAD3+DEAD4+DEAD5
      RO=DELLVF(IPOP,RPOP,NPOP,SURPOPD,DELPOP,DELPPOP,DT,KP)
      IPOP=DELLVF(FP,RFP,NFP,SURFPSD,DELPF,DELPPF,DT,KFP)
      DEADM=DELLVF(MA,RMA,NML,SURMLD,DELMLG,DELPMLG,DT,KM)
      DM=DM+DEADM
      DET=DET+DEADT
      MA=DELLVF(MP,RMP,NMP,SURFPSD,DELMP,DELPMP,DT,KFP)
      PE=PE+IPOP+MA
      FP=DELLVF(FL3,RL3,NFL3,SURL3D,DELL3,DELPL3,DT,KL3)
      MP=DELLVF(ML3,RLM3,NML3,SURL3D,DELL3,DELPL3,DT,KL3)
      FL3=0.0
      L3=DELLVF(L2,RL2,NL2,SURL2D,DELL2,DELPL2,DT,KL2)
      L2=DELLVF(L1,RL1,NL1,SURL1D,DELL1,DELPL1,DT,KL1)
      L1S=DELLVF(EGGSS,RE,NEGGSS,SUREGGD,DELES,DELPES,DT,KEA)
      L1A=DELLVF(EGGA,REA,NEGGA,SUREGAD,DELEA,DELPEA,DT,KEA)
      L1=L1S+L1A
      NL3=NML3+NFL3
      SUMFP=NFP
      SUMNML=NML
      SUMRO=SUMRO+RO
```

Table E. 1 continued

```
      AM(BIN)=0.0
      SUML1=NL1
      SUML2=NL2
      SUML3=NML3+NFL3
      SUMMAP=NMP
11    CONTINUE
      IF(SUMNRO.LE.0.1 .AND. SUMRO.LE.0.1)GO TO 19
      CALL EGGRATE(IDAY,BIN)
      DO 10 L=1,5
10    AM(L)=0.0
      AM(BIN)=SUMRO
19    CONTINUE
      NROLEF=NROLEF1+NROLEF2+NROLEF3+NROLEF4+NROLEF5
      SUMNRO=NROLEF
      TPOP=NPOP+NML+NROLEF
      TPP=NFP+NMP
      DM=0.0
      DET=0.0
      NUMEGG1=0.0
      IF(NROLEF1.GT.0.0)NUMEGG1=NROLEF1*0.75
      NUMEGG2=0.0
      IF(NROLEF2.GT.0.0)NUMEGG2=NROLEF2*2.5
      NUMEGG3=0.0
      IF(NROLEF3.GT.0.0)NUMEGG3=NROLEF3*4.0
      NUMEGG4=0.0
      IF(NROLEF4.GT.0.0)NUMEGG4=NROLEF4/2.0
      NUMEGG5=0.0
      EGG=NUMEGG1+NUMEGG2+NUMEGG3+NUMEGG4+NUMEGG5
      IF(EGG.GT.0.0)EGGSS=0.65*EGG
      IF(EGG.GT.0.0)EGGA=EGG-EGGSS
      IF(DDTOT.GT.2400.)EGGSS=0.
      IF(DDTOT.GT.2400)EGGA=0.0
      SUMRO=0.0
      SUMLT=SUML1+SUML2+SUML3
      SUMOM=SUMNPO+NROLEF
      TOTPUP=SUMMAP+SUMFP
      TOTEGG=NEGGSS+NEGGA
*
*    OUTPUT SECTION
*
      WRITE(3,9999)IDAY,DDTOT,SUMNPO,NROLEF,
     +SUMLT,SUMOM,TOTEGG,TOTPUP,TPOP,TPP,PE
9999  FORMAT(2I5,8F10.2,F10.4)
      WRITE(5,666)IDAY,DDTOT,NL1,NL2,NL3,NEGGSS,NEGGA,
     +NROLEF1,NROLEF2,NROLEF3,NROLEF4
666   FORMAT(2I5,9F9.2)
      IF(IDAY.EQ.214)GO TO 16
      GO TO 9
16    CONTINUE
      STOP
      END




      FUNCTION DELLVF(RIN,R,STRG,PLR,DEL,DELP,DT,K)
*
*  -  TIME VARYING DISTRIBUTION DELAY WITH ATTRITION.
*  -  THIS FUNCTION RETURNS A LAGGED VARIABLE GIVEN AN INPUT OF AN
*     UNLAGGED VARIBLE
*  -  THE DELAY ADJUSTS GRADUALLY TO CHANGES IN THE INPUT SUCH THAT
*     THE AGGREGATE FLOW SUBJECT TO DELAY VARY FROM ENTITY TO ENTITY
*  -  A TIME VARYING DELAY PARAMETER IS USED
*
*     GLOSSARY:
*
*       DEL=DEVELOPMENTAL TIME (DAYS)
*       DELLVF=OUTPUT OF DELAY (RETURNED TO MAIN PROGRAM)
*       DELP=PREVIOUS DEVELOPMENTAL TIME (DEL)
*       DT=DELTA T (TIME INCREMENT)
*       I=STAGE
*       K=NUMBER OF DELAY STAGES
*       PLR=MORTALITY CONSTANT (INSTANTANEOUS SURVIVAL)
*       R=RATE OUT OF THE I-TH STAGE
*       RIN=RATE INTO THE DELAY
*       STRG=STORAGE (NUMBER OF ENTITIES IN EACH STAGE)
*
      DIMENSION R(1)
      VIN=RIN
      FK=FLOAT(K)
      B=1.+(DEL-DELP)/(FK*DT)
      A=FK*DT/DEL
      DELP=DEL
      DO 10 I=1,K
      DR=R(I)
      R(I)=DR+A*(VIN-DR*B)
```

Table E. 1 continued

```
      VIN=OR
10    CONTINUE
      STRG=0.0
      DO 30 I=1,K
      R(I)=R(I)*PLR
      STRG=STRG+R(I)*DEL/FK
30    CONTINUE
      DELLVF=R(K)
      RETURN
      END
```

```
      SUBROUTINE DEGDAY(XMAX,XMIN,BASE,IHEAT)
*
*  -  CALCULATES DEGREE DAY ACCUMULATION FROM AIR TEMP DATA (MAX,MIN)
*     FOR EACH DAY
*
*     GLOSSARY:
*
*       A=SIN FUNCTION
*       BASE=39 F (BASE DEVELOPMENTAL TEMPERATURE)
*       XMAX=MAXIMUM TEMPERATURE
*       XMIN=MINIMUM TEMPERATURE
*       XHEAT=DEGREE DAY
*
      DATA TPIE/6.283181/, HPIE/1.570795/
      IF (XMAX .GT. BASE)GO TO 1
      IHEAT=0
      RETURN
* IF MAXIMUM TEMPERATURE GREATER THAN BASE COME HERE
1     Z=XMAX-XMIN
      XM=XMAX+XMIN
      IF (XMIN .LT. BASE)GO TO 2
      XHEAT=XM/2.-BASE
* ROUNDOFF  ODD UP, EVEN DOWN
10    IHEAT=XHEAT
      CHECK=IHEAT
      IF(XHEAT-CHECK-0.5)8,6,7
6     HALF=IHEAT/2
      IF(HALF-CHECK/2.0) 7,8,8
7     IHEAT=IHEAT+1
8     RETURN
* IF MINIMUM LESS THAN BASE COME HERE
2     TBASE=BASE*2.0
      A=ASIN((TBASE-XM)/Z)
      XHEAT=(Z*COS(A)-(TBASE-XM)*(HPIE-A))/TPIE
* GO ROUND-OFF AND RETURN
      GO TO 10
      END
```

```
      SUBROUTINE EGGRATE(DAY,BIN)
*
*  -  CALCULATES WHICH FECUNDITY DELAY REPRODUCING ADULTS ARE PLACED IN
*  -  NUMBER OF EGGS OVIPOSITED IS DETERMINED BY TEMPERATURE EXPOSURE
*     DURING PRE-OVIP STAGE
*
*     GLOSSARY:
*
*      BIN=EGG CLASS (1,2,3,4,5)
*      CUMMDD=TOTAL DEGREE DAYS DURING PRE-OVIP DEVELOPMENT
*      DAY=DAY NUMBER
*      N=NUMBER OF DAYS TILL 120 DEGREE DAYS
*      TOTAL=SUM OF AVERAGE DAILY TEMPERATURES FOR PRE-OVIP PERIOD
*
      INTEGER DAY,DEGDAYS,BIN,CUMDD
      REAL MAXTEMP,MINTEMP
       COMMON /WEATHER/DEGDAYS(300),MAXTEMP(300),MINTEMP(300)
      CUMDD=0
* GO BACK IN TIME UNTIL 120 DEGREE DAYS ARE REACHED
      DO 100 N=1,100
      CUMDD=CUMDD+DEGDAYS(DAY-N)
      IF (CUMDD .GE. 120)GO TO 200
100   CONTINUE
* NOW N=THE NUMBER OF DAYS TO FIND AN AVERAGE TEMP. FOR
200   M=DAY-N
      TOTAL=0.0
      S=FLOAT(N)
      NDAY=DAY-1
      DO 300 I=M,NDAY
      TOTAL=TOTAL+(2.0*MAXTEMP(I)+MINTEMP(I)+MINTEMP(I+1))/4.0
300   CONTINUE
```

Table E. 1 continued

```
      BIN=INT(0.5+TOTAL/S/10.0)-4
      IF ((BIN .LT. 1 ).OR.( BIN  .GT. 5))BIN=5
      RETURN
      END




      SUBROUTINE SPRAY
*
*  -  CALCULATES EFFECTIVENESS OF A FOLIAR SPRAY WHEN APPLIED
*  -  APPLIES A SPRAY WHEN CALLED
*
*     GLOSSARY:
*
*      APEST=FOLIAR PESTICIDE (1=MALATHION, 2=PARATHION, 3=DIAZINON)
*      CPDAY=NUMBER OF DAYS BETWEEN SPRAYS
*      FREQ=FREQUENCY OF SPRAY
*      MFREQ=RESIDUAL EFFECTIVENESS OF SPRAY APPLIED
*      PDAY=INTERNAL COUNTER
*      PMORTE=MORTALITY DUE TO SPRAY
*
      COMMON/PESTS/PDAY,PMORTE,A,APEST,FREQ,MFREQ
      INTEGER PDAY,FREQ
      INTEGER APEST
      TYPE REAL MFREQ
      I3=APEST
      A=A+1
      IF(A.EQ.1)GO TO 10
      IF(PDAY.EQ.FREQ)GO TO 10
      PDAY=PDAY+1
5     CPDAY=PDAY
      PMORTE=1.00-0.96*EXP((-CPDAY)*(0.69314)/MFREQ)
      RETURN
10    PDAY=0
      GO TO 5
      END
      FUNCTION TABEXE(VAL,SMALL,DIFF,K,DUMMY)
*
*  -  TABLE LOOK-UP FUNCTION THAT DOES EXTRAPULATION FROM A SET OF DATA
*  -  ELEMENTS OF ARGUMENT ARRAY ARE EQUALLY SPACED
*
*     GLOSSARY:
*
*      DIFF=DIFFERENCE BETWEEN ADJACENT ELEMENTS
*      DUM=DIFFERENCE BETWEEN DUMMY ARGUMENT AND SMALLEST VALUE (SMALL)
*      DUMMY=ARGUMENT VALUE (X VALUE INPUT)
*      SMALL=MINIMUM VALUE OF ARGUMENT ARRAY
*      TABEXE=RETURNED VALUE TO MAIN PROGRAM
*      VAL=ARRAY (VALUE RETURNED AS VAL)
*
      DIMENSION VAL(1)
      DUM=DUMMY-SMALL
      I=MIN0(MAX1(1.0+DUM/DIFF,1.0),K)
      TABEXE=(VAL(I+1)-VAL(I))*(DUM-FLOAT(I-1)*DIFF)/DIFF+VAL(I)
      RETURN
      END


      FUNCTION TABEX(VAL,ARG,DUM,K)
*
*  -  TABLE LOOK-UP FUNCTION THAT DOES EXTRAPULATION WHERE THE VALUES A
*     UNEQUALLY SPACED
*  -  A VALUE ARRAY AND ARGUMENT ARRAY ARE NEEDED
*
*     GLOSSARY:
*
*      ARG=ARGUMENT ARRAY
*      DUM=DUMMY UNLESS DUMMY IS TOO LARGE OR TOO SMALL
*      TABEX=RETURNED VALUE TO PROGRAM
*      VAL=ARGUMENT ARRAY
*
      DIMENSION VAL(1),ARG(1)
      DO 1 J=2,K
      IF(DUM.GT.ARG(J))GO TO 1
2     TABEX=(DUM-ARG(J-1))*(VAL(J)-VAL(J-1))/(ARG(J)-ARG(J-1))
     + +VAL(J-1)
      RETURN
1     CONTINUE
      TABEX=(DUM-ARG(K-1))*(VAL(K)-VAL(K-1))/(ARG(K)-ARG(K-1))
     ++VAL(K-1)
      RETURN
```

Table E. 1 continued

```
      END


      SUBROUTINE TEMCAL(MAX,MIN,M,T)
*
*  -  CALCULATES AIR TEMPERATURE FOR EACH DT BY FITTING A SINE CURVE TO
*     MAX AND MIN TWELVE HOURS APART
*
*     GLOSSARY:
*
*      MAX=MAXIMUM DAILY AIR TEMPERATURE
*      MIN=MINIMUM DAILY AIR TEMPERATURE
*      T=RETURNED AIR TEMPERATURE PER DT
*      TIME=HOUR OF THE DAY
*
      TYPE REAL MAX,MIN
      A=MAX-MIN
      TIME=2.4*FLOAT(M)
      S=TIME+3.1416
      T=MIN+A/2.0+(A/2.0*COS(S))
      RETURN
      END


      SUBROUTINE INPUTER(IVAL,M)
*
*  -  SPECIFIC TO CYBER 750 AND IT HANDLES THE INPUT FOR THE PROGRAM
*  -  FTN.   HAL=EASYIN.   LGO.   RUN PROGRAM
*     TAPE1=AIR TEMPERATURE DATA, TAPE88=SOIL TEMPERATURE DATA
*
      DIMENSION IVAL(1)
      N=1
10    CONTINUE
      CALL EASYIN(IVAL,N,J)
      IF(J.EQ.M)RETURN
      WRITE(61,1000)
1000  FORMAT(*  INPROPER TYPE, TRY AGAIN*)
      GOTO 10
      END
      SUBROUTINE SSTEMP(STEMP,LX)
*
*  -  THIS SUBROUTINE CALCULATES AN ARRAY OF SOIL TEMPERATURE VALUES
*     FOR EACH DAY IT IS CALLED.  REAL SOIL TEMPERATURE VALUES ARE
*     ENTERED FROM TAPE88.
*
      DIMENSION STEMP(13)
      IF (LX.GT.0) GOTO 100
      SCUM=0
      DO 10 I=1,13
      READ(88,50) STEMP(I)
10    CONTINUE
      GO TO 30
100   CONTINUE
      STEMP(1)=STEMP(13)
      DO 20 I=2,13
      READ(88,50) STEMP(I)
20    CONTINUE
30    CONTINUE
50    FORMAT(F2.0)
      DO 60 I=2,13
      IF (STEMP(I).LE.40 .AND. STEMP(I-1).LE.40) GOTO 60
      IF (STEMP(I).LE.40) GOTO 55
      IF (STEMP(I-1).LE.40 ) GOTO 66
      SCUM=SCUM+((ABS(STEMP(I)-STEMP(I-1))/2+AMIN1(STEMP(I),STEMP(I-1))
     +-40)/12
      GOTO 60
55    DIF=STEMP(I-1)-STEMP(I)
      YDIF=STEMP(I-1)-40
      SCUM=SCUM+(YDIF/2)*(YDIF/DIF)/12
      GOTO60
66    DIF=STEMP(I)-STEMP(I-1)
      YDIF=STEMP(I)-40
      SCUM=SCUM+(YDIF/2)*(YDIF/DIF)/12
60    CONTINUE
      WRITE (6,9898) SCUM
9898  FORMAT(1X,F10.4)
      RETURN
      END
```

APPENDIX F

A COLLECTION OF STUDIES ON THE BEHAVIOR OF ONION MAGGOT IMMATURES UNDER GREENHOUSE CONDITIONS

INTRODUCTION

Most of the published behavioral studies in regards to the onion maggot, Hylemya antigua (Meigen), have been directed at elucidating the response repetoire of the adult. Foraging and ovipositional behavior in response to the host plant, (Peterson 1924, Kastner 1930, Soni and Finch 1976, Vernon et al. 1978, Dindonis and Miller 1978, and Whitfield 1981), weather and spatial configuration of the habitat (Carruthers 1981 and Whitfield 1981), as well as, the modification of the flies behavior in response to disease (Carruthers 1981) have contributed greatly to understanding the biology of the onion maggot. Despite the direct effect of adult behavior upon the biology of the next generation of immature onion maggots only limited predictions can be made in regard to the larval population responses in a field situation. Little is known about the behavioral repetoire of the larvae. Behavioral studies conducted with the immatures to this date have been concerned with the response of the larvae to their host plant. Kendall (1932) was one of the first investigators to discover the phenomenon of underground migration of larvae from one onion to another. Workman (1958) continuing in this vein looked at the consumption rate of onion maggot larvae but failed to separate feeding rate within a single onion plant with the larva's dispersal from one destroyed plant to the next. This led him to studying the searching behavior of the larvae for the host plant. Based on his findings, Workman concluded that migrating onion maggots locate bulbs randomly. This was found to be suspect when Matsumoto and Thorsteinson (1968) found that newly hatched larvae in petri dishes orientate to organic sulfur compounds similar to those that readily volatalize from the onion plant. Reported here are the results from six experiments designed to provide a

preliminary account of the onion maggot larva's responses to stimuli emanating from the host plant, other larvae, and the soil environment.

LARVAL SUCCESS IN COLONIZING SPECIFIC CULTIVARS OF *ALLIUM CEPA* L. AND *ALLIUM FISTULOSUM* L.

Materials and Methods

Eleven cultivars of onion, *Allium cepa* and one cultivar (Nebuka) of *Allium fistulosum* (see Table F1), were selected for testing the ability of first instar larvae to become established. The study (as well as the five other investigations) was conducted in a greenhouse at the Pesticide Research Center, Michigan State University during the Winter of 1978. The temperature ranged between 15° and 27° C and the relative humidity averaged approximately 85%. Air was circulated by an electric fan. Seeds were sown in flats of steam sterilized Houghton muck soil. Seedlings were transplanted to three inch pots, then when the plants were approximately 3/4 cm. in diameter at the basal portion of the plant, eggs were introduced singly into each pot with the use of a camel hair brush. The onion maggot population was a laboratory reared strain (see Carruthers 1979) for at least two generations (originally obtained from Grant, Michigan as pupae). The experimental design consisted of three blocks of replicates in which plants from all cultivars were represented (blocking variable being time of inoculation). Each replicate for every cultivar consisted of 150 potted plants from which a percent establishment was calculated seven days after the placement of the eggs. A colonization was determined successful if and only if plant damage was associated with a living larva.

Table **F1**. Success[1] of individual first instar onion maggot larvae at colonizing various cultivars of *Allium cepa* L. and *Allium fistulosum* L.

Cultivar	Mean % success	standard error
Downing Yellow Globe	48.0	2.3
Nebuka	44.0	4.2
Southport White Globe	40.7	7.1
White Spanish Ringmaster	42.7	2.4
Danvers Yellow Globe	44.7	1.8
Ruby Red	46.0	3.5
Spartan Banner	44.7	3.3
Spartan Sleeper	49.3	2.9
White Sweet Spanish	45.3	3.5
Early Yellow Globe	41.3	2.9
Yellow Sweet Spanish	44.7	2.4
Northern Oak	47.3	4.8

[1] 50 plants/cultivar with one larva per plant for each replicate, three replicates/cultivar.

Results and Discussion

A summary of the results is depicted in Figure F1. Upon analysis of the data ($F_{(11,22)} = 0.49$, $P = 0.89$) sufficient evidence was not found to support a contention that varietal differences in resistance exist. The low level of colonization ($\bar{\bar{x}} = 44.89\%$) over all the varieties may have been due to excessive egg mortality in handling or dessication. It was evenly distributed among the treatments. Several investigators have tested various species of Allium for resistance to onion maggot attack. Ellis and Eckenrode (1979) in reviewing these studies state that Allium cepa L. (onion) is preferred for oviposition to Allium ascolonicum L. (shallot) and both of these species are more preferred than Allium porrum L. (Leek) or Allium sativum L. (garlic). The results of studies testing the resistance of onion varieties (Allium cepa L. and Allium fistulosum L.) have been quite variable, as well as, contradictory. Susceptability to damage by onion maggots appears to be a complex phenomenon resulting from the attractiveness of the host by gravid females, especially in the case of A. fistulosum which does not appear to be a preferred host (Perron et al. 1958, Perron et al. 1960, Ellis and Eckenrode 1979, and Ellis et al. 1979). The attractiveness of the varieties is not a stable character and can be effected by factors such as planting date, plant vigor, seed size, plant density, and microorganism colonizers (Ellis and Eckenrode 1979). The findings of this study support those of Ellis et al. (1979) in that true resistance to attack by colonizing larvae does not exist, regarding those varieties of A. cepa and A. fistulosum tested. However, possibilities of incorporating resistance into onion plants through altering the amino acid content in the onion so as to make it unsuitable for larval development or to manipulate microbial populations associated with

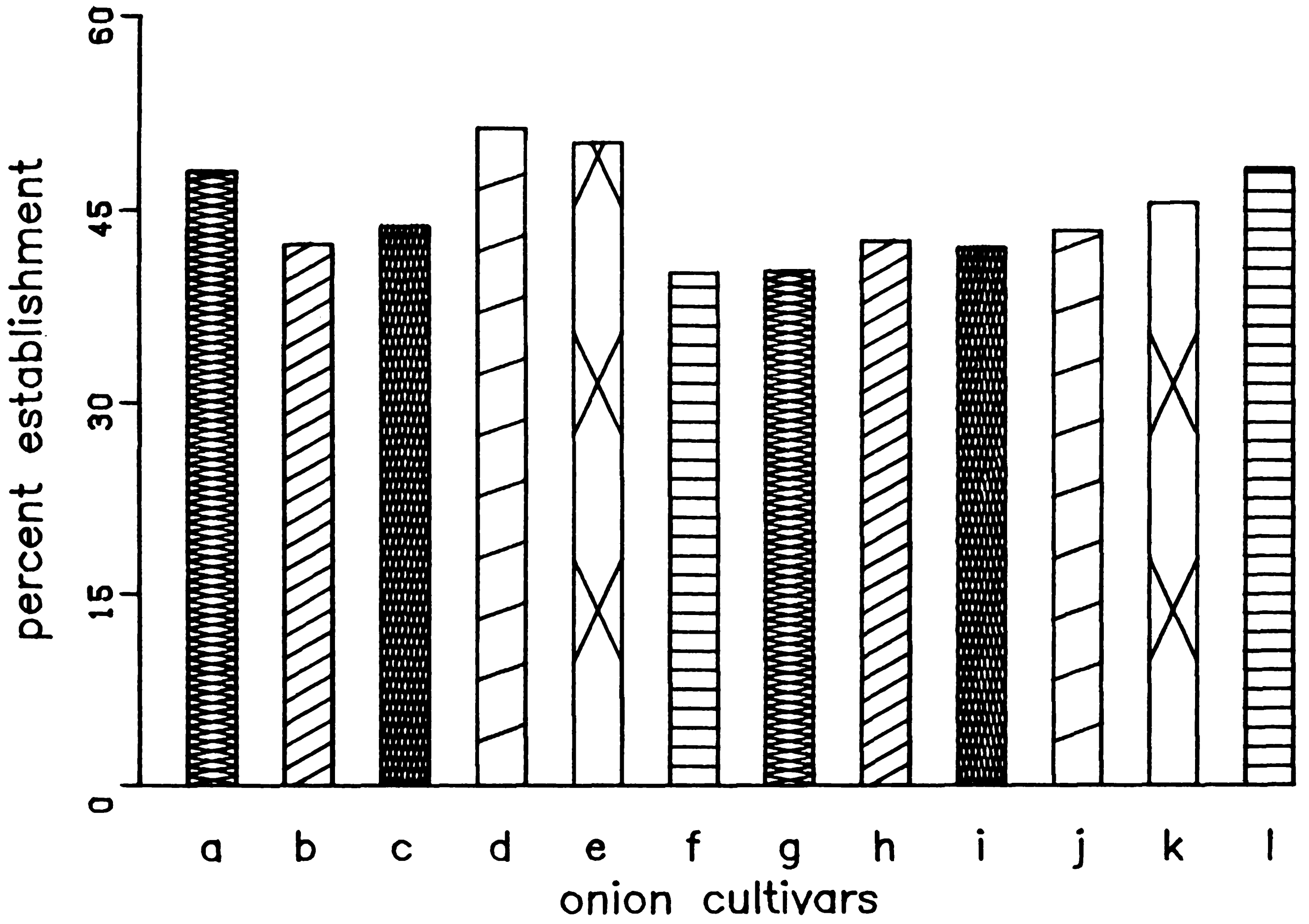

Figure F1. The relative susceptability of twelve onion cultivars to attack by newly hatched onion maggot larvae, cultivars: a - Northern Oak, b - White Spanish Ringmaster, c - Nebuka, d - Spartan Sleeper, e - Downing Yellow Globe, f - Southport White Globe, g - Early Yellow Globe, h - Danvers Yellow Globe, i - Yellow Sweet Spanish, j - Spartan Banner, k - White Sweet Spanish, l - Ruby Red.

onion plants inorder to decrease their attractiveness to the female fly have been suggested (Ellis and Eckenrode 1979, and Ellis et al. 1979).

LARVAL SURVIVAL IN RELATION TO ONION BULB SIZE

Materials and Methods

Onion plants of the cultivar Downing Yellow Globe, transplanted in sterilized Houghton muck soil as seedlings to 7.5 cm. pots and ranging in size (cross-sectional bulb diameter) from seedlings (1/4 cm.) to mature bulbs (5.0 cm.) were inoculated with first, second, and third instar onion maggot larvae. The experimental design consisted of four replicates or blocks and each treatment within a block was randomized, consisting of a group of 25 plants. Each plant had one larva in a particular stage of development introduced at the onset of the study. The use of four replicates (time as a blocking variable) allowed all treatments to be evaluated simultaneously with a limited number of larvae available at periodic intervals. Conditions in the greenhouse were similar to those in the previous study. Again, a successful colonization was considered if and only if a damaged plant and the surviving larva (or pupa in the case of third instar introductions) were found in association together at the end of a four day trial period.

Results and Discussion

Success of colonization does not appear to be influencd by bulb diameter in regard to second and third instar larvae ($H_o: B=0$, T=0.41, P=.91; T=0.9, P=.80 for second and third instar larvae respectively). There does seem to be a relationship between colonization success of first instar larvae and bulb diameter

(see Figure F2, raw data summary in Table F2). A drop in larval survival is most pronounced at bulb diameters of 1.0 cm. and larger. Exponential least squares can be used to approximate the change in colonization success over the whole range of bulb diameters ($Y=7.68 + 56.8e^{-1.2x}$, RSS=786.4 for N=24), although I feel that the qualitative form of the relationship may be more relevant than the quantitative description of the relationship in the general case. It has been suggested that factors such as soil texture (Perron 1972), soil moisture (Sleesman and Gui 1931), and the rate of onion plant growth (Ellis and Eckenrode 1979) all regulate this phenomenon. None of these were taken into account in the design of the experiment and thus I feel that one must be cautious in interpreting the results in too specific a manner. The low survival of second instars over the range of onion bulb treatments in comparison to that of the third instar larvae (significantly different at .95 confidence level, see Table F3), suggests that stresses (soil moisture or sterile soil) could have been present in the study differentially affecting first, second, and third instar larvae. If the relationship between onion bulb size and the colonizing ability of newly hatched larvae is a true trend it might be explained either by a change in nutritive value of the onion (Ellis and Eckenrode 1979) or a change in the physical characteristics of the leaf tissue that compose the bulb (leaf initiation is from the center of the bulb, thus the outside epidermal layers are the oldest parts of the plant separating from the bulb and drying with age). Dynamics such as these may be associated with the oviposition behavior of the adult fly: seedlings and young onions are a preferred oviposition host (Ellis and Eckenrode 1979). When only mature onions are available the preferred oviposition site becomes already infested onions, therefore it is possible that these choices are optimizing first

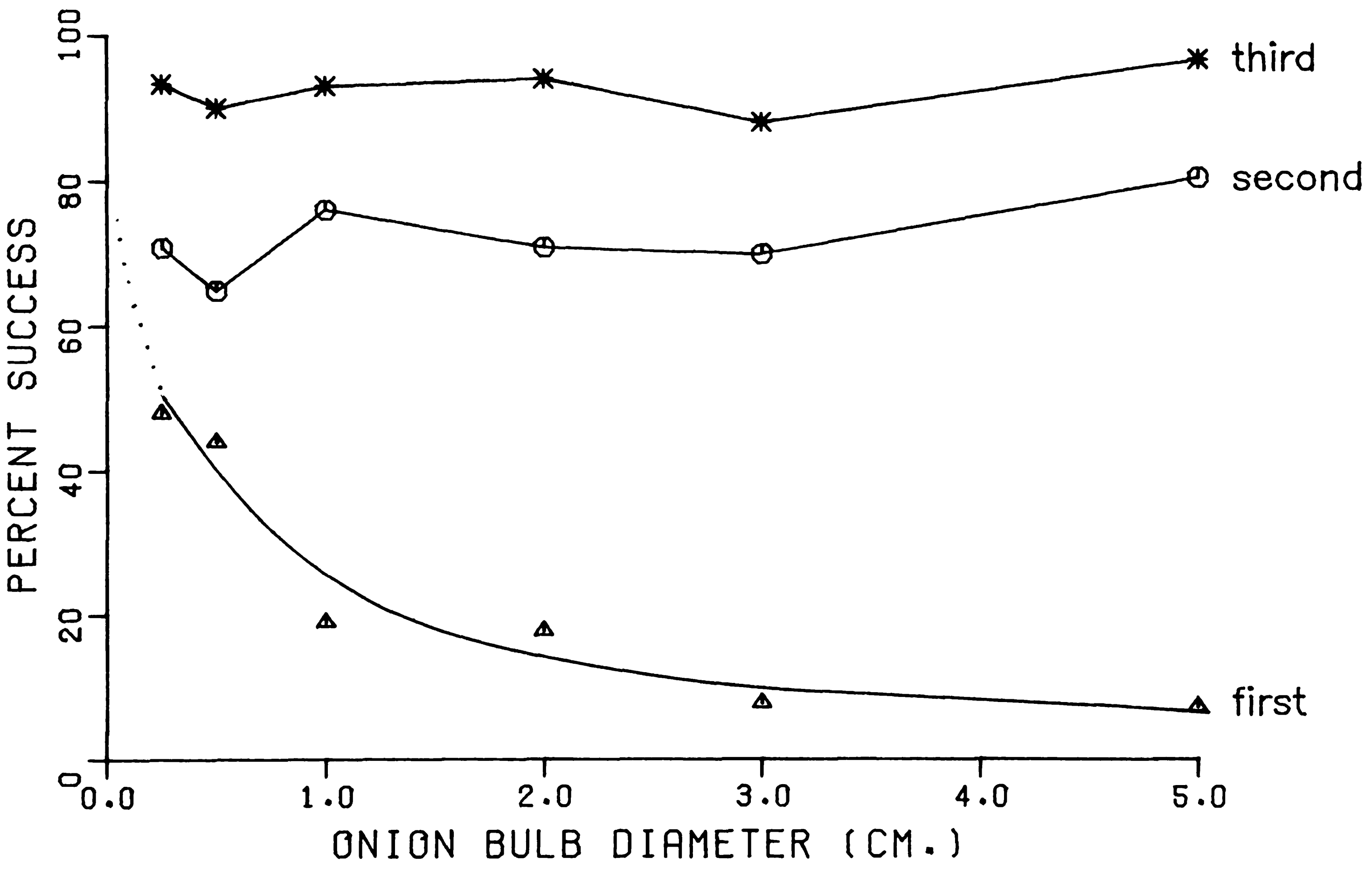

Figure F2. Successful colonization of first, second, and third instar larvae as a function of onion (Downing Yellow Globe) bulb diameter (only means plotted, n=4).

Table F2. Success of onion maggot larvae at colonizing Downing Yellow Globe onion plants of different bulb diameters.

Stadium	Bulb diameter (cm.) .25	.50	1.0	2.0	3.0	5.0
First	48.0±2.5[1]	44.0±2.9	19.0±4.6	17.8±1.7	7.8±1.7	7.3±1.3
Second	70.8±3.5	64.8±3.2	76.0±5.6	70.8±7.8	69.8±12.3	80.3±2.0
Third	93.3±1.8	90.0±1.8	93.0±1.9	94.0±2.2	88.0±2.8	96.5±0.9

[1] $\bar{x}$(in percent) ± S.E.(n=4)

Table F3. Migration as a function of third instar larval density.

	Third instar density[1]								
Replicate	5	10	20	30	40	50	75	100	150
1	0	1	0	4	1	2	21	7	31
2	0	0	2	5	2	2	6	13	19
3	0	0	4	6	3	3	16	3	23
$\bar{x}$	0	0.3	2.0	5.0	2.0	2.3	14.3	7.7	24.3
5$\bar{x}$	0	0.2	0.7	0.3	0.3	0.2	2.6	1.7	2.0

[1] number of third instar larvae introduced to a 2.5-3.0 cm. (bulb diameter) size plant.

instar survival partly due to the successful colonization of newly hatched larvae in a response to bulb size.

MIGRATION IN RELATION TO THIRD INSTAR LARVAL DENSITY

Materials and Methods

Onion plants (cultivar: Downing Yellow Globe) were grown in long troughs (600 cm. x 30 cm. x 20 cm.) filled with Houghton muck soil. Onions were set approximately 100 cm. from one another and when the bulb diameter attained a size of 2.5 - 3.0 cm. they were inoculated with varying densities of young third instar larvae (5, 10, 20, 30, 40, 50, 75, 100, and 150 larvae/onion). Twenty-four hours later dry bulb halves were placed 7.5 cm. from center in a circular perimeter manner surrounding each bulb. Twice a day the onion halves were lifted off the soil surface and inspected for newly arrived individuals which were then recorded and removed from the study. The experiment was terminated at the end of 20 days. Each treatment was replicated three times.

Results and Discussion

It was hypothesized that movement of larvae from an infested onion to another onion, for a given volume bulb, would be a density dependent response. Even if the response was density independent over a certain range of densities, it seems legitimate to assume that a density can be reached where the food source will be consumed necessitating migration or mortality. Figure F3 shows the fit of the data to the hypothesized model ($Y = -7.5 + 7.7e^{.009x}$, RSS=479.7, N=27). Over the range of densities tested, a linear model not supporting a density dependent relationship, appears to account for a large percentage of the

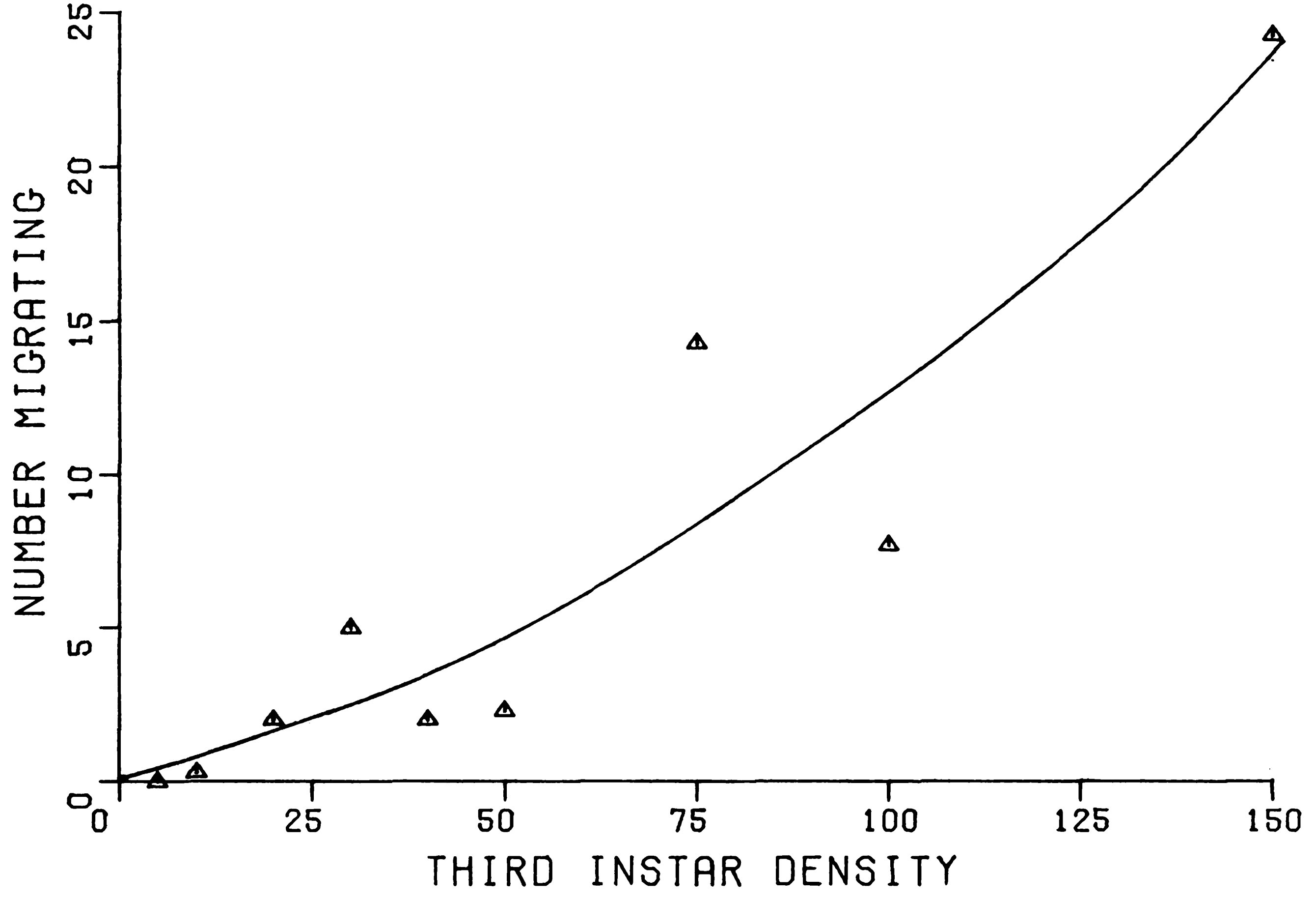

Figure F3. Relationship between the number of third instar larvae migrating and third instar density (2.5-3.0 cm. diameter Downing Yellow Globe Onion).

variation in larval migration ($Y = -1.8 + .15x$, $R^2=.71$, $N=27$). It is possible that the rate of migration due to crowding does not increase until extremely high densities are reached. The fairly constant rate of migration at the densities tested may be due to maggots feeding at the base of the bulb, randomly moving off of the feeding site and reorientating themselves toward a new onion. Movement of the larvae from onion to onion was first observed by Kendall (1932). He observed the phenomenon on seedling onions by noting that as the early growing season progresses, a few onion seedlings that were just starting to show damage symptoms contained large larvae. Workman (1958) set up greenhouse experiments with various age seedlings and documented migration as the number of seedlings consumed throughout the life stage of the maggot. The reason for testing to see if migration occurred in large, nearly mature onion bulbs was based on a hypothesis formulated from the results of the study concerned with first instar survival on large onion bulbs, as well as, previous conclusions about adult female oviposition preference of infested large size onions compared with healthy noninfested onions (Carruthers 1979). The hypothesis was that a mechanism such as migration of older larvae (second and third instar) from desirable but densely populated oviposition sites to uninfested onions would create a new "preferred" oviposition site and a host that would maximize survival for the newly hatched larvae. The rate of damage as well as pupal densities on a per onion basis during the second generation of the onion maggot (Carruthers 1979 and Whitfield 1981) lend support to the contention that a evolutionary mechanism such as this may be operating as a means of maximizing survival.

RATE OF LARVAL MOVEMENT

Materials and Methods

Mixtures of Houghton muck soil and white sand ranging from 0% muck soil (100% sand) to 100% muck soil (0% sand) were moistened and placed in a slanted root zone observation box (Bird, 1978). First, second, and third instar larvae were introduced along the plexiglass surface and the point of introduction was recorded. The plexiglass was then covered with a section of black polyethylene for thirty seconds, after which the location of the larvae if still adjacent to the plexiglass was recorded. Larvae that strayed away from the plexiglass surface were not included in the study. Ten replicates (different larvae) were run for each soil mixture for the first and second instars. Five replicates of third instar larvae were used. The data were transformed to rates on an hourly basis for analysis.

Results and Discussion

Kendall (1932) mentioned that larvae older than seven days but under twelve days in age could find onions at a distance of 25 cm. within 24 hours. Researchers that have described larval movement suggest that it is a phenomenon restricted to within a row in contrast to across rows (Loosjes, 1976). Third instar larvae, based on a conservative estimate (rate of movement assumed a straight line path) were found to migrate at a rate of 50-60 cm. per hour in a high muck/sand soil mixture (Table F4)). Figure F4 (statistics listed in Table F5) shows that a high rate of mobility is characteristic in most soil conditions. There is, however, an increase of the impact of soil mixture on the rate of movement in relation to the younger larvae. An interesting field observation

Table F4. Rate of larval movement in different soil mistures.

	Muck/sand Ratio										
	0	10	20	30	40	50	60	70	80	90	100
First Instar[1]											
$\bar{x}$	4.4	4.7	6.1	6.1	7.6	7.0	7.5	8.0	8.4	8.0	8.8
SE	0.5	0.4	0.6	1.0	.08	0.7	1.1	1.2	1.4	0.6	0.6
Second Instar											
$\bar{x}$	6.1	6.8	7.1	9.8	21.9	18.4	23.6	24.8	25.4	19.4	21.8
SE	1.1	0.9	0.6	1.7	3.5	1.4	2.4	3.0	4.4	1.7	3.1
Third Instar											
$\bar{x}$	9.4	11.2	9.8	20.2	28.2	41.4	51.4	49.4	62.4	55.8	67.4
SE	1.2	2.5	1.4	3.8	5.9	10.5	12.9	3.69	9.5	12.9	14.3

[1] First and second instar menas based on 10 individuals, third instar means based on 5 individuals.

Table F5. Regression statistics for the relationship between log movement of the first, second, and third onion maggot instars and soil mixture.

Instar	Regression Statistics				
	n	A	B	P(Ho:B=o)	R^2
First	110	.66 ± .02	.003 ± .0005	.10E-6	.19
Second	110	.79 ± .02	.007 ± .001	.48E-16	.48
Third	55	.96 ± .03	.009 ± .001	.48E-11	.62

pertaining to larval mobility took place in the Winter of 1979. I was inspecting onion culls for larvae, the air temperature was approximately -2° C and quite a few of the cull onions were frozen on the outside surface even though the soil temperature was approximately 8°-10° C. In quite a few instances maggots had moved out of the onions down into the soil where it was warmer. Later on in the day when the sun had come out and the air temperature had risen considerably almost all of the larvae were found within the onions. This suggests that larvae respond fairly rapidly to a differential in temperature. Later on in the season, however, most of the larval mortality due to freezing occurred in the onion.

DETECTION RADIUS

Materials and Methods

This greenhouse study was aimed at determining whether chemicals from an onion, leached into the surrounding soil serve as a means by which immature onion maggots can locate the host. Downing Yellow Globe onions planted as described in the materials and methods for the migration study were allowed to grow with water being supplied only by mist so that minimum disturbance of any chemicals in the soil around the onion resulted. When the onions were approximately one centimenter in diameter groups of five larvae (larvae of the same developmental stage were tested together) were released 5 cm. under the soil at varying distances from the test onion (0.5 cm. - 25 cm.). Twenty-four hours later the onion was excavated and the number of larvae found recorded.

Results and Discussion

The results shown in Figure F4 suggest that with the growth of an onion plant chemicals attractive to onion maggot larvae produced by the plant accumulate in the soil. This is contrary to the findings of Workman (1958) from which he concluded that the search for host plants by larvae was of a random nature. More recent studies in the laboratory have indicated that onion maggot larvae do orientate towards chemical cues. Matsumoto and Thorsteinson (1968) found that newly hatched larvae moved more consistently towards various sulfides, disulfides, and mercaptan compounds when compared to a control. These organic sulfides have been reported as being present within onion tissue (Boelens et al. 1971). The larvae observed in Matsumoto and Thorsteinsen's study appeared to have no trouble in detecting the chemicals at a distance of 1.5 cm. from the source. The interpretation of the data colected in this experiment has to be done cautiously as only the end result of the behavior was observed and not the searching behavior itself. The hypothesis of random search given the onion maggot larva's cross-sectional diameter being small compared to the 1 cm. diameter of the host (in a two dimensional case) 1, 2, 3, 5, 10, and 20 cm. do not support a hypothesis of random search for first instar larvae up to a 5 cm. distance (P=.005 at .5cm., P=.0001 at 1 cm., P=.31 at 2 cm., P=.07 at 3 cm., and P=.73 at 5 cm., χ^2 test). Similar results apply to second instar larvae (P=.005 at .5 cm., P=.0001 at 1 cm., P=.0001 at 2 cm., P=.0001 at 3 cm., and P=.73 at 5 cm., χ^2 test). Analysis of the third instar data suggest that there is a large probability that search is not random at all distances up to 10 cm. (P=.03, raw data in Table F6). As mentioned previously, due to the design of the experiment in which no attempt was made to measure search time or pattern, the data must

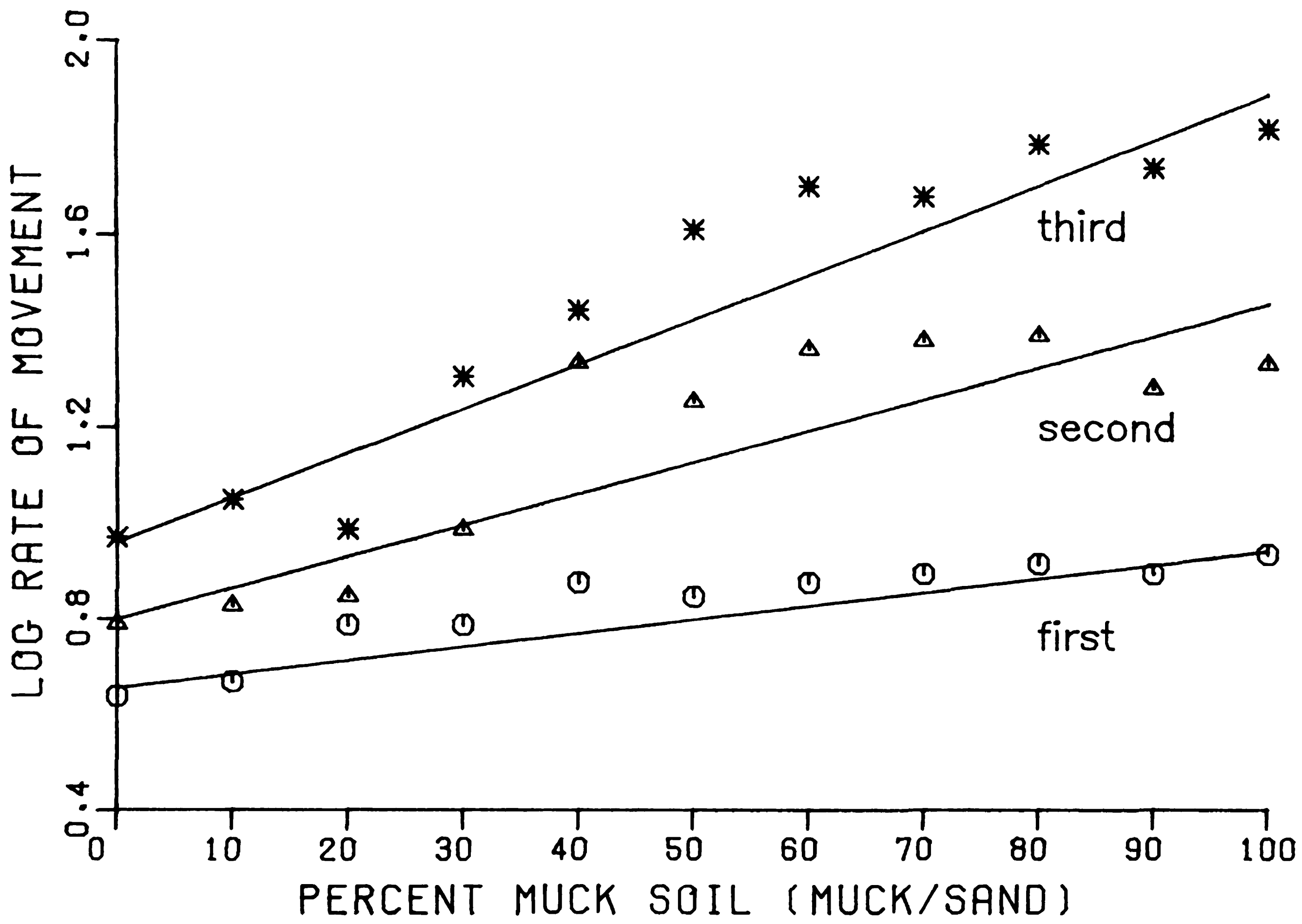

Figure F4. Relationship between the rate of larval movement (three instars) underground (per hour) and the muck soil to sand ratio (only means plotted).

Table F6. Detection of a 1 cm. diameter onion plant at various distances by onion maggot larvae.

Distance (cm.)	Responses (out of 5 possible)		
	First Instar	Second Instar	Third Instar
0.5	5	5	5
0.75	3	5	5
1.0	5	5	2
1.5	2	3	5
2.0	1	5	5
2.5	1	2	5
3.0	2	5	3
3.5	0	1	5
4.0	0	0	4
4.5	0	0	5
5.0	0	0	4
6.0	1	0	3
8.0	0	0	4
9.0	0	0*	1
10.0	0	0	2
15.0	0	0	0
20.0	0	0	0
25.0	0	0	0

*only three individuals used.

be interpreted cautiously. There is evidence to support a nonrandom search pattern, but the quantification of the zone of attraction is suspect (Figure F5). The greater detection difference found with third instar larvae predict initial probabilities of .35, .17, .09, .06, .04, and .02 in regards to larvae finding the host from introduction distances of 0.5 cm., 1 cm., 2 cm., 5 cm., 10 cm., and 20 cm. respectively. The three dimensional case (taking depth of soil into account) is much more complex than this given the dimensions of the test arena and the unknown response of larvae to soil depth and to the effect of onion plant root systems, but it can be assumed if roots are not an important factor that the probabilities of encounter will be much less than the two dimensional case. The binomial distribution was used as the theoretical model to determine expectations of proportions for comparison of the observed data with the expected probabilities due to random search. Expansion of the binomial for the expectations for 0.5, can not be explained. It may be that the third instar larvae can detect lower concentrations of organic sulfides due to more highly developed sensory organs or the larger detection radius could in fact be an artifact (in magnitude) due to a more efficient search effort per unit time based on the speed of movement.

LARVAL PREFERENCE FOR SOIL MOISTURE

Materials and Methods

A "choice" arena was devised for bioassay of the third instar preference for four levels of soil moisture. The arenas were constructed from plastic petri dishes (10 cm. in diameter). A four-way divider made from single edge razor blades that could be easily introduced into the arena and removed, separated the

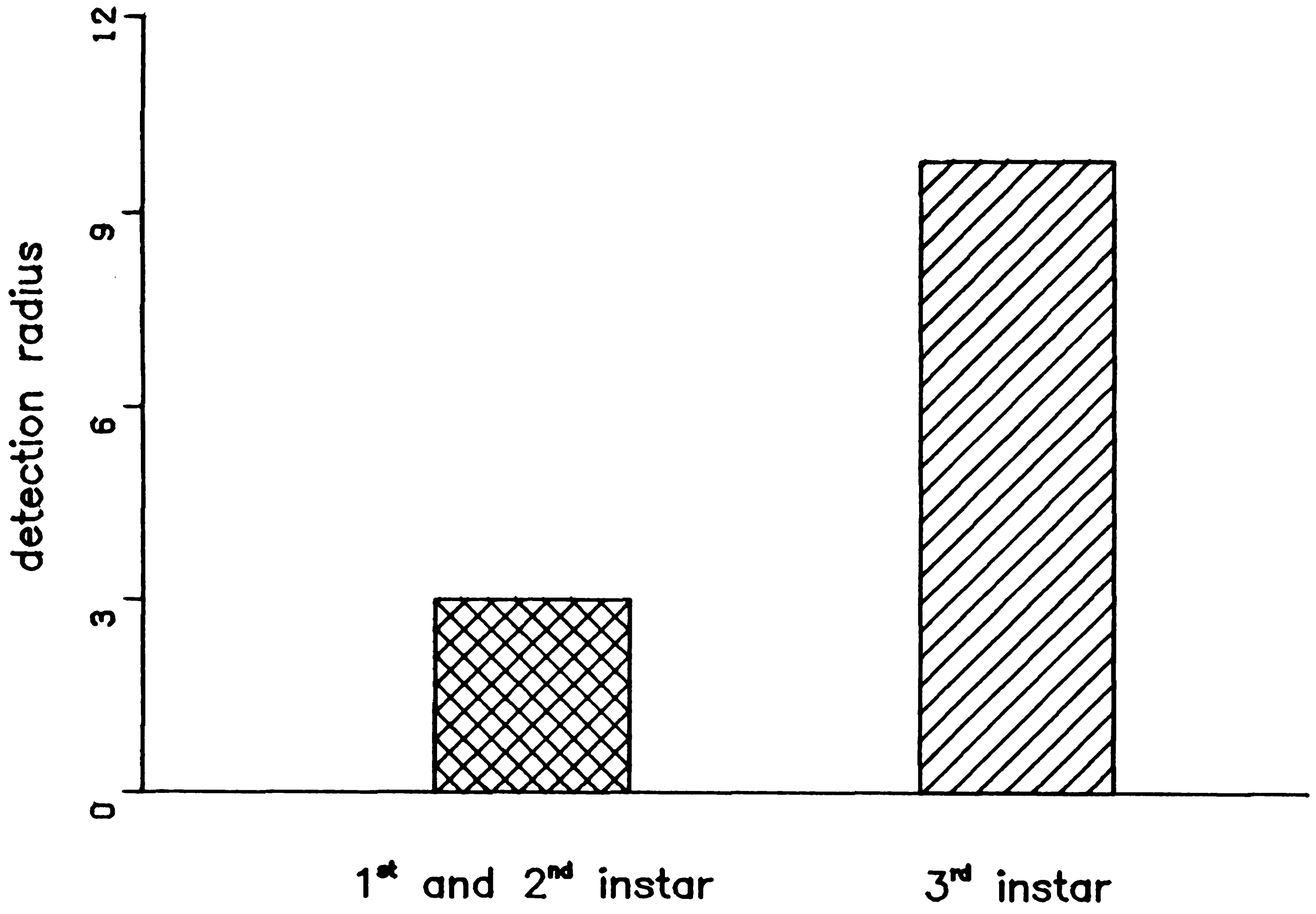

Figure F5. Maximum distance at which onion maggot larvae can detect a young onion plant (1 cm. diameter).

dish into identical quarters. Water was added to Houghton muck from which four levels of soil moisture were created: 0.94 grams/cm^3, 1.60 grams/cm^3, 3.0 grams/cm^3, and 4.5 grams/cm^3. Equal amounts of each soil moisture type were put into the four sections. Five third instar larvae were added to each section after which the divider was removed. Two hours after the start of the experiment the divider was put back in place and each compartment was sifted for larvae. The experimental design contained four replicates.

Results and Discussion

The results are illustrated in Figure F6. The only treatments that are significantly different from one another (based on confidence interval approximations, see Table F7) are soils of mass 0.92 grams/cm^3 and 3.0 grams/cm^3. There were no significant differences between any of the other treatment combinations. This may suggest that given extremes of choice larvae can select their preferred soil environment. An experiment such as this, independent of the host plant, may not be relevant to the biology of the onion maggot under field conditions. The original intentions for designing this experiment was to obtain a preliminary notion on whether soil moisture could play an important factor in the dynamics of migration of larvae from infested onions. These findings support that possibility.

Summary and Conclusions

The results of the greenhouse studies, while by no means complete, offer a basis from which a theory on the dynamics of onion attack can be built upon. The oviposition behavior of the adult female onion maggot may be very closely

Table F7. Percent[1] of larvae found in four soil moisture levels given a choice.

Replicate	Soil Mass 0.9	 1.6	 3.0	 4.5
1	10	30	50	10
2	20	20	20	40
3	5	10	60	25
4	5	20	45	30
$\bar{x}$	10	20	43.8	26.3
SE	3.5	4.1	8.5	6.3

[1] n=20/replicate

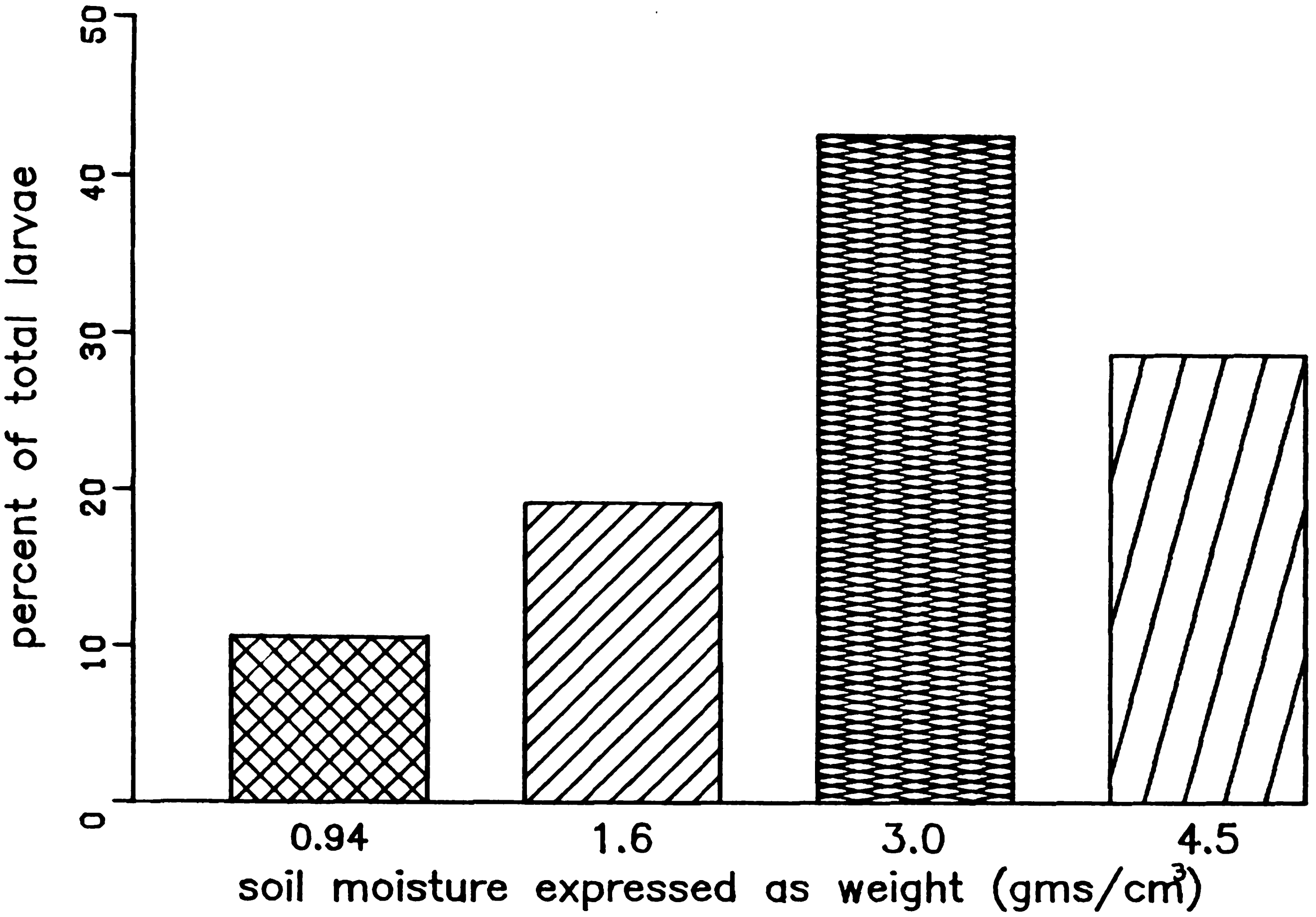

Figure F6. The relationship between soil moisture and third instar incidence.

linked to the bionomics and behavior of the immatures in an evolutionary sense. Without the presence of volunteer onions or soil granular insecticides, oviposition preference appears to be random among seedling onions of the same age in the spring (Loosjes 1976 and Carruthers 1979). Food resources on a per onion basis are limiting (Workman 1958) and newly hatched onion maggot larvae appear to have no difficulty in colonizing the host, therefore extreme aggregated behavior may be of a disadvantage in the early spring. With the progression of the season the oviposition behavior of the female results in a much more aggregative distribution of immatures. The carrying capacity of each onion is very high compared to the spring (Carruthers 1979). The advantages to aggregation at this time may be due to poor larval survival in regards to first instars colonizing new hosts as found in the greenhouse and or it may be due to a more nutritious food quality caused by microbial invasion of the onion plant (Zurlini and Robinson 1978). In this situation the older larvae may serve the function of creating preferred oviposition sites by colonizing new hosts (migration) and thus enlarging the available resource. This scenario probably does not occur in the post-harvest environment due to the large distances between onion bulbs and also due to the differential effect of sprouting onions on female oviposition behavior (see Fall study).

In concluding I would like to mention some factors that I believe are important to take into consideration in future studies in this area. The behavioral repetoire of these larvae appear to be so variable independent of exogenous changes that large numbers of individuals should be used inorder to estimate mean responses. Preconditioning of individuals used in these experiments was not taken into consideration and may have a profound effect on

subsequent behaviors. Zurlini and Robinson (1978) found that microbial colonizers played an important role in conditioning the onion. The experiments discussed in this appendix utilized sterilized soil which may have influenced the outcome of the results. Other environmental factors that shold be considered are the quality of the onion (Ellis and Eckenrode 1979), soil moisture, and temperature and photoperiod (shown to induce diapause therefore possibly effecting the physiology of the larvae (Ramakers 1973).

APPENDIX G

Footnotes for Figures 2G and E1.

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Footnote 7:

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Footnote 8:

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Appendix H.

All raw data can be found stored on magnetic tape at the Michigan State University Computer Center. The tape identification numbers are UP1819 and UP1820. Complete file listings along with individual file documentation can be obtained from the author or Mr. Ken Dimoff, Department of Entomology, Michigan State University. Raw data from which the following summaries (Tables H1 - H7) have been catalogued under the file names:

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CDDAMSUMUCKDEGREEDAYS1979AIRTEMPS
CCDASTORAGE
CCDAFALLLIFESTAGESAMPLINGDATAFIELDRILEY
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APPENDIX H

DATA SUMMARY

PLEASE NOTE:

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Table H1.

Julian Day	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Julian Day	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H1. (cont.)

Julian Day	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H2.

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp

Table H2. (cont.)

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H2. (cont.

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
261	21.00	[illegible]	[illegible]	[illegible]	[illegible]
262	24.00	[illegible]	[illegible]	[illegible]	[illegible]
263	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
264	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
265	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
266	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
267	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
268	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
269	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
270	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
271	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
272	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
273	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
274	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
275	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
276	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
277	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
278	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
279	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
280	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
281	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
282	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
283	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
284	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
285	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
286	1.00	[illegible]	[illegible]	[illegible]	[illegible]
287	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
288	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
289	4.02	[illegible]	[illegible]	[illegible]	[illegible]
290	10.44	[illegible]	2202.15	31.00	[illegible]
291	11.00	[illegible]	[illegible]	[illegible]	[illegible]
292	14.00	[illegible]	[illegible]	[illegible]	[illegible]
293	20.00	[illegible]	[illegible]	[illegible]	[illegible]
294	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
295	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
296	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
297	[illegible]	4110.00	[illegible]	[illegible]	[illegible]
298	2.01	[illegible]	[illegible]	[illegible]	[illegible]
299	1.12	[illegible]	[illegible]	[illegible]	[illegible]
300	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
301	.15	[illegible]	[illegible]	[illegible]	[illegible]
302	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
303	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
304	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
305	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
306	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
307	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
308	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
309	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
310	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
311	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
312	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
313	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
314	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
315	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
316	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
317	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
318	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
319	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
320	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
321	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
322	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
323	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
324	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
325	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
326	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
327	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
328	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
329	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
330	1.27	[illegible]	[illegible]	[illegible]	[illegible]
331	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
332	1.44	[illegible]	[illegible]	[illegible]	[illegible]
333	.12	[illegible]	[illegible]	[illegible]	[illegible]
334	.00	[illegible]	[illegible]	[illegible]	[illegible]
335	.00	[illegible]	2301.54	[illegible]	[illegible]
336	.00	[illegible]	[illegible]	[illegible]	[illegible]
337	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
338	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
339	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
340	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
341	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
342	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
343	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
344	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
345	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
346	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
347	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
348	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
349	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
350	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H2. (cont.)

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H3.

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H3. (cont.)

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
171	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H3. (cont.)

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp	Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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274	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table H3. (cont.)

Julian Day	DDay(F)	Acc. DDay(F)	Acc. DDay(C)	Min Temp	Max Temp
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible

Table H4. Onion storage data summary for 1979.

DAMAGE CODE KEY

Code	Description
MD	Mechanical damage
MC	Miscolor (sunscald--green onion)
SPR	Sprouter
TH	Thickskin (due to shrinkage)
PE	Peeler
SPI	Spindle (cigar shaped)
SO	Soft onion (not due to rotting)
TN	Thickneck (improperly dried or nitrogen fertilizer late in season
DO	Multiple centers
ST	Stained other than SS or WS
WS	Water stained
SS	Sun Scorch
NR	Neck Rot
OM	Onion Maggot
SM	Onion >1" in diameter
SU	Onion <4" in diameter
BR	Basal Rot
NEW	New roots developing and growing
BO	Black onion fly
PB	Purple Blotch

Table H4.

Date Sorted Grower	MD	MC	SPR	TH	PE	SPI	SO	TN	DO	ST	WS	SS	NR	OM	SM
	# %	# %	# %	# %	# %	# %	# %	# %	# %	# %	# %	# %	# %	# %	# %
3/14 Plakmeyer	106-18.6	93-16.3	13-2.3	31-5.4	357-62.5	51-8.9	21-3.6	11-1.9	0-0	33-6.3	63-11.0	11-1.9	1-0.2	37-6.5	84-16.2
3/29 Plakmeyer	43-12.6	76-22.3	3-0.8	19-5.5	81-23.8	4-1.2	73-21.4	2-0.5	5-1.5	10-2.9	62-18.2	36-10.6	48-14.1	12-3.5	8-2.3
4/10 Plakmeyer	7-6.0	14-12.1	9-7.8	48-41.4	74-63.8	4-3.4	12-10.3	1-0.8	1-0.8	6-5.2	53-45.7	5-4.3	2-1.7	23-19.8	16-13.8
4/5 Jackson	27-5.9	56-12.2	19-4.1	25-5.4	339-73.8	8-1.7	67-14.6	2-0.4	3-0.6	9-1.9	112-24.4	15-3.3	43-9.4	8-1.7	11-2.4
4/10 Beaukamp	7-4.8	20-13.8	24-16.6	7-4.8	71-43.9	24-16.6	29-20.0	0-0	1-0.7	6-4.1	34-23.4	14-9.6	1-0.7	6-4.1	13-8.9
3/16 Beaukamp	196-37.9	26-5.0	0-0	1-0.2	139-26.8	87-16.8	15-2.9	4-0.7	5-0.9	15-2.9	159-30.7	15-2.9	4-0.7	31-5.9	69-13.3
3/19 Bolthouse	19-6.6	94-32.4	8-2.7	63-21.7	127-43.8	20-6.9	61-21.0	4-1.4	21-7.2	23-7.9	83-28.6	47-16.2	3-1.0	3-1.0	35-12.0
3/16 Brink	295-18.6	162-10.2	12-0.7	56-3.5	672-42.5	238-15.0	98-6.2	18-1.1	27-1.7	135-8.5	257-16.7	40-2.5	9-0.6	90-5.7	177-11.2
3/21 Brink	10-8.6	33-28.4	2-1.7	36-31.0	44-37.9	7-6.0	26-22.4	3-2.6	23-19.8	17-14.6	---	12-10.3	7-6.0	11-9.5	2-1.7
3/27 Brink	17-5.3	123-38.6	12-3.7	85-26.6	90-28.2	22-6.8	75-23.5	12-3.7	31-9.7	36-11.3	80-25.1	47-14.7	2-0.6	48-15.0	40-12.5
3/29 Brink	44-13.7	84-26.3	20-6.3	74-23.2	110-34.5	5-1.6	79-24.7	11-3.4	13-4.0	11-3.4	123-38.6	14-4.3	8-2.5	51-15.9	36-11.3
4/5 Brink	57-9.8	64-11.0	9-1.5	88-15.2	75-12.9	32-5.5	120-20.7	12-2.1	6-1.0	19-3.3	123-21.2	131-22.6	10-1.7	76-13.1	68-11.7
3/15 Dyk	37-22.6	5-3.0	1-0.6	2-1.2	56-34.2	25-15.2	30-18.3	8-4.8	13-7.9	7-4.3	6-3.6	1-0.6	7-4.3	5-3.0	0-0
3/21 Dyk	12-10.3	23-19.8	4-3.4	12-10.3	72-62.1	6-5.2	27-23.3	9-7.8	5-4.3	26-22.5	14-12.1	3-2.5	7-6.0	4-3.4	14-12.1
3/12 Plasier	80-12.7	21-3.4	3-0.5	4-0.6	81-12.9	137-21.8	13-2.0	4-0.6	2-0.3	13-2.0	95-15.0	43-6.8	5-0.8	13-2.0	50-7.9
3/15 Plasier	54-13.5	26-6.5	7-1.8	17-4.3	97-24.3	246-61.5	65-16.3	15-3.8	3-0.8	54-13.5	24-6.0	22-5.5	11-2.8	12-3.0	67-16.8
4/5 Kedding	13-7.1	17-9.3	51-27.8	10-5.5	116-63.4	1-0.5	32-17.5	1-0.5	2-1.1	5-2.7	5-2.7	44-24.0	4-2.2	2-1.1	0-0
4/12 Palmbos	24-4.9	140-28.7	45-9.2	68-13.9	193-39.5	42-8.6	62-12.7	39-7.9	5-1.0	9-1.8	203-41.6	50-10.2	9-1.8	8-1.6	28-5.7

Table H4. (cont.)

Date Sorted Grower	TU	BR	NEW	BO	PB	Total Culls Sorted
	# %	# %	# %	# %	# %	
3/14 Plakmeyer	8-1.4	0-0	2-0.3	0-0	0-0	571
3/29 Plakmeyer	0-0	9-2.6	0-0	0-0	0-0	341
4/10 Plakneyer	0-0	0-0	0-0	0-0	0-0	116
4/5 Jackson	0-0	7-1.5	1-0.2	0-0	42-9.2	459
4/10 Beaukamp	4-2.7	4-2.7	1-0.7	0-0	0-0	145
3/16 Beaukamp	33-6.4	0-0	29-5.6	0-0	0-0	517
3/19 Bolthouse	13-4.4	1-0.3	0-0	3-1.0	0-0	290
3/16 Brink	61-3.9	6-0.4	25-1.5	0-0	0-0	1582
3/21 Brink	1-0.8	1-0.8	0-0	1-0.8	0-0	116
3/27 Brink	6-1.8	8-2.5	0-0	1-0.3	0-0	329
3/29 Brick	5-1.6	39-12.2	1-0.3	0-0	0-0	319
4/5 Brink	7-1.2	75-12.9	0-0	1-0.2	0-0	580
3/15 Dyk	11-6.7	1-0.6	0-0	0-0	0-0	164
3/21 Dyk	2-1.7	1-0.8	0-0	0-0	0-0	116
3/12 Plasier	1-0.2	17-2.7	0-0	0-0	0-0	629
3/15 Plasier	2-0.5	0-0	0-0	0-0	0-0	400
4/5 Redding	0-0	3-1.6	31-16.9	0-0	0-0	183
4/12 Palmbos	9-1.8	10-2.0	14-2.9	0-0	0-0	489

Table H5. Life stage densities[1] of the onion maggot in Eaton Rapids during the fall of 1979.

Date D Day	Field	Statistic	Egg	Instar 1	Instar 2	Instar 3
9/18 1940						
	R	$\bar{x}$	61.5	3.2	0.7	1.3
		s	38.9	3.0	1.5	1.2
	K	$\bar{x}$	43.7	0.7	1.5	1.4
		s	36.2	1.1	2.7	2.6
9/22 1970						
	R	$\bar{x}$	40.1	6.2	1.2	2.6
		s	57.6	5.8	1.2	3.7
9/26 2000						
	R	$\bar{x}$	71.2	8.1	1.7	2.0
		s	56.9	9.2	2.4	2.4
	K	$\bar{x}$	62.5	13.1	1.1	5.5
		s	42.2	15.3	1.9	6.4
9/30 2044						
	R	$\bar{x}$	20.3	6.8	4.5	1.7
		s	23.6	10.5	9.8	1.9
10/1 2057						
	K	$\bar{x}$	1.8	2.7	0.6	0.3
		s	3.1	3.7	0.8	0.5
10/2 2072						
	R	$\bar{x}$	17.7	10.1	4.9	12.0
		s	20.8	5.8	10.7	17.2
10/4 2091						
	R	$\bar{x}$	16.1	16.5	5.7	4.5
		s	23.4	17.2	3.2	3.3

Table H5. (con't)

Date D Day	Field	Statistic	Egg	Instar 1	Instar 2	Instar 3
	K	$\bar{x}$	8.9	5.4	2.9	0.2
		s	6.8	4.7	4.7	0.4
10/10 2129	R	$\bar{x}$	8.5	9.3	11.1	2.5
		s	8.0	15.7	13.6	3.6
	K	$\bar{x}$	33.1	6.9	12.0	0.6
		s	42.3	11.6	17.5	0.7
10/17 2147	R	$\bar{x}$	11.0	3.7	8.2	8.9
		s	8.2	4.4	7.4	10.6
	K	$\bar{x}$	7.9	1.1	5.9	2.9
		s	7.1	1.5	7.7	3.5
10/24 2224	R	$\bar{x}$	1.7	2.1	3.0	10.5
		s	3.6	3.4	3.1	10.5
	K	$\bar{x}$	0.0	0.2	1.5	2.5
		s	0.0	0.4	1.9	5.4
10/29 2239	R	$\bar{x}$	0.0	0.4	1.3	8.5
		s	0.0	0.5	1.7	6.9
	K	$\bar{x}$	0.0	0.2	1.3	1.4
		s	0.0	0.4	1.7	1/8
11/8 2272	R	$\bar{x}$	0.0	0.0	0.2	1.7
		s	0.0	0.0	0.6	2.2
	K	$\bar{x}$	0.0	0.0	0.2	1.1
		s	0.0	0.0	0.4	1.2

Table H5. (con't)

Date D Day	Field	Statistic	Egg	Instar 1	Instar 2	Instar 3
11/15 2276	R	$\bar{x}$	0.0	0.0	1.1	1.2
		s	0.0	0.0	1.4	1.9
	K	$\bar{x}$	0.0	0.0	0.1	0.7
		s	0.0	0.0	0.3	0.9
11/23 2295	R	$\bar{x}$	0.0	0.0	0.4	0.9
		s	0.0	0.0	0.5	1.1
	K	$\bar{x}$	0.0	0.0	0.2	0.5
		s	0.0	0.0	0.4	0.9
12/12 2317	R	$\bar{x}$	0.0	0.0	0.4	0.2
		s	0.0	0.0	0.9	0.4
	K	$\bar{x}$	0.0	0.0	0.1	0.5
		s	0.0	0.0	0.3	0.7

[1] $\bar{x}$ and s are computed on a per cluster basis (20 onions/ cluster and 10 clusters/sample date).

Table H6. Life stage densities[1] of the onion maggot in Laingsburg during the fall of 1979.

Date D Day	Field	Statistic	Eggs	Instar 1	Instar 2	Instar 3
9/18 1993	R	$\bar{x}$	0.3	0.2	0.0	0.3
		s	0.4	0.4	0.0	0.7
9/26 2062	R	$\bar{x}$	0.0	0.0	0.0	0.2
		s	0.0	0.0	0.0	0.4
10/1 2124	R	$\bar{x}$	0.5	0.2	0.1	0.0
		s	0.7	0.6	0.3	0.0
10/4 2154	R	$\bar{x}$	2.1	0.5	0.4	0.1
		s	3.4	0.7	0.7	0.3
10/10 2182	R	$\bar{x}$	0.8	0.7	0.4	0.9
		s	1.0	0.7	0.9	1.3
10/16 2196	P	$\bar{x}$	4.0	2.1	0.7	1.6
		s	5.3	1.9	1.1	1.3
10/17 2202	R	$\bar{x}$	1.4	0.6	0.7	1.1
		s	1.9	0.9	0.9	2.5
10/22 2254	P	$\bar{x}$	2.7	3.3	2.1	1.9
		s	2.5	3.7	2.5	2.3

Table H6. (con't)

Date D Day	Field	Statistic	Eggs	Instar 1	Instar 2	Instar 3
10/24 2284	R	$\bar{x}$	0.3	0.1	0.1	0.9
		s	0.7	0.3	0.3	1.9
10/29 2290	R	$\bar{x}$	0.2	0.0	0.2	0.3
		s	0.4	0.0	0.4	0.7
	P	$\bar{x}$	0.0	2.4	0.9	1.4
		s	0.0	2.6	1.3	2.4
11/8 2322	R	$\bar{x}$	0.0	0.0	0.1	0.6
		s	0.0	0.0	0.3	0.4
	P	$\bar{x}$	0.0	0.6	0.3	0.9
		s	0.0	0.8	0.5	0.9
11/15 2322	R	$\bar{x}$	0.0	0.0	0.0	0.0
		s	0.0	0.0	0.0	0.0
	P	$\bar{x}$	0.0	0.2	0.1	0.7
		s	0.0	0.4	0.3	0.7
11/23 2351	R	$\bar{x}$	0.0	0.0	0.0	0.3
		s	0.0	0.0	0.0	0.4
	P	$\bar{x}$	0.0	0.0	0.2	0.5
		s	0.0	0.0	0.4	0.7
12/13 2370	R	$\bar{x}$	0.0	0.0	0.0	0.4
		s	0.0	0.0	0.0	0.9
	P	$\bar{x}$	0.0	0.0	0.1	0.2
		s	0.0	0.0	0.3	0.4

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[1] $\bar{x}$ and s are computed on a per cluster basis (20 onions/ cluster and 10 clusters/sample date).

Table H7. Life stage densities[1] of the onion maggot in Grant during the fall of 1979.

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
9/19 1918						
	R	$\bar{x}$	6.3	0.8	0.3	0.1
		s	6.8	2.2	0.7	0.3
	1	$\bar{x}$	0.8	1.3	0.0	0.0
		s	2.3	1.4	0.0	0.0
	3	$\bar{x}$	7.5	0.0	0.0	0.0
		s	4.7	0.0	0.0	0.0
	6	$\bar{x}$	17.3	2.1	0.4	0.1
		s	20.2	2.3	0.8	0.3
9/21 1933						
	R	$\bar{x}$	4.1	0.2	0.1	0.3
		s	3.0	0.4	0.1	0.5
	3	$\bar{x}$	4.4	0.6	0.0	0.3
		s	8.1	1.1	0.0	0.9
	6	$\bar{x}$	16.9	3.6	1.8	0.3
		s	15.1	4.0	2.4	0.7
9/24 1959						
	R	$\bar{x}$	2.9	0.5	0.6	1.1
		s	4.1	0.7	0.9	2.1
	1	$\bar{x}$	1.3	0.1	0.0	0.0
		s	1.9	0.3	0.0	0.0
	3	$\bar{x}$	2.9	0.9	0.0	0.3
		s	4.3	1.3	0.0	0.7
	6	$\bar{x}$	14.9	2.7	1.5	0.2
		s	16.0	3.3	2.1	0.6
9/26 1974						
	R	$\bar{x}$	1.8	0.7	0.6	0.4
		s	3.5	1.3	1.1	0.9
	1	$\bar{x}$	1.8	0.4	0.2	0.0
		s	2.9	0.9	0.4	0.0
	2	$\bar{x}$	2.1	0.0	0.0	0.7
		s	3.4	0.0	0.0	2.1
	3	$\bar{x}$	4.6	1.1	0.5	0.7
		s	6.8	2.5	0.7	1.5

Table H7. (con't)

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
	4	$\bar{x}$	2.4	0.4	1.1	0.0
		s	2.8	1.3	2.3	0.0
	5	$\bar{x}$	6.4	0.1	0.0	1.4
		s	6.9	0.3	0.0	2.5
	6	$\bar{x}$	16.3	4.3	2.2	0.3
		s	9.5	4.7	3.5	0.9
10/1 2034	R	$\bar{x}$	2.7	0.3	1.3	0.7
		s	3.2	0.5	1.9	1.1
	1	$\bar{x}$	3.7	1.6	1.3	0.0
		s	7.8	3.2	2.9	0.0
	2	$\bar{x}$	18.8	1.6	0.2	0.0
		s	24.2	3.0	0.6	0.0
	3	$\bar{x}$	9.5	0.6	0.8	0.4
		s	7.8	1.1	0.8	0.7
	4	$\bar{x}$	4.9	2.5	0.9	0.0
		s	3.5	3.3	2.1	0.0
	5	$\bar{x}$	21.0	3.1	3.9	0.0
		s	15.6	4.1	3.9	0.0
	6	$\bar{x}$	30.9	6.8	3.2	0.2
		s	34.5	6.9	3.9	0.4
10/4 2065	R	$\bar{x}$	4.2	0.6	1.1	1.3
		s	7.1	0.9	1.5	1.9
	1	$\bar{x}$	2.3	1.6	1.0	0.1
		s	4.2	2.6	1.8	0.3
	2	$\bar{x}$	25.5	2.0	0.0	0.5
		s	25.6	2.5	0.0	1.3
	3	$\bar{x}$	19.1	6.2	2.1	0.5
		s	17.6	7.9	3.4	0.7
	4	$\bar{x}$	4.9	2.5	0.9	0.0
		s	3.5	3.3	2.1	0.0
	5	$\bar{x}$	33.6	8.1	5.9	0.3
		s	26.6	7.4	5.1	0.7
	6	$\bar{x}$	28.3	9.3	6.9	0.5
		s	24.6	12.5	9.1	0.9

Table H7. (con't)

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
10/7 2080						
	R	$\bar{x}$	3.9	0.9	1.7	1.9
		s	4.8	1.9	3.4	1.8
	1	$\bar{x}$	0.8	2.3	1.3	0.5
		s	1.5	4.7	2.2	0.9
	2	$\bar{x}$	18.1	2.4	1.5	0.1
		s	28.6	2.8	2.3	0.3
	3	$\bar{x}$	16.2	5.4	3.1	0.7
		s	17.3	7.4	5.9	1.5
	4	$\bar{x}$	7.9	3.4	1.7	0.2
		s	5.5	3.3	2.1	0.4
	5	$\bar{x}$	17.5	12.8	0.8	0.1
		s	13.9	11.9	1.8	0.3
	6	$\bar{x}$	39.7	8.0	7.5	0.9
		s	36.8	5.6	6.7	2.2
10/10 2090						
	R	$\bar{x}$	4.9	1.9	3.2	0.4
		s	6.2	1.9	3.1	0.5
	1	$\bar{x}$	1.1	1.4	1.6	0.8
		s	1.4	2.2	4.4	1.9
	2	$\bar{x}$	54.0	8.3	2.7	1.2
		s	33.6	9.8	2.9	1.8
	3	$\bar{x}$	26.1	8.6	3.8	1.2
		s	28.2	7.5	7.1	1.5
	4	$\bar{x}$	2.9	6.9	1.5	0.3
		s	3.5	9.4	3.1	1.0
	5	$\bar{x}$	43.7	15.8	15.3	1.4
		s	34.9	13.6	20.1	1.4
	6	$\bar{x}$	49.7	9.5	3.7	2.1
		s	71.2	10.0	3.3	2.3
10/12 2093						
	R	$\bar{x}$	8.4	3.2	2.5	0.5
		s	9.6	3.8	5.0	0.5
	3	$\bar{x}$	30.7	6.9	6.9	1.8
		s	34.1	7.3	8.2	2.8
	6	$\bar{x}$	24.0	3.3	6.2	3.3
		s	26.8	2.8	9.3	3.8

Table H7. (con't)

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
10/15 2097	R	$\bar{x}$	6.1	1.9	1.5	1.1
		s	5.2	3.4	3.1	1.9
	1	$\bar{x}$	0.4	0.4	1.7	1.1
		s	0.9	0.9	2.6	1.9
	2	$\bar{x}$	16.6	6.8	2.8	1.9
		s	15.6	1.9	3.7	3.0
	3	$\bar{x}$	12.1	3.2	3.0	2.4
		s	12.5	3.7	2.7	2.7
	4	$\bar{x}$	1.3	5.0	2.2	0.6
		s	2.2	3.0	2.9	0.8
	5	$\bar{x}$	9.9	9.1	5.2	0.8
		s	6.6	3.3	8.9	1.3
	6	$\bar{x}$	31.8	2.5	7.2	4.6
		s	17.6	4.1	6.8	2.6
10/19 2117	R	$\bar{x}$	3.7	0.8	4.1	3.4
		s	5.7	1.3	7.2	4.1
	1	$\bar{x}$	0.5	0.6	1.8	1.8
		s	1.1	1.9	2.3	1.9
	2	$\bar{x}$	5.2	3.6	3.7	1.2
		s	5.3	5.3	3.4	1.7
	3	$\bar{x}$	9.0	7.2	5.9	1.8
		s	12.3	11.3	4.9	2.0
	4	$\bar{x}$	0.9	3.6	4.2	0.5
		s	1.5	4.3	6.8	1.1
	5	$\bar{x}$	5.8	3.3	7.8	1.7
		s	4.2	3.9	5.8	1.9
	6	$\bar{x}$	24.7	2.0	6.0	5.1
		s	34.1	2.2	4.6	4.1
10/22 2154	R	$\bar{x}$	1.6	0.7	2.9	4.3
		s	1.7	1.3	4.3	4.3
	3	$\bar{x}$	4.4	4.9	5.6	3.6
		s	5.6	5.7	8.1	3.5
	6	$\bar{x}$	7.1	1.3	0.8	6.3
		s	9.2	2.4	1.7	8.0

Table H7. (con't)

ate						
Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
0/24 181						
	R	$\bar{x}$	3.1	1.1	2.4	3.3
		s	2.5	2.8	3.1	4.2
	1	$\bar{x}$	0.0	0.4	1.4	1.6
		s	0.0	0.9	3.8	4.1
	2	$\bar{x}$	3.1	5.7	4.0	4.7
		s	4.2	5.7	3.4	3.4
	3	$\bar{x}$	2.5	1.8	3.0	6.1
		s	2.7	1.6	3.4	6.8
	4	$\bar{x}$	0.7	0.8	4.5	1.1
		s	1.9	1.9	4.8	1.5
	5	$\bar{x}$	2.8	6.2	9.5	4.2
		s	2.9	7.3	7.5	4.7
	6	$\bar{x}$	0.3	0.4	1.8	9.6
		s	0.9	0.8	2.3	12.1
0/29 186						
	R	$\bar{x}$	0.0	0.9	1.1	4.1
		s	0.0	1.7	2.3	6.2
	1	$\bar{x}$	0.0	0.0	1.3	1.2
		s	0.0	0.0	2.2	2.9
	2	$\bar{x}$	0.3	1.5	2.6	5.2
		s	0.9	3.1	3.2	5.5
	3	$\bar{x}$	0.4	0.8	1.1	5.1
		s	0.9	2.2	1.5	5.8
	4	$\bar{x}$	0.0	1.7	6.1	0.6
		s	0.0	2.6	8.9	0.8
	5	$\bar{x}$	0.1	0.0	4.0	2.3
		s	0.3	0.0	6.0	3.0
	6	$\bar{x}$	0.0	0.0	1.3	6.1
		s	0.0	0.0	2.3	6.1
1/1 197						
	R	$\bar{x}$	0.0	0.5	0.9	2.9
		s	0.0	0.9	1.3	4.3
	3	$\bar{x}$	0.0	0.0	2.1	4.3
		s	0.0	0.0	3.4	4.9
	6	$\bar{x}$	0.0	0.0	1.0	5.1
		s	0.0	0.0	1.3	4.7

Table H7. (con't)

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
11/5 2210						
	R	$\bar{x}$	0.0	0.0	0.4	0.4
		s	0.0	0.0	0.7	0.5
	1	$\bar{x}$	0.0	0.0	0.3	1.0
		s	0.0	0.0	0.9	1.5
	2	$\bar{x}$	0.0	2.2	2.4	5.2
		s	0.0	2.9	5.0	3.6
	3	$\bar{x}$	0.0	0.5	1.1	5.0
		s	0.0	0.9	2.3	2.6
	4	$\bar{x}$	0.0	0.5	2.7	0.9
		s	0.0	1.3	3.9	1.5
	5	$\bar{x}$	0.0	0.0	1.8	1.8
		s	0.0	0.0	2.8	1.9
	6	$\bar{x}$	0.0	0.0	0.0	3.3
		s	0.0	0.0	0.0	6.3
11/10 2217						
	R	$\bar{x}$	0.0	0.0	0.3	0.5
		s	0.0	0.0	0.5	1.0
	1	$\bar{x}$	0.0	0.0	1.3	1.2
		s	0.0	0.0	1.9	1.6
	2	$\bar{x}$	0.0	1.3	1.8	4.3
		s	0.0	2.0	2.4	3.9
	3	$\bar{x}$	0.0	0.0	1.8	3.5
		s	0.0	0.0	2.1	5.2
	4	$\bar{x}$	0.0	0.0	0.4	0.8
		s	0.0	0.0	0.4	1.8
	5	$\bar{x}$	0.0	0.0	0.9	2.2
		s	0.0	0.0	1.9	2.7
	6	$\bar{x}$	0.0	0.0	1.0	4.6
		s	0.0	0.0	2.0	2.5
11/17 2218						
	R	$\bar{x}$	0.0	0.0	0.2	1.1
		s	0.0	0.0	0.4	1.5
	1	$\bar{x}$	0.0	0.0	0.3	0.7
		s	0.0	0.0	0.9	1.6
	2	$\bar{x}$	0.0	0.3	1.5	2.4
		s	0.0	0.7	2.3	3.2

Table H7. (con't)

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
	3	$\bar{x}$	0.0	0.0	0.3	4.0
		s	0.0	0.0	0.7	3.3
	4	$\bar{x}$	0.0	0.0	0.0	1.1
		s	0.0	0.0	0.0	1.9
	5	$\bar{x}$	0.0	0.0	1.3	0.9
		s	0.0	0.0	1.9	2.0
	6	$\bar{x}$	0.0	0.0	1.4	2.0
		s	0.0	0.0	2.5	2.7
11/23 2239						
	R	$\bar{x}$	0.0	0.1	0.1	0.2
		s	0.0	0.3	0.3	0.3
	1	$\bar{x}$	0.0	0.0	0.1	0.8
		s	0.0	0.0	0.3	1.5
	2	$\bar{x}$	0.0	1.3	1.8	4.3
		s	0.0	2.0	2.4	3.9
	3	$\bar{x}$	0.0	0.0	0.5	3.3
		s	0.0	0.0	0.9	4.2
	4	$\bar{x}$	0.0	0.0	0.0	1.6
		s	0.0	0.0	0.0	2.6
	5	$\bar{x}$	0.0	0.0	0.6	0.5
		s	0.0	0.0	0.8	2.3
	6	$\bar{x}$	0.0	0.0	0.7	4.6
11/30 2245						
	R	$\bar{x}$	0.0	0.0	0.1	0.3
		s	0.0	0.0	0.3	0.6
	1	$\bar{x}$	0.0	0.0	0.1	0.5
		s	0.0	0.0	0.3	1.1
	2	$\bar{x}$	0.0	0.0	1.2	4.0
		s	0.0	0.0	2.9	6.1
	3	$\bar{x}$	0.0	0.0	0.4	2.7
		s	0.0	0.0	0.6	4.9
	4	$\bar{x}$	0.0	0.0	0.5	1.2
		s	0.0	0.0	0.9	1.6
	5	$\bar{x}$	0.0	0.0	0.0	0.0
		s	0.0	0.0	0.0	0.0
	6	$\bar{x}$	0.0	0.0	0.0	0.3
		s	0.0	0.0	0.0	0.6

Table H7. (con't)

Date D Day	Field	Statistics	Egg	Instar 1	Instar 2	Instar 3
12/5 2245						
	R	$\bar{x}$	0.0	0.0	0.0	0.9
		s	0.0	0.0	0.0	2.2
	1	$\bar{x}$	0.0	0.0	0.0	0.3
		s	0.0	0.0	0.0	0.7
	2	$\bar{x}$	0.0	0.0	0.5	1.3
		s	0.0	0.0	1.1	2.8
	3	$\bar{x}$	0.0	0.0	0.2	0.5
		s	0.0	0.0	0.6	1.1
	4	$\bar{x}$	0.0	0.0	1.1	0.5
		s	0.0	0.0	2.3	1.0
	5	$\bar{x}$	0.0	0.0	0.0	0.7
		s	0.0	0.0	0.0	1.9
	6	$\bar{x}$	0.0	0.0	0.0	0.5
		s	0.0	0.0	0.0	0.7
12/12 2247						
	R	$\bar{x}$	0.0	0.0	0.1	0.3
		s	0.0	0.0	0.3	0.6
	1	$\bar{x}$	0.0	0.0	0.0	0.7
		s	0.0	0.0	0.0	1.3
	2	$\bar{x}$	0.0	0.0	0.0	0.2
		s	0.0	0.0	0.0	0.6
	3	$\bar{x}$	0.0	0.0	0.0	0.8
		s	0.0	0.0	0.0	1.5
	4	$\bar{x}$	0.0	0.0	0.0	0.3
		s	0.0	0.0	0.0	0.7
	5	$\bar{x}$	0.0	0.0	0.0	0.0
		s	0.0	0.0	0.0	0.0
	6	$\bar{x}$	0.0	0.0	0.2	0.6
		s	0.0	0.0	0.4	1.0

[1] $\bar{x}$ and s (for fields 1-6) are computed on a per cluster basis (20 onions/cluster and 10 clusters/sample date) and with 200 onions/cluster for field R.

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