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THE BIOLOGY AND ECOLOGY OF
ENTOMOPHTHORA MUSCAE (COHN) IN
THE ONION AGROECOSYSTEM

presented by

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THE BIOLOGY AND ECOLOGY OF *ENTOMOPHTHORA MUSCAE* (COHN) IN THE ONION AGROECOSYSTEM

by

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ABSTRACT

THE BIOLOGY AND ECOLOGY OF
ENTOMOPHTHORA MUSCAE (COHN) IN
THE ONION AGROECOSYSTEM

by

Raymond I. Carruthers

Entomophthora muscae was identified as a common fungal pathogen of the adult onion maggot, Hylemya antiqua, and the adult seed corn maggot, H. platura, throughout Michigan. The general disease cycle is described including the etiology, symptomatology and phenology. In vivo and in vitro laboratory culture and transmission techniques are also given.

Field investigations revealed high levels of E. muscae infection in natural host populations. Although high infection levels were noted, actual E. muscae-induced mortality in the overall adult population was significantly lower due to other mortality factors preempting death by mycosis. The importance of E. muscae-induced mortality to population regulation was found to be highly significant, as its effect on the reproductively mature females, thus fecundity was greatest.

A conceptual model of E. muscae in the onion agroecosystem was developed and used as a basis in hypothesis development for specific experimentation. Functional relationships were identified and quantified for use in the development of a multiple host-pathogen simulation model.

Experimental results include characterization of the temperature-dependent disease incubation period, pre-mortality effects of E. muscae on fecundity, and temperature and moisture-induced effects on E. muscae conidial production, rate, and phenology of sporulation, germination and mortality. Further studies examine the spatial interactions of the host and pathogen under field conditions. Identification of important microhabitats and quantification of their impact on disease spread and development are also examined.

The experimental results of this study have been linked with data from the literature and synthesized into a computer simulation model of the onion maggot-seed corn maggot-E. muscae life system. The model was constructed in free-body form to allow component-by-component evaluation and easy linkage with other models associated with the onion agroecosystem. Model formulation, validation, and application are discussed, with several simulation results presented.

DEDICATION

To Dr. D. M. MacLeod
an inexhaustible source of inspiration

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I wish to express my sincere appreciation to the entire faculty and staff of the Department of Entomology as all of you have greatly added to my professional and personal development.

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I also extend thanks to all of my colleagues, especially Tom Ellis, Julia Pet, Bill Ravlin, and Gary Whitfield, who provided constant support, encouragement, and friendship: you made the hard times easier.

To Susan Battenfield, Marie Pane, and Cathy Stewart, thank you for putting this thesis to rest.

Most importantly, I express my love and appreciation to my wife Diane, the single person who has given the most toward the completion of this goal.

Cycles within cycles, independent yet interacting, the large encompassing the small, the small fusing into the large. Each moment of life is shaped by everything that has gone before. No act or circumstance stands alone; each has been influenced by the past and, in turn, will affect the future. There is no living thing, no biological or environmental event, condition or process, that deviates from this universal principle. Interdependence is the supreme law of nature (Edward R. Ricciuti, from The Peaceable Kingdom).

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I. INTRODUCTION

Entomogenous fungi have long been known to play an important role in regulating insect numbers (Steinhaus 1954). Over the past century, widespread attention has been drawn to natural epizootics, induced by fungal pathogens, and their potential for suppressing insect pests (Steinhaus 1956), although few controlled successes have been realized (Ferron 1978). One of the primary limitations has been the lack of knowledge associated with the dynamic interactions of the host-pathogen complex under field conditions.

Epizooticological studies have been infrequent with few underlying causal mechanisms identified. Such has been the case with Entomophthora muscae (Cohn) Fresenius, a common pathogen of several adult dipterans. Since its first description (Cohn 1855), E. muscae has been noted inducing epizootics in numerous host species including the common house fly, Musca domestica (Thaxter 1888, Yeager 1939, Baird 1957, Miller and McClanahan 1959, Kramer 1971, Berisford and Tsao 1974, Wilding and Lauckner 1974). The incidence of E. muscae in field populations of Hylemya antiqua (Meigen), the onion maggot (OM), has been well documented (Miller and McClanahan 1959, Perron and Crete 1960, Kramer 1971, Loosjes 1976). Although it is considered a major mortality factor of adult flies, virtually no research has been conducted on its field biology or its impacts on the host organism.

During outbreak years, the OM has been known to cause serious damage to onions (80-90%) (Perron et al. 1955, Metcalf et al. 1962). In Michigan, endemic populations annually cause between 5-20% loss despite intensive control programs (Carruthers et al. 1981). In response to problems associated with the present control strategies--OM insecticide resistance (Harris and Svec 1976), the economics of current pesticide applications, future pesticide development,

and the associated environmental and health hazards (Metcalf 1980)--an intensive program was initiated to study the population dynamics of the OM in the onion pest-crop agroecosystem (Haynes et al. 1980). Due to its importance in the population dynamics of the OM, E. muscae has been included as a major component of that program. The goal of this study is to research the pathogen's role as it relates to the regulation of OM populations in the onion pest-crop agroecosystem.

The "systems approach" (Churchman 1968, Tummala et al. 1975, Manetsch and Park 1977) was used as the underlying research philosophy of study which necessitated a cooperative, transdisciplinary-oriented project. Researchers from various disciplines (botany-plant pathology, economics, entomology, nematology, and electrical engineering-systems science) have been involved in developing an overall research program interlocking the disciplines through the common base of systems modeling. The scope of this subproject has been highly augmented by the cooperative nature of this project within and beyond the Department of Entomology.

Specific cooperation with Mr. G. H. Whitfield (PhD candidate, Department of Entomology) and Ms. J. J. Pet (MS candidate, Department of Electrical Engineering and Systems Science) on various aspects of the population dynamics of the OM allowed an in-depth evaluation of the impact of E. muscae in the onion agroecosystem. This evaluation led to the experimentation necessary for developing the biological models for this host-pathogen life system.

II. OBJECTIVES

1. Research the basic life system of Entomophthora muscae in the onion agroecosystem.
2. Determine the abiotic and biotic factors that influence the occurrence, viability, movement and mortality of E. muscae.
3. Utilize experimental procedures that produce the quantitative results necessary for the construction of a free-body model.
4. Develop a simulation model of the within season dynamics of the E. muscae life system in the onion agroecosystem and utilize this model to aid in the development of pest management strategies.

III. RESEARCH RATIONALE AND APPROACH

Crop protection in the United States has centered around chemical control supplemented by (1) cultural control methods, (2) chemically-oriented host plant resistance and (3) biological control strategies (McGovran et al. 1969). The rationale for this approach is based on the notion that chemical controls are inexpensive (based on cheap energy), effective, and implementable with a minimum lag time. However, it has been estimated that approximately $18.2 billion or 33% (35% on a worldwide basis) of the crops produced in the United States are lost to insects, pathogens and weed pests despite extensive pest control operations--including an annual application of approximately 1.2 billion pounds of pesticides (Pimentel 1976). Also, during the past thirty years, insecticide usage has increased eleven-fold while preharvest loss to insects has more than doubled (van den Bosch 1978). These statistics indicate that present pest control strategies (chemical control) fail a significant amount of the time.

This situation, coupled with the rapid increase in energy costs over the past ten years, casts serious doubt on the viability of the chemical control approach for future crop protection.

By conventional definition the onion agroecosystem is one of a group of relatively insignificant components of the American agricultural system, representing only 0.5% of total farm production. By defining the crop's significance from an ecological and energetic perspective, however, this system becomes extremely valuable from a research standpoint as it represents an agricultural microcosm that is the epitome of the state of American agriculture. The existing production system is the result of several decades of energy-intensive cropping practices that have been supported primarily by petroleum-based products. Pest control is no exception. Agrochemical pesticides dominate other management strategies (Haynes et al. 1980).

Insect pests, plant pathogens, and weeds are the three major pests in this ecosystem. On organic soils (e.g., Michigan, Ontario, and New York) the major crop pest is the OM. Efforts to control the OM with chemical agents are numerous, but, with few remaining exceptions, ineffective. The variety of agents used to control the OM represents the evolution of pesticides in the United States:

pre-1930's - Natural mortality and cultural practices

1930's - Oil sprays and corrosive sublimates (Kendall 1932)

1940's - Mercurous chloride and oil bordeaux emulsion (Perron and La-France 1960)

1950's - DDT, Aldrin, Dieldrin, etc.: the chlorinated hydrocarbon complex (Doane and Chapman 1952)

1960's - Organophosphates: Parathion, Ethion, etc. (Guyer and Wells 1959, Perron and LaFrance 1962)

1970's - Thiophosphates: Dasanit, Dyfonate, etc. (Cress et al. 1976).

The constant substitution of insecticides does not stem from the development of more efficient pesticides, but rather to the loss of effectiveness or the failure of an insecticide to control OM infestations over an extended period of time. The reduced effectiveness of chemical control has been attributed to increasing pesticide resistance within OM populations (Brown 1958, Harris 1972, Harris et al. 1962, Harris and Svec 1976, Harris et al. 1963, Howitt 1958, Guyer and Wells 1959).

Resistance to many chlorinated hydrocarbons (including DDT and the Aldrin-Dieldrin complex) was documented by Drew and Guyer (1958). This resistance stimulated research to find a substitute--the organophosphate (OP) insecticides. OP insecticides were highly effective during the first few years of use, as were the chlorinated hydrocarbons in the early fifties (Guyer and Wells 1959, Allen 1962). However, following the same pattern exhibited by the CH compounds, the effectiveness dropped dramatically with continued use (Harris and Svec 1976).

Harris and Svec (1976) noted substantial increases in the levels of OM resistance in relation to many organophosphate and carbamate insecticides between 1965 and 1972, including several populations from Michigan onion-producing regions. Dasanit, a thiophosphate which has been used extensively since 1970 as a soil insecticide for OM control in Michigan, now gives very low levels of control and is no longer being formulated for use on onions (Wells 1977). Carbofuran, a carbamate insecticide, has shown excellent control in field

testing, but field resistance is expected to develop (Harris and Svec 1976). Similarly, the synthetic pyrethroid insecticides produced excellent initial control of dipteran pests, but with continued selection pressure resistance develops rapidly (Solomon 1981). Neither chemical type is now felt to offer long-term OM control, and they are no longer being actively pursued for OM registration.

If future management is going to be an extension of present-day strategies, no long-term pest control can be expected. However, the failure of this approach does not lie exclusively with the use of chemicals. The philosophies and techniques that direct chemical use are equally responsible and need to be altered. Typically, agricultural chemicals are applied in a crop protection mode (often as "insurance" sprays) as opposed to a population regulation mode that utilizes information regarding the pest population and its dynamics. The crop protection philosophy accelerates the normal adaptive processes of the pest directly against the pest control method by applying continual selective pressure—even when unnecessary. This same philosophy has been carried directly over to biological control programs--creating a similar set of problems, the most apparent similarity being the development of host immunity or resistance to biological control (Ratcliffe 1959, Messenger and van den Bosch 1964, Pimentel and Stone 1968).

Less apparent, but probably more important, is the lack of knowledge concerning the true operation of the control system. This lack of understanding allows the system to establish its own unpredictable trajectory, which leads to an unmanageable outcome. Numerous examples of parasite release are cited in the literature where little or no prior knowledge of the host-parasite dynamics existed. The long-term results of such release programs are quite variable with

only a few classic examples giving adequate control (the vedalia lady beetle-cottony cushion scale system or Chrysolina-Klamath weed system). Documentation of biological control attempts in Canada show only a 10% measureable economic success rate associated with introduced parasitoids and predators (Beirne 1975). Viewed in retrospect, multiple-species parasite releases indicate that direct and indirect interference between competing parasites often lowers overall mortality rates in the host (Turnbull and Chant 1961, Zwolfer 1963, Gage 1974). Actually, any type of mortality (parasitism, predation, or that caused by the abiotic environment) at the right point in a life cycle can raise the overall host survival by relieving the density-dependent mortality stresses of a later life stage.

The chemical control philosophy (Doutt and Smith 1969) in biological control has recently focused on the field of insect pathology. A large portion of present microbial research is being directed toward developing spray tank-compatible microbes with long shelf-lives for commercial use. Applying insect microbes in this manner presents no direct problems and may prove to be a valuable method for future pest management programs. However, the problem arises because the unilateral control philosophy (the use of a single control technique) long associated with chemical control is being directly carried over with other spray technology. Not only are microbes being applied in a unilateral fashion, but they are typically used without an adequate understanding of their population biology and host interactions. Some leaders in the field (Allen et al. 1978) have recently become aware of this trend and are working to establish a more holistic balance within the discipline.

An alternative approach to direct chemical or biological control using

similar philosophies may be found by studying the population dynamics of the pest and the natural mortality factors regulating their numbers. In this way, directed pest mortality can be interjected into the production system when necessary with the least amount of disruption to other components within the agroecosystem. If the aforementioned problems are to be avoided, understanding these mortality factors and utilizing them in a multifactorial manner should be the basis for developing and implementing specific pest management strategies.

Control strategies for a single pest may act as stimuli not only for the target organism but for many other organisms within the agroecosystem. Management practices other than pest control also exhibit similar impacts on non-target portions of the agroecosystem; therefore, research programs dealing with agricultural management are, or should be, transdisciplinary in nature (Jantsch 1970, Bird 1979). Even if transdisciplinary programs exist, they may provide only short-term solutions unless the dynamics of the overall production system are considered. Such an approach to agroecosystem design and management (Haynes et al. 1980) is much more complex than what agricultural scientists have dealt with in the past. This complexity necessitates an overall methodology to guide and manage the development and implementation of such projects. Although new to agricultural scientists, the philosophical and practical basis for this methodology has been developed and used for some time in the field of systems engineering. The problem-solving process commonly referred to as the "systems approach" (Churchman 1968, Tummala et al. 1975, Manetsch and Park 1979) offers a highly structured format within which complex problems are considered, needs are identified, alternative solutions are evaluated, and final programs are implemented.

The systems approach originated from the military operations research programs of World War II and developed rapidly in the postwar industrial sector (Churchman 1968). Originally, the primary function was designing and implementing physical or information processing systems to meet specific user needs. Its utility in an analytical mode soon became evident. This analytical mode of the systems approach gave biologists the ability to consider and evaluate the complex relationships associated with ecological problems.

Ecological systems belong to a special subset of real world problems where the system structure is pre-existing but unknown. Scientific experimentation is the primary methodology used to identify the underlying structure and the functional processes linking that structure. Mathematical modeling, a component of the systems approach, has been used successfully to guide and link such experimentation, thus helping to develop a more comprehensive understanding of the system and its operation (Patten 1971, Tummala et al. 1975, Ruesink 1976).

The systems approach, however, is much more than just applying mathematical modeling to complex problems. It is a problem-solving methodology that begins with a set of objectives and, through a structured process, results in an operational system capable of satisfying original or slightly modified needs based on resource limitations and constraints (Manetsch and Park 1977). The problem-solving process is composed of several interconnected decision-making phases including (1) feasibility evaluation, (2) abstract modeling, (3) implementation design, (4) implementation, and (5) operation. Each phase is iterative in nature and composed of numerous sub-phases (Manetsch and Park 1977).

For ecological problems, after carefully outlining objectives, the emphasis

is on system identification, the first step of feasibility analysis. Conceptualization and system-environment dichotomization are the primary processes of this phase which allow the researcher to specify what components are to be considered, their levels of interest, and how they interact with the environment (variables external to the system). The conceptualization process begins with a general description of components in biological terms and ends with the transformation of this model into a functional block diagram that represents the actual structural linkages between components.

The second phase of system identification is the parameterization of the functional block diagram, e.g., evaluating the present scientific understanding of the biological components and processes involved in the system. In essence, this is a qualitative and quantitative literature review from which actual system transfer functions can be formulated. In most cases, system conceptualization and parameterization identify areas where data gaps exist and additional research is necessary, which leads to the next sub-phase of feasibility analysis: problem formulation. At this stage, it is clear what research components are necessary to complete the biological model. If no resource limitations exist, research experimentation can be used to identify the missing data for the transfer functions. Normally this is not the case, and the original objectives with the given resource constraints must be reevaluated. This evaluation is the essence of any feasibility analysis and exemplifies the iterative nature of the systems approach.

Once objectives, constraints, and system understanding have been balanced, model parameterization can be completed and abstract modeling begun. Abstract modeling involves determining model type (e.g., simulation model,

mathematical model, stochastic model, etc.), computer implementation, program verification, model validation, and model use (including evaluation of control variables and sensitivity analysis of system parameters). The final results or output of abstract modeling is an identified set of plans for implementation or a set of further research objectives to clarify additional components found to be of importance in system response.

The systems approach is a highly structured system that is organized to aid in rational planning and informed decision-making. The two prominent attributes of this approach are:

1) It overtly seeks to include all factors that are important in arriving at an acceptable problem solution, thus promoting a transdisciplinary philosophy.
2) It makes use of qualitative and quantitative models including computer representations when deemed appropriate (Manetsch and Park 1977).

The systems approach has been used as the overlying methodology in the development of the onion pest-crop agroecosystem project of which this study is a sub-project. The first two phases of the systems approach (feasibility analysis and abstract modeling) were used throughout this study to direct research goals and specific experimentation relating to the population biology of E. muscae and its major hosts in the onion pest-crop agroecosystem. It is hoped that this study will provide system alternatives to be utilized in the overall onion agroecosystem project, will add biological information to the field of epizootiology, and will provide insight into the use of the systems approach in biological research.

IV. BACKGROUND

The OM is the major insect pest component of the onion agroecosystem. Records indicate that the OM has been a major pest of onions for over 100 years in Europe and the United States (Fitch 1867). The larval stage feeds directly on the onion bulb. Although the majority of the damage occurs from direct feeding by the larva, the adult is also a key factor in the spread of the damp rot bacteria, Erwinia corotovora (Jones) (Gorlenko et al. 1956).

Scott (1969) assembled an extensive bibliography for H. antiqua which covers most of the published material with the exception of taxonomic citations and actual spray calendars. Several authors (Doane 1953, Tozloski 1954, Workman 1958, Ellington 1963, Loosjes 1976, Carruthers 1979, Ellis and Eckenrode 1979) have reviewed and collated much of the important biological literature on H. antiqua.

Michigan typically has three distinct generations of H. antiqua per year which overlap due to the longevity of the adult flies. The adults emerge from overwintering pupae in late April or early May. The exact date and length of the emergence period depends on temperature and depth of the overwintering pupae in the soil. As the soil profile warms, the pupae break diapause. The pupae closest to the surface emerge first. Developmental zero for the diapaused pupae is close to 40°F (Eckenrode, Vea and Stone 1975). Newly emerged adults are soft-bodied and require a day to dry and harden. At this time flies emigrate to field borders and feed on pollen. The preovipositional period lasts about 10 days (Theunissen 1976) varying slightly with microclimatic fluctuations (103 degree day, base 4.4°C) (Robinson and Zurlini 1979, Carruthers 1979).

When gravid females move back into the onion field, they lay their eggs on the soil surface around the base of the plant and in the leaf axils. After

eclosion, the newly hatched, first instar larvae move into the base of the onion bulb and feed. This disrupts the tissue in the onion bulb, creating acute water stress. Necrotic lesions then open on the bulb surface which allow microorganisms, primarily soft rot bacteria such as E. corotovora, to enter. The microorganism development increases the rate of tissue degeneration within the onion and increases symptomatic damage. Doane (1953) described OM soft rot damage symptoms.

Onion damage is characterized by flaccid leaves, followed by leaf tip yellowing, and then extreme foliage dehydration. With prolonged damage, the bulb can be completely consumed by the OM soft rot attack, leaving only the desiccated leaf tissue and the outer bulb sheath. At this point the maggot moves into the soil and pupates or migrates to succeeding onions until fully developed (Workman 1958). In the early part of the growing season, one OM may consume up to 28 onion seedlings in the loop stage (Workman 1958), resulting in a high rate of plant damage and mortality. As the season progresses and bulb size increases, one onion can support many more maggots (Loosjes 1976, Carruthers 1979). Kendall (1932) reported that 96.6% of second generation flies reinfest previously infested onions.

Perron (1972) discussed several parasitoids and predators of the OM that were present in non-pesticide, organic soil plots in the Ste. Clotilde region of Quebec (1951-1966). A staphylinid beetle, Alerochara bilineata (Gyllo), was most effective. (A. bilineata, as a larval parasitoid, is capable of destroying 20% of the overwintering pupae (Perron 1972). It becomes a predator as an adult.) A braconid wasp, Aphaereta pallipes, was the second most effective parasitoid, capable of destroying 12% of the overwintering pupae. Several other parasitoids and predators were listed along with a short evaluation of each.

Ritcey (personal communication, 1979, University of Guelph) stated that less than 10 parasitized individuals were observed from several thousand field-collected pupae in Ontario commercial production areas. This same condition is found throughout Michigan, with the exception of non-pesticidal research plots. Heavy pesticide use (soil treatment at planting and weekly foliar applications) has effectively eliminated the natural enemy complex of the onion maggot from these commercial production areas (see Appendix A).

Entomophthora muscae (Cohn) has been identified as a naturally-occurring fungal pathogen of H. antiqua (Miller and McCallahan 1959, Perron and Crete 1960, Krammer 1971) and is presently the only known natural biotic control agent that has a major impact on populations throughout Michigan's commercial onion production system. MacLeod et al. (1976) summarized Entomophthora species with muscae-like conidia; life histories, species identification, and a thorough bibliography are included.

Entomophthora muscae is believed to overwinter in soil via the environmentally-resistant, thick-walled azygospore. In the spring, by a still unknown stimulus-response mechanism, the azygospores germinate in the soil possibly producing germ conidia (Tyrrell and MacLeod, 1975) which cause primary infection of the host. This initial infection takes place in either the developing pupal stage or the newly emerging imago as it moves to the soil surface. After initial contact, the pathogen penetrates the host cuticle and enters the host's body cavity, initiating the disease cycle. Upon entry into the haemocoele, the hyphae begin fragmenting into hyphal bodies. This vegetative stage multiplies rapidly by a budding process and completely fills the host's body cavity before death. An exoenzyme, secreted into the haemocoele, digests most of the host's internal tissue. Eventually, each of these hyphal bodies produces a conidiophore

which penetrates the host integument, then produces a single conidium at its tip (MacLeod 1963). The conidia are forcibly discharged with a mucilaginous coating that allows the conidia to adhere to any object they contact. If the conidium contacts a suitable host, it will germinate, produce a germ tube and penetrate the host cuticle, thus initiating a secondary infection cycle. This cycle may be repeated numerous times throughout the growing season.

The pathogen is known only to be transmitted between adults; no translarval transmission has been noted through experimental procedures (Baird 1957). In the late stages of disease development, the host's behavior is modified such that dying flies orient to elevated loci (tips of grass leaves, small plants, or other material over 1/3 m above the ground) where they attach themselves to the substrate by salivary secretions, a fungal byssus, and a characteristic body and leg configuration (Berisford and Tsao 1974). Host death and fungal sporulation immediately follow. This peculiar behavior modification just prior to spore discharge characterizes many Entomophthora species-host interactions and enhances fungal inoculum dispersal (Steinhaus 1954, MacLeod 1963).

> Under still undetermined conditions, conidial formation may be interrupted by a sudden change in morphology (Dustan 1924, 1927) and physiology (Speare and Colley 1912, Ullyott and Schonker 1940) of some of the hyphal bodies. Instead of producing conidiophores, they produce either zygospores or azygospores (MacLeod 1963).

With azygospore production in H. antiqua, the fly behavior modification differs from that of conidial production. The flies do not orient to or attach on any substrate, instead they fall to the ground when dead. The insect abdomen, which is completely filled with the thick-walled spores, fragments and releases the spores into the soil where they either germinate immediately or lie dormant as in the overwintering condition.

Epizootiological data concerning E. muscae in relation to H. antiqua are

lacking, with little, if any, known quantifiable relationships. Numerous qualitative assessments of the dynamics of E. muscae with various hosts appear contradictory as, i.e., epizootics have been typified as occurring only under wet conditions (Gough 1946, Kramer 1971, Petch 1934, Roubaud 1922, Yeager 1939) and as occurring in warm dry conditions, in field (Perron and Crete 1960) and laboratory conditions (Baird 1957). In a more quantitative study, Wilding and Lauckner (1974) found no clear relationship between weather variables and disease incidence in three Entomophthora species, including E. muscae, attacking the wheat bulb fly in England. A significant positive correlation was found between disease levels and host densities. High OM densities have been noted during epizootics (Miller and McClanahan 1959, Perron and Crete 1960) although moderate population levels have also been noted with epizootic fungal conditions (Loosjes 1976).

Clearly, disease monitoring and gross correlation with abiotic and biotic environmental factors cannot explain the observed response of such a complex association. Only when detailed analyses are coupled in some structural framework or model, can the operative components of such a system by synthesized, understood, and used effectively in a management program.

Classically, insect pathologists and plant pathologists have emphasized the importance of analysis that explores into the microscopic depths, factors that cause variations in host-pathogen interactions. Until recently, little effort has been placed on synthesizing this material to a system level. Without such synthesis, the usefulness of in-depth research is extremely limited and possibly misdirected. One of the first comprehensive models synthesizing an insect-pathogen relationship was developed by Kish and Allen (1978). Their approach recognized intricate relationships while keeping the system as a whole in mind.

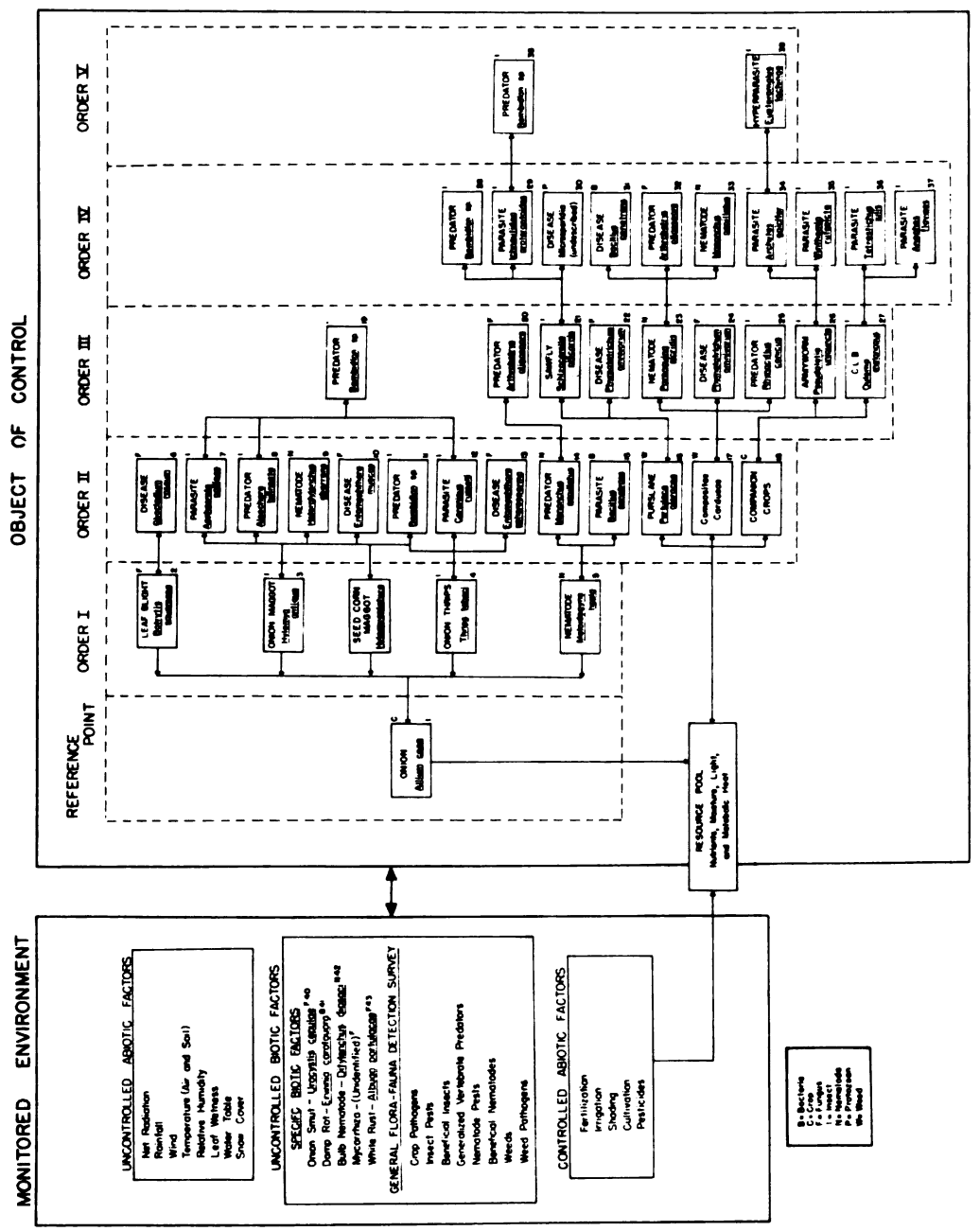
The effect was system-directed analyses that were capable of being linked to provide an overall evaluation of the experimental system.

V. SYSTEM IDENTIFICATION

The first step in system identification is dichotomizing the universe of concern into the system of interest (object of control) and its environment. This process includes defining controlled and uncontrolled factors that affect the object of control and identifying the structural components of the system and their causal linkages (Manetsch and Park 1977, Tummala and Haynes 1977). The object of control in Figure 1 represents the structural features of an onion pest-crop agroecosystem and the levels of interaction within that system (Haynes et al. 1980). The onion pest-crop agroecosystem is characterized as a set of interacting components (such as the onion plant, onion maggot, onion leaf blight, etc.) connected through several orders of interaction. First order interactions are the organisms that directly attack or damage the onion (reference point). Historically, agricultural research on crop pests has dealt principally with direct pests or first order interactions. As the research emphasis moves away from this level, it is more difficult to assess the relationships as they affect the reference point. As pointed out earlier, control strategies for any single component stimulate many other components within the same system, thus it is necessary to obtain a more comprehensive view.

For example, several different fungicides, such as mancozeb or chlorothalonil which are recommended for application on onions for protection from the direct attack of Botrytis squamosa, have an undetermined influence on Gliodium roseum, a fungal pathogen of Botrytis; Entomophthora muscae, the reference point of this study; Entomophthora sphaerosperma a fungal pathogen

Figure 1. Structural features showing levels of interaction within an onion agroecosystem design (object of control) and the monitored environment. Numbers refer to footnotes containing specific references (Appendix B) (from 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
SPECIES BIOTIC FACTORS
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
OBJECT OF CONTROL
REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
ORDER V
RESOURCE POOL
Nutrients, Moisture, Light, and Metabolic Heat

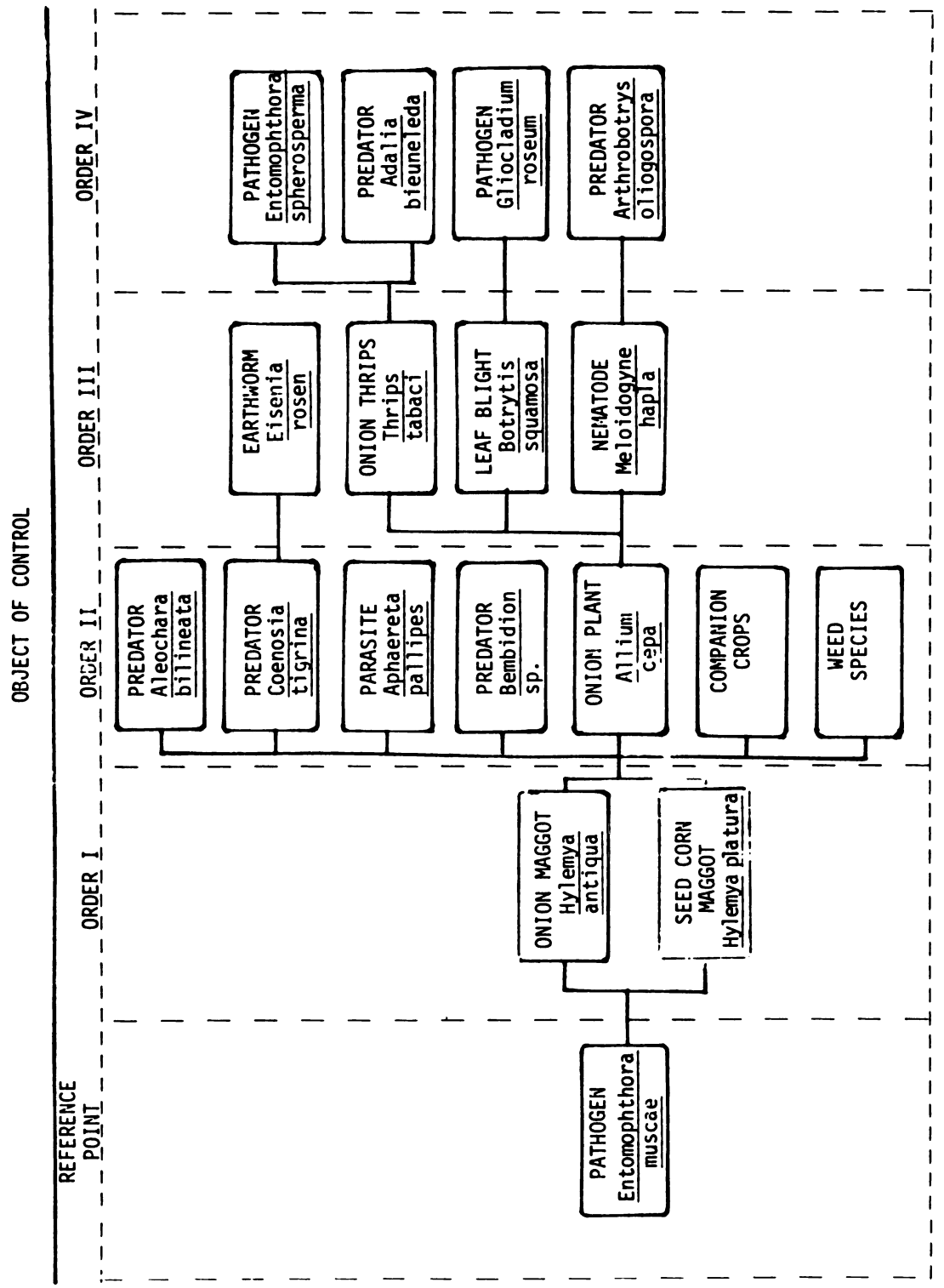
of onion thrips; and Arthrobotrys oligospora a fungal predator of the northern root-knot nematode, Meloidogyne hapla, thus the resultant impact of a fungicide treatment on an onion crop is unclear.

The goal of the systems approach is to quantify the structural linkages between these biological components so that they may be manipulated in mathematical form to test the effects across levels of interaction. The key to developing an effort of this type is to conduct the necessary research to provide the linkages or transfer functions between each of the components. In this way, individual components or groups of components can be researched in free-body form and then linked together to represent the overall system.

A scaled down reorganization of the object of control of Figure 1, with E. muscae as the reference point (Figure 2) creates a more explicit picture of the linkage between E. muscae and other organisms within the onion agroecosystem. To develop an adequate understanding of E. muscae dynamics in the onion agroecosystem, the seed corn maggot (SCM), H. platura (Meigen) must be considered in both research and model form even though it is presently insignificant as a direct pest to the onion plant.

Keeping the overall system in mind, a detailed functional block diagram (Figure 3) was constructed showing the relationship between E. muscae and a single host. Wherever possible the transfer functions have been indicated. Initially, specific data concerning E. muscae was very limited; much of the information has been gathered during this study or taken from other Entomophthora species. In essence, Figure 3 provides the experimental design and literature review of this research project. Each component is documented by the experimental study that provides either the necessary data for implementation or the experimental techniques capable of acquiring that data (numbers refer to

Figure 2. Conceptualization of the object of control for an onion agroecosystem using Entomophthora muscae as the reference point.


OBJECT OF CONTROL
REFERENCE POINT
ORDER I
ORDER II
ORDER III
ORDER IV
PATHOGEN Entomophthora muscae
ONION MAGGOT Hylemya antiqua
SEED CORN MAGGOT Hylemya platura
PREDATOR Aleochara bilineata
PREDATOR Coenosia tigrina
PARASITE Aphaereta pallipes
PREDATOR Bembidion sp.
ONION PLANT Allium cepa
COMPANION CROPS
WEED SPECIES
EARTHWORM Eisenia rosen
ONION THRIPS Thrips tabaci
LEAF BLIGHT Botrytis squamosa
NEMATODE Meloidogyne hapla
PATHOGEN Entomophthora spherosperma
PREDATOR Adalia bieuneleda
PATHOGEN Gliocladium roseum
PREDATOR Arthrobotrys oligospora

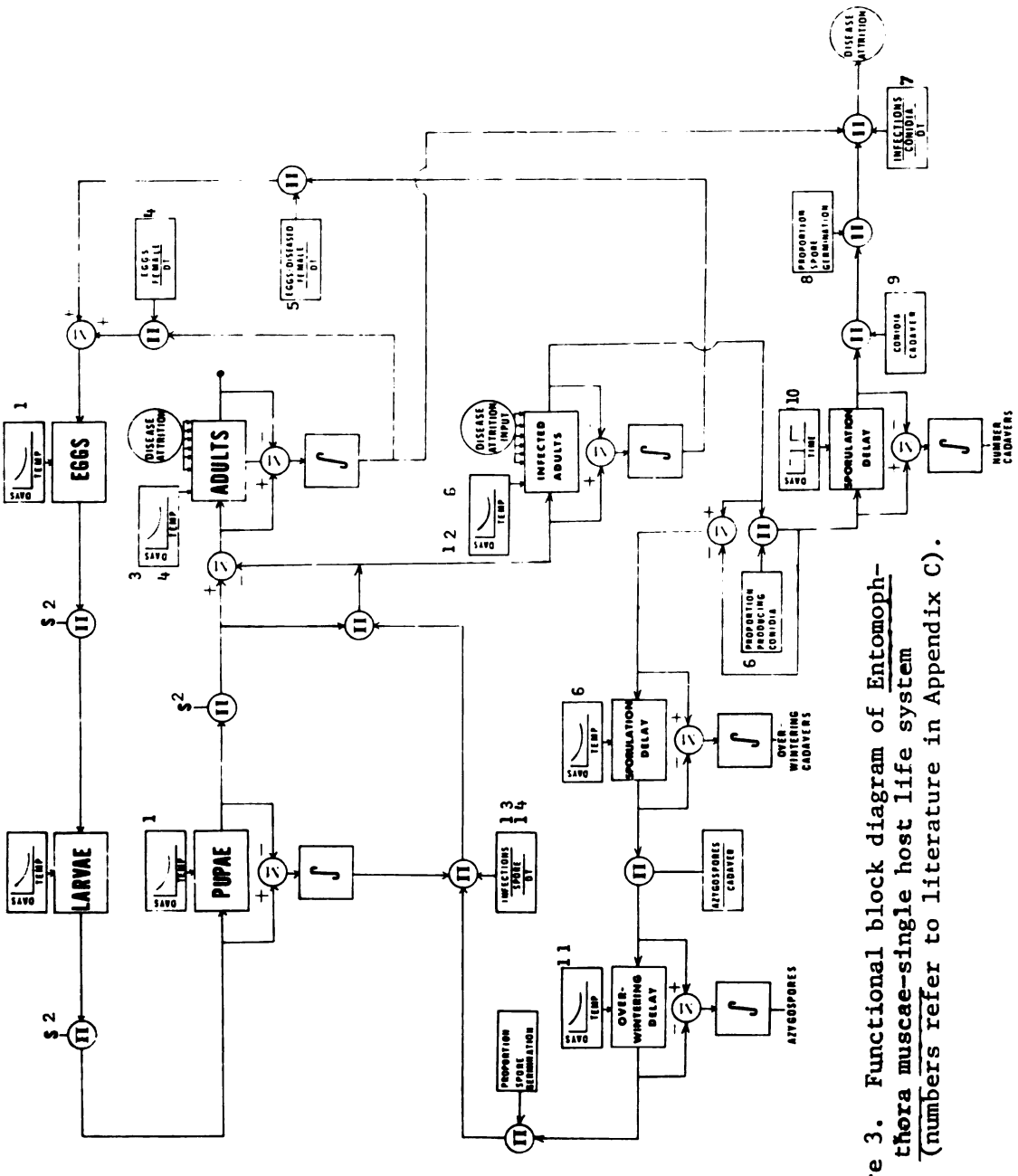


Figure 3. Functional block diagram of Entomophthora muscae-single host life system (numbers refer to literature in Appendix C).

literature in Appendix C).

Space, an added dimension not directly depicted in Figure 3, is extremely important in epizootiology, as many of the transfer functions are spatially dependent (i.e., the influence of spatially distributed habitat on microclimatic factors such as temperature and relative humidity, as well as the spatial distribution, thus population overlap, of the host and pathogen). The concept of spatial orientation of pathogens has been considered by numerous researchers primarily in plant pathology. Much of the work has centered on spore dispersal and disease development in host crop systems (Ingold 1971, Zadoks and Schein 1979). Insect pathogens present a somewhat different situation as the host may be extremely mobile. Little or no work has been done to evaluate the spatial interactions of such a system, although its importance in disease development, thus management, seems critical.

VI. PROBLEM FORMULATION

Actual data on E. muscae in the onion agroecosystem are relatively nonexistent other than some documentation of its presence during epizootic conditions for specific years and locales. Basic life history information which defines the actual life cycle and host interactions in the onion agroecosystem is of primary importance. It is also necessary to understand its natural distribution, abundance and impact on host populations. Further detailed experimentation concerning parameter measurement and estimation, as described in Figure 3, is also of extreme importance in defining the exact functional relationships between E. muscae, H. antiqua, H. platura, and the environment within the onion pest-crop system.

Explicitly, research needs can be separated into three major categories:

a) Identifying unknown system components and their linkage, including disease etiology and definition of the basic life system.

b) Studying the response of the natural system, including detection sampling to determine the presence or absence of E. muscae in measureable levels throughout Michigan onion production regions; regional surveys to determine relative abundance, distribution and host identification for different production areas; and field-level sampling to determine the impact of E. muscae on limited host populations and the effect of host and pathogen spatial patterns.

c) Conducting specific experiments to parameterize the functional relationships such as the effects of environmental parameters on spore germination and infection, pathogen development within the host, host response, and the other relationships graphically described in Figure 3.

VII. EXPERIMENTAL PROCEDURES AND RESULTS

A. Etiology and Disease Life System

Characterization of the natural disease cycle, including identification of the pathogen, specification of its life stages and their relationship to the host organism, is basic to understanding their biology. As discussed by Matanmi and Libby (1975), few investigations have clearly defined host-pathogen interactions as they occur under natural field conditions. This certainly is the case with the infection of root maggot adults by E. muscae, even though its importance in pest regulation has been realized for over two decades (Miller and McClanahan 1959, Perron and Crete 1960).

METHODS: Onion maggot adults, naturally infected with a fungal pathogen later identified as E. muscae, were first collected from an onion field near Grant, Michigan (Grant Township, Newaygo County), in the spring of 1977. Microscopic examination revealed masses of hyaline, multinucleate ellipsoidal conidia, with a papillate apex and flattened base, protruding from the highly distended abdomen of the flies. Conidiophore penetration was limited to the membranous ventral aspect of the abdomen and dorsally in the intersegmental areas (Figure 4, A-D). One hundred conidia were measured microscopically for width and length and used for pathogen identification (MacLeod et al. 1976).

Field-collected adult flies were acquired from the original collection site by sweepnet and taken to the Insect Pathology Research Institute, Sault Sainte Marie, Ontario, Canada. With assistance from Dr. D. M. MacLeod and Ms. M. A. Welton, isolation techniques (Welton and Tyrrell 1975) as described below were followed. Newly sporulating cadavers were attached to the inner lid of a sterile 100 mm petri dish via sterile petroleum jelly. The lid was placed over its original base containing a sterile distilled water-soaked filter paper used to maintain saturated atmospheric conditions within the petri dish. Sporulating conidia were collected over five minute intervals in 5 ml of Grace's insect tissue culture media (supplemented with 5% (v/v) heat denatured, fetal bovine serum and a wide spectrum antibiotic, gentomycin (50 micrograms/ml)), held directly below the sporulating cadaver in a 60 mm diameter petri dish. The medium containing the conidia was then transferred to standard 30 ml tissue culture flasks to which 10 ml of additional media was added. The flasks were incubated at laboratory temperature (ca 21^{o}C) under ambient lighting. At two week intervals, 5 ml portions of the isolate were added to 10 ml of fresh tissue culture media in sterile culture flasks to maintain a continuous supply of the pathogen.

Figure 4, A-F. Conidial life stage of Entomophthora muscae, parasitic on the adult onion maggot (Hylemya antiqua).

A. Female fly infected with E. muscae in the process of sporulation. Note the conidiophore penetration only on the membranous ventral aspect of the abdomen and dorsally between the tergites (fungal growth, whitish area on abdomen, 5x).

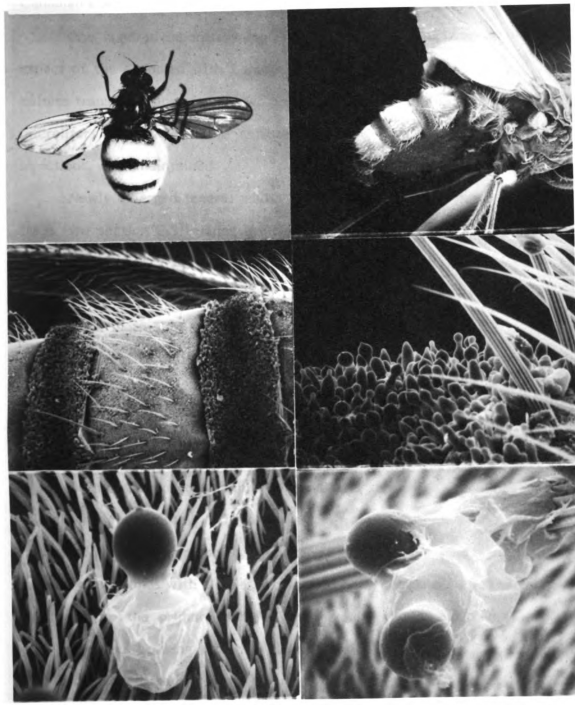
B-C. Lateral views of a male fly infected with E. muscae in the process of sporulation. The area of fungal growth (darkened area in the SEM) is again restricted to the membranous areas of the abdomen (B, 10X and C, 45X).

D. Conidiophore penetration in the intersegmental area of the abdomen. Note the singularly borne conidia in various stages of development from the immature fingerlike conidiophore to the mature bell-shaped conidia (235X).

E. Single E. muscae conidium attached on the thoracic region of an onion maggot adult. The conidia are forcibly ejected from the conidiophores and adhere readily to most substrates. Note the mucilaginous material attached to the base of the conidia and the point of separation from the parent conidiophore. The SEM gives a different perspective, showing a lower separation point, than is seen in light micrographs (Fig. 5A) (1000X).

F. Two E. muscae conidia attached to an abdominal setae of a fly showing the adhesive nature of the mucilaginous protoplasm attached to the conidia (1000X).

A	B
C	D
E	F



To insure a stable, long-term supply of the isolate, a subculture was also placed in liquid nitrogen storage at the Forest Pest Management Institute (FPMI), Canadian Forest Service, Environment Canada.

One hundred laboratory-reared OM adults were injected in the ventral aspect of the abdomen with 2 microliters of the above culture (five days after culture transfer) using glass-drawn needles. Two control treatments, one with 2 microliters of sterile tissue culture media injected and the other with no injections, were maintained.

Newly emerged teneral adults were collected using live catch emergence traps (see section B.3) placed around areas of known OM infestation. These adults, along with adults acquired by sifting pupae from adjacent soil, were held in the laboratory and evaluated for primary E. muscae infection. Microscopic examination (both SEM and light) were used to characterize the fungal stages in vivo.

RESULTS: Based on conidial dimensions (mean length: 22.7 $\pm$ 1.4 µm, mean width: 17.8 $\pm$ 1.1 µm) and shape (Figures 4, E-5A), the pathogen was identified as E. muscae, using the keys provided by MacLeod et al. (1976).

Germination of the conidia released into the insect tissue culture media was noted approximately 9-12 hours after transfer to the culture flasks. A variety of germination responses were seen including the production of secondary conidia, many times with elongate, branched germ tubes, germ tubes developing directly from the primary conidia, and conidia-producing vegetative clusters with branchlets growing out in a radial pattern (Figure 5, B-C). Vegetative growth developed readily in the tissue culture media, producing small mycelial-like colonies (Figures 5, D and 6, A, E-F). Conidial formation was never noted in the tissue culture media although, several months after isolation, hyphal

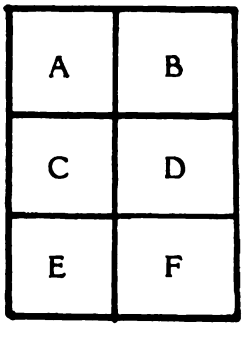
Figure 5, A-F. Phase contrast micrographs of Entomophthora muscae in Grace's insect tissue culture medium supplemented with 5% fetal bovine serum.

A. Single conidium just after ejection from conidiophore. Note the mucilaginous protoplasmic material surrounding the conidium and the apparent separation point from the conidiophore (contrast with the SEM of Fig. 4, E-F, 410X).

B-C. Conidia in the process of germination in tissue culture media. Note the long singular germ tube arising from the secondary conidium in B. The formation of secondary conidia seem to be the normal mode of germination although some conidia produce germ tubes directly, as in C. The germ tubes are found both singularly and branched independent of secondary conidia formation (B + C - 410X).

D. Initial hyphal growth develops from branchlets radiating from the germination point. Hyphal fragments or buds are broken off of the original colony and released into the media (410X).

E-F. Several months after the initial isolation, numerous hyphal fragments divided, forming spherical bodies, possible precursors of the thick-walled azygospores (410X, 820X).



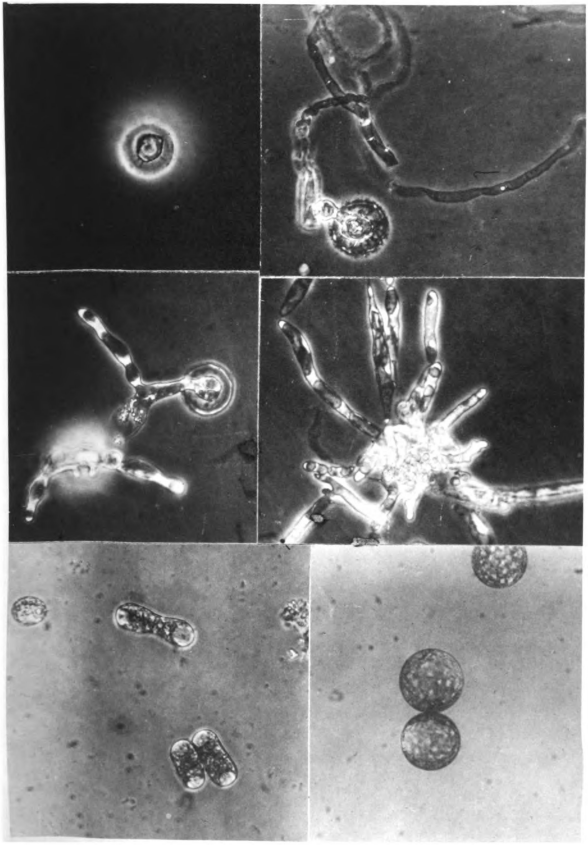
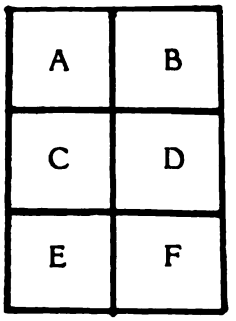
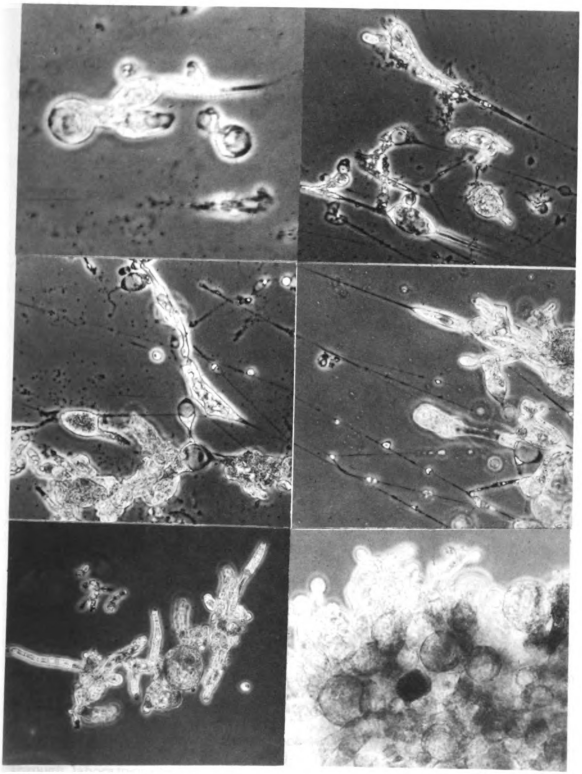


Figure 6, A-F. Entomophthora muscae in Grace's insect tissue culture media (A-F, 300X).

A, E-F. Typical mode of E. muscae growth in tissue culture flasks. The pathogen grows in colonies that are mycelial-like although it tends to form spheres (hyphal bodies) which continue to bud.

B-D. E. muscae held under slight pressure induced by a coverslip tends to develop thread-like forms similar to the protoplast phase of other Entomophthora spp. (see Fig. 7).





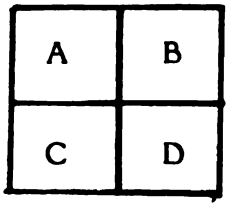
fragments divided and formed spherical bodies, possibly precursors of thick-walled resting spores (Figure 5, E-F).

When vegetative hyphal material is placed under slight pressure (induced by the addition of a cover-slip) the fungal material tends to develop thread-like forms (Figure 6, B-C) similar to the protoplast phase of other Entomophthora spp. (Figure 7, A-D) (Tyrrell and MacLeod 1972, Tyrrell 1977, MacLeod et al. 1980). In vivo development of E. muscae is still not well understood, and the presence of protoplasts in the hemolymph of host flies has not yet been identified, although microscopic examination of infected hosts has revealed identifiable hyphal material only the day prior to death. The lack of hyphal bodies or fragments within the abdomen of the host suggests the existence of such a protoplasmic stage during the early stages of E. muscae infection. Further research is necessary to clarify its mode of in vivo development.

Injecting OM adults with tissue culture containing the above isolate in a vegetative state resulted in only six flies dying of fungal mycosis (four in the conidial state and two in the azygospore state (Figure 8, A-D)). This mycosis, although low in percentage, was highly significant as it completed the requirements associated with Koch's postulates. No explanation presently can be given for the low success rate of infection through injection, although subtle changes in osmotic pressure, pH, and nutrient content of the microhabitat are sure to play a distinct role.

Infection of teneral adults at the time of emergence is common, although the habitat and its microclimate exert major effects on the observed infection levels (see section B.3). Host flies, obtained by collecting pupae from areas of known E. muscae presence, never became infected when allowed to emerge through laboratory-sterilized soil (N=512), suggesting that host-pathogen inter-

Figure 7, A-D. Typical protoplast cultures of Entomophthora spp. provided by Dr. D. M. MacLeod. Note the similarity between these protoplasts and the forms produced by E. muscae-induced by the addition of slight pressure.



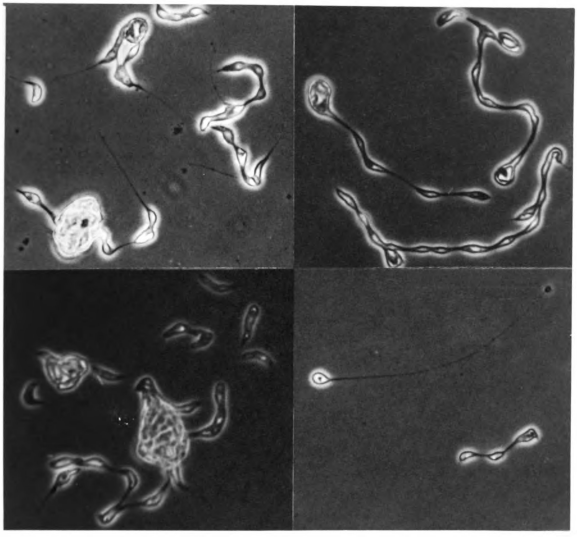
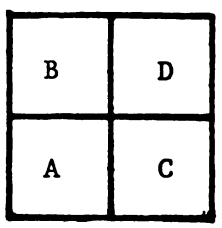


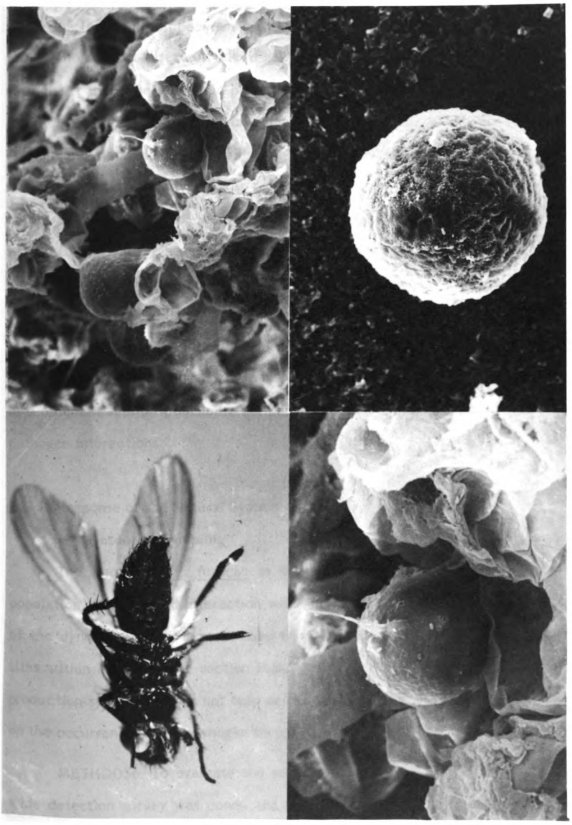
Figure 8. Azygospore life stage of Entomophthora muscae from natural mycosis of onion maggot adults (Hylemya antiqua).

A. Female fly containing E. muscae azygospores internally in the abdomen. Note the dark coloration and shriveled nature of the abdomen (7.25X).

B-C. Azygospores of E. muscae imbedded in the internal abdominal tissue of the host fly (700X, 1600X).

D. Azygospore isolated from heavily inoculated muck soil via centrifugation-flotation techniques (2275X).





actions (presumably azygospores or germ conidia originating from azygospores) infect the fly in the soil between the pupal case and soil surface.

The overall disease cycle (Figure 9) consists of host emergence in the spring. At this time, a certain proportion are infected (primary infection) from interaction with overwintering azygospores, possibly in the form of germ conidia (Tyrrell and MacLeod 1975). Following the incubation period, host death occurs, and either conidia or azygospores result. Conidial production results in host fly attachment to elevated loci, active spore liberation, germination and, if successful, secondary host infection. If azygospore production occurs, the flies die on the ground, the abdomen turns black, becomes very brittle, and then fractures open, releasing azygospores back into the soil. The cycle is continuous throughout the season, although periods occur when E. muscae infection is below detectable levels. Further details concerning the disease cycle will be discussed in subsequent sections, outlining the phenology and spatial relations of the host-pathogen interactions.

B. Response of the Natural System

1. Detection Sampling

The impact of E. muscae in the onion agroecosystem is based on its population dynamics and interaction with various host species. Detailed analysis of the dynamics of this system have been conducted in three primary research sites within Michigan (see section B.2). The full impact on the Michigan onion production system depends not only on localized population interactions, but also on the occurrence of the pathogen throughout the state.

METHODS: To evaluate the natural distribution of E. muscae, a state-wide detection survey was conducted during the spring of 1978 throughout all

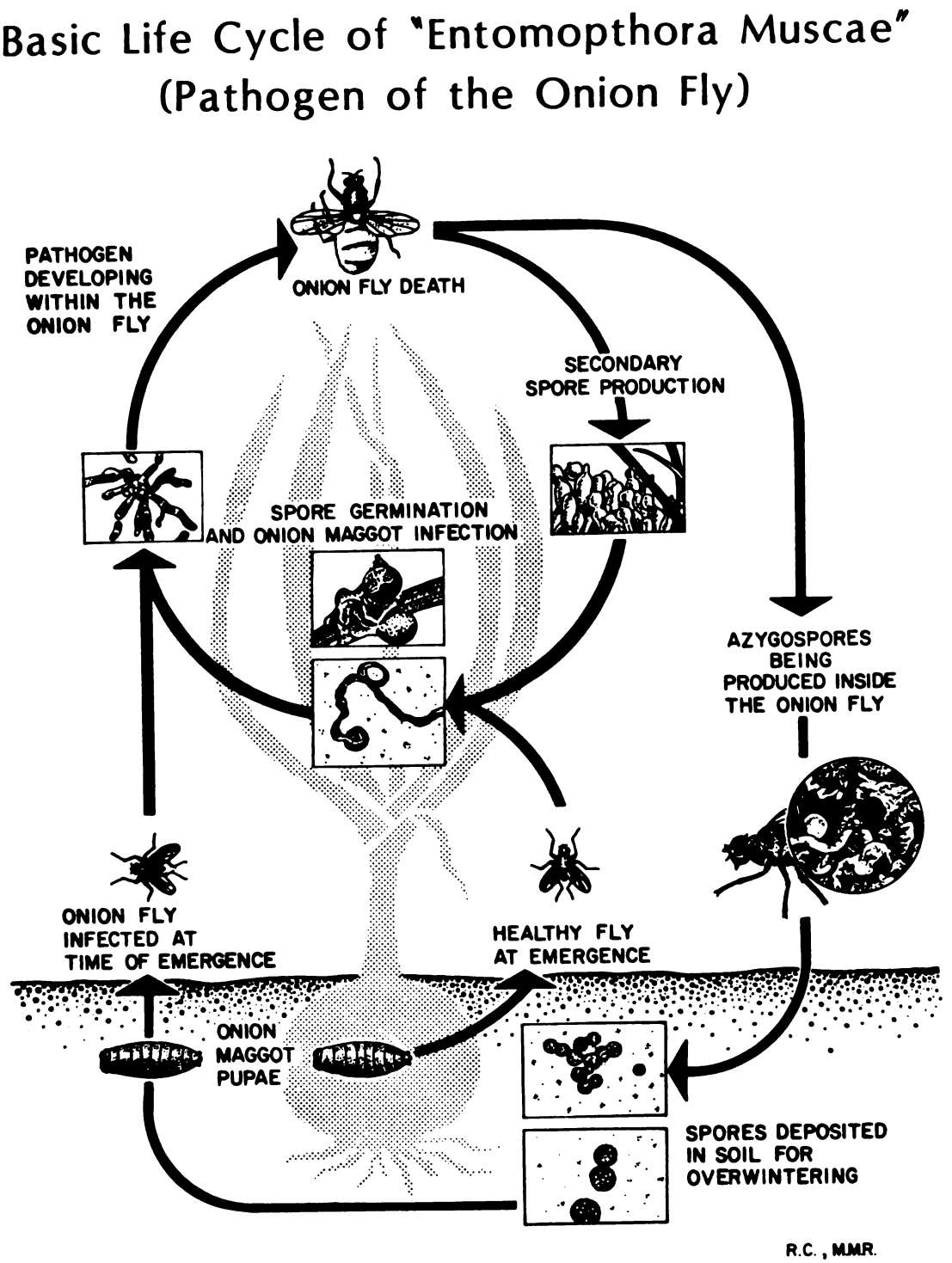


Figure 9. Disease cycle associated with Entomophthora muscae mycosis of Hylemya antiqua.

major onion production areas within Michigan. Pest management field assistants were trained to recognize and collect adult dipteran cadavers exhibiting the characteristic death patterns associated with E. muscae mycosis (Berisford and Tsao 1974). The specimens collected in the survey were preserved in alcohol, labeled with date and locale, and forwarded to the laboratory for identification of both host and pathogen. Host identification was made using common Dipteran keys (Huckett 1971) and comparative specimens from the Michigan State University insect museum with assistance from Dirk Spillemaeckers. The keys provided by MacLeod et al. (1976) were used for pathogen identification with sample material being verified by Dr. D.M. MacLeod of the Forest Pest Management Institute, Sault Sainte Marie, Ontario, Canada.

RESULTS: Twenty-six Michigan counties were sampled during 1978 in the southern lower peninsula. Entomophthora muscae was found naturally occurring in every county sampled including the ten counties where most of Michigan's onions are produced (Table 1, Figure 10). In onion production areas, E. muscae was identified in association with the OM and the SCM. From counties where samples were collected in the absence of onions, the SCM was the primary host identified, although the cluster fly, Pollenia rudis, was also found as a host in six counties, and Coenosia tigrina, the tiger fly, was found in two counties. Numerous other host species are known to be associated with E. muscae, although this survey found no other hosts, probably due to the type of habitats sampled and the level of effort exerted.

2. Field Level Monitoring for E. muscae Infection

Entomophthora muscae is known to cause substantial mortality in populations of both the OM (Miller and McClanahan 1959, Perron and Crete 1960,

Table 1. Counties sampled in 1978 *Entomophthora muscae* detection survey, listed with identified host species.

County Name	Host Flies			
	Hylemya antiqua	*Hylemya platura*	*Pollenia rudis*	*Coenosia tigrinia*
Allegan	X	X		
Barry		X		
Berrien		X		
Calhoun		X		
Cass		X		
Clinton	X	X	X	X
Eaton	X	X	X	
Genesee		X		
Huron		X		
Ingham	X	X	X	
Ionia		X		
Jackson	X	X		
Kalamazoo		X	X	
Kent	X	X		
Lake		X		
Lapeer	X	X		
Lenawee		X		
Monroe		X		
Montcalm		X		
Muskegon	X	X		
Newago	X	X	X	X
Ottawa	X	X		
Sanilac		X		
Shiawassee		X		
Tuscola		X	X	
Van Buren		X		

Figure 10. Distribution of Entomophthora muscae in Michigan based on detection sampling of infected host flies.

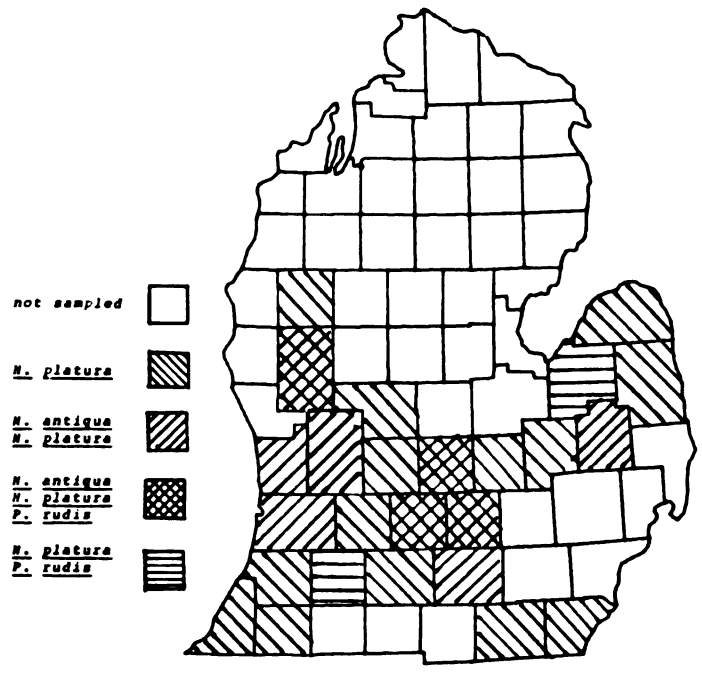
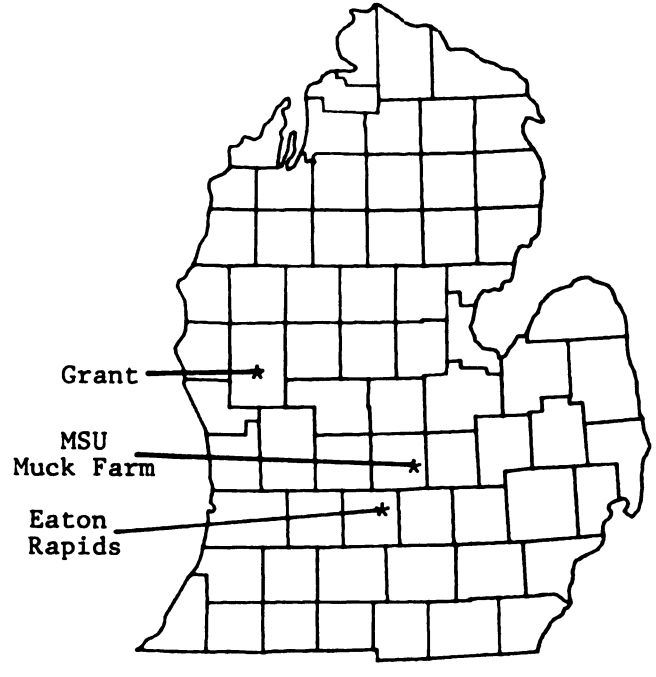


Figure 11. Primary research sites monitored for population levels of Entomophthora muscae in the onion agroecosystem.



Loosjes 1976) and the SCM (Beresford and Tsao 1974), although no detailed assessment of infection level or its effect on the population dynamics of these hosts has been conducted.

The response of the natural system under a variety of conditions and a more thorough understanding of its operation is essential if E. muscae is to be used in pest management programs or even if such programs are developed independent of its effect.

METHODS: To determine the incidence of E. muscae infection in host fly populations, three Michigan onion production regions were monitored during 1978 and 1979 (Figure 11). The primary study site was located in the Rice Lake vegetable production region (Grant Township, Newaygo County) where commercially maintained fields, adjacent border areas, and specific research plots were monitored (Figure 12). Because commercial onion fields are typically maintained using large amounts of chemical pesticides for control, a 4-acre field was acquired for research purposes and kept free of foliar insecticides and fungicides.

The second study site was located on an organic onion production farm near Eaton Rapids, Michigan (Eaton Rapids Township, Eaton County). This area was maintained completely free of any chemical inputs including pesticides and commercial fertilizers. Pest control was conducted using the standard operating procedures of the grower: primarily cultural control tactics (delayed planting, cultivation, rotation, strip-planting, etc.). The third study site was located at the Michigan State University, Organic Soils Research Farm near Laingsburg, Michigan (Bath Township, Clinton County). A 4-acre research plot was planted with onions, maintained pesticide-free, and allowed to develop naturally with no attempt to control pest populations or damage.

Figure 12. Aerial photograph of the Rice Lake vegetable production region (Grant Township, Newaygo County), with specific study sites labeled for identification. (R = primary research site; BR = adjacent nonagricultural research site; * = field laboratory; and 1-7 = commercial fields monitored).

1 mile
N
1
2
3
4
5
6
7
R
BR

These study sites were used by numerous researchers and evaluated for pest populations, natural enemies, onion growth, crop damage and several other biological parameters of interest in the overall onion agroecosystem project. Environmental monitoring equipment including a 3 point soil thermograph, an air hygrothermograph and a pyreheliometer were maintained at each study site. Leaf wetness meters were also installed, but due to equipment failure (sensitivity to electrical storms), very limited data is available. Additional meteorological data including rainfall and wind velocities was available through local National Weather Service monitoring stations.

Samples were collected from each of the study sites approximately twice a week, using either a "D-vac" sampler (Dietrick 1961) or a tractor-mounted suction sampler (Figure 13) constructed after the design by Cobb and Ruppel (1976). The suction sampler was driven through the habitat of interest and operated at a speed sufficient to catch adult muscoid flies without causing severe physical injury. The insects captured in the collection net were transferred to cages and transported to the laboratory where samples of flies known to be hosts of E. muscae were taken. The flies (100 per species when available) were placed by lots of 25 in 20 cm glass lantern globes containing 5-12 cm tall barley seedlings as a substrate. The flies were held under laboratory conditions of 21 $\pm$ 1°C, 80% R.H. and a 16-8 light-dark photoperiod throughout the incubation period of the disease (see Experiment 3). Water and food (honey and brewer's yeast) were provided in conjunction with daily observations for fly mortality. Dead flies were removed from the containers, examined (microscopically when necessary) for the presence of E. muscae infection, and data recorded as to host species, sex, date of death and presence of E. muscae. At the end of the incubation period, the remaining flies were counted, recorded

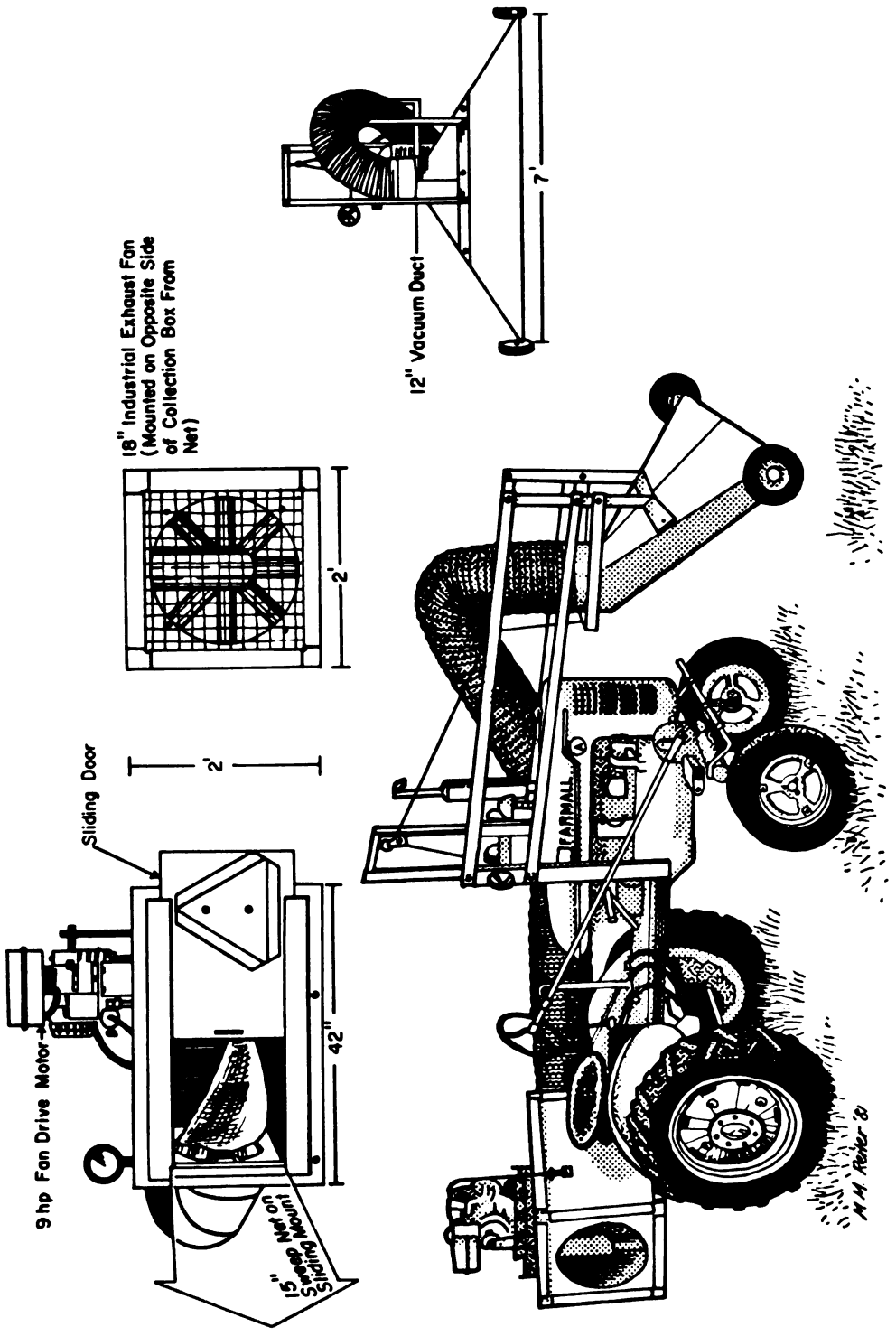


Figure 13. Tractor-mounted suction sampler used for live collection of host flies.

and then discarded or used for other purposes.

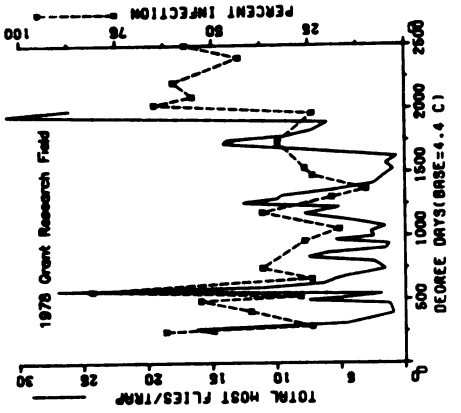
Host fly populations were monitored approximately twice a week in each of the study areas using a variety of sampling devices including emergence traps, activity traps, flight interception traps, sticky board traps, rotary flight traps, and sweepnet samples (see Whitfield 1981 for specific trapping details).

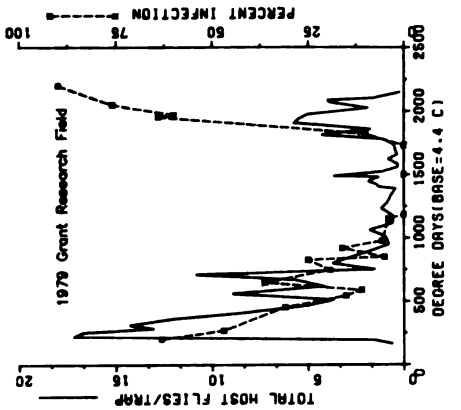
RESULTS: Fifteen sets of E. muscae infection data were collected over the 1978-79 sampling seasons for adult populations of both the OM and SCM. Percent infection and the associated sample variance were calculated and are listed by year, collection location, host type, and sample date in Appendix D. These data were used in conjunction with the adult population estimates from Whitfield (1981) (Grant Research Field, Figures 14-19, other fields plotted in Appendix D).

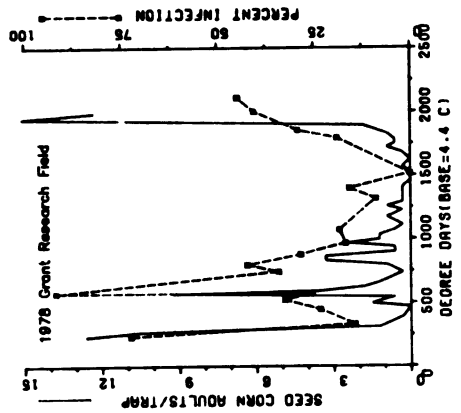
Visual examination of these data suggest a lagged, density-dependent response of infection level with host number. This response is clearly reflected in the field data sets from the 1978-1979 Grant research field (Figures 14-19). Increases in adult OM numbers, primarily in the second and third generations, are followed by a lagged disease response (Figure 14). This effect is not noted in the first generation of OM flies until the adult SCM population is considered (Figure 15). Total host density (OM + SCM) clearly suggests that the two populations are responding to a common pathogen population in a lagged, density-dependent manner (Figure 16).

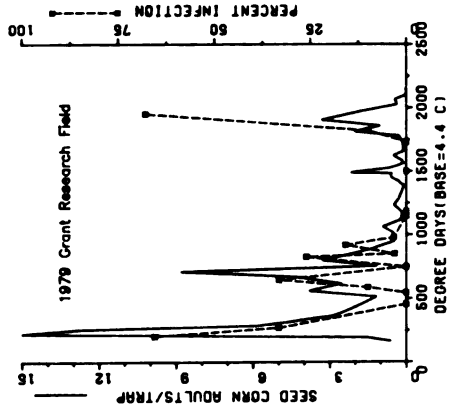
Multivariable techniques were used to regress several independent variables (Table 2) including total host density, several abiotic parameters, and estimated inoculum densities (predicted from the infection data as the number of flies expected to die of E. muscae over a projected time interval) against the proportion infection, lagged by the length of the incubation period (see Experi-

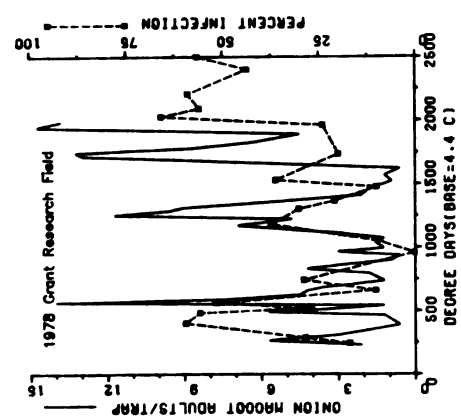
Figures 14-19. *Entomophthora muscae* infection and host fly population levels in the Grant research field 1978-1979.


1978 Grant Research Field
TOTAL MOST FLIES/TRAP
PERCENT INFECTION
DEGREE DAYS(BASE=4.4 C)


1979 Grant Research Field
TOTAL MOST FLIES/TRAP
PERCENT INFECTION
DEGREE DAYS(BASE=4.4 C)


1978 Grant Research Field
SEED CORN ADULTS/TRAP
PERCENT INFECTION
DEGREE DAYS(BASE=4.4 C)


1979 Grant Research Field
SEED CORN ADULTS/TRAP
PERCENT INFECTION
DEGREE DAYS(BASE=4.4 C)


1978 Grant Research Field
ONION MAGGOT ADULTS/TRAP
PERCENT INFECTION
DEGREE DAYS(BASE=4.4 C)

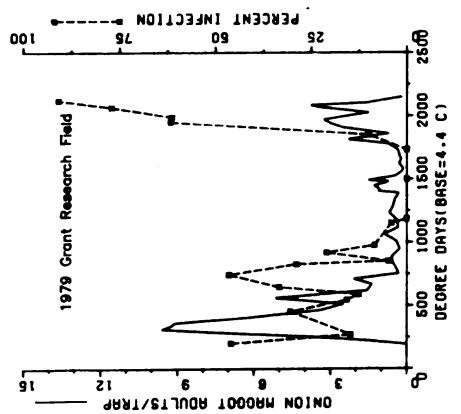

1979 Grant Research Field
ONION MAGGOT ADULTS/TRAP
PERCENT INFECTION
DEGREE DAYS(BASE=4.4 C)

Table 2. Multivariable regression statistics and variables examined for prediction of lagged *E. muscae* infection.

Variables Examined	
DEN = Total Host Density	AHUM = Average Relative Humidity
CAD = Cadaver Density	HOURS = Consecutive Hours Above 95% RH
ATEMP = Average Temperature	MAXH = Maximum Relative Humidity
MAXT = Maximum Temperature	MINH = Minimum Relative Humidity
MINT = Minimum Temperature	

Variable	F to Enter	Multiple r^2	B
LOG10(DEN)	28.05***	.5557	13.79
CAD	24.23***	.6508	.49
(Constant)			17.79
y = 17.79 + 13.79LOG10(DEN) + .49CAD			

*** ($p<.001$)

ment 3). Host density and inoculum density were the only variables eliciting a significant response ($p = .05$). Abiotic variables, including temperature and moisture levels, were found to have no significant effects in explaining any of the variability associated with population infection levels during the 1978 season. The effect of abiotic variables will be discussed in some length in other sections, although the lack of significance in this analysis is probably because abiotic conditions conducive to infection are almost always present in the microenvironment inhabited by these populations. Host and pathogen density seem to be the predominant variables in the development of this disease and many other infections caused by Entomophthora spp. (Perron and Crete 1960, Wilding and Lauckner 1976, Soper and MacLeod 1980).

The relationship of host-pathogen density is much more complex than discussed above, because the "effective density," (that density sensed by the organisms in restricted habitats (Ravlin 1980)), changes differentially throughout the season with respect to absolute density (on a fieldwide per hectare basis). The spatial distribution of host and pathogen is of key importance in regulating the effective density and thus in developing a more complete understanding of the operation of the natural system response.

3. Host-Pathogen Spatial Patterns and Areas of Interaction

Fly mycosis occurs naturally by contact between the host and pathogen under favorable environmental conditions. Two distinct modes of contact (Figure 9), primary infection (via contact with azygospores at emergence) and secondary infection (via contact with infective conidia after emergence) produce the infection levels observed under field conditions.

As mentioned in the previous section, the spatial distribution of host and

pathogen populations is a key factor in disease initiation and development. To better understand the actual host-pathogen spatial interactions, a major effort was made to characterize how these organisms are distributed on a meso scale and in what types of microhabitats they are found, and thus overlap and interact.

a. Infection at Emergence

Primary infection is induced by host-pathogen contact in the soil, presumably by the interaction of azygospores with teneral adults as they move from the pupal case to the soil surface. The exact mode of contact is still unknown although inoculum density and microhabitat are known to influence the infection rate of other Entomophthora species (Wilding 1975; Soper and MacLeod 1981).

METHODS: Centrifugation-flotation techniques commonly used to extract nematodes and spores of endomycorrhizal fungi (Bird 1978, class notes), were evaluated for use in measuring azygospore densities from field soil samples. Silica sand and field-collected muck soil were both heavily inoculated with E. muscae azygospores obtained from infected, field-collected, OM adults. The samples were processed using the techniques described by Bird and evaluated using light microscopy (lactophenol-aniline blue stain) and SEM.

Primary infection levels were estimated using live-catch emergence traps (Figure 20) to capture teneral host flies at emergence. The traps (20 per generation) were placed over areas of known onion damage in the Grant research field for all three OM generations during 1979 and 1980. The flies were collected on a daily basis and transferred to laboratory rearing facilities where they were individually held in 20 cm tall glass globes containing five, 11 cm tall barley seedlings. The flies were held in the laboratory under controlled

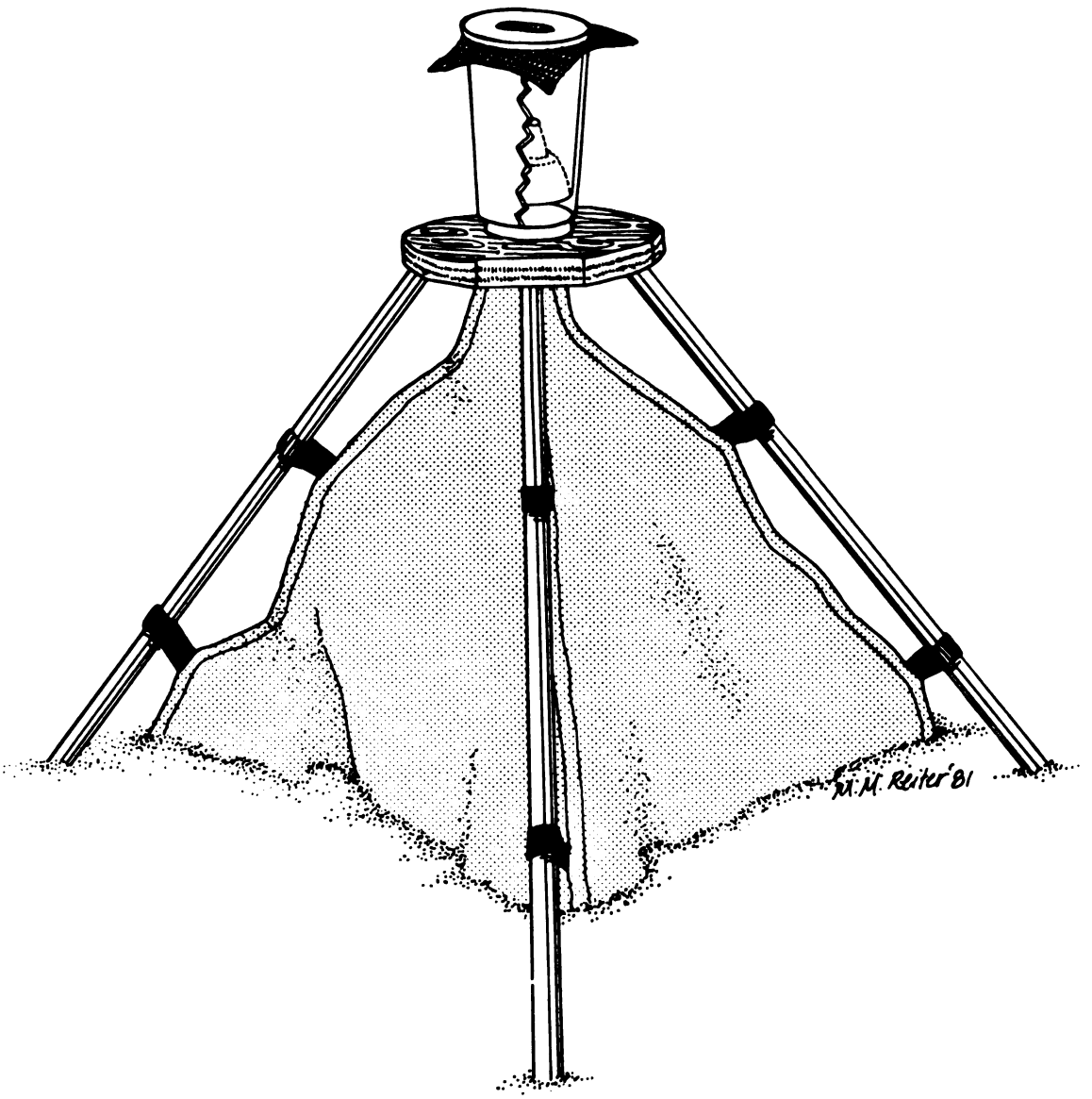


Figure 20. Live catch emergence traps used to capture newly emerging host flies.

conditions (21 ± 1° C, 80% R.H. and a 16-8 light-dark cycle) during the disease incubation period (see Experiment 3). The flies were fed, watered and monitored for mortality on a daily basis.

Overwintering spatial patterns of E. muscae and the resultant infection levels stratified by habitats (onion field-field borders) were evaluated using a bioassay technique. One hundred, laboratory-reared, disease-free, OM pupae were placed into diapause and then buried within marked plots within onion fields and field borders in late October of 1979. The following spring (1980), live-catch emergence traps were placed over the plots and teneral adults were trapped and monitored as described above. This procedure was replicated five times within each habitat and across four fields (3 commercial fields and the research field in Grant).

RESULTS: Azygospores were readily extracted and identified from the silica sand, although extractions from the muck soil proved difficult to evaluate due to the diversity of spore types of similar size and configuration to E. muscae azygospores. If such extraction methods are to be used for estimating azygospore densities in field samples, additional experimentation is necessary in the areas of spore separation by flotation or identification using differential staining techniques.

Primary infection from the Grant research field was found to be too variable to accurately estimate daily infection rates or correlate to daily weather patterns. The variance was compounded by low emergence numbers on a daily basis in combination with variable infection levels between emergence traps presumably due to the spatial distribution of the pathogen. Aggregating these data by trap across each generation, infection levels for each emergence period were calculated (Table 3). The between-trap, variance-to-mean ratios ere

Table 3. Estimated levels of primary E. muscae infection in Hylemya antiqua adults (pooled by generations across traps for the Grant, Michigan, research field). Between-trap variance/mean ratio.

Emergence Period	Total Flies Trapped (N)	Estimated % Infection	Standard Error	Between Trap Variance/Mean Ratio
1979				
1st Generation	67	32.84	5.7	17.8
2nd Generation	137	10.2	2.6	21.34
3rd Generation	333	27.3	2.1	12.43
1980				
1st Generation	132	15.2	3.12	14.93
2nd Generation	210	13.33	2.4	18.27
3rd Generation	3550	32.79	0.8	16.77

also calculated and used as a measure of the spatial distribution of host infection. These ratios are considered to reflect the spatial pattern of azygospores as environmental conditions between traps were considered stable and fly densities per trap were not significantly different from random, $\alpha = .05$). The large variance-to-mean ratios for each generation (Table 3) suggest an aggregated distribution of azygospores within the field. Such a pattern is expected as spores are released to the soil in aggregates from OM cadavers.

Further characterization of this spatial pattern was achieved in combination with the evaluation of the overwintering distribution of E. muscae. It must be noted that the infection levels at emergence in the Grant research field (Table 3) do not reflect the average condition throughout commercial production areas. This field was maintained under different growing practices (see section B.2) resulting in low chemical input and substantial foliage cover in and around the field both during the season and after harvest. For that reason both border samples and onion field samples from the research field were pooled and considered to represent border areas in this analysis.

Due to the extended period of time between establishment of the overwintering plots (late October) and the time of emergence trap placement (late April), several plot markers were lost or destroyed by farm vehicles. The remaining plots (25 out of 40) were monitored between May 1 and June 30.

These data could not be normalized as the mode was equal to zero, therefore two nonparametric tests (the median test, and the Mann-Whitney U-Wilcoxon rank sum w test) were used to test for infection level differences between habitats (Siegal 1956). Significant differences were indicated in each test (Table 4) which substantiated the hypothesis that there are differences in primary infection betwen habitats (border $\bar{x}$ = 26.3% infection, onion field $\bar{x}$ =

Table 4. Non-parametric test for primary infection levels between onion fields and field borders.

Median Test - cases above and below the median

	Onion Fields	Field Borders	N = 25
Greater than	1.	11.	Exact
Less than	10.	3.	2-tailed probability=.001

Mann-Whitney U-Wilcoxon Rank Sum W Test

	Onion Field	Field Border	MW - U = 4.0
Mean Rank of Subgroup	6.36	18.21	W rank sum = 70.0
			2 corrected for ties = 4.1355
			Exact 2-tailed Probability = .0001

2.02% infection). Although E. muscae spore densities were not actually measured and, as mentioned above, differences could be due to differential success in host infection between habitats, it is felt that these results reflect actual spatial patterns of the pathogen. The spatial pattern of the overwintering azygospores is directly dependent on the spatial pattern of the infected flies at the time of death. As they are highly aggregated in border areas during the third generation (see section B.3.b), the observed pattern closely follows the expected pattern.

Although further experimentation is necessary to determine the exact causal relationships, the 13-fold increase (26.3% / 2.02%) in primary infection between border areas and onion fields and the similarly high infection levels in the Grant research field (Table 3) suggest management options such as cull manipulation in the fall or companion planting used to manipulate host and pathogen spatial patterns to increase infection.

b. Spatial Patterns Associated With Secondary Infection

Secondary E. muscae infection is induced by host contact with the asexually-produced conidia. The areas of contact are variable as both host and pathogen are mobile during this phase of interaction. The spatial patterns of both organisms, therefore, are of key importance in determining when and in what areas population interaction occurs.

METHODS: Host fly populations were sampled approximately twice per week in seven different fields in the Grant region during 1979. Within each field, three different microhabitats were sampled: 1) the onion field, 2) adjacent carrot fields (the other major crop in the Grant vegetable production region), and 3) grassy field borders. The samples were collected using the tractor-mounted

suction sampler previously described (Figure 13). The suction engine was run at full speed to increase the collection efficiency. High suction causes physical injury to the flies collected in the sampler, but because density determination was the only variable of interest, fly mortality was unimportant. Ten samples 30 m in length were collected from each microhabitat each sampling period. The flies were preserved in alcohol at the collection site and returned to a field laboratory for identification and enumeration.

RESULTS: Distinct density differences between microhabitats were apparent throughout the season for both the OM and SCM populations (analysis of variance for Grant field 4 presented, Tables 5 & 6). A significant interaction term was also noted indicating changes in relative fly densities between habitats through the season.

Early in the season (May-June), virtually no habitat cover was available in either the onion or carrot fields due to the small size of the plants and their planting densities. This lack of cover induced high OM adult aggregation in field borders where dense vegetation provided shelter from direct solar radiation and high temperatures. Such aggregation created artifically high densities (artificial in the sense that host numbers associated with large acreages are temporarily restricted to very small areas) within field borders. As the season progressed, the crop canopies developed and provided more suitable cover, thereby allowing the fly populations to become more evenly dispersed. The fly density levels between onion fields and the surrounding border areas followed the general pattern illustrated by field 4 (Figure 21). The largest differences occurred during the first generation when crop canopies were small and again during the third generation after normal onion foliage died back and harvest occurred (Figure 21, Julian day 240).

Table 5. Two-way analysis of variance table for onion maggot adult density in differing habitats through the season. (Grant Field 4).

Source of Variation	Sum of Squares	DF	Mean Square	F
Main Effects	7745.1	17	455.6	25.18***
Date	5779.7	15	385.3	21.32***
Habitat	2644.8	2	1322.4	73.20***
Interaction				
Date x Habitat	5197.0	12	433.1	23.90***
Residual	5041.2	279	18.1	
Total	17983.3	307	58.6	

*** (p<.001)

Table 6. Two-way analysis of variance table for seed corn maggot adult density in differing habitats through the season.

Source of Variation	Sum of Squares	DF	Mean Square	F
Main Effects	41343.4	17	2431.9	48.6***
Date	27745.9	15	1849.7	34.8***
Habitat	17443.7	2	8721.5	163.9***
Interaction				
Date x Habitat	20146.4	12	1678.8	31.6***
Residual	14844.8	279	53.2	
Total	76334.5	307	248.7	

*** (p<.001)

Figure 21. Density of onion maggot adults between field borders and the onion field throughout the 1979 season (field 4).

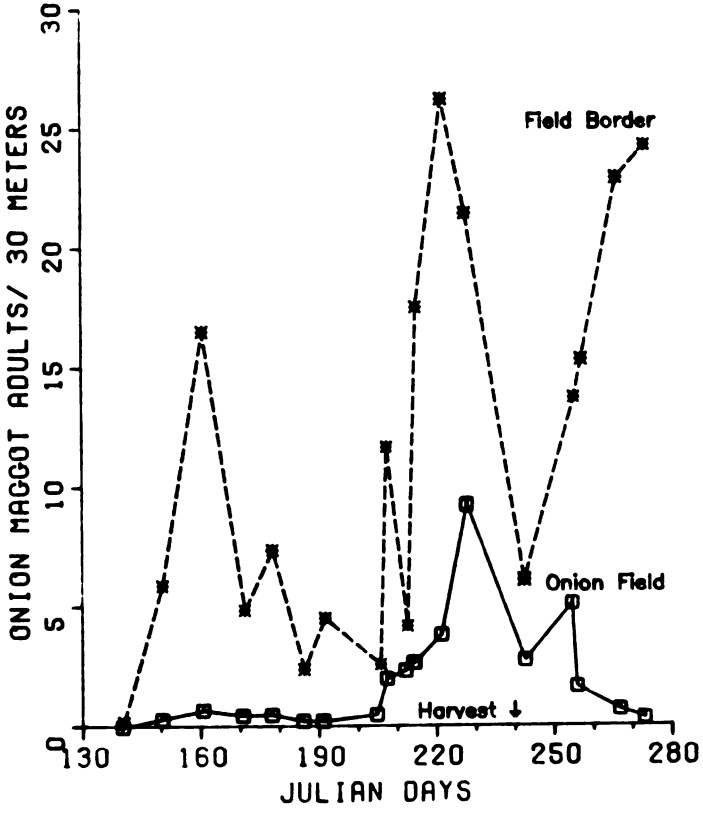
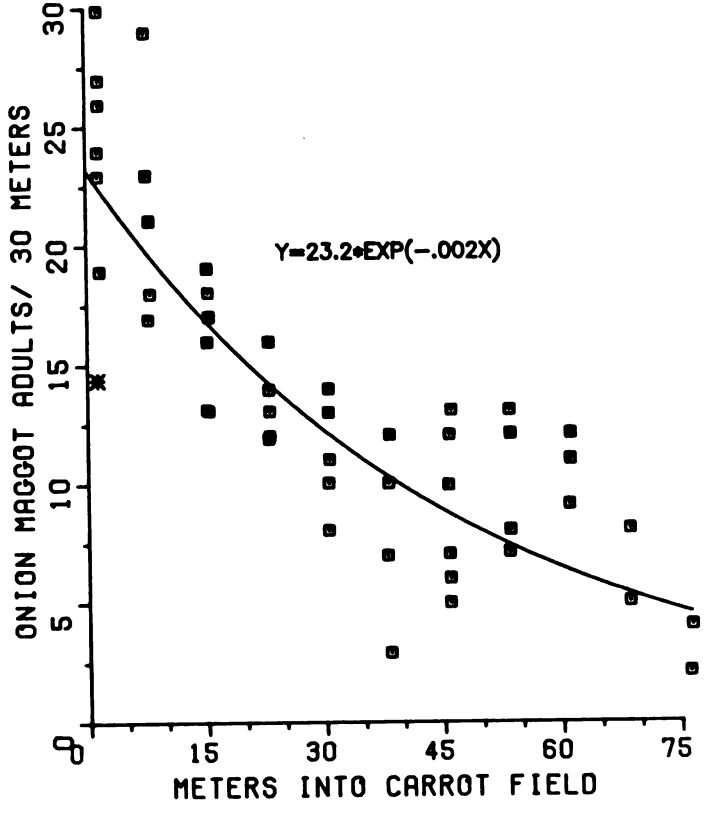


Figure 22. Spatial pattern of onion maggot adults in a carrot canopy adjacent to an onion field during second generation (research field).



Due to the openness of the onion canopy, even during mid-season when the onion canopy was at its peak, the border areas still maintained higher fly densities. This relationship changed through the season in the carrot canopy due to the dense foliage produced after mid-season, creating the significant interaction term noted in the analysis of variance. During mid-season, the carrot canopy provided a habitat very similar to that found in adjacent border areas, thus similar fly densities were noted (Figures 21 & 22). As OM adults were restricted to onions for oviposition, a gradient effect was seen in adjacent carrot fields. Nearly twice the fly densities associated with onion fields were found in the interface areas, dropping exponentially as the distance into the carrots increased (Figure 22).

As the distribution of the pathogen was highly dependent on the infected host, the patterns discussed above were generally followed throughout the incubation period. Departure from this pattern occurred shortly before host death as the infected flies began searching for elevated attachment sites. If suitable attachment sites are available within the habitat, the infected flies attach, die, and sporulate there. If not, they move to an area where suitable sites are available. As spore dispersal under normal conditions was fairly limited (see Experiment 7), the distribution of infective conidia closely resembled that of the cadavers.

As mentioned in Section IV, suitable attachment sites typically must be 1/3 m or more above the ground, with the preferred elevation being approximately 3/4 m. Common substrates for attachment include the tips of grass leaves, stems of herbaceous plants, and onion leaves over 1/3 m in length (carrots are not an acceptable site). Under certain conditions, this behavioral specificity in attachment substrates definitely altered the spatial pattern of E. muscae-

infected flies. For example, early in the season, both healthy and infected flies were found primarily in grassy border areas. These areas also provided adequate cadaver attachment sites, and thus produced excellent population overlap and high effective densities (flies/m to cadavers/m) between the host and pathogen. Although this system seems to operate in favor of onion producers by increasing infection, and thus lowering OM population levels, it is typically disrupted by normal agricultural practices. One standard onion production procedure is border area maintenance, which is primarily a cosmetic practice that includes mowing or spray-down of these areas. Such practices do not eliminate these areas as refuge sites for the OM, but alter the sites in relation to the pathogen density at the time of sporulation. Mowing or herbicide spray-down eliminates adequate cadaver attachment sites which causes an outward migration of diseased flies just prior to sporulation. This practice alters the effective densities of these populations by significantly lowering the population spatial overlap at a critical time.

Later in the season, host flies may be found in large numbers in carrot fields where no attachment sites are available. The result is a migration of diseased flies out of the carrots and into areas where such sites exist. The final result is an aggregated pattern of E. muscae cadavers on onion leaf tips along interface areas between onions and carrots (Figure 23). This high aggregation pattern of cadavers along these areas has been noted by several authors (Miller and McClanahan 1959, Perron and Crete 1969, Loosjes 1976) and is felt to enhance infection during mid-season, when host populations are dispersed much more uniformly than either earlier in the season or after harvest. If sporulating cadavers were spread uniformly over the entire area of host distribution (borders, onion fields and carrot fields), the effective density (flies/m to

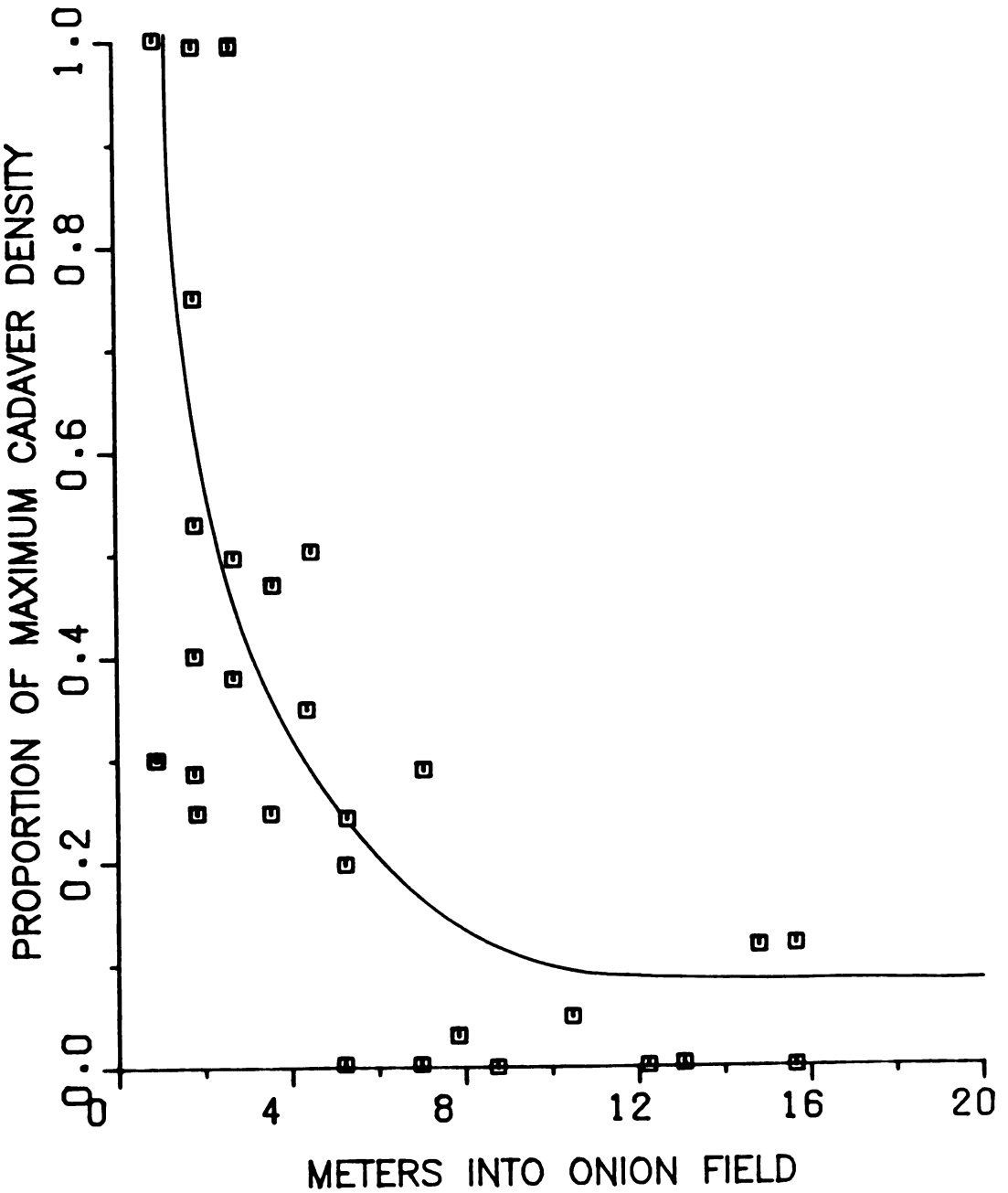


Figure 23. Spatial pattern of E. muscae infected onion maggot cadavers in onion fields adjacent to carrot canopies and border areas during second generation.

cadavers/m) would be extremely low. Aggregation along these interface areas creates much more host-pathogen interaction, as a large number of host flies actually pass back and forth through this area of high cadaver density while moving from the preferred resting habitat of the carrot canopy into the onion fields where oviposition occurs.

Further experimentation to quantify host diffusion between these habitats is necessary to fully understand this interaction, although, as shown in experiment 10, a great deal of the host-pathogen interaction is linked to host movement within microhabitat areas after sporulation has occurred.

Unless host densities are high, as in 1978 (Figure 16), host dispersion over the entire available habitat produces very low effective densities and little host-pathogen interaction occurs. This lowers the infection levels, as in 1979 (Figure 19). For pest management purposes, strip-planting onions and carrots is expected to increase fly infection by increasing interface areas between these crops and allowing more movement of flies through zones of high pathogen density.

4. Host Mortality and the Impact of E. muscae Infection on Fecundity

Direct interpretation of E. muscae infection levels measured in the field provides little information regarding its impact on the population dynamics of the host. Infection does not directly translate to host mortality, because other compounding mortality factors (parasites, predators, or abiotic factors) frequently terminate the host before the mycosis. Similarly, the time of host infection after emergence dictates the ovipositional pattern of adult females causing differential ovipositional responses between early-infected and late-infected individuals. Thus the possible extreme of 100% E. muscae mortality

could result in no viable eggs being produced or the maximum number of eggs being produced.

Interpretation of the impact of E. muscae is a confusing problem which requires an independent measurement of host mortality as it impacts fecundity. Cage studies have been used by numerous authors (Perron 1961, Wilding and Lauckner 1974, and Loosjes 1976) to estimate mortality of adult Anthomyiidae, including the OM. However, adult flies maintained in field cages must be supplied with artificial food and water sources, they are sheltered from harsh abiotic conditions, are protected from natural enemies, and do not maintain normal flight activities. Thus mortality estimates made using field cage experiments must be viewed as biased (Loosjes 1976).

The need for more realistic adult mortality measurements has required that detailed population assessments be evaluated to provide an alternate method of determination.

METHODS: Adult population assessments (Whitfield 1981), including field emergence rates and population density estimates from adult flight curves, were used jointly to estimate adult mortality through the season.

Mortality estimates of adult flies were calculated by using adult emergence curves to determine the proportion of new recruitment allocated to the adult population over the intervals between population density estimates. In the absence of mortality, the cumulative emergence curve and the adult population density curve (both plotted as a percent) would track the same function. In reality, mortality naturally occurs following a lagged negative exponential decay function (Robinson and Zurlini 1979). In the field, flies emerge over an extended period of time (several weeks) which compounds the observed mortality because mixed ages of adults occur simultaneously. Mortality of the mixed age

population is directly measureable as the difference between the projected population estimated from the emergence curves and the measured population density over the sample interval. Using this method, the assessment of adult mortality is a cumulative process throughout the entire generation as new estimates must be adjusted by previous mortality (Figure 24).

Assessing adult mortality in this manner provides an estimate of total adult mortality including that caused by E. muscae. These mortality estimates are the best that can be derived from the available data. They are not absolute, however, because they depend on several assumptions: 1) population immigration equals emigration; 2) sufficient trap numbers are used to estimate the population means (Whitfield 1981); and 3) environmentally adjusted trapping data (Whitfield 1981) provides stable estimates within any single generation.

Separation of the mortality induced by E. muscae was accomplished using a computer program which uses the above emergence data, total mortality estimates and percent infection data (Appendix D). The program stochastically simulates a population of 1000 flies emerging and developing through a single adult generation. Using the above mortality estimates, the program first calculates a continuous population density curve which by definition fits the estimated population density data from which it was originally derived. The program then simulates the E. muscae infection measured in the field over 10 DD intervals. The result is a lower population density curve caused by redundancy of the mortality produced by E. muscae (E. muscae mortality was previously accounted for in the original mortality estimates). The program then resimulates the process keeping the E. muscae levels constant, while iteratively lowering the generalized mortality coefficients until the adjusted curve fits the original population density curve. This process fractionates the mortality into

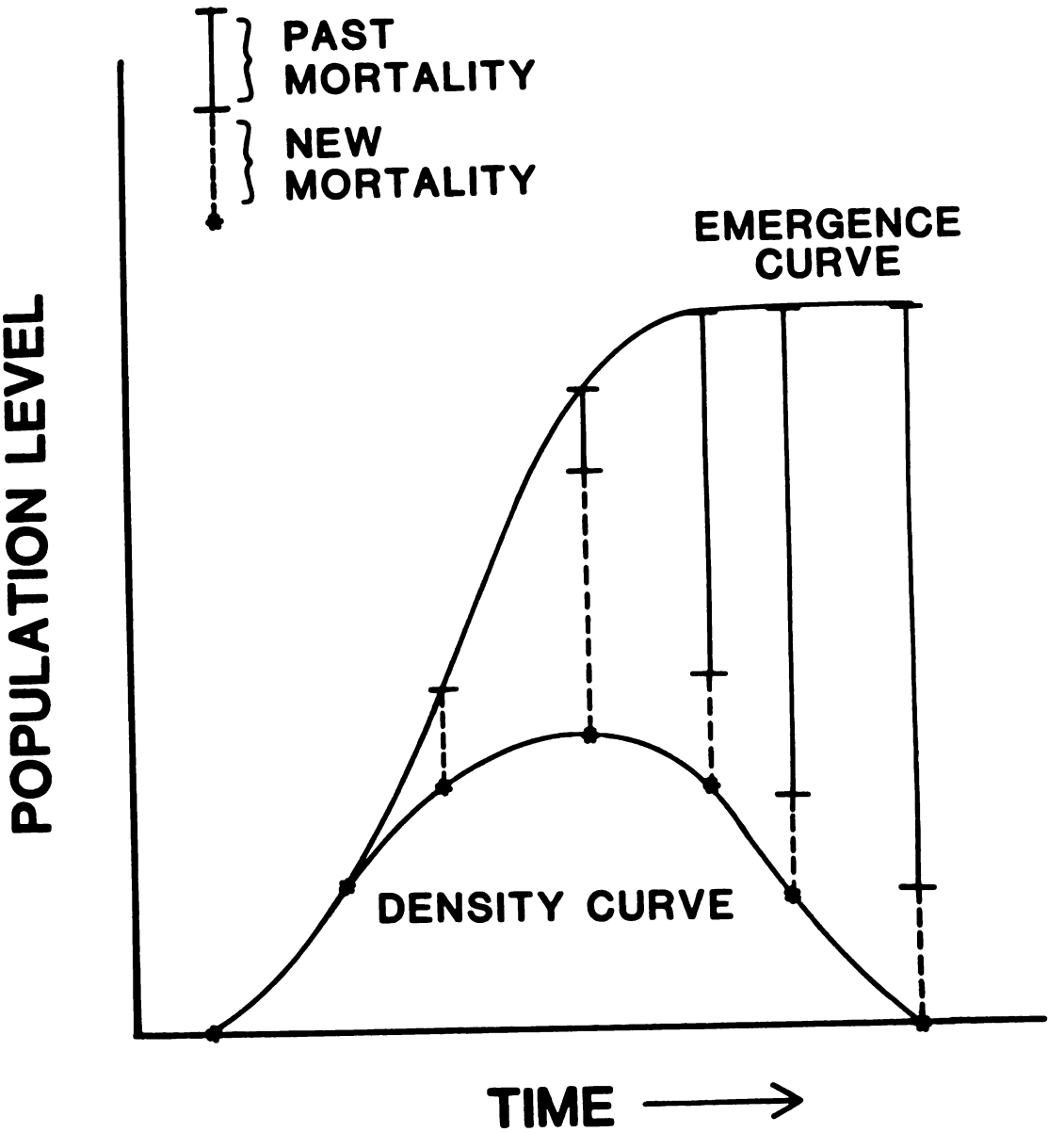


Figure 24. Graphical representation of analytical method used to calculate total field mortality from population assessment information. Note that the mortality from all previous time intervals must be used to adjust each estimate.

the proportion caused by E. muscae and that caused by other factors. Similarly, oviposition was calculated both in the presence and absence of E. muscae infection, based on the data given by Robinson and Zurlini (1979) and the data of Experiment 4.

RESULTS: As emergence data is only available for 1979-1980 and E. muscae field infection data for 1978-1979, this analysis was restricted to the 1979 Grant research field. These data were evaluated separately for males and females as longevity differences were known to occur (Robinson and Zurlini 1979). The females were also of separate interest due to the effect of mortality on oviposition.

The percent mortality by sex was calculated at each sample date and divided by the time interval in DD over which the sample was taken. These mortality coefficients were then used in the program described above to estimate the actual mortality caused by E. muscae infection. Although infection levels within the population were high in 1979 (Figure 17), the actual mortality caused by E. muscae mycosis was rather low until late in each generation (1st and 3rd generation presented as 2nd generation revealed little E. muscae infection (Figures 25 & 26)). Calculation of the percent mortality caused by E. muscae over each generation revealed low levels of mortality in the overall host population due to the high rate of mortality caused by other factors (Table 7). These average mortality coefficients for each generation were used to calculate the population half-life (median longevity) for each generation. In all cases, the half-life was found to be substantially less than the incubation period of the disease with only a small portion of the population living long enough to die of E. muscae mycosis (Table 7).

A more relevant measure of the impact of E. muscae infection is the

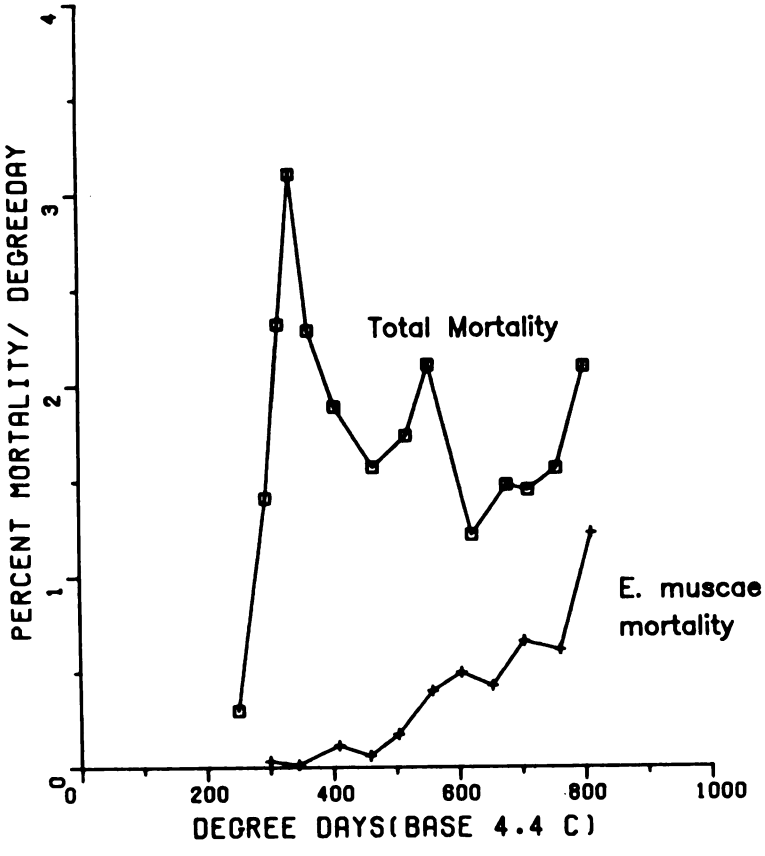


Figure 25. Total first generation onion maggot adult mortality and the estimated mortality caused by E. muscae.

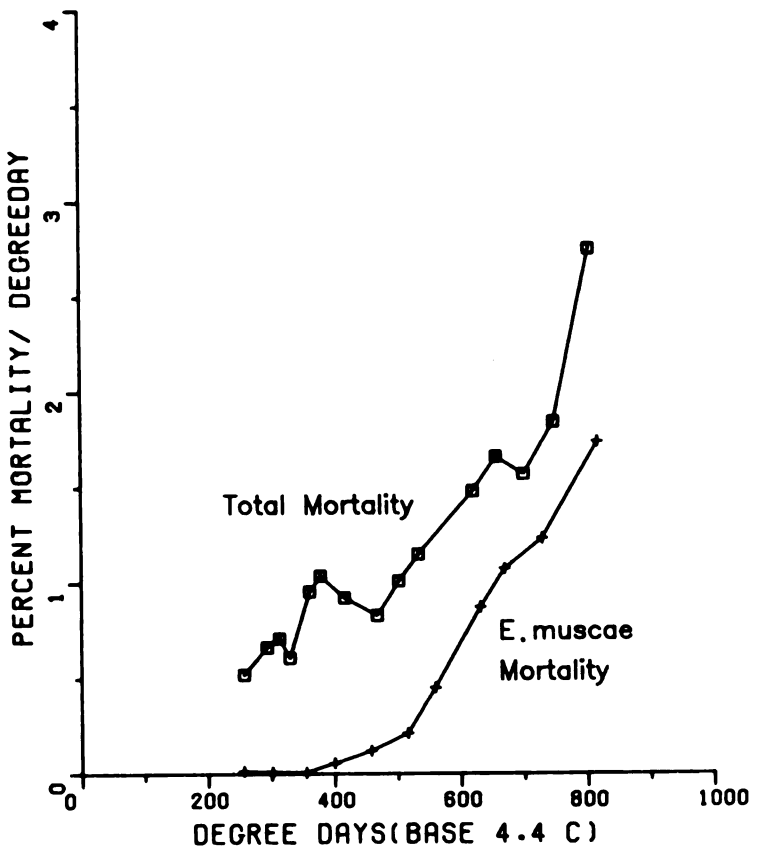


Figure 26. Total third generation adult mortality and the estimated mortality caused by E. muscae.

Table 7. Adult mortality separated into that caused by E. muscae and other mortality factors for the 1979 Grant Research Field. Estimates of adult half-life, percent of adults living longer than 105 degree days, E. muscae mortality of mature adults (older than 105DD), and percent reduction in fecundity caused by E. muscae included.

Generation	Sex	Overall E. muscae Mortality	Other Mortality	Estimated Population Half-life	% Adults Surviving 105DD	% E. muscae Mortality of Mature Adults	Estimated % Egg Reduction
1st	M	6.8	93.2	40.	16.2	41.9	--
1st	F	12.4	87.6	54.	24.9	49.8	34.1
2nd	M	2.1	97.9	37.	13.9	15.1	--
2nd	F	3.2	96.8	41.	16.9	18.9	13.0
3rd	M	16.4	83.6	52.	24.1	68.1	--
3rd	F	23.1	76.9	73.	36.3	63.6	49.3

mortality associated with reproductive females and the associated reduction in fecundity. As the OM has a preovipositional period of approximately the same length as the incubation period of the disease (103 to 105 degree days, respectively), the effect of E. muscae cannot be expressed in younger flies nor can younger flies contribute viable offspring to the following generation.

As described above, only a small portion of the total female population survive past the preovipositional period (Table 7). Those females that do, have a highly increased probability of E. muscae mortality. The mortality levels of E. muscae in mature flies (predicted from above program) are much higher than the levels affecting the overall population. The resulting impact is a substantial reduction of mature flies by E. muscae, thus reducing the actual fecundity levels. During 1979, OM fecundity levels were reduced as much as 50% over the levels estimated in the absence of E. muscae. As mortality caused by other factors drops (possible in other years or localities), the high E. muscae infection levels would produce increased mortality as more adults would live past the 105 DD preovipositional period.

C. Specific Experimentation

Experiment 1. Laboratory transmission of E. muscae.

Transmission studies between E. muscae-infected and healthy host flies have presented inconsistent results (Gussow 1913, Yeager 1939, Baird 1957, Kramer 1971). In all these studies, healthy flies were infected, but with variable levels of success and no continued repeatability. Kramer (1971) summarized the environmental conditions surrounding these past successful transmissions, which exemplify their extreme variability, and suggested that the inconsistency was due to subtle micro-environmental changes. Under moisture conditions as dry as

50% R.H., fly-to-fly transmission was achieved (Baird 1957). These results seem inconsistent with the data of Experiment 8 where free water was mandatory for spore germination. Although not mentioned by Baird, free moisture must have been available as a water source for the host flies and probably was the medium for spore germination, thus host infection, in this and other studies.

METHODS: Free moisture was felt to be the key factor in developing laboratory techniques to produce consistently high levels of disease transmission. To produce adequate free moisture levels similar to those found under field conditions, a cold mist water vaporizer was installed in a semi-airtight, 36 cu ft, plexiglass chamber. Distilled water was run through the vaporizer to form a dense fog cloud. This fog cloud was easily maintained by the vaporizer as the only water loss was due to condensation in the bottom of the chamber. Ten replicates of 25 laboratory-reared, disease free, OM adults were placed in 20 cm tall, glass chimney globes with five E. muscae-infected OM adults ready to sporulate. The globes were covered with a double layer of cheesecloth to inhibit spore movement between globes (Baird 1957) and then placed over 9 cm diameter Dixie• cups, each containing five, 12 cm tall barley seedlings. The barley seedlings acted as attachment sites for the E. muscae sporulating cadavers and as substrates for the healthy flies. Ten control globes were maintained in the infection chamber and in isolation. Flies were maintained in the mist chamber for 12 hours (7:00 p.m.-7:00 a.m.) at 21 $\pm$ 2°C under total darkness, after which they were removed from the chamber and incubated under 21 $\pm$ 2°C, 80% R.H. with a 16-8 light-dark photoperiod maintained with fluorescent lighting. Honey and brewer's yeast were provided as food upon removal from the infection chamber, and water was given daily by wetting the cheesecloth tops of the globes with a mist sprayer. The globes were observed daily for fly death. Dead

flies were examined for E. muscae mycosis using microscopic techniques when necessary.

RESULTS: Nine of the ten replicates produced 100% mortality of the OM adults due to E. muscae. The tenth replicate indicated 96% mortality from fungal mycosis as only one OM adult did not die from E. muscae infection. No E. muscae infection was found in either control set, giving an overall infection rate of 99.6%. Subsequent infection studies have given an average transmission rate well above 95%, with a minimum of 87%.

Experiment 2.

Laboratory cross infection of E. muscae between OM and SCM adults.

Host specificity in the Entomophthorales is highly developed with most Entomophthora spp. being limited to a narrow set of possible host organisms. The development of races or strains within a given species has been known to increase a pathogen's specificity to limit its function to a single host population (Fargues and Remaudiere 1977). Because E. muscae was found infecting both H. antiqua and H. platura in large numbers throughout the same geographic area, it was felt that a single pathogen population (strain) was probably infective to both hosts.

METHODS: Field collections from Grant, Michigan, of E. muscae-infected host flies (both OM and SCM adults) were used to acquire the pathogen sources used in the initial cross infections. Four sets of 25 flies (OM and SCM each held separately) were exposed to five E. muscae-sporulating cadavers of the opposite species. Secondary crossback infections of the original host species were also conducted to check for continued pathogen viability. Laboratory-reared, disease-free, OM adults were used in the infection studies. Because laboratory cultures of the SCM were not available, collections from field populations (Eaton

Rapids, Michigan) were used and compared to nontreated controls. The glass globes containing the experimental treatments were placed at 21 $\pm$ 2°C for the length of the incubation period (Experiment 3) and monitored on a daily basis. Test flies showing E. muscae infection symptoms were removed from the containers before sporulation to inhibit noncontrolled infection.

RESULTS: These data (Table 8) indicate that under the laboratory conditions described above, field populations of E. muscae contain sufficient genetic variability to infect both OM and SCM adult populations. Field data seem to further substantiate that cross infection occurs under natural conditions (section VII.B.2). Under current population genetic theory, such strain differentiation would not be expected to occur. Possible differences in relative efficacy between hosts would be expected, yet the development of host-specific strains in an area of continued population intermixing, thus presumably genetic exchange, is doubtful.

Experiment 3. Temperature-dependent development of E. muscae in vivo.

The developmental phase of E. muscae from initial spore contact until host death and sporulation is considered to be the incubation period of the disease. Vegetative growth in the Entomophthorales is known to be temperature-dependent (Hall and Bell 1960, 1961) thus affecting the in vivo incubation period (Stimmann 1968).

METHODS: To determine the effect of temperature on the duration of the in vivo incubation period, 11 sets of 25, laboratory-reared, OM adults (2-5 days old) were placed on a barley substrate (five, 12 cm tall plants) and covered with a cheesecloth-topped, 20 cm glass chimney globe. Five OM adults infected with E. muscae were added to each globe just prior to sporulation and then placed into the infection chamber described in Experiment 1. The globes containing the test

Table 8. *Entomophthora muscae* cross infection between *Hylemya antiqua* and *Hylemya platura* under laboratory conditions. Infection adjusted for control mortality as suggested by Abbott (1925).

Original Host Species							
Hylemya antiqua				*Hylemya platura*			
Initial cross to *H. platura*				Initial cross to *H. antiqua*			
Replicate	N	Percent Infection	Adjusted Infection	Replicate	N	Percent Infection	Adjusted Infection
1	25	100.0	92.0	1	25	96.0	96.0
2	25	96.0	91.7	2	25	100.0	100.0
3	25	92.0	91.3	3	25	88.0	88.0
4	25	100.0	92.0	4	23	91.3	91.3
Control	25	8.0	--	Control	25	0.0	--
Crossback to *H. antiqua*				Crossback to *H. platura*			
Replicate	N	Percent Infection	Adjusted Infection	Replicate	N	Percent Infection	Adjusted Infection
1	25	96.0	96.0	1	25	96.0	95.8
2	25	100.0	100.0	2	19	100.0	96.0
3	25	92.0	92.0	3	25	100.0	96.0
4	25	100.0	100.0	4	24	95.8	95.8
Control	25	0.0	--	Control	25	4.0	--

flies were maintained in the infection chamber at 21 $\pm$ 2°C (with a saturated atmosphere throughout the 12-hour exposure period). After exposure, the globes were removed and placed with a duplicate nonexposed control at equally spaced temperatures ranging from 4.4°C to 32.22°C (5.6°C increment).

The globes were checked daily for fly mortality: abdominal samples were taken from dead flies, stained with lactophenol-aniline blue, and microscopically examined for the presence of E. muscae mycosis. In addition to the day of death, and presence of mycosis, data concerning the spore type found in the examinations was recorded.

RESULTS: Entomophthora muscae mycosis was noted in 100% of the 275 OM adults exposed within the infection chamber. No mycosis was noted in the control sets. No premature mortality caused by other factors was present in the treated flies, although four flies in the 32.22°C control died before the experiment ended. Due to the high survival of the treated flies, natural mortality adjustments were not necessary and the control data were discarded.

The only spore types found were conidia, although each fly was evaluated for azygospores even in the presence of conidia. The duration data (Appendix E) were found to be homogeneous in a nontransferred form state using both Bartlett's Box F and Cochran's C tests (α = .05). A one-way analysis of variance was used to test for treatment differences (Table 9). These data were then transformed to percent development per day and evaluated using multivariable regression techniques (Table 10). Significance was indicated for a second order polynomial function of temperature (equation 1, Figure 27) providing a multiple r^2 of .944 between the data limits of 4.4°C and 30°C.

$$\text{Percent Development} = 0.0152 * \text{Temp} - 0.00173\ \text{Temp}^2 - 0.06883 \quad \text{(Eq. 1)}$$

Table 9. One-way analysis of variance for incubation period versus temperature. Student-Newman-Keuls multiple range test included.

Variable	DF	Sum of Squares	Mean Square	F
Temperature	10	31875.0	3187.50	1864.4***
Residual	264	451.4	1.71	
Total	274	32326.4		

*** ($p<.001$)

Temperature Treatment C^{o}	Mean Days for Development*
4.40	0.00a
7.20	40.90b
10.00	17.20c
12.81	11.40d
15.60	7.60e
18.30	7.44e
21.10	7.00ef
23.90	6.36f
26.70	6.24f
29.40	6.16f
32.20	0.00a

*Means followed by the same letter are not significantly different ($\alpha=.05$)

Table 10. Multivariable regression statistics for prediction of the incubation period of the pathogen Entomophthora muscae in vivo.

Analysis of Variance	DF	Sum of Squares	Mean Square	F
Regression	2	.80440	.26813	1389.6***
Residual	247	.04747	.00019	

Variable	F to Enter	Multiple r^2	B
Temperature	69.12***	.9258	.015203
$Temp^2$	12.09*	.9717	-.001729
(Constant)			-.06883
	$y = .015203Temp - .001729Temp^2 - .06883$		

*($p < .05$)
***($p < .001$)

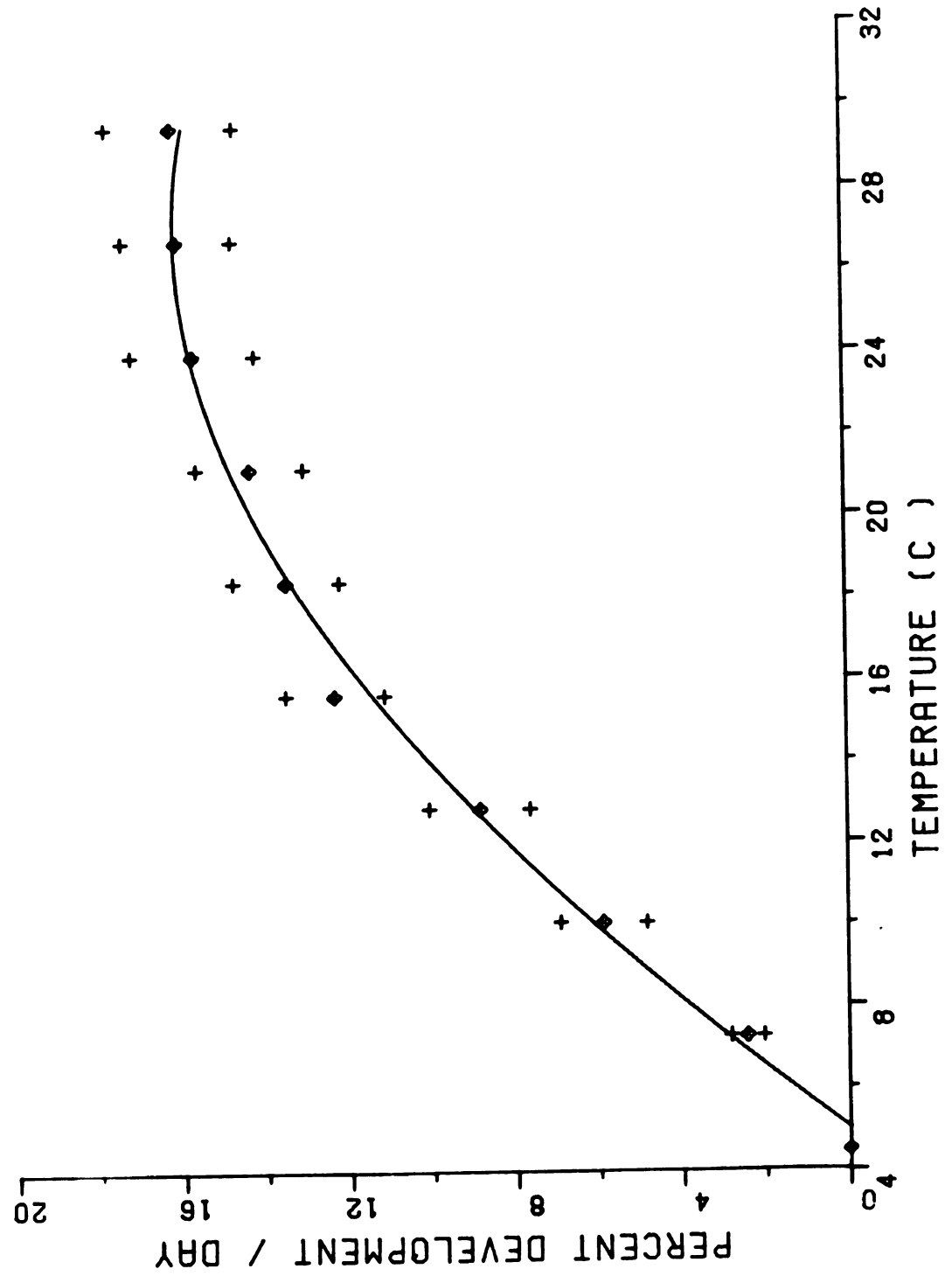


Figure 27. Temperature dependent relationship of the incubation period (percent of total development per day) of E. muscae in adult onion maggots.

Setting the percent development per day (y) equal to zero and solving equation 1 using the quadratic equation, a developmental base of 4.86°C was estimated.

Using this base temperature, DD estimates were obtained on the original 275 flies over the test temperatures. A mean developmental time of 105 DD with 95% confidence limits of 3.14 DD was predicted.

Experiment 4. The effects of E. muscae on onion maggot fecundity.

Onion maggot population studies under field cage conditions indicate that E. muscae significantly reduces total population fecundity (Perron and Crete 1960). Since OM eggs are deposited in a prolonged, cyclic ovipositional pattern, E. muscae can reduce total population fecundity levels in two ways. First, mortality induced by E. muscae directly shortens adult longevity, thus the number of ovipositional days available for the population. Second, E. muscae may induce physiological damage to the adult reproductive organs, thus reducing fecundity rates of infected hosts even before host death. The effect of reduced longevity on fecundity was discussed in section VII.B.4. This experiment was designed to test for and quantify any premortality effects on the overall population fecundity rate.

METHODS: Mature OM adults (late 2nd generation, 1980) were collected live from the research field in Grant, Michigan, using the tractor-mounted, insect collection device described in Figure 13. At the time of collection E. muscae was assessed between 20 and 25% infection in the research field. When the flies were returned to the laboratory, the females were separated out and placed individually in cheesecloth-covered, 40 ml souffle cups containing moist sand and a small onion slice in the bottom. The flies were maintained at 21 $\pm$ 2°C over the following ten-day experimental period. The flies were transferred daily to clean cups with the old onions and sand closely examined for egg

deposition. The fecundity rates for each fly were tabulated individually as was a record of fly mortality including day of death and mortality induced by E. muscae.

RESULTS: Seven hundred and two, female, OM adults were captured and reared over the 10-day experimental period. One hundred and seventy three flies (24.6%) were infected with E. muscae. Fecundity estimates on a per day basis were calculated for OM adults not dying of E. muscae over the experimental period, (thus presumed not infected) and for those flies which died of E. muscae on each subsequent day after the experiment began. Fecundity was fairly stable over the first 50 DD of infection, with no significant differences from the noninfected proportion of the population (all represented by the single point on the Y axis (Figure 28)). A significant reduction in fecundity occurred just short of 70°C DD after infection. No egg-laying occurred after that point, which resulted in approximately a 50% fecundity reduction before death.

Experiment 5. Characterization of sporulation rate.

Host death and the initiation of E. muscae sporulation occurs within very precise time limits during a day. Diseased flies are typically found searching out attachment sites only during early evening hours (5-7 p.m.). Host death occurs approximately 30 minutes after the flies attach to an acceptable substrate. Conidial production and sporulation quickly follow, with conidia being released throughout the night. This phenomenon is widespread in Entomophthora sp. (Hamilton 1959, Wilding 1969, 1970, Newman and Carner 1974) producing high conidial densities during night time hours when environmental conditions are most favorable for conidial germination, thus host infection (Newman and Carner 1974).

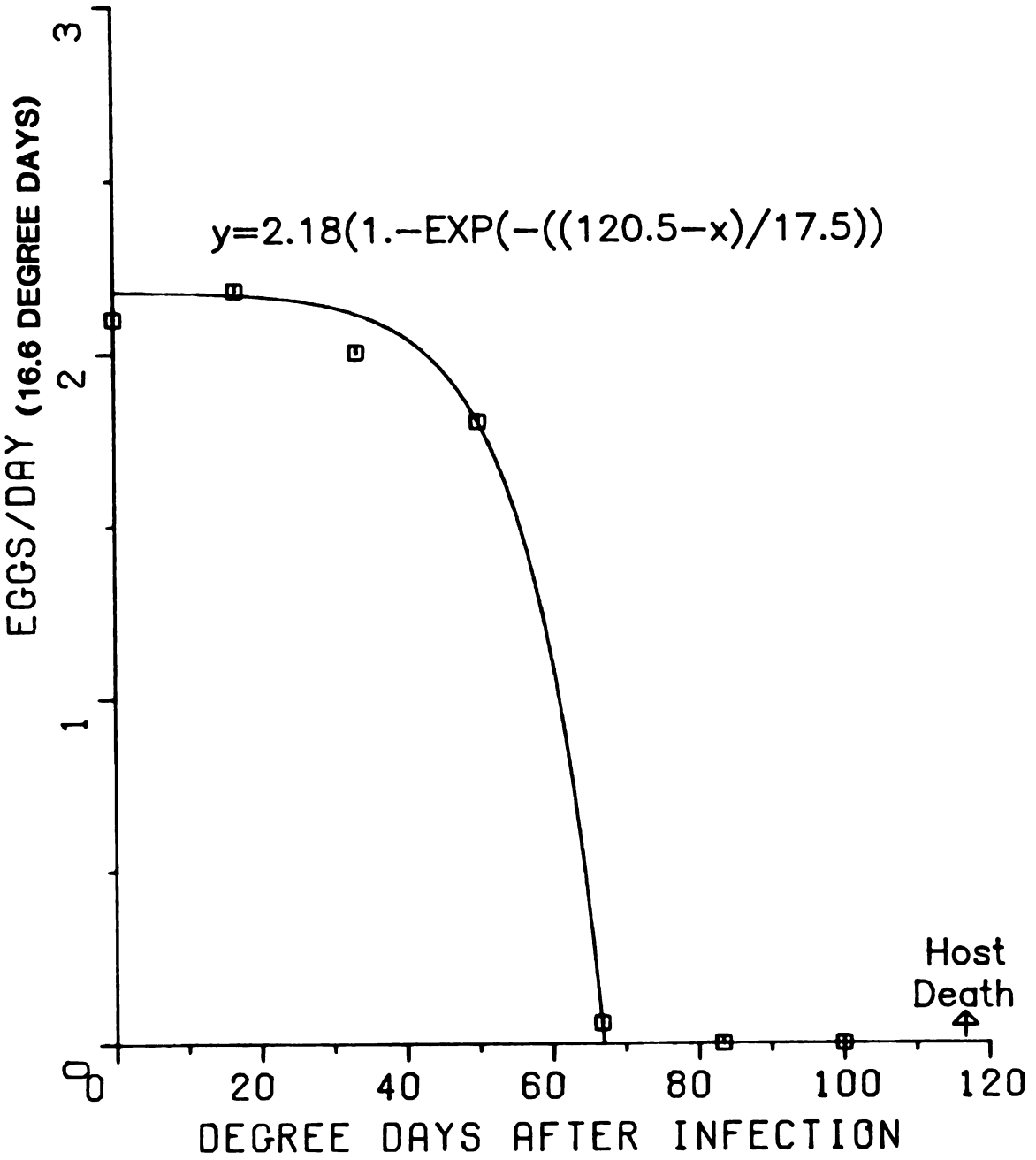


Figure 28. Premortality effects of E. muscae mycosis on the fecundity rate of onion maggot females. The fecundity of noninfected flies is represented by the point on the Y axis (mean of 529 samples).

METHODS: To characterize this sporulation rate, six male and six female E. muscae-infected cadavers were collected from their attachment sites in the Grant research field, prior to the initiation of conidial formation, and placed above hourly-monitored spore traps (adapted from Reidl et al. 1976). Two spore traps, each with six input monitoring ports fitted with a single cadaver (conidia collected by free fall impact on acetate sheets), were maintained under field conditions between 7:30 p.m. the night of collection and 7:30 a.m. the following morning. The hourly conidial samples were returned to the laboratory the morning following the experiment where ten randomly selected microscope fields (2.19 sq. mm each) were subsampled for conidial density to estimate sporulation rate per cadaver.

RESULTS: Two sampling periods (August 8-9 and August 17-18) were evaluated during the 1978 growing season. These data (Appendix F) were transformed to proportions of the total sporulation over the sampling period by cadaver to equalize any between-cadaver density effects not of interest in this experiment. The data were then adjusted in time to represent the mean release time per sample (conidia trapped between 7:30 and 8:30 are representive of the 8:00 sporulation rate). Bartlett's Box F and Cochran's C tests both indicated that these data were homogeneous; therefore, a 3-way analysis of variance (Table 11) was used to evaluate the effect of sex, day of experimentation, and time of conidial release on the rate of sporulation. No significance ($P = .05$) was indicated by either host sex or day of experimentation. It should be noted that only two days were evaluated; therefore, between-day differences were possible and even expected due to varying environmental conditions (see Experiment 11). Time of day was found to be highly significant ($P = .001$) in relation to sporulation rate, with the multiple classification analysis (Table 12) suggesting a

Table 11. Three way analysis of variance table for Entomophthora muscae sporulation rate evaluated for day of sample, time of sample, and sex of the sporulating onion maggot cadaver.

Source of Variation	Sum of Squares	DF	Mean Square	F
Main effects	.716	13	.055	28.39***
Day	.0005	1	.0005	.185
Sex	.0005	1	.0005	.185
Time	.715	11	.065	33.55***
Interactions	nonsignificant pooled in residual error			
Residual	.590	215	.0027	
Total	1.306	239	.005	

*** ($p<.001$)

Table 12. Multiple classification analysis for analysis of sporulation rate for day of sample, time of sample and sex of the sporulating onion maggot cadaver.

Variable	Category	Sign	N	Adjusted Deviation	Beta
Day		NS			
Sex		NS			
Time		***			.74
	1		20	-.07	
	2		20	-.05	
	3		20	-.02	
	4		20	.04	
	5		20	.08	
	6		20	.09	
	7		20	.06	
	8		20	.02	
	9		20	-.01	
	10		20	-.03	
	11		20	-.05	
	12		20	-.07	

*** ($p<.001$)
NS = not significant ($p>.05$)

normal distribution of conidial release over the night hours (group 1 = 8:00 p.m., group 2 = 9:00 p.m., . . . , group 12 = 7:00 a.m.). These data were fit to normal distributions by experimental data and pooled across dates using regression analysis on data transformed as probits of the cumulative sporulation versus hours (8:00 p.m. = 1, 9:00 p.m. = 2, . . . , 7:00 a.m. = 12) (Tables 13-15 and Figures 29-31). The regressions over individual sampling dates provided the highest r^2 values. This information suggests an increase in variance due to day of sample, but, as was indicated in the analysis of variance, no significance from the pooled analysis can be justified in this case. Using probit values of 5.0 (50%) and 5.99 (84%) in the estimated regression equation of Table 13, the mean and variance of the described normal distribution were calculated as 12:50 a.m. and 4.13 hours, respectively. Therefore, 95% of the sporulation occurs between 9:00 p.m. and 5:00 a.m. the following morning. Using these parameters, the estimated normal distribution was calculated and used to simulate the expected sporulation rate for an example data set (Figure 32).

Experiment 6. E. muscae sporulation as a function of temperature.

Conidial production in Entomophthora spp. is both temperature and moisture dependent (Newman and Carnes 1975, Wilding 1970). In the onion agroecosystem, temperature is assumed to be the primary controlling variable as moisture conditions are typically not limiting during the growing season. Eliminating moisture as a variable is justified because: 1) little differential effect in sporulation rate is noted in Entomophthora spp. for atmospheric moisture conditions greater than 80% R.H. (Newman and Carnes 1975), and 2) atmospheric moisture conditions in the low-lying, Michigan muck soil, onion production areas normally reaches saturated conditions during the sporulation period (Table 16).

Table 13. Regression statistics for probit of cumulative sporulation versus time for the data sets pooled across experimental day.

Source	DF	Sum of Squares	Mean Square
Regression	1	687.20	687.20
Residual	238	74.22	.312
Total	239	761.40	

y intercept (a) = 2.158 ± .0365 r^2 = .9025
slope (b) = .4862 ± .01036 y = 2.158 + .4862x

Table 14. Regression statistics for probit of cumulative sporulation versus time for experimental day 8/8/78.

Source	DF	Sum of Squares	Mean Square
Regression	1	295.18	295.18
Residual	118	18.72	.294
Total	119	313.90	

y intercept (a) = 2.78 ± .04132 r^2 = .947
slope (b) = .4469 ± .01154 y = 2.78 + .4469x

Table 15. Regression statistics for probit of cumulative sporulation versus time for experimental day 8/17/78.

Source	DF	Sum of Squares	Mean Square
Regression	1	368.20	368.20
Residual	118	14.40	.122
Total	119	382.60	

y intercept (a) = 1.78 ± .0455 r^2 = .96
slope (b) = .5011 ± .01318 y = 1.78 + .5011x

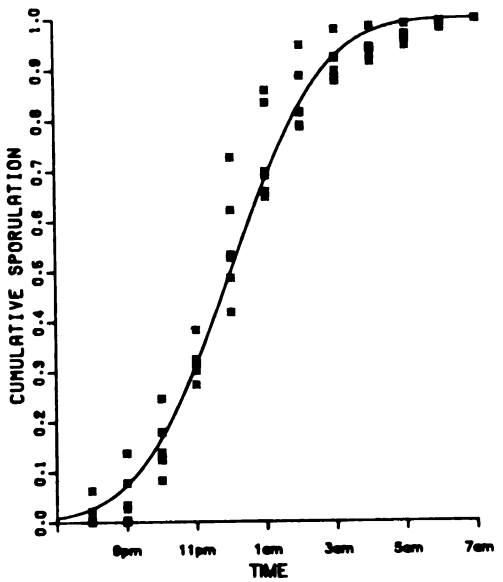


Figure 29.

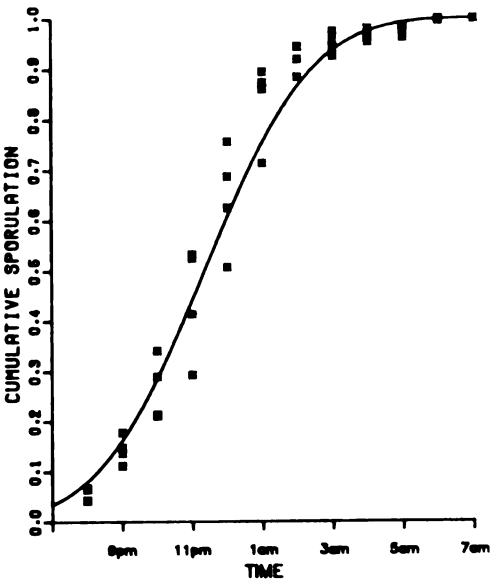


Figure 30.

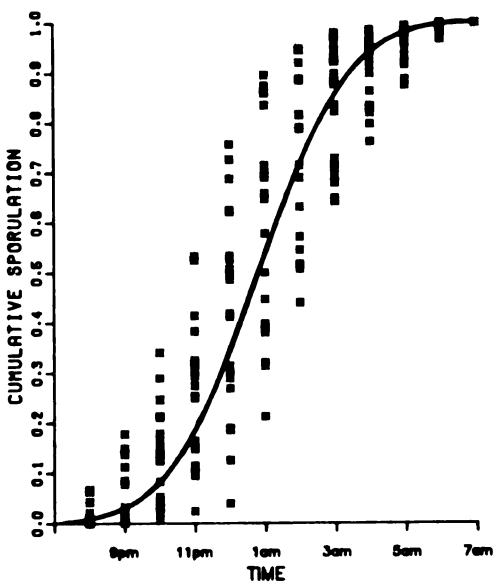


Figure 31.

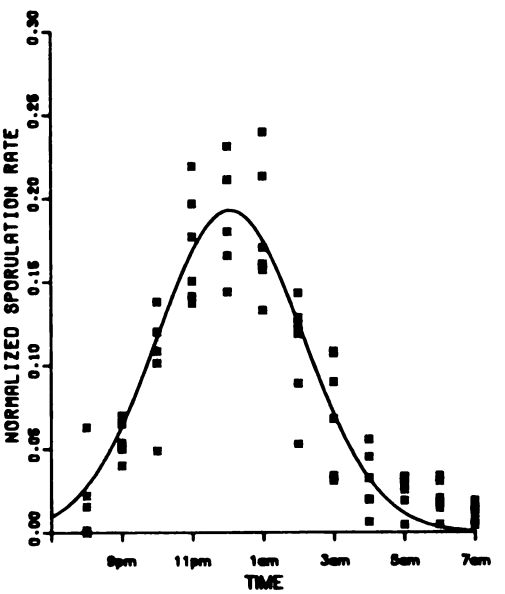


Figure 32.

Figures 29-30. Cumulative sporulation of E. muscae through a 12 hour period for two representative sample dates (8/8/78 and 8/17/78).
Figure 31. Cumulative sporulation of E. muscae through a 12 hour period for these data pooled across sample dates.
Figure 32. Estimated normal distribution compared to actual rate of sporulation.

Table 16. Frequency table for continuous hours of 100% relative humidity within a 24-hour period (12 noon to 12 noon) for Grant, Michigan, from May 1 to September 15 for 1978 and 1979. Note that over 80% of the days during this period have 8 hours or more of continuous 100% relative humidity.

Continuous Hours of 100% R.H.	Observed Frequency	Cumulative Frequency	Continuous Hours of 100% R.H.	Observed Frequency	Cumulative Frequency
13	5.0	77.5	0	2.1	2.1
14	4.3	81.8	1	0.4	2.5
15	3.6	85.4	2	0.4	2.9
16	2.5	87.9	3	0.4	3.2
17	3.2	91.1	4	1.1	4.3
18	2.5	93.6	5	2.1	6.4
19	1.8	95.4	6	2.9	9.3
20	1.4	96.8	7	3.2	12.5
21	0.4	97.1	8	7.5	20.0
22	0.4	97.5	9	10.0	30.0
23	1.1	98.6	10	20.4	50.4
24	1.4	100.0	11	11.1	61.4
--	--	--	12	11.1	72.5

METHODS: To evaluate the effect of temperature on E. muscae conidial sporulation, saturated atmospheric conditions were simulated in the laboratory using 40 ml, sealed souffle cups filled with 30 ml of distilled water. Onion maggot cadavers infected in the laboratory (see Experiment 1) were attached via petroleum jelly to the inside lid of each 40 ml container just prior to sporulation. The cadavers were placed very close to the water's surface (not touching) so the ejected conidia would fall directly into the water beneath. After a 12-hour sporulation period, the cadavers were removed from the containers. Lactophenol-aniline blue stain was added to stop germination, and two drops of Basic H•, a surfactant, was added to break the surface tension of the water to augment total spore dispersion. Ten subsamples were extracted from each container after agitation and evaluated for conidial density using a Bright Line hemacytometer. Estimates of the total conidia released per fly were made by weighting each subsample by the total volume (30 ml) of distilled water in each container.

RESULTS: These data (Appendix G) were tested for homogeneity of variance and found acceptable ($\alpha = .05$) in the nontransformed state. A one-way nested analysis of variance was conducted to test for treatment differences while partitioning out the subsample variation (Table 17).

A significant level of variation ($P = .001$) was found at both levels. No effort was made to differentiate between host sex. Because a size difference between male and female is apparent, some of the between-fly variation is assumed to originate from that source. Visual observation of the data suggested a normal distribution of sporulation as a function of temperature. Transformation to probits of the cumulative curve allowed the application of linear regression to estimate the mean and variance of the observed function

Table 17. One-way nested analysis of variance for total sporulation versus temperature with flies (subsamples) nested.

Variable	DF	Sum of Squares	Mean Square	F
Main effects	7	.847E + 14	.121E + 14	5.73**
Temperature	7	.847E + 14	.121E + 14	5.73**
Nested				
Flies/Temp.	32	.73952E + 14	.2311E + 13	15.61**
Residual	360	.5328E + 14	.148E + 12	
Total	399	.2118R + 15		

**($p<.01$)

Table 18. Regression statistics for probit of cumulative sporulation versus temperature.

Source	DF	Sum of Squares	Mean Square
Regression	1	36.95	36.95
Residual	6	1.518	.25
Total	7	38.46	

y intercept(a) = .7883 $\pm$ .1778

slope(b) = .2553 $\pm$ .02112

r^2 = .96

y = .7883 + .2553x

(Table 18). Using these estimates, a normal probability density function was calculated and plotted against the mean sporulation over temperature (Figure 33).

Under field conditions, this temperature response interacts with the diurnal pattern of spore release (Experiment 5) for total spore production. Within-day temperature differences between 8 p.m. and 7 a.m. are usually not of the magnitude to create major deviations from the diurnal pattern. Between days, however, total spore output is significantly altered (see Experiment 11 and model formation).

Experiment 7. Entomophthora muscae conidial dispersion.

Conidial dispersion in the Entomophthorales is primarily anemochorous, aided by an active spore liberation mechanism (MacLeod 1963). Active liberation mechanisms are known from various fungi, with some producing ejection velocities up to 100 m/sec (Zadoks and Schein 1979). The combined effect of this ejection mechanism and the air movement at the time of sporulation dictate the dispersal pattern and distance of these propagules, which indicates the effective area of possible infection surrounding a sporulating host cadaver. Characterizing the effective area of infection and the resultant conidial densities within this area is extremely important in developing a more thorough understanding of the spatial dimensions associated with host-pathogen interactions and their associated epizootiology.

METHODS: To evaluate conidial dispersal under still-air conditions (thus the dispersal caused by active liberation), an impact spore sampler (Raynor 1979) (Figure 34) was designed to capture E. muscae conidia on plexiglass sample strips (82 cm high x 2.54 cm wide) from 5 to 33 cm (by 2.54 cm intervals) away from a point release source. A cluster of ten sporulating E. muscae-infected, OM

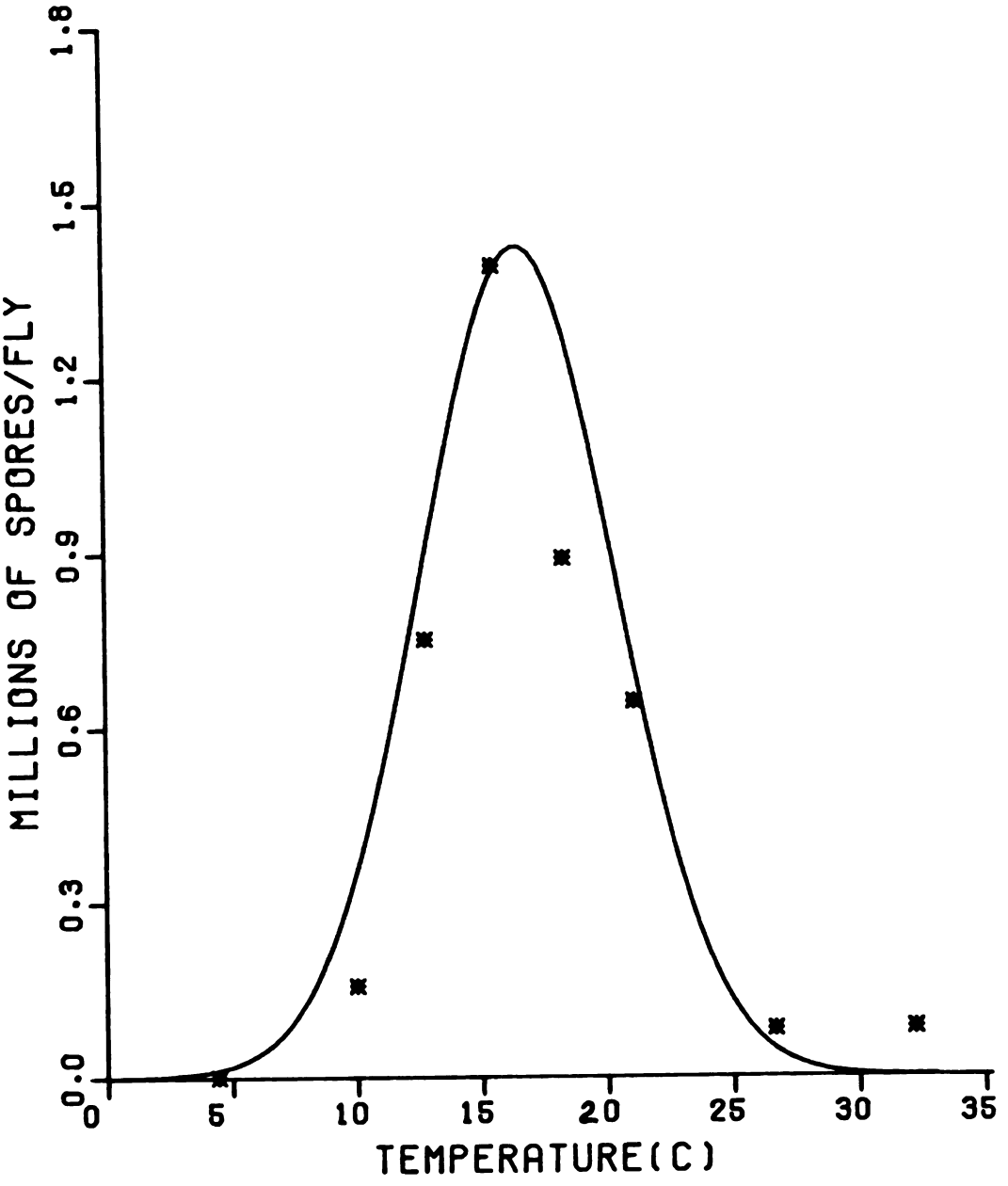


Figure 33. Estimated normal distribution fit to actual spore production response of E. muscae infected onion maggot adults held under differing temperature regimes.

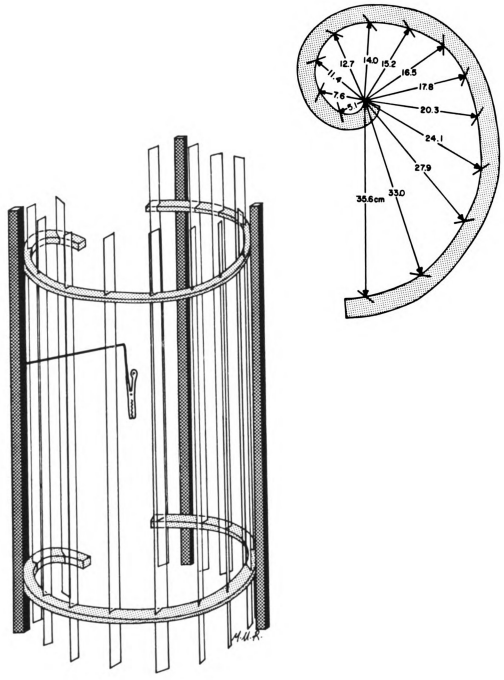


Figure 34. Impact spore sampler used to measure E. muscae conidial dispersal from a point source.

cadavers were attached in a radially symmetrical pattern at a central release point, 50 cm above the base of the sampler. The impact sampler with attached cadavers was placed into a plexiglass cloud chamber (see Experiment 1) where saturated atmospheric conditions were maintained at 21 $\pm$ 2°C, under total darkness for a 12-hour experimental sporulation period. Upon termination of the experimental period, the plexiglass impact strips were microscopically examined, with spore densities evaluated within 32 blocks (2.54 cm intervals) along each sampling strip. Conidial densities were estimated by counting conidia within 3 sub-samples (3-2.19 sq mm microscope fields) per block.

RESULTS: These data were transformed using a weighting factor (tan -1)* (width of the sample strip/its distance from the source) to equalize the radial area in degrees measured by each plexiglass sampling strip. From the weighted data, the proportional rate of conidial density over distance from the source was calculated for impact at ground level (50 cm below the release point (Table 19)). Assuming uniform dispersion in all directions, the resultant pattern on a horizontal plane 50 cm below a point release source approaches a circular Poisson distribution with a mean of 12.86 cm and variance 12.94 (Figure 35, A and B). The maximum range noted was 34 cm in any direction, which represented an area of influence of approximately .5 sq m. Under still air field conditions, the actual area of influence would be substantially reduced as conidia are expected to impact on and adhere to vegetation well above ground level (Zadoks and Schein 1979). By adding the wind velocity factor, the pattern of conidial dispersal becomes more complex, although rough estimation may provide a reasonable estimate of the area of influence.

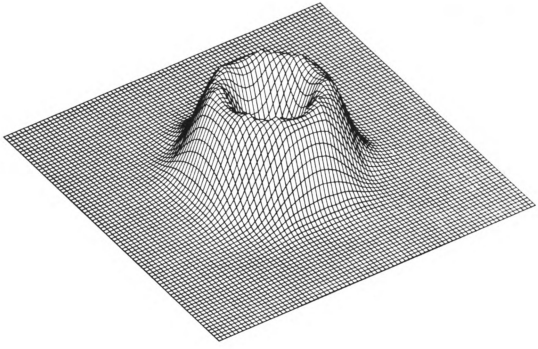
Weather data from the National Weather Service (Lansing, Michigan) was evaluated from May 1 to September 30, 1980, over the time of maximum

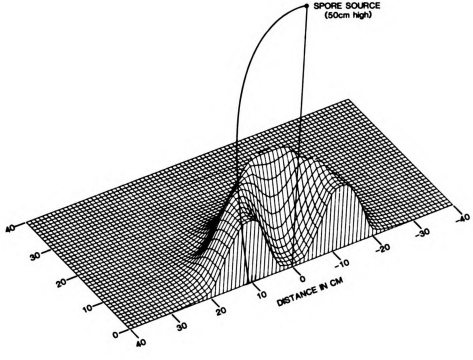
Table 19. Spore density measured on a transect through a horizontal plane 50 cm below a point spore source (see Figure 35).

Distance in cm	0	6.4	9.5	12.0	13.4	14.6	15.9	17.5	19.05	22.23	26.0	30.0
Percent Total Spore Density	0	.0186	.2021	.2566	.3962	.0354	.0327	.0147	.0098	.0188	0	.003

Figure 35. A. Pattern of E. muscae conidial dispersal on a horizontal surface 50 cm below a fixed release point.

B. Sectional view showing the poisson distributional pattern in a single direction (height of graph represents spore density, see Table 19).




SPORE SOURCE
(50cm high)
40
30
20
10
0
40
30
20
10
0
-10
-20
-30
-40
DISTANCE IN CM

sporulation (10 p.m. - 4 a.m.). The data showed extremely low wind velocities (Table 20). Over the time interval examined, the mode was always equal to 0 (34-38%), with over 50% of the days having wind velocities during the sporulation period of 1.5 m/sec or below. Settling velocities of spores in the E. muscae conidia size range (ca 20 µm) are on the order of 2-5 cm/sec (Chatigny et al. 1979). Using the average expected settling velocity (3.5 cm/sec), a dispersal distance of 2.86 m is estimated before a 10 cm drop in surrounding vegetation at a wind speed of 1 m/sec. With higher wind velocities, more turbulence is expected and the outcome of spore dispersal is difficult to determine (Zadoks and Schein 1979). Under the majority of weather conditions that occur in Michigan onion production regions, spore dispersal is expected to be short range, producing an effective area similar in size to Figure 35 and in close proximity to the original spore source.

Experiment 8.

The effects of moisture and temperature on E. muscae spore germination.

Spore germination in most fungi directly depends on the availability of free water, although for some fungi (e.g., powdery mildews) free water is actually inhibitory (Zadoks and Schein 1979). In the Entomophthorales, reports indicate a wide range of responses in relation to moisture conditions. Sawyer (1929) found that E. sphaerosperma and other unnamed Entomophthora spp. were capable of conidial germination in relative humidities lower than 75%. Baird (1957) reported that primary conidia of E. muscae could germinate even under dry conditions (no quantification given). Yendol (1968) evaluated conidial germination for several Entomophthora spp. and found that extremely high relative humidities were necessary for germination to occur (100% R.H. for all species examined except E. coronata which germinated under 95% R.H.). Such

Table 20. Frequency tables for wind velocities between 10p.m. and 4a.m. from May 1 to September 30, 1980. Note the mode is always zero (34-38%).

Frequency km/sec	10:00p.m.	1:00a.m.	4:00a.m.
0.0	34	35	38
.5	13	12	21
1.0	8	11	18
1.5	7	4	12
2.0	8	7	6
2.5	4	7	4
3.0	7	5	0
3.5	4	3	0
4.0	6	4	1
4.5	5	4	--
5-above	4	8	--

high relative humidities suggest the presence of free water in the germination chambers, but this information was not given.

METHODS: To examine the germination potential of E. muscae conidia in relation to both temperature and moisture conditions, slide germination procedures (Yendol 1968) were used. Conidia were obtained from field-collected (Grant, Michigan) onion maggot adults. The infected adults were held under mass-caged, laboratory conditions (21 $\pm$ 2°C, 75% R.H.) until the evening of host death and sporulation. Sporulating cadavers were transferred from the cage, each being attached on the upper, inside surface of a 20 cm disposable petri dish using petroleum jelly. The flies were attached by their heads which allowed the conidia-covered abdomen to be suspended freely over filter paper that was saturated with distilled water. The high relative humidity within the sealed petri dish stimulated sporulation and allowed several hundred conidia to be collected on standard, glass microscope slides during a ten minute time interval. After obtaining an estimated minimum conidial density of 100 per slide, the slides were placed in pint containers, then suspended on plastic racks over sodium hydroxide-distilled water solutions that were used to regulate humidities within the containers (Solomon 1951, Winston and Bates 1960). Distilled water was used to generate 100% R.H., and free water treatments were obtained by placing water droplets on the upper surface of the slides directly covering the attached conidia. Ten replicates (in some cases only seven) per container were obtained from different sporulating cadavers to insure between-cadaver variation that represented the true population and to provide the necessary number of replicates simultaneously. The pint containers were then sealed and returned to growth chambers for incubation (all containers were maintained at the experimental temperature of interest at least three hours prior to testing to allow the

salt solution to stabilize at the test temperature). Temperatures ranging from 0°C to 35°C were evaluated over free water conditions, saturated atmospheric conditions (100% R.H.) and under a series of atmospheric moisture levels ranging from 0 to 2.11 mm vapor pressure deficit (95% R.H. over the treatment temperature ranges). Containers were removed from each treatment (temperature x moisture) every 3 hours over the 12-hour experimentation period. When removed from the temperature chambers, germination was terminated using a lactophenol-aniline blue stain and then evaluated for germination under a compound microscope. A minimum germ tube length (2 x spore diameter) or the formation of a secondary conidium was used as the germination criterion.

RESULTS: No germ tubes were formed under less than saturated atmospheric conditions, although a limited number of secondary conidia were formed under lower vapor pressure deficits. The upper and lower conidial germination limits were found to be 32.2°C and 4.4°C, respectively. Conidia below 4.4°C were found intact but nongerminated, while conidia incubated at 32.2°C and above were fragmented and no longer easily identified. The dependent variable (data in Appendix H), proportion germination, was linearized using an arcsin transformation, then evaluated for homogeneity of variances using both Cochran's C and Bartlett's F test. The assumption of unequal variances was rejected. The analysis was continued using an analysis of covariance testing for differences between the free water treatment and the 100% R.H. treatment while controlling for the metric variables, temperature and time. Significant differences (Table 21) were indicated; therefore, these data were divided into two separate sets and evaluated for linear effects using multivariable techniques (Tables 22-23). Significant linear responses were indicated using third order polynomials for both time and temperature. Three

Table 21. Analysis of covariance for arcsin spore germination by moisture condition (free water, 100 R.H.) while controlling for the metric variables of temperature, temperature squared and time.

Source of Variation	Sum of Squares	DF	Mean Square	F
Covariates	46962.8	3	15654.3	137.28***
Temp	25677.7	1	25677.7	225.2***
$Temp^2$	27503.7	1	27503.7	241.2***
Time	19146.9	1	19146.8	167.9***
Main effects				
Water	10287.2	1	10287.2	90.2***
Residual	37631.6	330	114.04	
Total	94908.2	334	284.16	

*** ($p < .001$)

Table 22. Multiple regression statistics for spore germination under free moisture conditions predicted by temperature and time.

Variable	F to Enter	r^2	B
Time	5.49*	.3239	-.04993
$Time^2$	19.71***	.3722	.00620
$Temp^2$	7.51**	.3905	.00345
$Temp^3$	17.33***	.6915	-.0000932
Constant			.05628

$y = .05628 - .04993Time + .00620Time^2 + .00345Temp^2 - .0000932Temp^3$

* ($p < .05$)
** ($p < .01$)
*** ($p < .001$)

Table 23. Multiple regression statistics for spore germination under 100% relative humidity moisture conditions predicted by temperature and time.

Variable	F to Enter	r^2	B
Time	3.78*	.1809	.01938
$Temp^2$	6.57**	.1999	.001529
$Temp^3$	13.52***	.4246	-.0000388
Constant			-.018568

$y = -.018568 + .01938Time + .001529Temp^2 - .0000388Temp^3$

* ($p < .05$)
** ($p < .01$)
*** ($p < .001$)

dimensional surface plots were generated for both moisture conditions using Surface II graphics (Sampson 1975) (Figures 36-37). Alteration of these germination rates due to fungicides commonly applied in the onion agroecosystem was also tested (Appendix A and Experiment 9).

Experiment 9.

Conidial germination and viability in various habitats of concern.

As discussed in Section VII.B.3, the crop and border area canopy cover changes throughout the season, affecting not only the distribution of the host and pathogen, but also the viability of the spores within them. The vegetation type and canopy cover highly alter temperature and moisture conditions that regulate conidial germination and protect the spores from lethal ultraviolet radiation. Conidial germination and the ability to withstand deleterious environmental conditions is a key factor in understanding the interrelationships associated with host-pathogen interactions under field conditions.

METHODS: Conidial germination and viability were evaluated in onion, carrot and border canopies using slide germination tests (Altman 1966). Sporulating OM cadavers were collected from the field and attached via petroleum jelly to the upper surface of petri dishes that contained distilled, water-soaked filter paper to maintain saturated atmospheric conditions. Standard glass microscope slides were placed directly under the sporulating cadavers to collect a minimum of 100 conidia per slide (approximately 5-10 minutes). Ten slides containing conidia were placed on wooden frame stands set at high (top of canopy), medium (center of canopy) and low (ground level) within the three habitats of interest. The slides were set out into the field at approximately 10 p.m. the night of experimentation. Two slides were removed from each site at 6 a.m., 8 a.m., 10 p.m., 12 p.m. and 6 p.m. One slide from each pair was treated

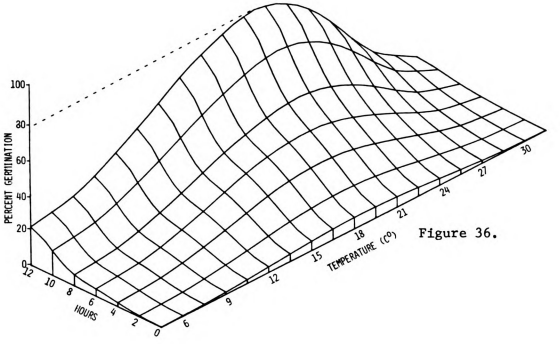


Figure 36.

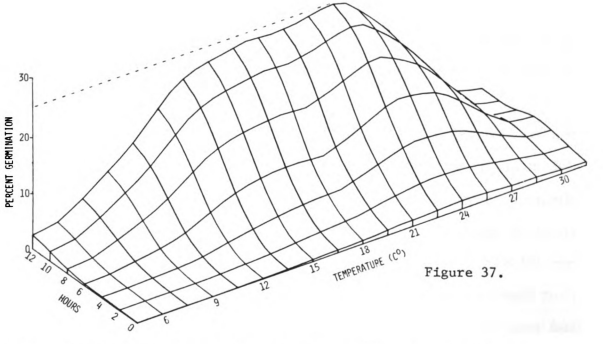


Figure 37.

Figures 36 and 37. E. muscae conidial germination as a function of time and temperature for both free water conditions (Figure 36) and 100% relative humidity (Figure 37).

with lactophenol-aniline blue stain and evaluated for percent germination. The other was placed under free moisture conditions (21 ± 5°C) and allowed to develop for 12 additional hours after which it was also evaluated for percent germination. Spores were considered germinated if a secondary conidia was present or if the germ tube was 2x the spore diameter. The experimental process was replicated five times for each experimental date. Control treatments were maintained in the field laboratory at 21 ± 5°C under free moisture conditions throughout the experimental period.

RESULTS: The experiment was conducted four times during the 1980 growing season (June 16, July 16 and 23, and August 21) to characterize the effect of habitat development on spore germination and viability. On the second experimental date (July 16), the grower maintaining the research plots inadvertently applied a fungicide application to the experimental area at 6:30 a.m. just following the morning sampling period. This data set, although not formally designed, represents the impact of fungicide-induced mortality of E. muscae conidia and will be analyzed separately (all four data sets are listed in Appendix I).

Spore germination (after 14 hours of exposure) between habitats and location within habitats was examined using analysis of variance (Table 24). Significant differences were noted between the treatments for each experimental date. The multiple range tests (Table 25) reflected the habitat groupings as they affect overall spore germination. Early in the season (June 16), the border areas provided near-optimal conditions (not significantly different from control) for spore germination, while the more open crop canopies were less favorable (ca. 1/3 control) for spore germination. The reduced germination in those spores held at the top of the border canopy reflect moderation between the

Table 24. One-way analysis of variance for arcsin of observed spore germination in carrot, border and onion canopies.

June 16

Variable	DF	Sum of Squares	Mean Square	F
Canopy Habitats	9	75601.4	8400.2	140.94***
Residuals	40	2382.0	59.6	
Total	49	77983.4		

***(p<.001)

July 23

Variable	DF	Sum of Squares	Mean Square	F
Canopy Habitats	9	88996.9	9988.5	106.9***
Residuals	40	3701.6	92.5	
Total	49	92698.5		

***(p<.001)

August 21

Variable	DF	Sum of Squares	Mean Square	F
Canopy Habitats	9	94268.5	10474.3	457.4***
Residuals	40	914.0	22.9	
Total	49	95182.5		

***(p<.001)

Table 25. Student-Newman-Keuls multiple range tests for spore germination by Canopy-Habitat treatments (untransformed mean presented).*

Habitat-Canopy Treatment	Mean Percent Spore Germination by Test Date		
	June 16	July 23	August 21
Onions-Top	25.1a	26.9d	21.4h
Middle	21.4a	22.6d	23.6h
Bottom	23.4a	32.7e	23.0h
Carrots-Top	21.0a	38.1e	39.9i
Middle	19.6a	70.1f	80.1jk
Bottom	20.2a	78.6fg	73.1j
Border-Top	40.1b	29.4e	52.0i
Middle	74.8c	73.4f	73.1j
Bottom	74.4c	77.6fg	72.8j
Control	83.6c	82.8g	86.2k

*Means followed by the same letter are not significantly different (α=.05).

two habitat groupings, probably due to a moderate buffering from dessication and direct exposure to ultraviolet radiation. The third and fourth experimental dates (July 23 and August 21) reflected the same basic germination pattern and will be discussed as a unit. The protection provided by both the border area and carrot canopies produced near optimal (not significantly different from the control) spore germination in the low and mid-canopy heights. The upper portion of the canopies were found to produce significantly less germination than both the control and the lower canopy, although greater than the onions showing the same gradient effect or buffering from harmful environmental conditions shown above. Conidial germination in the onion canopy was still approximately 1/3 the level of the control, again reflecting less than optimal environmental conditions.

The overall effect of habitat type and spore location on germination is best represented graphically as percent germination by treatment over the experimental dates (Figures 38-40). Further characterization of spore germination within the day provides additional insight into the differential response between habitats. Conidial germination is a cumulative function of time, thus any leveling effect (decrease in germination rate) can be readily identified.

A series of one-way ANOVAs (germination by habitat) for each sampling period (6 a.m. - 6 p.m.) was used to examine between-habitat differences over time (a single experimental day, July 23, is presented because the trend holds over all sample dates (Table 26)). No significant differences between habitats were found until the 8:00 sample period, which suggests that favorable environmental conditions were present until approximately the 6:00 sampling period (Figure 41).

Differential spore germination between habitats can be explained by either spore mortality, nongermination, or a combination of both. Identifying the

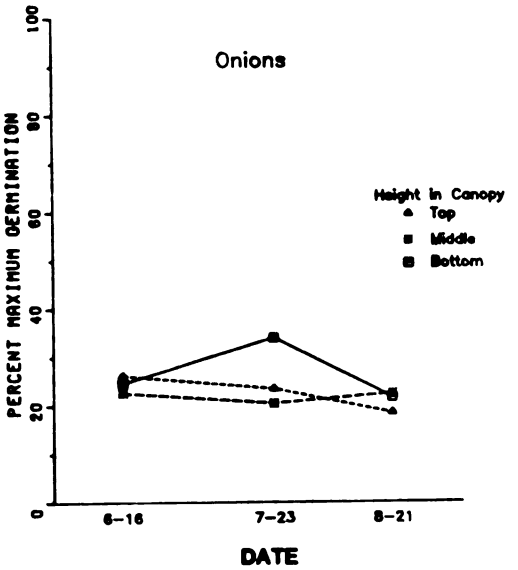


Figure 38.

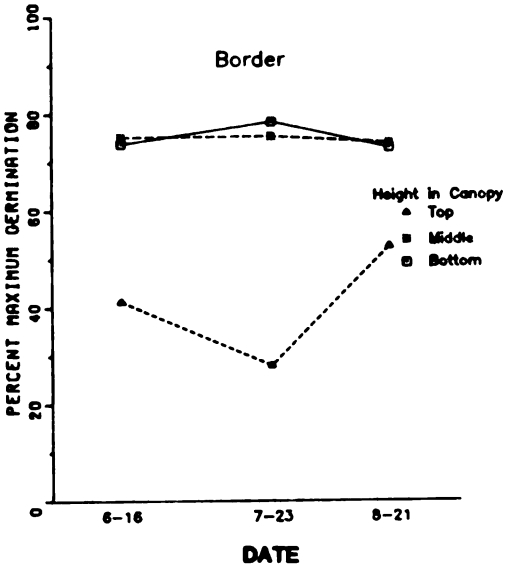


Figure 39.

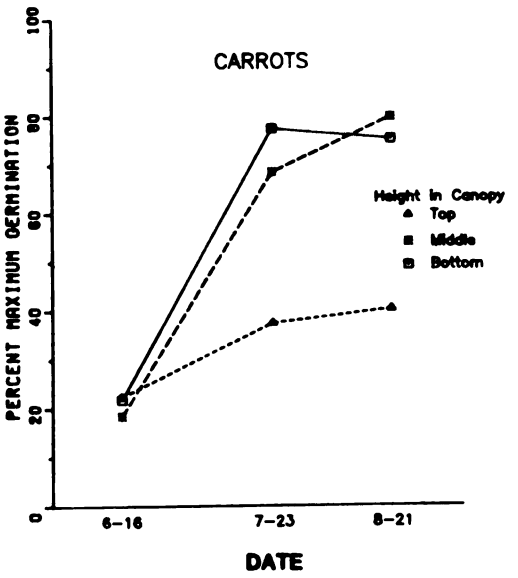


Figure 40.

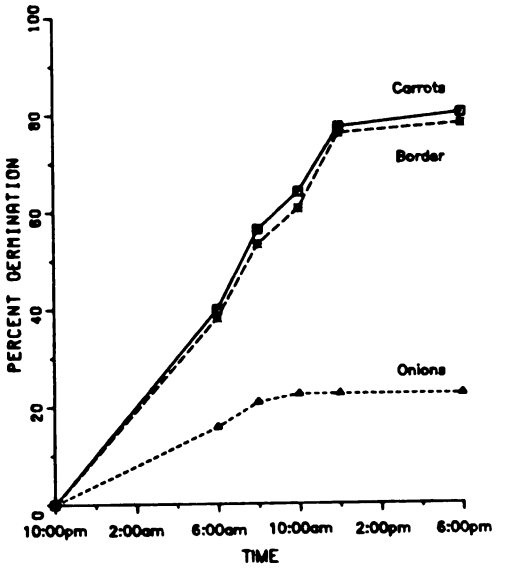


Figure 41.

Figures 38-40. E. muscae conidial germination in three canopy levels for onion, carrot and border habitats.

Figure 41. E. muscae conidial germination through time of day for onion, carrot and border habitats.

Table 26. One-way analysis of variance for arcsin spore germination on July 23, between onion, carrot and border canopies. Anova tables presented for 6:00 and 8:00 a.m. Student-Newman-Keuls multiple range tests provided for all five time intervals.

6:00 a.m.

Variable	DF	Sum of Squares	Mean Square	F
Habitat	3	15918.0	5306.1	2.51NS
Residuals	46	97257.8	2114.3	
Total	49	113175.8		

NS = Not significant

8:00 a.m.

Variable	DF	Sum of Squares	Mean Square	F
Habitat	3	10528.7	3509.6	3.47*
Residuals	46	46524.4	1011.4	
Total	49			

*($p<.05$)

Student-Newman-Keuls Multiple Range Test*

	Time of Sample				
Treatment	6:00 a.m.	8:00 a.m.	10:00 a.m.	12:00 p.m.	6:00 p.m.
Onions	19.4a	20.8c	22.4	22.4	22.4
Carrots	39.9a	56.3d	61.1	77.1	80.1
Border	38.1a	53.3d	60.6	75.6	78.3
Control	58.0b	70.1e	80.0	82.8	81.9

*means followed by the same letter are not significantly different ($\alpha=.05$)

actual response is important because spore mortality is terminal, while nongermination allows viable spores to accumulate until favorable conditions are present.

Conidial mortality was separated from nongermination by comparing actual field germination with germination in the field treatments that were allowed to continue germination under free moisture conditions and the laboratory control. Conidial mortality was estimated as:

CM = (1. - (LABG-FIELDG)/(MAXG-FIELDG)) * 100.

Where: CM = percent conidial mortality

FIELDG = germination of field sample

LABG = germination of field sample held an additional 12 hours under free moisture conditions

MAXG = laboratory control germination (maximum possible)

Plotting the mean percent spore mortality by habitat (pooled across height within habitats) (Figures 42-44) shows that the majority of spore mortality occurred after 8:00 a.m. Mortality was delayed in protected habitats (those with thick canopy covers) although by the 6:00 p.m. sampling period, spore mortality approached 100% in all habitats.

The effect of fungicide applications on spore viability is represented by the July 16 data set where a fungicide treatment was applied directly over the conidia placed within the onion field. The field border plots were also affected as they were directly adjacent to the sprayed onion plots. The carrot plots were not affected; they were located in plots several hundred meters away from the sprayed area. The mortality (Figure 45) pooled across height within the habitat approached 100% immediately after spray application (8:00 a.m. samples). The effect of fungicides has been shown under laboratory conditions to cause 100%

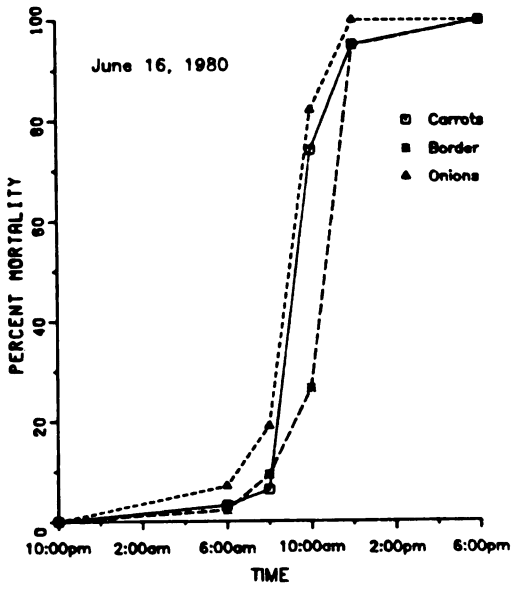


Figure 42.

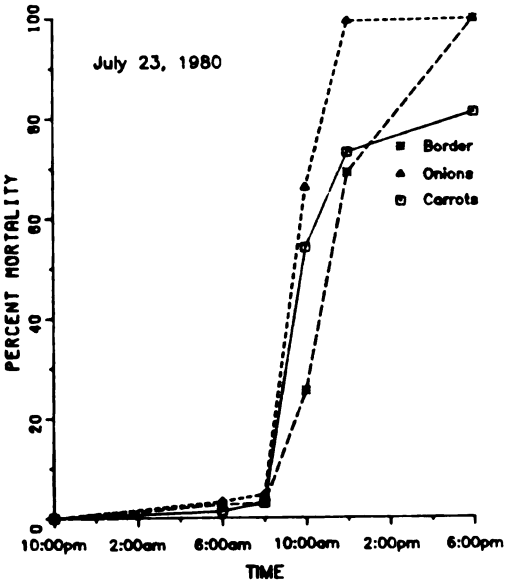


Figure 43.

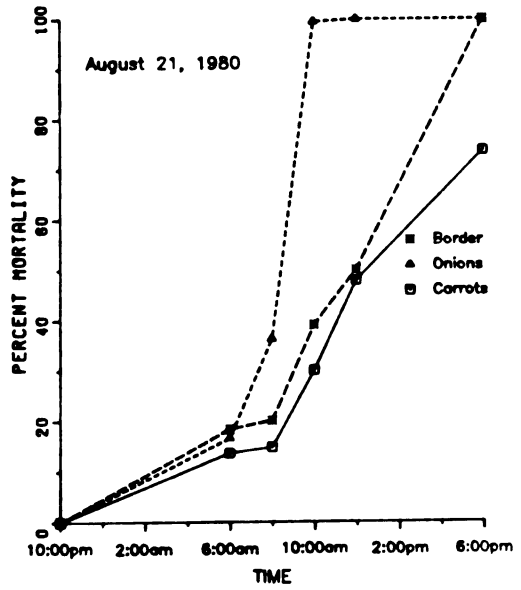


Figure 44.

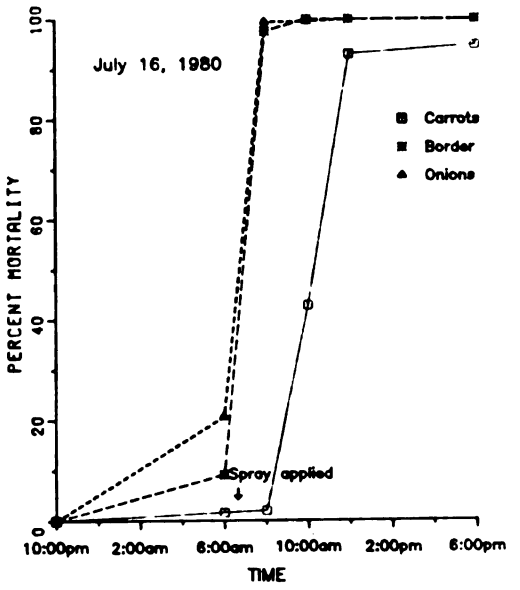


Figure 45.

Figures 42-44. E. muscae conidial mortality as a function of exposure time for three different sample dates during the 1980 season.
Figure 45. The impact of fungicide application on E. muscae conidial mortality (application time indicated by arrow).

spore mortality down to concentrations as low as 1/100 of the recommended field rate (Appendix A).

Experiment 10. Host-pathogen interaction.

Secondary E. muscae infection depends on host contact with the infective conidial stage of the pathogen, successful germination, and penetration of the host's cuticle. Little is known about the actual process of conidia-host contact in nature. Although most authors imply that the conidia directly strike the host at the time of sporulation, the probability of conidia directly striking a viable host the size of an OM adult is extremely small. Assuming one cadaver emitting one million spores over a 1 cu m volume of habitat, the probability of conidia striking any host the size of an OM adult is less than 5%. The addition of dense foliage in the same volume of habitat would lower that probability by aggregating spores closer to the cadaver. An alternative mode of host-pathogen contact could occur during times of host activity (movement through the foliage). This would increase the exposure time (contact after sporulation ends) and the active area of spore influence (increased in terms of the area covered by host movement and the increased surface area of the germinating conidia). The ease with which the germ tube and secondary conidia separate from an attached primary conidia suggests that such a mechanism may have evolved due to an increased success rate in attaching to viable hosts. Since OM adults are not active during the night hours, a comparison of infection over various time intervals should show differences.

METHODS: Five OM adult cadavers infected with E. muscae in the laboratory were attached to the tips of grass leaves in 12 (6 treatments x 2 replicates) 1 sq m border plots at the Eaton Rapids research field on June 18, 1979. Emergence cages were placed over these plots where sporulation occurred

overnight. In treatments 1 and 2, 100 laboratory-reared, OM adults were sealed in the emergence cages prior to sporulation and removed at 6 a.m. and 2 p.m., respectively, the following day. A single control treatment with 100 flies and no cadavers was maintained throughout the experiment. The emergence cages were removed from treatments 4-6 at 6 a.m. to allow normal drying and sunlight exposure to the plot beneath. The cadavers were removed from all treatments at 6 a.m. The cages were replaced as the plots were used later in the day. In treatments 3-6, 100 flies were added at 6 a.m., 8 a.m., 10 a.m. and 12 p.m., respectively. All flies were removed, and the experiment terminated at 2 p.m. The flies were taken to the laboratory immediately after being removed from the emergence cages and maintained under 21 $\pm$ 2°C, 75% R.H., with an 16-8 hour photoperiod (treatment 2 flies which were removed at 6 a.m. were moved to untreated plots and held in the same type of habitat until 2 p.m.).

The flies were fed, watered and monitored daily for presence of E. muscae.

RESULTS: No E. muscae-induced mortality was found in the control; therefore, the original data (Appendix J) were transformed to arcsins to meet the assumptions of the analysis of variance. A one-way analysis based on exposure time was performed with significant differences indicated between the means (P = .05). A Student-Newman-Keuls multiple range test was used to separate the treatment differences (Table 27).

As hypothesized, treatment 1 caused significantly less E. muscae infection than treatment 2, indicating host-pathogen contact after sporulation ceased. Treatments 3-6 substantiated this hypothesis as the flies within those treatments were never exposed to sporulating cadavers. It was hoped that there would be differences between treatments 3-6 so that number of active hours could be

Table 27. One-way analysis of variance for arcsin of observed infection versus time of host-pathogen interaction. Student-Newman-Keuls multiple range test given on untransformed means.

Variable	DF	Sum of Squares	Mean Square	F
Exposure Times	5	5767.5	1153.5	26.2***
Residuals	12	528.0	44.0	
Total	17	6295.5		

*** ($p<.001$)

Treatment	Exposure Time	Mean Proportion Infected*
1	7:00pm-6:00am	.1560a
2	7:00pm-2:00pm	.7450b
3	6:00am-2:00pm	.5147c
4	8:00am-2:00pm	.5660c
5	10:00am-2:00pm	.5410c
6	12:00am-2:00pm	.0255d

*Means followed by the same letter are not significantly different ($\alpha=.05$)

related to infection. The only significant difference, however, was that associated with treatment 6. Infection levels in treatment 6 (exposure between 12 a.m. and 2 p.m.) were below 3% infection--much lower than any of the other treatments. Several hypotheses for this difference have been generated. The most probable is that actual conidial mortality due to environmental factors, such as ultraviolet radiation and dessication, had occurred (see Experiment 9).

Experiment 11. Conidial dose for infection of onion maggot adults.

Numerous methods including injection, topical application of a conidial suspension, exposure to conidia discharged from in vitro cultures and exposure to conidia discharged from infected insects have been used to evaluate conidial density to infection in test insects. These procedures, although accurate, are of little use in relating field conidial densities to natural infection, because they do not account for the mode and habitat of host-pathogen interaction. Measuring infection under field conditions is extremely important, because the habitat of infection exerts a dominant role in the contact, germination and infection process.

METHODS: Adult OM cadavers infected with E. muscae were collected from the research field in Grant, Michigan, just prior to the time of sporulation. These cadavers were attached to the tips of grass leaves within 1 sq m cheesecloth enclosures (.75 m high). The enclosures were situated in a field border area representative of an area where the majority of host infection was believed to occur (see section VII.B.3). Treatment densities were composed of 0, 1, 2, 4, 6, 8 and 10 cadavers per enclosure, each replicated three times. One hundred OM adults, collected from field 1 in Grant (an area of low E. muscae infection), were placed within each enclosure for 18 hours (8 p.m. - 2 p.m.). At the end of the experimental period, the flies were removed and maintained under

laboratory conditions (21 $\pm$ 2°C, R.H. 75 $\pm$ 3%, 16-8 hour photoperiod) over the necessary incubation period. The flies were fed, watered and evaluated daily for mortality. This experimental procedure was repeated twice during the 1980 growing season (June 16, 1980 and June 28, 1980).

RESULTS: Over the exposure period and while removing flies from the field cages, several individuals escaped from each cage, which produced an unbalanced data set. Although numerous cases were missing, it presented no analysis problems as the data was evaluated using the proportion infected of the total recaptured. Control mortalities (0 cadavers per enclosure) of 8.9% and 12.03% were measured from the first and second sample period data sets, respectively. The data were corrected for control mortalities using the methods suggested by Abbott (1925) (Table 28). An analysis of covariance was used to evaluate between-day infection differences while controlling for cadaver density using the arcsin of proportion infection. A significant difference between days ($p = .05$) was indicated (Table 29).

A probit regression conducted on the pooled data sets (Figure 46) shows the variation caused between days. Because the weather conditions were not in ranges that limited spore germination, an assumption was made that actual number of conidia produced per cadaver might be different between the experimental periods. Linking the sporulation rate curve (Experiment 5) with the data on cumulative sporulation as an instantaneous function of temperature (Experiment 6) and evaluating the relationship using hourly temperature data from the research site, a 2.53 fold difference in total conidia per cadaver was estimated. Weighting each cadaver by the estimated number of conidia produced on the day of experimentation provided a variance stabilizing factor between experimental periods (see analysis of covariance, Table 30). It also predicted the

Table 28. Observed and adjusted mortalities for onion maggot adults exposed to various E. muscae conidial doses in field cages. Mortalities adjusted for background infection using the method suggested by Abbott (1925).

June 16, 1980					June 28, 1980				
Cadavers per plot	Replicate	N	Percent Infection	Adjusted Infection	Cadavers per plot	Replicate	N	Percent Infection	Adjusted Infection
1	1	47	25.5	18.1	1	1	97	41.2	32.0
	2	50	18.0	9.9		2	93	60.2	54.8
	3	43	44.2	38.7		3	76	69.7	65.6
2	1	50	40.0	34.1	2	1	100	78.0	75.0
	2	41	51.2	46.4		2	91	67.0	62.5
	3	38	55.0	50.6		3	83	48.2	41.1
4	1	49	49.0	44.0	4	1	61	91.8	90.7
	2	31	54.8	50.3		2	74	72.9	69.2
	3	43	81.4	79.6		3	97	69.1	64.9
6	1	50	80.0	78.0	6	1	70	91.4	90.2
	2	37	65.0	61.5		2	87	100.0	100.0
	3	33	87.9	86.7		3	91	96.7	96.3
8	1	37	100.0	100.0	8	1	76	97.4	97.1
	2	50	98.0	97.0		2	98	100.0	100.0
	3	29	79.3	77.3		3	92	92.4	91.4
10	1	32	100.0	100.0	10	1	93	98.9	98.8
	2	37	97.3	97.0		2	71	98.7	98.5
	3	44	72.7	70.0		3	52	94.2	93.4
0	1	43	9.3	---	0	1	87	16.1	---
(control)	2	50	12.0	---	(control)	2	73	6.8	---
	3	38	5.3	---		3	91	13.2	---

Table 29. Analysis of covariance for arcsin proportion infection by day of experimentation while controlling for the metric variable, cadaver density.

Source of Variation	Sum of Squares	DF	Mean Square	F
Covariate				
Cadaver density	24.01	1	24.01	85.64***
Main Effects				
Days	2.99	1	2.99	10.68**
Residual	9.25	33	.28	
Total	36.25	35	1.036	

** (p<.01) *** (p<.001)

Table 30. Analysis of covariance for arcsin proportion infection by day of experiment while controlling for the metric variable, estimated spore density.

Source of Variation	Sum of Squares	DF	Mean Squares	F
Covariate				
Estimated Spore Density	21.24	1	21.24	49.46***
Main Effects				
Days	.84	1	.84	1.96NS
Residual	14.17	33	.429	
Total	36.25	35	1.036	

*** (p<.001) NS = Not significant (p>.10)

Table 31. Regression statistics for probit mortality versus log spore dose (*1 million).

Source	DF	Sum of Squares	Mean Square
Regression	1	24.15	24.15
Residual	34	9.99	.294
Total	35	34.15	

y intercept(a) = 4.86 $\pm$ .019 r^2 = .7072
slope(b) = 2.03 $\pm$ .224 y = 4.86 + 2.03x

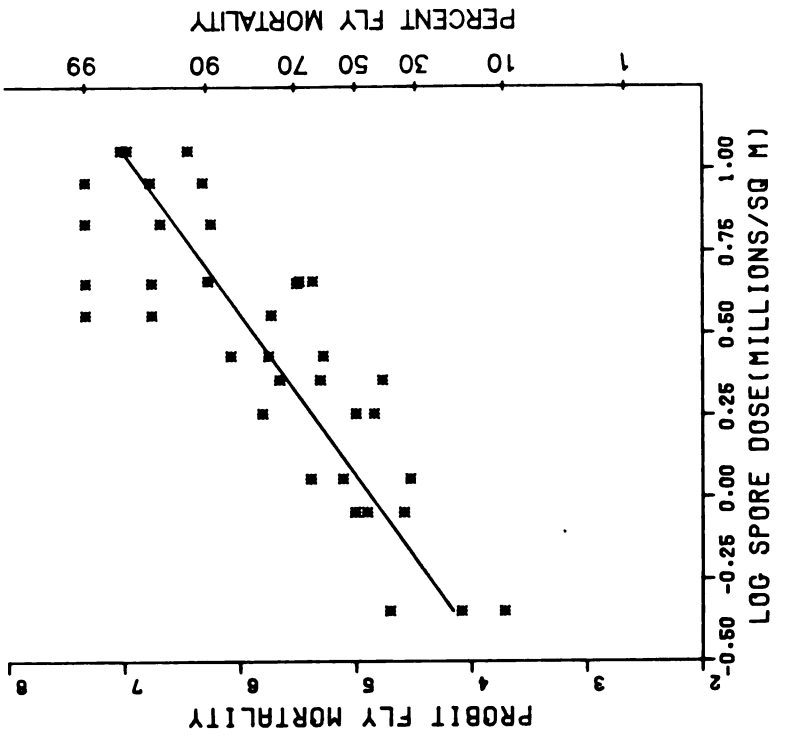


Figure 47. Probit fly mortality versus log of estimated spore dose from field infection studies.

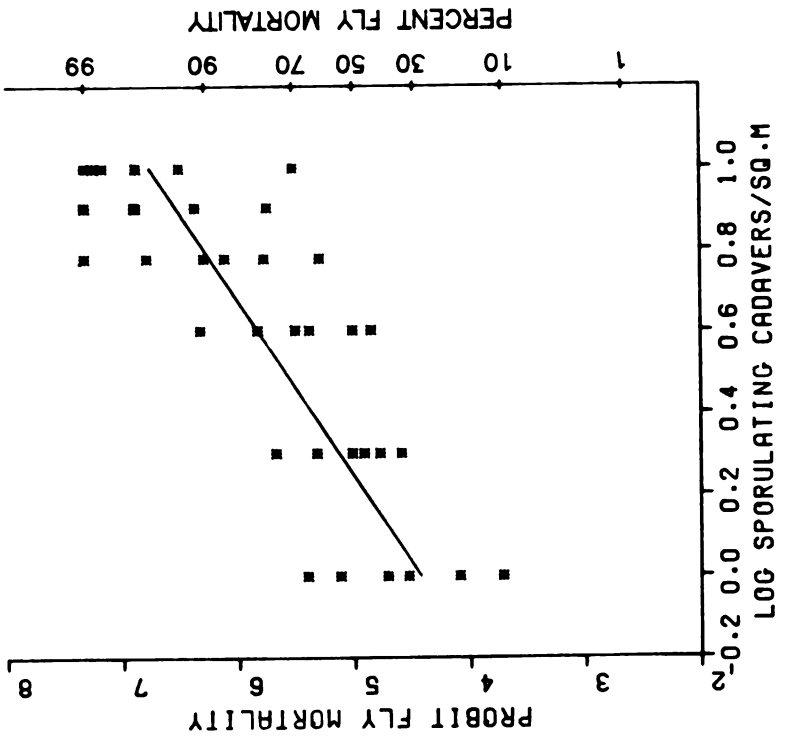


Figure 46. Probit fly mortality versus log of sporulating E. muscae cadavers from field infection study.

actual conidia density to produce the observed infection. A probit regression analysis was applied to the spore density-percent infection data (Table 31, Figure 47) (note the reduced variation due to the differential conidial production between days). Using this relationship to predict host infection under differing conidial loads, the infection process can be modeled. For example, 1.17 million spores (less than that produced by 1 cadaver under optimal conditions) per meter produces 50% host mortality. This experiment may have overestimated the actual field infection due to the buffered environment within the experimental enclosures.

VIII. ABSTRACT MODELING

The complexity of biological processes, particularly at the ecosystem level, hampers direct conceptual interpretation of overall system response to changing environmental conditions. Populations of specific organisms respond differentially to various environmental stimuli, as do individuals within each of these populations. Characterization of these responses both within and between species is important in developing a comprehensive understanding of how organisms interact within their environment. Although numerous detailed studies have been conducted for many organisms, synthesis of this information back to a system level has been hindered primarily due to a lack of available techniques. The development of biological modeling (Patten 1971 and Tummala et al. 1975) has recently provided a medium for such synthesis. Individual subcomponents of a system may be evaluated in detail, described mathematically and linked through computer modeling with other subcomponents for evaluation of overall system response.

The necessity to develop more precise agricultural management programs,

including pest management, requires a thorough understanding of overall system response to both controlled and uncontrolled stimuli. Agricultural design and management are the focus of the onion pest crop agroecosystem project (Haynes et al. 1980), thus necessitating such a level of understanding. Systems modeling is being used in this project as the primary integration method between subcomponents. Each subcomponent is modeled and evaluated in free-body form (Tummala et al. 1975) and then linked to provide a better understanding of overall system response.

Model development in this subproject follows the above format closely. The three primary components, OM, SCM and E. muscae, are each conceptualized and modeled in free-body form and then linked to provide insight into their response as a unit. Model development and evaluation was conducted in cooperation with Ms. J.J. Pet and Mr. G.H. Whitfield. Only a brief synopsis of model formation validation and use will follow as it will be the central theme for Ms. J.J. Pet's Master of Science degree in the Department of Electrical Engineering and System Science at Michigan State University. (For more technical details, complete validation and use, please refer to Ms. Pet's thesis (projected completion date, 1982).)

A. Simulation Model Formulation

Actual model formulation involves the transformation of biological concepts and processes into mathematical form which can be linked and evaluated numerically. Numerous techniques are available to construct such models, including both "black box" and structural approaches (Manetsch and Park 1977). The structural approach, which explicitly defines subcomponents, their interconnections and constraints, provides the most biologically intuitive methods, and thus was used throughout this study whenever possible. When in-

depth system structure was not necessary or was unknown, time series were evaluated and black box approximations used (Manetsch and Park 1977, Varadarajan 1979).

The modeling process begins with system conceptualization (section V, Figures 1-3), where the exact components of interest and the level of consideration are determined. For this model, the OM and E. muscae were considered in the detail described by the exact functional block diagram representing their life system (Figure 48). The SCM was considered to have the same response to E. muscae although only the adult life stages were modeled (time series representation) as much of its population dynamics occurs externally to the onion system and is presently unknown.

The pest and pathogen components of the system are each composed of several life stages (Figure 48). These life stages (eggs, larvae, adults, spores, etc.) represent "states" (Patten 1971) of the biological system (the density of the organism by life stage) at any given time (t). The transformation of these organisms between different states is controlled by various biological processes referred to as rates. Common to each life stage is the process of development (physiological maturation). The development of each life stage is highly correlated with prevailing environmental conditions, predominantly temperature (Experiment 3, Carruthers 1979). Development occurs only when the temperature, T(t), exceeds a threshold, T_0, that is characteristic of each particular organism. Thus, each life stage requires a specific amount of heat accumulation above the threshold in order to complete development and pass from one life stage to the next.

Once these developmental rates are estimated (Experiment 3, Carruthers 1979), the development can be modeled as discrete delays using difference

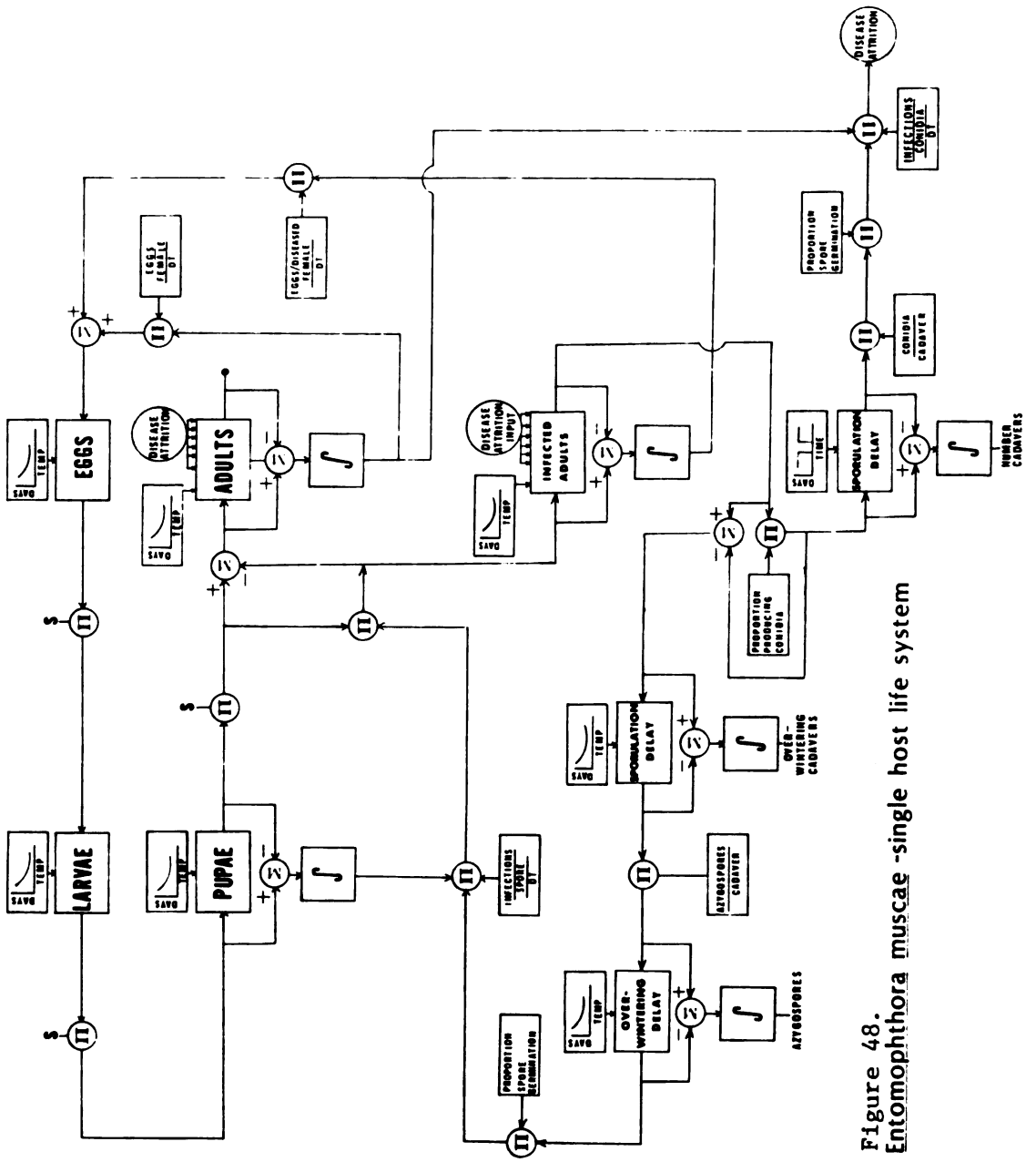


Figure 48.
Entomophthora muscae -single host life system

equations or delay-differential equations. The underlying assumption in using a discrete delay to model insect development is that all individual entities of the population at any one stage develop in an identical manner. In other words, we assume that the insects move as homogeneous groups from one life stage to another. In reality, this seldom occurs. Organisms develop as heterogeneous groups; therefore, development differs between individuals. It is more realistic to model development considering aggregative behavior, which is characterized by a mean delay and associated variance. This mean delay is dependent on temperature, and hence, is time-varying. Consequently, the basic building blocks of the model are time-varying distributed delays (Forrester 1961, Abkin et al. 1972, Manetsch 1976, Ravlin et al. 1978, and Ravlin 1980) linked serially to form the basic model structure.

Parameterization of the model subcomponents was accomplished using the data provided by the experimental sections of this study in combination with previously known information (Figure 3, Appendix C). Stage-specific mortality (Ellington 1963, Whitfield 1981) was applied at the end of each immature life stage and as an instantaneous mortality rate (Fulton 1978) in the adult stage. Host fly populations were allocated between specific habitats (onion fields and border areas) using the data collected in relation to host spatial patterns (section VII.B.3, Figure 21). Relative field-border dimensions were considered as a model variable and adjusted differentially to examine the effect of limiting habitat size on overall system response.

Entomophthora muscae densities were initiated through host infection at the time of emergence and allowed to change freely based on interaction with host populations in the areas of population overlap. Conidial formation and sporulation were based on the time and temperature relationships outlined in

section VII.C (Experiments 5 & 6). Conidial densities associated with the sporulation period were integrated and allowed to interact with host fly densities. This interaction produced infection based on the experimental probit infection-spore density relationship (section VII.C, Experiment 11).

Two major deviations from the proposed model (Figure 48) were necessary for implementation: 1) the structural characterization of the azygospore section of the life cycle was not feasible due to the present lack of understanding of the biological processes controlling its operation, thus time series (section VI.B.3) were used to simulate primary host infection; and 2) further structural characterization of the adult OM was necessary to separate preovipositional and ovipositional adults.

The preovipositional adult stage in the OM lasts approximately 105°C DD, necessitating separate consideration in model form. Because infection time is critical in determining if adults will live long enough to reach ovipositional maturity, a special modeling component was necessary to describe the host-pathogen interaction during this stage. This component can best be described as two biological processes (adult development and pathogen development) simultaneously competing for the same resource. The process was modeled by developing a 2-dimensional extension of a standard, time-varying distributed delay.

B. Computer Implementation and Program Verification

The computer implementation of any model increases its abstraction from the real world process by imposing a variety of technological constraints on the conceptualized system (Manetsch and Park 1977). Care must be taken when choosing the programming language and the machine for implementation as well as critically evaluating the resultant output. The E. muscae-host life system

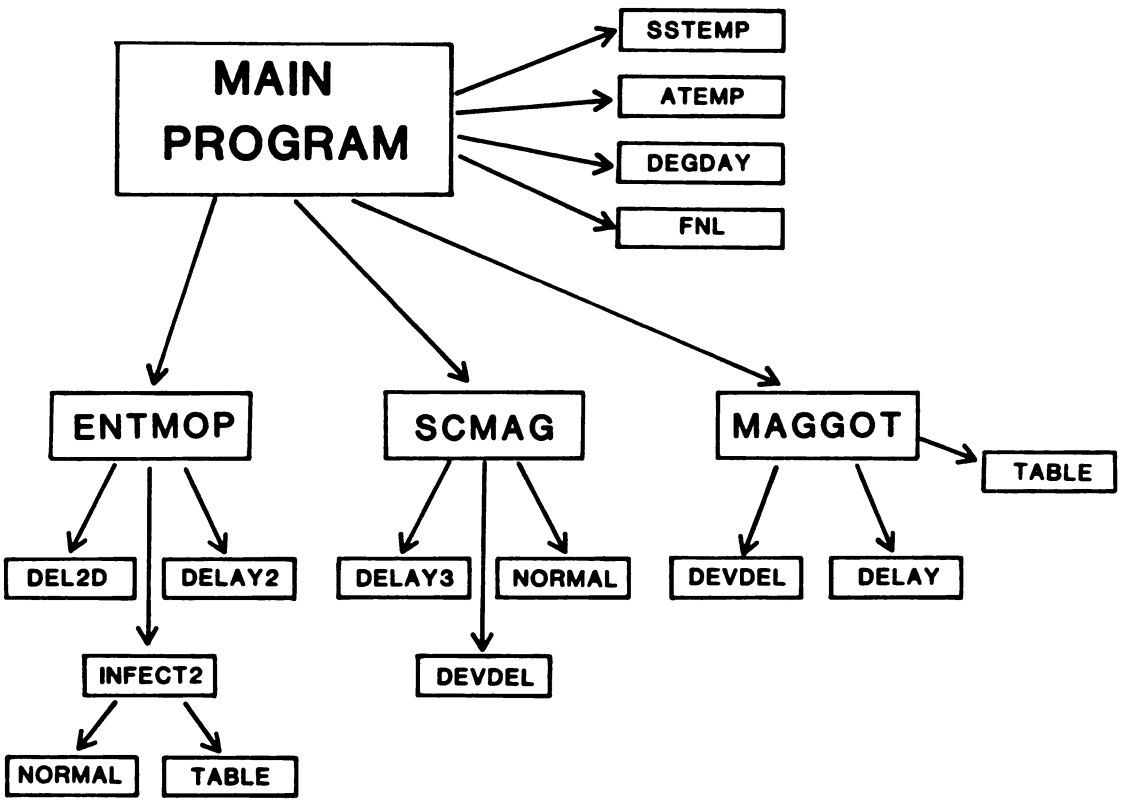
model described above was programmed in cooperation with Ms. J.J. Pet (Master of Science candidate, Department of Electrical Engineering and Systems Science) in Fortran V and implemented on the Michigan State University Cyber 750 computer. The program was constructed in a hierarchical manner with a driver program controlling free-body submodels of each biological component (Figure 49, program source code listed in Appendix L).

Program verification, a rigorous and time-consuming step, involved individual verification of each model subroutine before implementation into the final program followed by an overall evaluation when linked together through the driver program. Programming errors and model stability under various time increments (DT) were scrutinized for accuracy. Further program verification is linked with model validation before the model is acceptable for use.

C. Model Validation

Validation establishes whether or not the model is a valid representation of the actual system. The degree of model accuracy depends on the level of precision necessary for model use. For our purposes, conceptual evaluation, high precision (exact quantitative fit) was not mandatory, although desirable. In this instance, where the model was designed from experimentally-derived structural components, comparison with actual field data provided a measure of validity.

Each component of the free-body model was evaluated separately and in combination. Initial response of the OM component provided a rough approximation of the observed natural system. Emergence and population density estimates (Figures 50 & 51) predicted by the model accurately described the initiation of each generation, although as the season progressed, the model response deviated markedly from the observed field data. The pathogen component of the model increased accuracy by providing adult mortality that



COMMON BLOCK

1- COMMON/PASS1/TEMP,LX,DT
2- COMMON/PASS2/HTIME,DMAG
3- COMMON/PASS3/STRG,SQI,SQ2
4- COMMON/PASS4/RATES,DEL,DEGGS,SADULTS,OMOUT
5- COMMON/PASS5/SCRATE,DELSC,SCINF
6- COMMON/PASS6/SCSTOR
7- COMMON/PASS7/OM,STMP,PSUM
8- COMMON/PASS8/PUPA,PUPA1,PUPA2,CUMDD

Figure 49. Programming structure of Free Body Host-Pathogen Simulation Model listed in Appendix L.

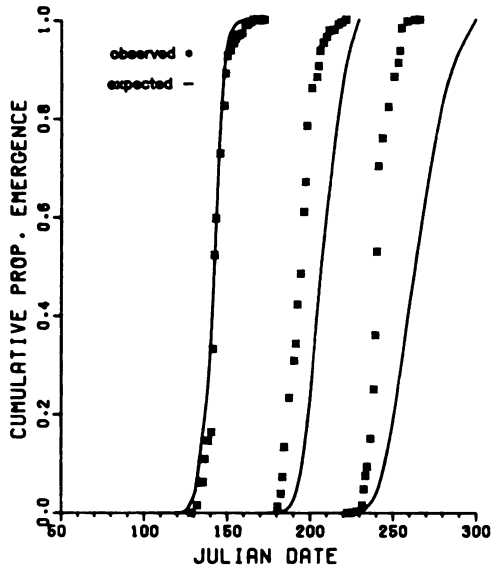


Figure 50.

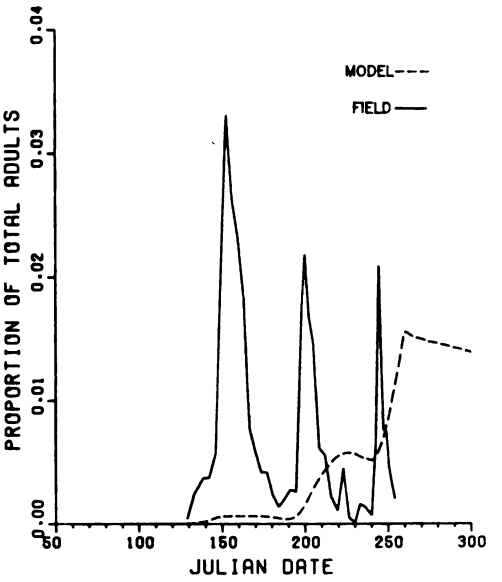


Figure 51.

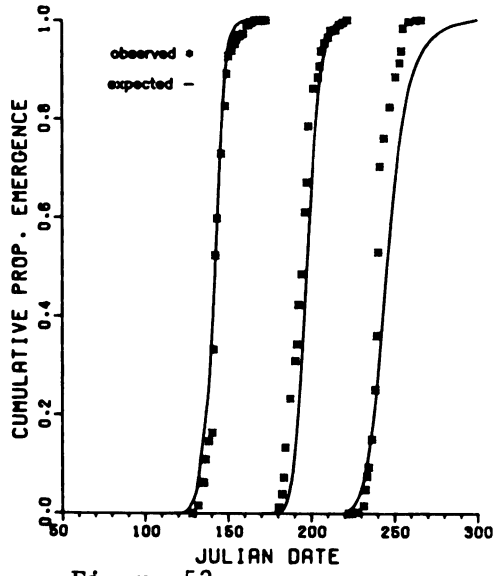


Figure 52.

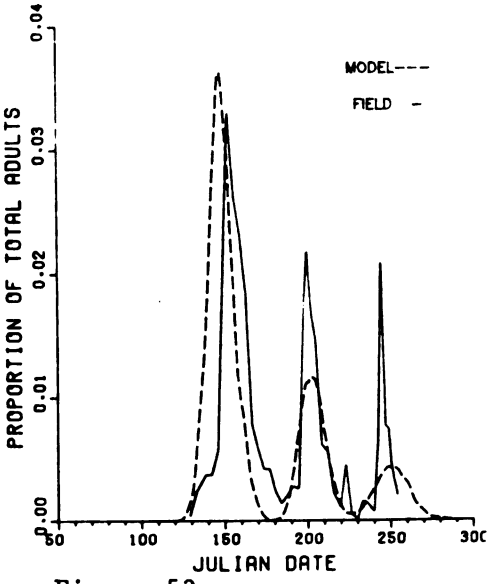


Figure 53.

Figure 50. Observed and simulated (expected) onion maggot emergence for Grant 1980. E. muscae not included in the simulation.

Figure 51. Observed and simulated onion maggot adult population levels for Grant 1980. E. muscae not included in the simulation.

Figure 52. Observed and simulated (expected) onion maggot emergence for Grant 1980. E. muscae included in the simulation.

Figure 53. Observed and simulated onion maggot adult population levels for Grant 1980. E. muscae included in the simulation.

was inherent in the natural system. The effect was a shifting of the predicted population curves and a much more realistic model response (Figures 52 & 53). Population infection levels (Figure 54) also followed observed field patterns (Figures 14-19) responding in a lagged, density-dependent manner (Section VII.B.2). Further model validation including the response of the immature OM life stages, and sensitivity analysis of the entire model is given by Whitfield (1981) and Pet (1982, projected date of masters thesis completion).

D. Model Application

An understanding of the system response to various environmental and human-induced conditions is necessary to develop and implement pest management strategies. Simulation of these conditions, although not absolute, can provide insight into the system response at an extremely small cost. Such insight may be useful for management decision-making or for developing hypotheses to be tested under field conditions.

Although the model is still in the process of being validated, example outputs (Figures 54-56) were generated using the 1980 Grant weather data as a standard for comparison. The effect of altering the initial OM population (Figures 54 & 55, note differing scales) on E. muscae follows the expected density-dependent pattern discussed in section VII.B. An initial population size of 5000 flies resulted in infection levels approaching 50%. The resultant second and third generations and the associated E. muscae infection levels were reduced to much lower densities. Simulation of the initial population density of 500 flies produced rather stable numbers between all three generations. The reduced infection level during the second generation is always less than the other two generations, due to the spatial aggregation (Figure 21) in border areas in early spring and late fall.

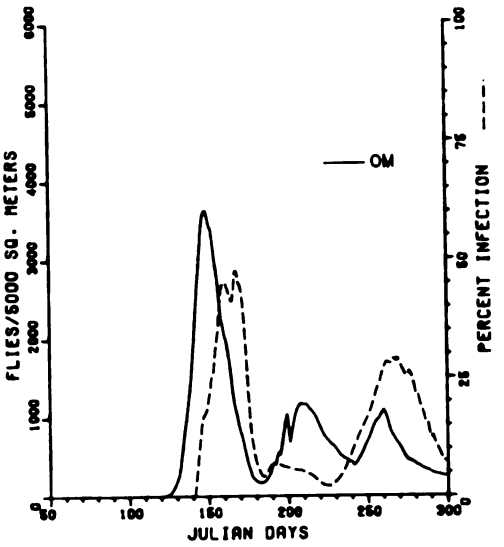


Figure 54.

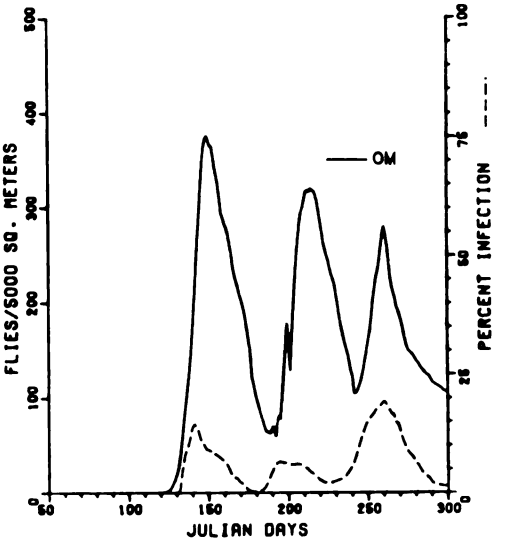


Figure 55.

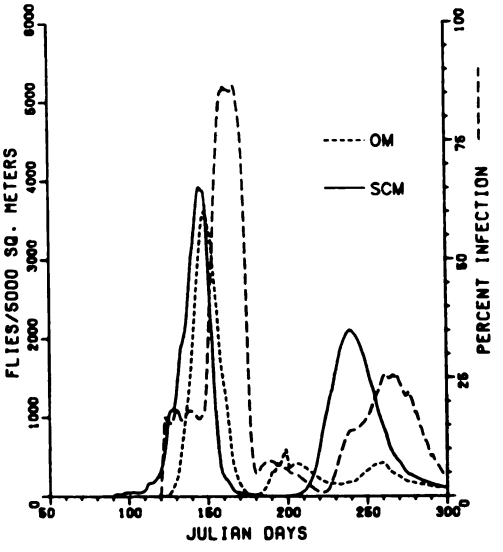


Figure 56.

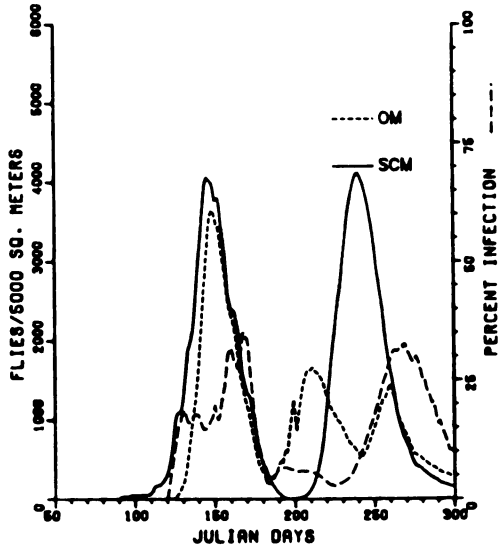


Figure 57.

Figure 54. Simulated onion maggot adult population with the predicted level of E. muscae infection. (Initial OM population = 5000).

Figure 55. Simulated onion maggot adult population with the predicted level of E. muscae infection. (Initial OM population = 5000).

Figure 56. Simulation results showing the augmentation of E. muscae infection due to the inclusion of the seed corn maggot. (Initial populations: OM = 5000; SC = 5000).

Figure 57. Simulation results showing the effect of fungicide application on E. muscae infection and the resultant fly population increase.

The impact of an alternate disease host can be clearly noted (Figure 56) with the addition of the SCM population. Using the same input parameters as in Figure 54, with the addition of 5000 SCM adults substantial increases in the infection levels were simulated, causing a further reduction in the second and third generations. The model was also developed to simulate the utilization of both insecticides and fungicides on the three populations. Two applications of an early season fungicide (applied on days 150 and 170 for downy mildew (Figure 57)) greatly reduced E. muscae levels, which altered both OM and SCM from their previously projected population levels (Figure 56).

These examples represent only a small proportion of the analysis possible upon final validation of the model. After completion, the model is to be linked to other models associated with the onion agroecosystem for evaluation of overall system response and the development of ecosystem level management strategies.

IX. SUMMARY

Entomophthora muscae was identified as a common fungal pathogen of the adult onion maggot, Hylemya antiqua, and the adult seed corn maggot, H. platura, during each of 4 study years (1977-80). Positive identifications made in every sample area indicated a well established, widespread distribution of the pathogen throughout Michigan's southern lower peninsula. In addition, two other flies commonly found in onion production regions, the cluster fly (Pollenia rudis) and the tiger fly (Coenosia tigrina) were identified as common hosts. Clearly, E. muscae is a common and integral biological component of the onion agroecosystem.

Intensive field-level monitoring revealed variable infection levels

throughout the season. Disease incidence, on the average, was highest during the spring and fall and lower during midsummer. Multivariable techniques were used to assess the effect of both abiotic and biotic environmental variables on disease occurrence. Host and inoculum densities were the only variables found to produce statistically significant infection patterns. Further experimentation indicated that changes in host and pathogen spatial patterns throughout the season directly affected the amount of population overlap. These changes in interaction in turn resulted in variable infection levels.

Although E. muscae infection levels were high under many conditions, overall host mortality due to mycosis was significantly reduced by other preempting mortality factors. Estimates ranging between 2.1% and 23.1% mortality due to mycosis were noted in the overall H. antiqua population during 1979. By considering only the adult flies reaching maturity (females older than the 105 DD preoviposition period), the range of E. muscae-induced mortality is increased to 15.1-68.1%. The significance of this pathogen from a population dynamics standpoint must then be considered as it affects the succeeding generation through a reduction in population fecundity. Using simulation methods, estimates of between 13.6 and 49.3% reduction in fecundity were obtained for the 1979 H. antiqua populations. In years when other mortality factors are not as effective and do not preempt E. muscae mycosis, the potential impact may be greater.

The development of a conceptual E. muscae/single-host life system model helped specify what further experimentation was necessary to parameterize the transfer functions used to complete an actual simulation model. In vivo and in vitro culture and transmission techniques were also developed to aid in specific experimentation.

A second order polynomial expression adequately described the temperature-dependent developmental relationship of E. muscae in vivo. Entomophthora muscae also caused a premortality reduction in H. antiqua fecundity. Noticeable reductions in fecundity of mature females occurred 40 DD after infection, with complete suspension around 70 DD (approximately 40 DD before host death).

Host death and the initiation of E. muscae conidial sporulation occurred only during evening hours. Dying flies locate attachment sites, fasten themselves to the substrate, and die between 5 and 8 p.m. Conidial production and sporulation quickly follow. Conidia are released throughout the night. Sporulation follows a cumulative normal distribution centered around 1:00 a.m., with 95% of the spores released between 9:00 p.m. and 5:00 a.m. the following morning. Although the sporulation phenology followed this basic pattern, the absolute number of spores produced was temperature and moisture dependent. Under optimal conditions, approximately 1.5 million spores per fly are produced. For modeling purposes, the phenology and density of conidial production was evaluated on an hourly basis for synchrony with environmental conditions producing spore dispersal and germination.

Conidial germination was evaluated under laboratory and field conditions. Free moisture was found to be necessary for conidial germination; temperature regulated the rate of development. Polynomial regressions were used to simulate the time-temperature-germination response surfaces. Conidial germination and survival were evaluated in onion, carrot, and field border plant canopies. Germination and survival rates were highest in carrot and border canopies (the primary site of host-pathogen interaction) due to increased canopy cover. Canopy cover provided protection from harsh environmental conditions.

In each of four experimental dates, almost complete conidial mortality occurred within a 24-hour period following the initiation of sporulation. This suggested that host-pathogen interactions must occur the day following sporulation for infection to develop.

Host-pathogen interactions were examined in border habitats. Experimental results indicated that a significant amount of infection occurs from host contact with conidia deposited on vegetation rather than only by direct contact at the time of sporulation. Field cage studies were used to estimate host mortality under differing conidial doses. Using probit analysis, 50% host infection level can be expected with a conidial load of 1.17 million conidia per meter. Under optimal conditions, 1.17 million conidia per meter converts to less than 1 cadaver per meter, which is well within observed field densities.

The multiple host-pathogen life system was simulated using free-body modeling techniques developed in cooperation with Dr. G.H. Whitfield and Ms. J.J. Pet. Preliminary model validation has been conducted component by comonent and in combined form. Results indicate that the model provides a reasonable approximation of the desired system. Further validation and testing are currently underway and readers are referred to Pet (in prep.) for a more detailed evaluation of results.

In conclusion, E. muscae is of prime importance in the population regulation of both OM and SCM in the onion agroecosystem. Utilization of this pathogen for pest management purposes is highly desirable due to its host specificity and natural abundance. Field infection levels can be enhanced by grassy border areas where host-pathogen interaction may occur, by possible augmentation of non-pest host species, and by limiting the use of foliar

insecticides and fungicides. Strip-planting onion with other crops such as carrot provides a more protected canopy for spore germination and host infection. It also increases infection levels, although further research is necessary in this area. Similarly, further research on manipulating onion culls in the fall may be useful in developing better host-pathogen spatial overlap, thus higher primary infection levels in the spring.

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APPENDIX A

The Impact of Pesticides On Natural Enemies of the Onion Maggot, *Hylemya antiqua*

The Impact of Pesticides On Natural Enemies of the Onion Maggot (Hylemya antiqua (Meigen))[1, 2]

By

R. I. Carruthers & D. L. Haynes

ABSTRACT

Pesticide–induced differential mortalities between the onion maggot (Hylemya antiqua (Meigen)) and several organisms associated with its natural control (H. platura (Meigen), Coenosia tigrina (Fabricius), Entomophthora muscae (Cohn), and Aphaereta pallipes (Say)) were evaluated under simulated field conditions. Direct and residual differential mortalities were examined for three herbicides (Chloro-IPC, nitrofen, and CDAA), three fungicides (maneb, chlorothalonil, and copper sulfate), and an insecticide (malathion). The recommended field application rates of these chemicals produced high differential mortality levels between H. antiqua and some of the natural mortality agents. Chloro-IPC, a preplant herbicide, induced 100% differential mortality between H. antiqua and A. pallipes over the three-day residual test period.

INTRODUCTION

An intensive use of chemical insecticides has long been known to disrupt the natural balance of host-parasitoid systems (Nicholson 1939, Pickett 1949, Ripper 1956, Van den Bosh and Stern 1962). Insecticide use also causes differential mortality, the temporary elimination of natural enemy food resources (host insects) and the secondary poisoning of natural enemies--known mechanisms of pest resurgence (Croft and Brown 1975). Disruptions such as these dominate contemporary agricultural production systems (Metcalf 1980).

Less apparent, yet just as significant, are the impacts associated with agrochemicals applied for purposes other than direct insect control. Of the present agricultural pesticide usage, herbicides compose ca. 52%, insecticides ca. 38%, and fungicides ca. 10% (McEwen and Stevenson 1979). The accelerated use of herbicides in recent years, combined with the current and predicted trend toward chemically maintained no-till production systems, is certain to cause increased side effects in the associated agroecosystem (Barney 1980). Direct toxicity as well as indirect effects (elimination of habitat, food resources, etc.) on non-target organisms are probable and must be considered when designing and managing agricultural production systems.

The onion production system in Michigan is a prime example of an agroecosystem with several direct pests as the focus of intensive, chemical control programs. Haynes et al. (1980) described the structural organization of the onion pest-crop agroecosystem, accentuating the interrelationship between the biotic components and the onion plant. In this system, antagonism between traditional disciplinary-oriented control strategies is apparent as many important biological control populations (parasitoids, pathogens, and predators) are frequently disrupted by the application of common agrochemicals.

This paper will quantify the differential effects of specific pesticides between Hylemya antiqua (Meigen), the primary insect pest associated with northern onion production, and several organisms associated with its natural mortality: Hylemya platura (Meigen) (alternate pathogen host), Entomophthora muscae (Cohn) (fungal pathogen), Coenosia tigrina (Fabricius) (predator) and Aphaereta pallipes (Say) (parasitoid).

METHODS

TEST SPECIES

A vacuum-operated, self-propelled, insect collection machine (Cobb and Ruppel 1976) was used to mass collect H. antiqua, H. platura, and C. tigrina adults from onion fields in Grant, Michigan. The flies were anesthetized with CO_2, sorted to species, and caged for transportation to the laboratory. The test species were maintained at 21 $\pm$ 2°C for a 48 h period prior to testing (food and water provided). Individuals identified as being infected with E. muscae were transferred to alternate storage areas before sporulation and used as pathogen sources for conidial sporulation and germination studies.

One hundred A. pallipes-parasitized onion maggot (OM) pupae were collected from onion fields in Grant Township, Newaygo County, Michigan, and reared through a single cohort of laboratory-reared OM larvae (Niemczyk 1964) to acquire the quantity necessary for testing.

APPLICATION TECHNIQUES

The pesticides tested represent the chemicals presently used in the Michigan onion production system. Commercially available formulations were used in all experiments with treatment doses designed to bracket recommended

field application rates (Cress et al. 1976, Putnam 1979). The chemical doses are presented as concentrations (percent solution) based on the amount of active ingredient applied to 1 ha in 470 liters of water (Table A1).

Bioassay procedures associated with the insect species tested used a Beltsville chain-drive sprayer to apply the test chemicals to barley seedlings. Wooden greenhouse flats containing 20 cups (each containing five 12 cm tall plants per 9 cm diameter Dixie• cup) were run through the sprayer at 40.5 m/min. A Tee Jet• 8004E nozzle, emitting 1.46 liter/min (27 g/cm^2 liquid pressure) was used to acquire the desired spray volume (470 liter/ha) (Anonymous 1977). All sprayer specifications were held constant throughout the experiment with the treatment doses adjusted by altering the spray solution concentration.

Test insects were placed on the barley substrate (1 cup/rep) immediately after spray application and covered with a screen-topped glass globe. The globes were held at 21 $\pm$ 2^{o}C for the test period with mortality assessments made at 12, 24, 36, and 48 h after initial contact. The insects were considered dead if they were unable to right themselves. The pesticide test series was compared to three control treatments for each chemical-insect combination: a) no spray, b) water spray, and c) non-contact. The non-contact control treatment consisted of treated barley (2x field rate) covered by glass lantern globes fitted with an internal screen divider separating the treated plants from the test insects. This was used to evaluate the contact versus fumigative mortality.

Additional barley cups, treated at the recommended field rates, were placed outdoors and allowed to age under natural field conditions (14 h photoperiod, clear skies, 0 precipitation, 27-5^{o}C temperature range). Residual activities were evaluated over a three-day period by introducing test insects after specific aging periods.

TABLE A1. Treatment levels (presented as percent solution) for common onion production pesticides.

Malathion (I)	Nitrofen (H)	CDAA (H)	CIPC (H)	Chlorothalonil (F)	Maneb (F)	Copper Sulfate (F)
.576	.960	2.88	2.88	1.08	1.14	.240[a,c]
.2886[a]	.480[a]	1.44[a]	1.44[a]	.54[a]	.57[a]	.024[c]
.1444	.240	.720	.72	.27	.285	.0024[c]
.0722	.120	.360	.36	.14	.143	
.0361	.06	.180	.18	.07	.072	
.018				.054[c]	.057[c]	
.009[b]				.0054[c]	.0057[c]	
.0045[b]						

a = recommended field application rate
b = treatment applied only to A. pallipes
c = treatment applied only to E. muscae conidia
I = insecticide
H = herbicide
F = fungicide

Standard slide germination tests (Altman 1966) were used to evaluate pesticide-induced disruption of E. muscae conidial germination. Glass microscope slides were dipped into chemicals at the test concentrations, air-dried, and then held under sporulating, E. muscae-infected, H. antiqua adults until a minimum of 100 conidia per slide was obtained. Five independent pathogen sources (infected flies) were used as replicates within each treatment. The slides were incubated by treatment in enclosed containers maintained at 21 $\pm$ 2°C and 100% R.H. under a 14-10 light-dark cycle. One hundred conidia per replicate were evaluated for spore germination. A minimum germ tube length (2x spore diameter) or the formation of a secondary conidium was used as the criterion for germination.

RESULTS AND DISCUSSION

Response to treatment stabilized after 24 hr, and this time interval was used for mortality assessment. Mortality levels between controls (no spray, water spray, and non contact) were not significantly different (analysis of variance-arcsin transformation) at the 95% level of confidence. Control mortalities were pooled and used to adjust each treatment replicate for natural mortality (Abbott 1925). Corrected dose-mortality data were linearized using log dose, probit mortality transformations and evaluated using regression analysis where sufficient mortality data was available (Figures A1 and A2). A complete summary of the experimental results, LD_{50} with 95% confidence limits, the no effect treatments, and the 100% mortality treatments are given in Table A2.

Malathion-induced differential mortality levels between H. antiqua and the other test insects are readily apparent (Figure A1). Due to organophosphate

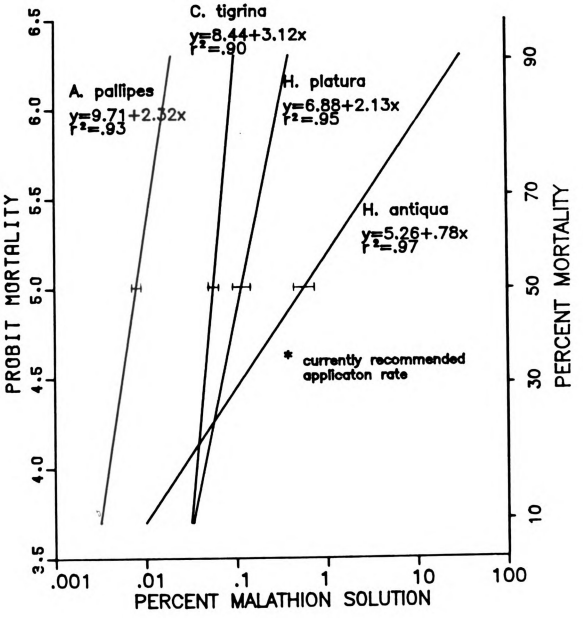

Figure A1. Log dose-probit mortality regressions for H. antiqua, H. platura, C. tigrina, and A. pallipes exposed to malathion-treated barley (see Table 2 for sample sizes).

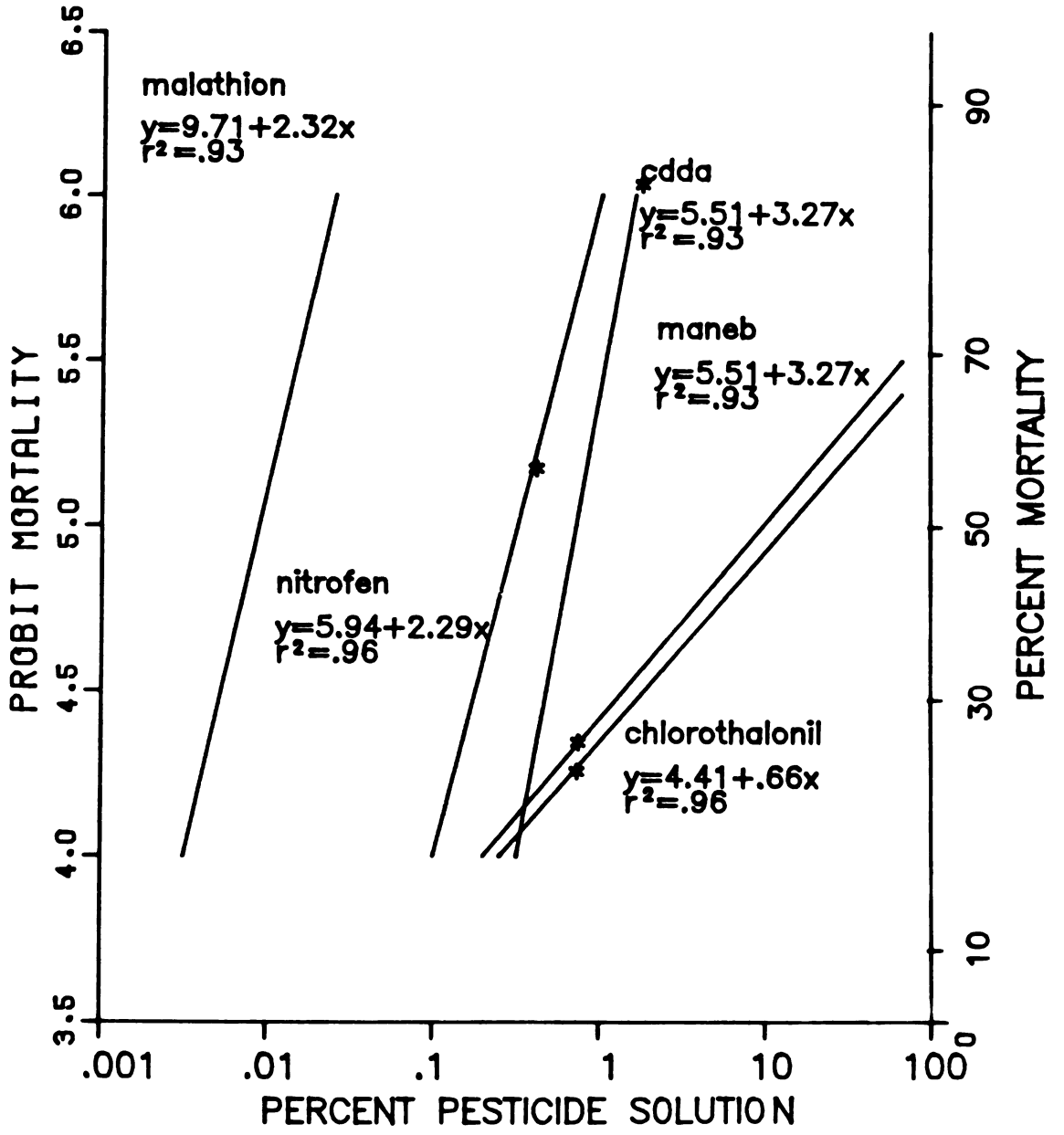

Figure A2. Log dose-probit mortality regressions for A. pallipes (see Table 2 for sample sizes).
*Recommended field application rates.

TABLE A2. Response levels and LD_{50} values with 95% confidence limits (CL) for all experimental treatments.

	A. pallipes[a]		C. tigrina[a]		H. antiqua[b]		H. platura[b]		E. muscae[b] infected H. antiqua		E. muscae conidia	
	LD_{50}	CL	LD_{50}	CL	LD_{50}	CL	LD_{50}	CL	LD_{50}	CL	LD_{50}	CL
Malathion (I)	.0093	.011 .0079	.0792	.0914 .0686	.460	.609 .347	.131	.155 .110	.452	.591 .331	NE	
Nitrofen (H)	.39	.698 .218	NE		NE		NE		-		-	
CDAA (H)	.66	.787 .557	NE		NE		NE		-		-	
CIPC (H)	.36	*	NE		NE		NE		-		-	
Chlorothalonil (F)	7.83	18.7 3.27	NE		NE		NE		-		.0054*	
Maneb (F)	13.10	37.4 4.6	NE		NE		NE		-		.0057*	
Copper Sulfate (F)		-		-		-		-		-	.0024*	

a = tabled valued based on 9 replicates per dose and 10 insects per replicate
b = tabled values based on 10 replicates per dose and 25 insects per replicate
NE = no effect noted at 2x recommended rate (not significantly different from control mortality, P = .05)
* = 100% mortality at tabled concentration (lowest rate tested)
- = not tested
I = insecticide
F = fungicide
H = herbicide

resistance, 10-15x (Harris and Svec 1976; Harris 1980, personal communication), in Michigan H. antiqua populations, the impact of legal field application rates (noted by * on graph) are highly reduced. Nontarget beneficial insects, however, are significantly affected at these rates, which inhibits their natural control potential.

Malathion produced no detectible reduction of E. muscae conidial germination or differential mortality between healthy and infected H. antiqua adults. However, a behavioral alteration was noted in H. antiqua adults at the time of pathogen sporulation (after 24 h test period). Nontreated flies climbed to the top of the barley plant, attached, and began sporulation in the characteristic E. muscae pattern (Miller and McClanahan 1959, Perron and Crete 1960). Malathion-treated, infected flies sporulated normally, but without exception, sporulated on the soil surface instead of attaching to the barley. This factor may be highly significant in relation to spore dispersal, thus disease spread and development in the field.

Entomophthora muscae conidial germination was completely inhibited by all fungicide treatments (chlorothalonil, copper sulfate, and maneb) typically applied to control plant pathogenic fungi (Table A2). Maneb and chlorothalonil produced significant mortality levels in A. pallipes, although low levels at the recommended field application rates. Aphaereta pallipes was also significantly affected by the herbicides chloropropam (CIPC), CDAA, and nitrofen (Figure A2 and Table A2). High A. pallipes mortality levels were induced by the recommended field application rate for each of these herbicides, producing even higher differential mortality than malathion. These herbicides appear to have no adverse effect on H. antiqua.

Pesticide activity over an extended time period (effective residual life)

produces further differential mortality effects between H. antiqua and the associated beneficial populations. Malathion decay follows a negative exponential function (Saini and Durough 1970, Casagrande and Haynes 1976) based on the daylight exposure time. By plotting percent malathion induced mortality versus daylight exposure after application, the residual differential mortalities between the test insects were apparent (Figure A3). The impact of this residual mortality must be evaluated with respect to the dynamics of the newly emerging and locally immigrating individuals after the time of application. For several hours after the original application, the mortality rates of the beneficial insect populations were much higher than that of the target, H. antiqua, population. The braconid parasitoid (A. pallipes) was differentially affected for 15 daylight hours after application. This finding is highly significant as many Michigan onion growers apply insecticides at three-day intervals.

Residual activities of the herbicides CIPC, CDAA, and nitrofen also produced mortalities in A. pallipes adults. Field rates of CIPC, a preplant herbicide, induced 100% mortality after a 72 h (42 daylight h) aging period. The high residual activity of CIPC is related to its chemical structure which provides an approximate soil half-life of 65 days (Mullison 1979). Nitrofen and CDAA, both post emergence herbicides with shorter decay periods (Mullison 1979), produced 17% and 20% mortality, respectively, after 24 h (14 daylight) with no significant effects detected at 48 h.

The pesticide-induced, differential mortality levels between H. antiqua and A. pallipes are best characterized as the difference between their associated mortalities through time (% mortality A. pallipes (t) - % mortality H. antiqua) (t) (Figure A4). These curves illustrate the differential response of these populations to the pesticides examined. Since CDAA, chlorothalonil, maneb and

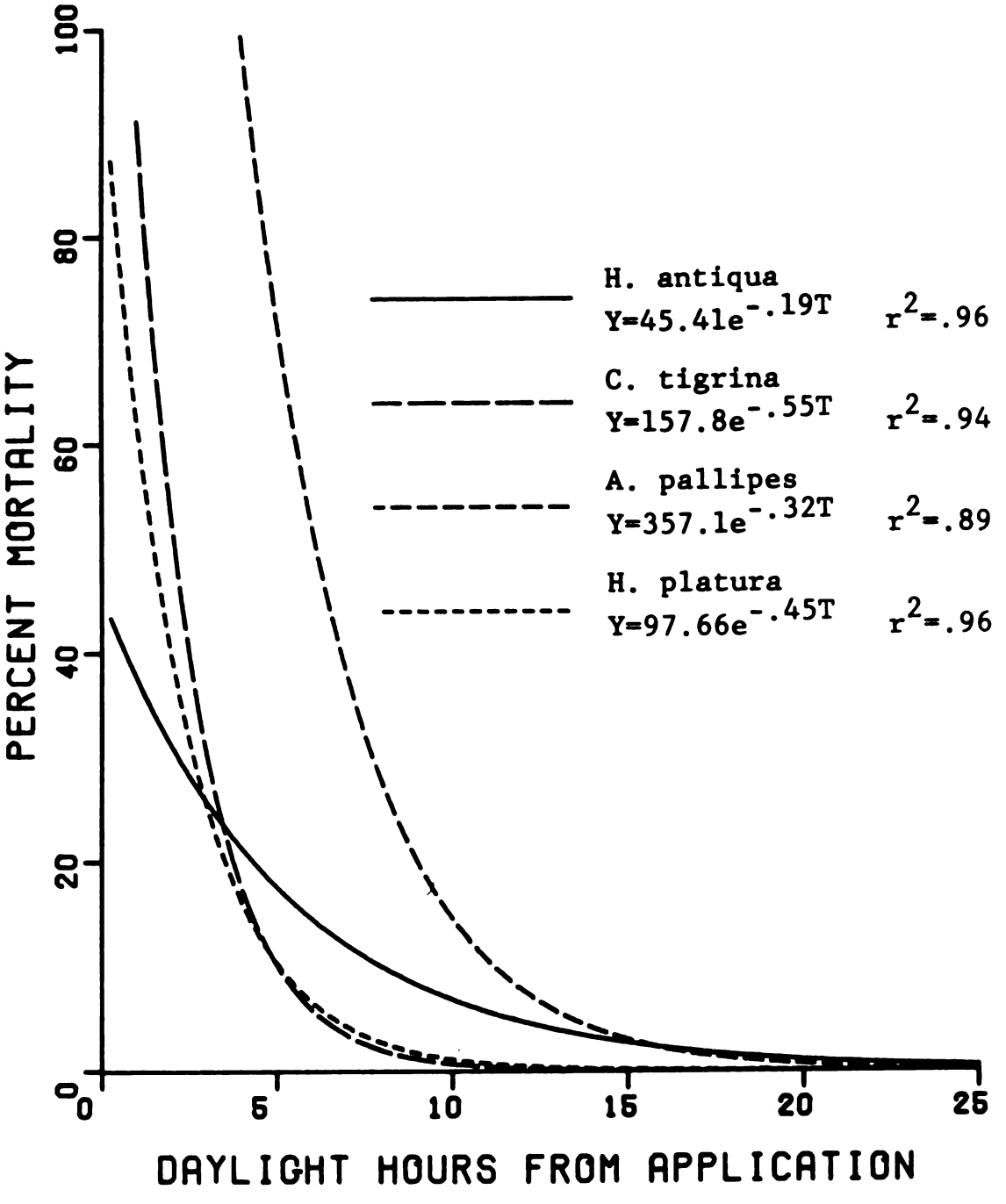

Figure A3. Residual mortality effects of malathion on H. antiqua. H. platura, C. tigrina, and A. pallipes adults. Exponential regressions based on original application rate of .2888% malathion solution.

nitrofen caused no mortality in H. antiqua, they are all characterized by monotonically decreasing functions equivalent to the residual mortality affects on A. pallipes. Similarly, the herbicide CIPC affected only A. pallipes, causing 100% differential mortality throughout the three day test period. This high differential mortality rate is due to the prolonged residual activity of CIPC and can be expected to extend beyond the chemical half-life, possibly throughout the entire season.

Malathion-induced differential mortality follows a different pattern with the response curve peaking several hours after application. The initial positive slope of this function is caused by the exponential reduction in H. antiqua mortality, while A. pallipes mortality remains fixed at 100% for several hours. Peak differential mortality corresponds with the time when the malathion residual last causes 100% mortality in A. pallipes.

Theoretically, a pesticide may actually favor the beneficial over the pest, thus producing negative differential (Figure A4). For pest management purposes, negative differential mortality is a desirable result of chemical application and can be used to manage host-parasitoid systems.

The effective residual life of these pesticides is expected to vary with changes in environmental conditions, although due to the long photoperiod and clear sky conditions during these tests, the breakdown rate is expected to be equal to or slower than the experimental rates found here (except as influenced by precipitation). Any delay in the breakdown rate would increase the differential mortality between H. antiqua and the beneficial populations examined.

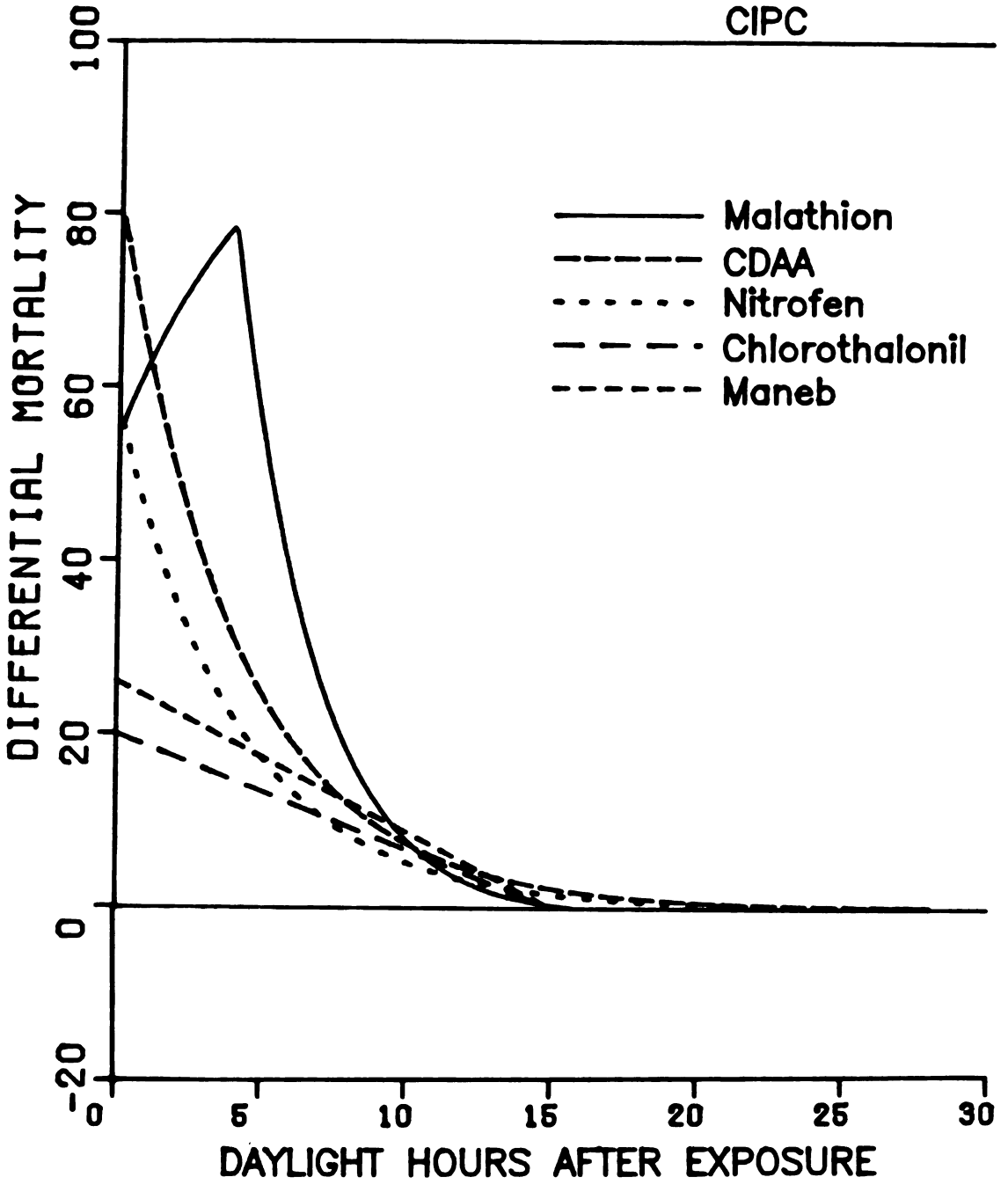

Figure A4. Pesticide-induced differential mortality between H. antiqua and A. pallipes.

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Appendix D.

Entomophthora muscae field infection data.

EWDA78ENTTABLES
EWDA79ENTTABLES

Raw data sets
CDDAENTOMOPHTHORASORTI
CDDA1979ENTOMOPHTHORAFINAL

All data files are located on UP2017 and UP2018 dump tapes at the Michigan State University Computer Center.

TABLE D1. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT RESEARCH FIELD — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	130	21	4	0	4	.19	.0081
2	138	38	5	0	5	.13	.0025
3	157	75	24	0	24	.32	.0025
4	163	21	4	1	5	.24	.0081
5	166	6	1	0	1	.17	.0225
6	170	21	7	0	7	.33	.0100
7	178	37	16	4	20	.54	.0064
8	184	29	9	0	9	.31	.0081
9	186	18	2	0	2	.11	.0049
10	191	18	6	0	6	.33	.0121
11	194	61	10	0	10	.16	.0025
12	205	98	4	0	4	.04	.0004
13	207	70	0	0	0	.0	.0000
14	230	17	0	0	0	.0	.0000
15	244	34	0	0	0	.0	.0000
16	256	40	3	1	4	.10	.0025
17	264	99	58	0	58	.59	.0025
18	269	70	34	9	43	.61	.0036
19	276	35	27	0	27	.77	.0049
20	291	11	7	3	10	.91	.0081

TABLE D2. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 1 — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	7	0	0	0	.0	.0000
2	170	12	1	0	1	.08	.0064
3	178	1	0	0	0	.0	.0000
4	186	5	0	0	0	.0	.0000
5	191	25	4	0	4	.16	.0049
6	205	62	0	0	0	.0	.0000
7	207	0	0	0	0	.0	.0000
8	221	0	0	0	0	.0	.0000
9	233	0	0	0	0	.0	.0000
10	254	78	30	5	35	.45	.0036
11	256	84	25	0	25	.30	.0025
12	264	99	73	0	73	.74	.0016
13	269	72	45	3	48	.67	.0036
14	276	20	15	0	15	.75	.0100

TABLE D3. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 2 — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	28	12	0	12	.43	.0081
2	170	31	17	0	17	.55	.0081
3	184	3	1	0	1	.33	.0729
4	199	83	0	0	0	.0	.0000
5	205	50	0	0	0	.0	.0000
6	207	0	0	0	0	.0	.0000
7	221	0	0	0	0	.0	.0000
8	233	0	0	0	0	.0	.0000
9	191	22	0	0	0	.0	.0000
10	254	79	43	0	43	.54	.0036
11	256	87	44	0	44	.51	.0025
12	264	98	44	0	44	.45	.0025
13	269	92	20	3	23	.25	.0025
14	276	43	30	0	30	.70	.0049
15	291	26	13	4	17	.65	.0081

TABLE D4. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 3 — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	9	3	0	3	.33	.0256
2	170	9	5	0	5	.56	.0289
3	186	8	1	0	1	.13	.0144
4	191	10	0	0	0	.0	.0000
5	199	11	5	0	5	.45	.0225
6	207	0	0	0	0	.0	.0000
7	221	0	0	0	0	.0	.0000
8	233	0	0	0	0	.0	.0000
9	256	43	6	0	6	.14	.0025
10	264	99	70	0	70	.71	.0025
11	276	44	26	0	26	.59	.0049

TABLE D5. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 4						HOST: ONION FLIES	
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	150	33	25	0	25	.76	.0049
2	157	35	15	0	15	.43	.0064
3	163	28	10	0	10	.36	.0081
4	170	51	16	0	16	.31	.0036
5	178	45	23	0	23	.51	.0049
6	186	71	27	0	27	.38	.0036
7	191	33	8	0	8	.24	.0049
8	207	50	0	0	0	.0	.0000
9	191	33	8	0	8	.24	.0049
10	212	71	0	0	0	.0	.0000
11	221	102	6	0	6	.06	.0004
12	227	40	3	0	3	.08	.0016
13	233	50	0	0	0	.0	.0000
14	242	98	19	0	19	.19	.0016
15	254	60	19	0	19	.32	.0036
16	256	93	15	0	15	.16	.0016
17	264	102	44	0	44	.43	.0025
18	269	60	16	1	17	.28	.0036
19	276	24	17	0	17	.71	.0081
20	298	3	2	0	2	.67	.0729

TABLE D6. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 5						HOST: ONION FLIES	
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	46	28	0	28	.61	.0049
2	170	12	6	0	6	.50	.0196
3	184	37	11	0	11	.30	.0064
4	199	57	15	0	15	.26	.0036
5	207	0	0	0	0	.0	.0000
6	221	0	0	0	0	.0	.0000
7	233	0	0	0	0	.0	.0000
8	254	95	23	0	23	.24	.0016
9	256	34	9	0	9	.26	.0064
10	264	98	33	0	33	.34	.0025
11	269	120	19	8	27	.23	.0016
12	276	50	38	0	38	.76	.0036
13	291	86	45	10	55	.64	.0025

TABLE D7. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 6						HOST: ONION FLIES	
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	21	13	0	13	.62	.0121
2	170	16	7	0	7	.44	.0144
3	184	20	0	0	0	.0	.0000
4	199	120	15	0	15	.13	.0009
5	207	35	0	0	0	.0	.0000
6	221	0	0	0	0	.0	.0000
7	233	0	0	0	0	.0	.0000
8	242	102	16	0	16	.16	.0016
9	247	104	3	0	3	.03	.0004
10	254	61	42	2	44	.72	.0036
11	256	99	90	1	91	.92	.0009
12	264	95	93	0	93	.98	.0001
13	269	49	32	1	33	.67	.0049
14	276	16	12	0	12	.75	.0121
15	291	18	5	1	6	.33	.0121

TABLE D8. 1979 ENTOMOPHTHORA INFECTION

AREA: GRANT BACKROAD						HOST: ONION FLIES	
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	135	67	2	0	2	.03	.0004
2	138	88	8	3	11	.13	.0016
3	145	110	24	0	24	.22	.0016
4	150	101	34	10	44	.44	.0025
5	157	141	56	1	57	.40	.0016
6	163	69	5	0	5	.07	.0009
7	166	8	4	0	4	.50	.0324
8	170	23	10	0	10	.43	.0100
9	178	10	2	1	3	.30	.0196
10	184	16	1	0	1	.06	.0036
11	186	28	7	0	7	.25	.0064
12	191	5	2	0	2	.40	.0484
13	194	4	0	0	0	.0	.0000
14	205	25	0	0	0	.0	.0000
15	207	27	0	0	0	.0	.0000
16	212	100	0	0	0	.0	.0000
17	233	52	0	0	0	.0	.0000
18	242	97	13	0	13	.13	.0009
19	254	85	19	4	23	.27	.0025
20	256	93	18	0	18	.19	.0016
21	264	98	76	0	76	.78	.0016
22	269	23	15	0	15	.65	.0100
23	276	46	31	0	31	.67	.0049

TABLE D9. 1979 ENTOMOPHTHORA INFECTION

AREA					HOST		
EATON RAPIDS					ONION FLIES		
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	137	4	2	0	2	.50	.0625
2	155	2	0	0	0	.0	.0000
3	161	1	1	0	1	1.00	.0000
4	173	2	2	0	2	1.00	.0000
5	183	14	10	0	10	.71	.0144
6	197	10	0	0	0	.0	.0000
7	208	6	0	0	0	.0	.0000
8	218	28	1	0	1	.04	.0016
9	228	15	0	0	0	.0	.0000
10	232	50	0	0	0	.0	.0000
11	239	101	0	0	0	.0	.0000
12	250	78	21	0	21	.27	.0025
13	263	52	19	0	19	.37	.0049
14	268	79	16	2	18	.23	.0025
15	289	101	15	4	19	.19	.0016

TABLE D10. 1979 ENTOMOPHTHORA INFECTION

AREA					HOST		
MSU MUCKFARM					ONION FLIES		
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	155	34	4	0	4	.12	.0036
2	190	1	0	0	0	.0	.0000
3	239	8	0	0	0	.0	.0000

TABLE D11. 1979 ENTOMOPHTHORA INFECTION

AREA					HOST		
GRANT RESEARCH FIELD					SEED CORN FLIES		
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	130	29	18	1	19	.66	.0081
2	138	3	1	0	1	.33	.0729
3	157	4	0	0	0	.0	.0000
4	163	11	0	0	0	.0	.0000
5	166	10	1	0	1	.10	.0081
6	170	21	7	0	7	.33	.0100
7	178	6	0	0	0	.0	.0000
8	184	23	6	0	6	.26	.0081
9	186	66	2	0	2	.03	.0004
10	191	44	7	0	7	.16	.0036
11	194	93	3	0	3	.03	.0004
12	205	2	0	0	0	.0	.0000
13	207	45	0	0	0	.0	.0000
14	230	32	0	0	0	.0	.0000
15	244	12	0	0	0	.0	.0000
16	256	48	4	0	4	.12	.0025
17	264	50	34	0	34	.68	.0049

TABLE D12. 1979 ENTOMOPHTHORA INFECTION

AREA					HOST		
GRANT FIELD 1					SEED CORN FLIES		
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	29	0	0	0	.0	.0000
2	170	49	5	0	5	.10	.0016
3	178	14	0	0	0	.0	.0000
4	191	69	9	0	9	.13	.0016
5	205	10	0	0	0	.0	.0000
6	207	0	0	0	0	.0	.0000
7	221	0	0	0	0	.0	.0000
8	233	0	0	0	0	.0	.0000
9	254	48	2	0	2	.04	.0009
10	256	11	3	0	3	.27	.0169

TABLE D13. 1979 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 2							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	78	42	0	42	.54	.0036
2	170	78	47	0	47	.60	.0036
3	184	71	7	0	7	.10	.0016
4	199	6	0	0	0	.0	.0000
5	205	28	0	0	0	.0	.0000
6	207	0	0	0	0	.0	.0000
7	221	0	0	0	0	.0	.0000
8	233	0	0	0	0	.0	.0000
9	191	74	1	0	1	.01	.0001
10	264	30	19	0	19	.63	.0081
11	269	12	2	0	2	.17	.0121

TABLE D14. 1979 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 3							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	63	30	0	30	.48	.0036
2	170	43	23	0	23	.53	.0064
3	191	4	0	0	0	.0	.0000
4	199	1	1	0	1	1.00	.0000
5	207	0	0	0	0	.0	.0000
6	221	0	0	0	0	.0	.0000
7	233	0	0	0	0	.0	.0000
8	256	22	4	0	4	.18	.0064

TABLE D15. 1979 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 4							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	138	62	18	0	18	.29	.0036
2	150	62	29	0	29	.47	.0036
3	157	50	23	0	23	.46	.0049
4	163	76	23	0	23	.30	.0025
5	170	13	8	0	8	.62	.0169
6	178	47	9	0	9	.19	.0036
7	186	26	6	0	6	.23	.0064
8	191	76	25	0	25	.33	.0025
9	212	14	0	0	0	.0	.0000
10	221	1	0	0	0	.0	.0000

TABLE D16. 1979 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 5							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	55	33	0	33	.60	.0049
2	170	16	8	0	8	.50	.0169
3	184	17	6	0	6	.35	.0144
4	199	20	1	0	1	.05	.0025
5	207	0	0	0	0	.0	.0000
6	221	0	0	0	0	.0	.0000
7	233	0	0	0	0	.0	.0000

TABLE D17. 1979 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 6							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	163	100	36	0	36	.36	.0025
2	170	48	11	0	11	.23	.0036
3	184	17	5	0	5	.29	.0121
4	199	20	0	0	0	.0	.0000
5	221	0	0	0	0	.0	.0000
6	233	0	0	0	0	.0	.0000
7	242	11	0	0	0	.0	.0000
8	247	25	0	0	0	.0	.0000

TABLE D18. 1979 ENTOMOPHTHORA INFECTION

AREA GRANT BACKROAD							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	138	21	3	0	3	.14	.0064
2	145	4	1	0	1	.25	.0484
3	157	31	1	0	1	.03	.0009
4	163	21	1	0	1	.05	.0025
5	166	16	5	1	6	.38	.0144
6	170	16	4	0	4	.25	.0121
7	178	37	24	1	25	.68	.0064
8	184	41	6	0	6	.15	.0036
9	186	28	9	0	9	.32	.0081
10	191	77	9	0	9	.12	.0016
11	194	14	1	0	1	.07	.0049
12	205	71	0	0	0	.0	.0000
13	207	21	0	0	0	.0	.0000
14	212	53	0	0	0	.0	.0000
15	233	23	0	0	0	.0	.0000
16	247	98	0	0	0	.0	.0000
17	254	50	2	0	2	.04	.0009
18	256	28	4	0	4	.14	.0049
19	264	34	30	0	30	.88	.0036

TABLE D19. 1979 ENTOMOPHTHORA INFECTION

AREA EATON RAPIDS							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	137	1	0	0	0	.0	.0000
2	155	21	2	0	2	.10	.0036
3	161	90	7	1	8	.09	.0009
4	165	39	10	0	10	.26	.0049
5	169	158	49	1	50	.32	.0016
6	173	120	53	1	54	.45	.0025
7	176	23	6	2	8	.35	.0100
8	183	114	18	0	18	.16	.0009
9	190	30	5	0	5	.17	.0049
10	197	6	0	0	0	.0	.0000
11	201	63	7	0	7	.11	.0016
12	204	91	3	0	3	.03	.0004
13	208	94	4	0	4	.04	.0004
14	211	100	0	0	0	.0	.0000
15	218	7	0	0	0	.0	.0000
16	228	6	0	0	0	.0	.0000
17	232	55	0	0	0	.0	.0000
18	239	98	0	0	0	.0	.0000
19	250	83	0	0	0	.0	.0000

TABLE D20. 1979 ENTOMOPHTHORA INFECTION

AREA MSU MUCKFARM							HOST SEED CORN FLIES
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	155	101	3	1	4	.04	.0004
2	176	101	39	5	44	.44	.0025
3	183	121	12	0	12	.10	.0009
4	239	99	0	0	0	.0	.0000

TABLE D21. 1978 ENTOMOPHTHORA INFECTION

AREA GRANT RESEARCH FIELD						HOST ONION FLIES	
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	139	30	5	0	5	.17	.0049
2	143	95	27	0	27	.28	.0025
3	144	0	0	0	0	.0	.0000
4	146	100	31	0	31	.31	.0025
5	150	100	60	0	60	.60	.0025
6	152	122	72	6	78	.64	.0016
7	157	93	49	3	52	.56	.0025
9	160	100	23	4	27	.27	.0016
10	164	54	27	1	28	.52	.0049
11	166	100	1	0	1	.01	.0001
12	171	100	9	1	10	.10	.0009
13	173	100	1	0	1	.01	.0001
14	177	17	3	2	5	.29	.0121
15	181	0	0	0	0	.0	.0000
16	187	2	0	0	0	.0	.0000
17	199	90	9	0	9	.10	.0025
18	206	100	34	3	37	.37	.0025
19	215	100	30	0	30	.30	.0025
20	221	142	26	4	30	.21	.0009
21	229	100	34	2	36	.36	.0025
22	234	92	22	0	22	.24	.0025
23	243	97	19	0	19	.20	.0016
24	249	106	17	2	19	.18	.0016
25	257	137	30	3	33	.24	.0016
26	262	100	66	0	66	.66	.0025
27	269	200	109	3	112	.56	.0016
28	289	100	59	0	59	.59	.0025
29	304	39	16	1	17	.44	.0064
30	314	23	9	4	13	.57	.0100

TABLE D22. 1978 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 6						HOST ONION FLIES	
SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	139	50	0	0	0	.0	.0000
2	143	33	0	0	0	.0	.0000
3	146	106	7	2	9	.08	.0009
4	150	51	9	6	15	.29	.0036
5	157	41	3	0	3	.07	.0016
6	160	40	8	0	8	.20	.0036
7	164	47	7	2	9	.19	.0036
8	166	21	0	0	0	.0	.0000
9	171	16	1	0	1	.06	.0036
10	173	2	0	0	0	.0	.0000
11	177	7	2	0	2	.29	.0289
12	187	5	1	0	1	.20	.0324
13	192	4	0	0	0	.0	.0000
14	199	85	10	0	10	12	.0009
15	206	186	46	0	46	.25	.0009
16	215	209	44	0	44	.21	.0009
17	221	132	13	0	13	.10	.0009
18	227	18	0	0	0	.0	.0000
19	229	96	4	0	4	.04	.0004
20	243	81	10	3	13	.16	.0016
21	249	47	0	0	0	.0	.0000
22	257	181	8	0	8	.04	.0004
23	262	132	63	1	64	.48	.0016
24	269	132	66	0	66	.50	.0016

TABLE D23. 1978 ENTOMOPHTHORA INFECTION

AREA: GRANT FIELD 7 — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	136	1	0	0	0	.0	.0000
2	143	1	0	0	0	.0	.0000
3	146	46	5	1	6	.13	.0025
4	150	95	21	6	27	.28	.0025
5	157	7	1	0	1	.14	.0169
6	160	17	7	0	7	.41	.0144
7	164	22	6	0	6	.27	.0081
8	166	19	3	0	3	.16	.0064
9	171	3	1	0	1	.33	.0729
10	173	6	0	0	0	.0	.0000
11	187	1	1	0	1	1.00	.0000
12	192	4	1	0	1	.25	.0484
13	206	115	5	0	5	.04	.0004
14	215	29	0	0	0	.0	.0000
15	249	9	0	0	0	.0	.0000
16	269	133	47	0	47	.35	.0016

TABLE D24. 1978 ENTOMOPHTHORA INFECTION

AREA: GRANT BACKROAD — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	139	1	0	0	0	.0	.0000
2	143	46	0	0	0	.0	.0000
3	144	1	0	0	0	.0	.0000
4	146	76	2	0	2	.03	.0004
5	150	42	7	0	7	.17	.0036
6	152	122	20	17	37	.30	.0016
7	157	14	3	0	3	.21	.0121
8	152	122	20	17	37	.30	.0016
9	160	68	13	2	15	.22	.0025
10	164	54	10	2	12	.22	.0036
11	166	13	0	0	0	.0	.0000
12	171	71	23	1	24	.34	.0036
13	173	5	0	0	0	.0	.0000
14	177	6	1	0	1	.17	.0225
15	181	15	4	0	4	.27	.0121
16	187	2	0	0	0	.0	.0000
17	199	90	21	1	22	.24	.0025
18	206	198	13	0	13	.07	.0004
19	215	33	3	0	3	.09	.0025
20	221	142	26	0	26	.18	.0009
21	229	10	0	0	0	.0	.0000
22	234	37	0	0	0	.0	.0000
23	243	97	11	0	11	.11	.0009
24	249	106	11	0	11	.10	.0009
25	257	137	11	0	11	.08	.0004
26	262	240	59	0	59	.25	.0009
27	269	212	128	0	128	.60	.0009

TABLE D25. 1978 ENTOMOPHTHORA INFECTION

AREA: EATON RAPIDS — HOST: ONION FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	145	7	2	0	2	.29	.0289
2	164	9	1	0	1	.11	.0100
3	171	7	3	0	3	.43	.0361
4	178	2	0	0	0	.0	.0000
5	198	159	1	0	1	.01	.0001
6	236	293	0	0	0	.0	.0000
7	208	17	0	0	0	.0	.0000
8	214	208	9	0	9	.04	.0001
9	218	7	0	0	0	.0	.0000
10	228	10	0	0	0	.0	.0000
11	233	21	0	0	0	.0	.0000
12	236	293	14	0	14	.05	.0001
13	250	56	0	0	0	.0	.0000
14	263	62	2	0	2	.03	.0004
15	271	31	1	0	1	.03	.0009

TABLE D26. 1978 ENTOMOPHTHORA INFECTION

AREA: GRANT RESEARCH FIELD — HOST: SEED CORN FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	139	100	70	2	72	.72	.0000
2	143	117	29	3	32	.27	.0016
3	146	100	14	0	14	.14	.0009
4	152	13	3	0	3	.23	.0144
5	160	3	1	0	1	.33	.0400
6	164	8	1	1	2	.25	.0225
7	166	20	19	0	19	.95	.0025
8	171	0	0	0	0	.0	.0000
9	173	0	0	0	0	.0	.0000
10	177	6	1	1	2	.33	.0361
11	180	24	7	3	10	.42	.0100
12	181	20	3	0	3	.15	.0064
13	186	50	11	3	14	.28	.0036
14	192	37	6	0	6	.16	.0036
15	199	29	4	1	5	.17	.0036
16	206	0	0	0	0	.0	.0000
17	215	22	2	0	2	.09	.0036
18	221	27	2	2	4	.15	.0036
19	229	14	0	0	0	.0	.0000
20	246	34	6	0	6	.18	.0049
21	250	30	9	1	10	.30	.0064
22	262	10	1	3	4	.40	.0225
23	271	7	3	0	3	.43	.0361

TABLE D28. 1978 ENTOMOPHTHORA INFECTION

AREA GRANT BACKROAD — HOST SEED CORN FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	139	10	0	0	0	.0	.0000
2	143	118	0	0	0	.0	.0000
3	146	10	0	0	0	.0	.0000
4	152	6	1	1	2	.33	.0361
5	160	4	1	0	1	.25	.0484
6	164	7	3	0	3	.43	.0361
7	166	4	0	0	0	.0	.0000
8	171	22	2	0	2	.09	.0036
9	173	3	0	0	0	.0	.0000
10	177	6	1	0	1	.17	.0225
11	180	24	0	0	0	.0	.0000
12	181	20	3	0	3	.15	.0064
13	187	3	0	0	0	.0	.0000
14	192	1	0	0	0	.0	.0000
15	199	29	3	0	3	.10	.0036
16	206	1	0	0	0	.0	.0000
17	215	1	0	0	0	.0	.0000
18	221	3	0	0	0	.0	.0000
19	229	14	0	0	0	.0	.0000
20	234	3	0	0	0	.0	.0000
21	243	4	0	0	0	.0	.0000
22	262	10	1	0	1	.10	.0081
23	269	2	2	0	2	1.00	.0000

TABLE D27. 1978 ENTOMOPHTHORA INFECTION

AREA GRANT FIELD 6 — HOST SEED CORN FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	139	13	0	0	0	.0	.0000
2	143	1	0	0	0	.0	.0000
3	146	10	1	0	1	.10	.0081
4	150	1	0	0	0	.0	.0000
5	157	2	0	0	0	.0	.0000
6	160	9	0	0	0	.0	.0000
7	164	27	2	0	2	.07	.0025
8	166	1	0	0	0	.0	.0000
9	171	1	0	0	0	.0	.0000
10	177	6	1	0	1	.17	.0225
11	187	12	1	0	1	.08	.0064
12	192	22	3	0	3	.14	.0049
13	199	57	2	0	2	.04	.0004
14	206	5	0	0	0	.0	.0000
15	215	11	1	0	1	.09	.0081
16	221	18	0	0	0	.0	.0000
17	227	5	0	0	0	.0	.0000
18	243	2	1	0	1	.50	.1225
19	249	5	0	0	0	.0	.0000
20	257	1	0	0	0	.0	.0000
21	262	1	0	0	0	.0	.0000
22	269	3	0	0	0	.0	.0000

TABLE D29. 1978 ENTOMOPHTHORA INFECTION

AREA EATON RAPIDS — HOST SEED CORN FLIES

SAMPLE	DATE	N	CONIDA	OW S.	TOTAL	INFEC	VAR
1	145	2	0	0	0	.0	.0000
2	164	19	0	0	0	.0	.0000
3	3171	1	1	0	1	.03	.0009
4	178	65	4	0	4	.06	.0009
5	174	11	0	0	0	.0	.0000
6	178	65	4	0	4	.06	.0009
7	198	4	0	0	0	.0	.0000
8	208	2	0	0	0	.0	.0000
9	214	8	0	0	0	.0	.0000
10	218	1	0	0	0	.0	.0000
11	228	65	1	0	1	.02	.0004
12	233	9	0	0	0	.0	.0000
13	236	3	0	0	0	.0	.0000
14	250	1	0	0	0	.0	.0000
15	263	19	0	0	0	.0	.0000
16	271	1	1	0	1	1.00	.0000

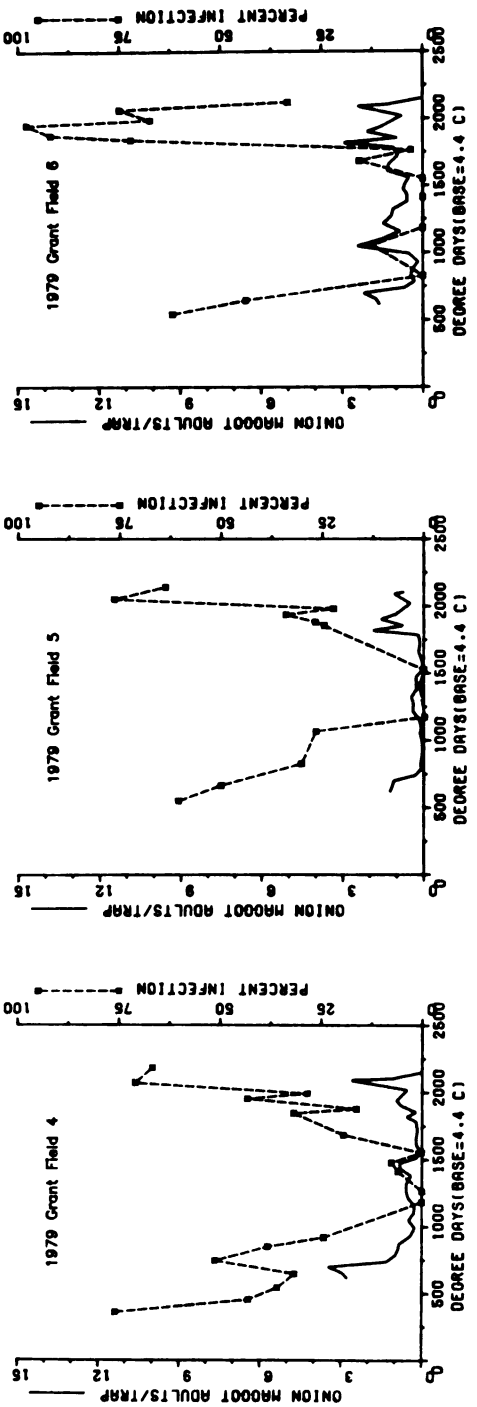

Figure D1.

Figure D3.

Figure D5.

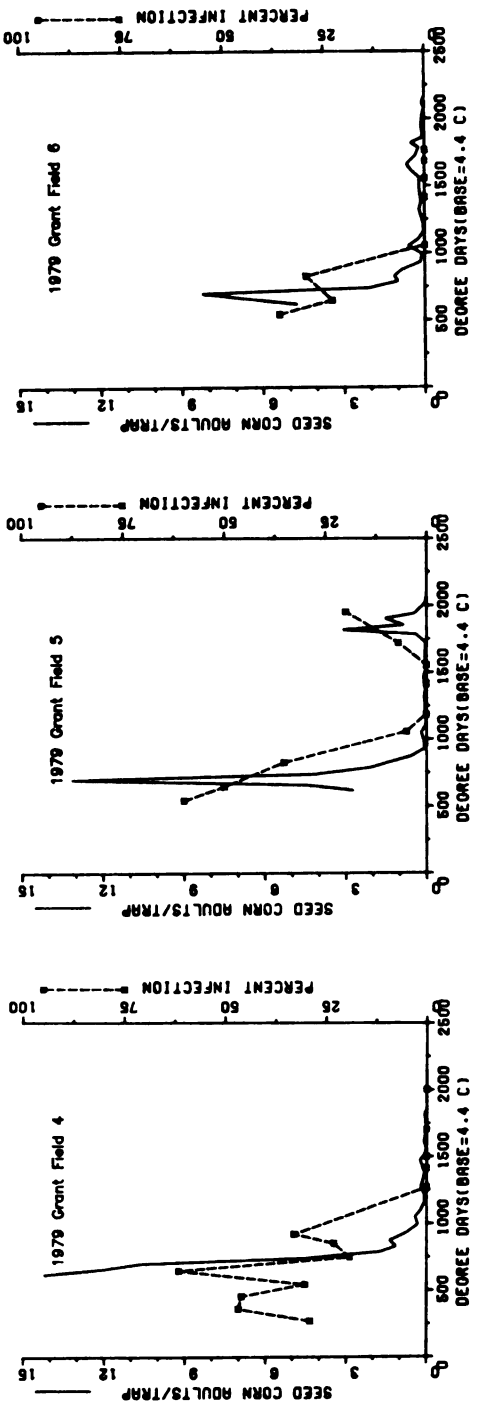

Figure D2.

Figure D4.

Figure D6.

Figures D1-D6. Entomophthora muscae infection and host fly population levels for Fields 1-3, Grant, Michigan, 1979.

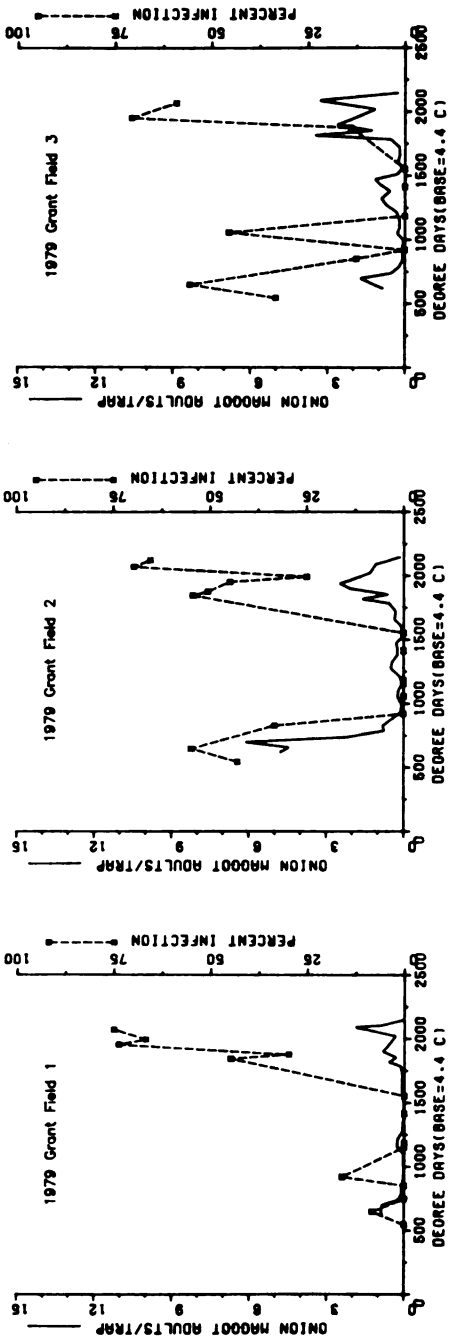

Figure D7.

Figure D8.

Figure D9.

Figure D10.

Figure D11.

Figure D12.

Figures D7-D12. Entomophthora muscae infection and host fly population levels for Fields 4-6, Grant, Michigan, 1979.

Appendix E.

Appendix E. Data for incubation period of E. muscae infecting onion maggot adults (See Experiment 3).
CDDALATENTPERIODEMUSCAE (1X, 3F10.5)

Table E1.

°F	°C	Days for Development	°F	°C	Days for Development
40.00000	4.44444	0.00000	50.00000	10.00000	16.00000
40.00000	4.44444	0.00000	50.00000	10.00000	16.00000
40.00000	4.44444	0.00000	50.00000	10.00000	17.00000
40.00000	4.44444	0.00000	50.00000	10.00000	17.00000
40.00000	4.44444	0.00000	50.00000	10.00000	17.00000
40.00000	4.44444	0.00000	50.00000	10.00000	17.00000
40.00000	4.44444	0.00000	50.00000	10.00000	18.00000
40.00000	4.44444	0.00000	50.00000	10.00000	18.00000
40.00000	4.44444	0.00000	50.00000	10.00000	18.00000
40.00000	4.44444	0.00000	50.00000	10.00000	19.00000
40.00000	4.44444	0.00000	50.00000	10.00000	19.00000
40.00000	4.44444	0.00000	50.00000	10.00000	19.00000
40.00000	4.44444	0.00000	50.00000	10.00000	20.00000
40.00000	4.44444	0.00000	50.00000	10.00000	20.00000
40.00000	4.44444	0.00000	50.00000	10.00000	21.00000
40.00000	4.44444	0.00000	50.00000	10.00000	21.00000
40.00000	4.44444	0.00000	50.00000	10.00000	22.00000
40.00000	4.44444	0.00000	55.00000	12.77778	9.00000
40.00000	4.44444	0.00000	55.00000	12.77778	10.00000
40.00000	4.44444	0.00000	55.00000	12.77778	10.00000
40.00000	4.44444	0.00000	55.00000	12.77778	10.00000
40.00000	4.44444	0.00000	55.00000	12.77778	10.00000
40.00000	4.44444	0.00000	55.00000	12.77778	11.00000
40.00000	4.44444	0.00000	55.00000	12.77778	11.00000
40.00000	4.44444	0.00000	55.00000	12.77778	11.00000
45.00000	7.22222	36.00000	55.00000	12.77778	11.00000
45.00000	7.22222	36.00000	55.00000	12.77778	11.00000
45.00000	7.22222	37.00000	55.00000	12.77778	11.00000
45.00000	7.22222	38.00000	55.00000	12.77778	11.00000
45.00000	7.22222	38.00000	55.00000	12.77778	11.00000
45.00000	7.22222	39.00000	55.00000	12.77778	11.00000
45.00000	7.22222	39.00000	55.00000	12.77778	12.00000
45.00000	7.22222	40.00000	55.00000	12.77778	12.00000
45.00000	7.22222	40.00000	55.00000	12.77778	12.00000
45.00000	7.22222	40.00000	55.00000	12.77778	12.00000
45.00000	7.22222	41.00000	55.00000	12.77778	12.00000
45.00000	7.22222	41.00000	55.00000	12.77778	12.00000
45.00000	7.22222	41.00000	55.00000	12.77778	12.00000
45.00000	7.22222	41.00000	55.00000	12.77778	13.00000
45.00000	7.22222	41.00000	55.00000	12.77778	13.00000
45.00000	7.22222	42.00000	55.00000	12.77778	13.00000
45.00000	7.22222	42.00000	55.00000	12.77778	14.00000
45.00000	7.22222	42.00000	60.00000	15.55556	6.00000
45.00000	7.22222	43.00000	60.00000	15.55556	7.00000
45.00000	7.22222	43.00000	60.00000	15.55556	7.00000
45.00000	7.22222	43.00000	60.00000	15.55556	7.00000
45.00000	7.22222	44.00000	60.00000	15.55556	7.00000
45.00000	7.22222	45.00000	60.00000	15.55556	7.00000
45.00000	7.22222	45.00000	60.00000	15.55556	7.00000
45.00000	7.22222	47.00000	60.00000	15.55556	7.00000
50.00000	10.00000	12.00000	60.00000	15.55556	7.00000
50.00000	10.00000	13.00000	60.00000	15.55556	7.00000
50.00000	10.00000	14.00000	60.00000	15.55556	7.00000
50.00000	10.00000	14.00000	60.00000	15.55556	8.00000
50.00000	10.00000	15.00000	60.00000	15.55556	8.00000
50.00000	10.00000	15.00000	60.00000	15.55556	8.00000
50.00000	10.00000	16.00000	60.00000	15.55556	8.00000
50.00000	10.00000	16.00000	60.00000	15.55556	8.00000

Appendix E. (con.)

°F	°C	Days for Development
60.00000	15.55556	8.00000
60.00000	15.55556	8.00000
60.00000	15.55556	8.00000
60.00000	15.55556	8.00000
60.00000	15.55556	9.00000
60.00000	15.55556	9.00000
60.00000	15.55556	9.00000
60.00000	15.55556	9.00000
60.00000	15.55556	10.00000
65.00000	18.33333	6.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	7.00000
65.00000	18.33333	8.00000
65.00000	18.33333	8.00000
65.00000	18.33333	8.00000
65.00000	18.33333	8.00000
65.00000	18.33333	8.00000
65.00000	18.33333	8.00000
65.00000	18.33333	9.00000
65.00000	18.33333	9.00000
65.00000	18.33333	9.00000
70.00000	21.11111	5.00000
70.00000	21.11111	6.00000
70.00000	21.11111	6.00000
70.00000	21.11111	7.00000
70.00000	21.11111	8.00000
70.00000	21.11111	8.00000
70.00000	21.11111	8.00000
70.00000	21.11111	8.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
70.00000	21.11111	7.00000
75.00000	23.88889	5.00000

°F	°C	Days for Development
75.00000	23.88889	8.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	7.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
75.00000	23.88889	6.00000
80.00000	26.66667	5.00000
80.00000	26.66667	5.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	7.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
80.00000	26.66667	6.00000
85.00000	29.44444	5.00000
85.00000	29.44444	5.00000
85.00000	29.44444	5.00000
85.00000	29.44444	7.00000
85.00000	29.44444	7.00000
85.00000	29.44444	7.00000
85.00000	29.44444	7.00000
85.00000	29.44444	7.00000
85.00000	29.44444	7.00000
85.00000	29.44444	7.00000
85.00000	29.44444	6.00000

Appendix E. (con.)

^{o}F	^{o}C	Days for Development
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
85.00000	29.44444	6.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000
90.00000	32.22222	0.00000

Appendix F.

Entomophthora muscae sporulation rate data (See Experiment 5).

CDDASLEASEMALEAUG8.
CDDASLEASEFEMALEAUG8.
CDDASLEASEMALEAUG17.
CDDASLEASEFEMALEAUG17.
(1X, 11F5.0)

-999 = missing data

Table F1.

August 8. Male.

Time	Ten replicates of spore density									
1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
1.	0.	0.	0.	1.	0.	0.	0.	1.	3.	0.
1.	1.	2.	0.	1.	0.	0.	0.	0.	0.	0.
1.	4.	4.	6.	6.	6.	2.	5.	5.	7.	4.
2.	0.	0.	0.	0.	0.	1.	0.	0.	0.	1.
2.	8.	5.	9.	12.	17.	8.	11.	6.	6.	10.
2.	0.	1.	1.	1.	1.	1.	2.	3.	1.	0.
2.	9.	16.	7.	11.	6.	3.	3.	2.	0.	1.
3.	2.	0.	0.	1.	14.	24.	43.	24.	117.	242.
3.	29.	33.	54.	59.	35.	59.	35.	20.	14.	31.
3.	31.	43.	38.	34.	21.	27.	72.	70.	70.	35.
3.	2.	3.	5.	0.	10.	25.	10.	19.	40.	40.
4.	94.	59.	59.	70.	59.	59.	35.	23.	47.	94.
4.	106.	106.	35.	59.	70.	35.	117.	70.	59.	59.
4.	94.	106.	59.	23.	12.	59.	59.	59.	35.	47.
4.	54.	88.	89.	106.	59.	59.	47.	82.	47.	59.
5.	59.	70.	59.	70.	35.	59.	47.	152.	94.	70.
5.	152.	152.	82.	106.	94.	59.	70.	164.	94.	106.
5.	59.	35.	12.	59.	35.	82.	35.	59.	59.	94.
5.	129.	106.	23.	70.	82.	94.	82.	70.	70.	2.
6.	47.	47.	82.	35.	35.	47.	94.	82.	106.	2.
6.	70.	59.	94.	94.	70.	59.	188.	82.	59.	1.
6.	152.	106.	129.	82.	94.	82.	82.	82.	70.	2.
6.	35.	35.	59.	35.	70.	59.	47.	70.	82.	3.

Time	Ten replicates of spore density									
7.	47.	47.	70.	59.	23.	12.	47.	47.	47.	3.
7.	41.	62.	34.	1.	6.	2.	34.	5.	4.	3.
7.	35.	35.	35.	82.	35.	35.	47.	59.	106.	3.
7.	47.	47.	47.	35.	47.	59.	35.	35.	35.	4.
8.	23.	35.	12.	35.	59.	35.	35.	70.	59.	4.
8.	9.	6.	4.	14.	18.	21.	22.	10.	15.	4.
8.	23.	70.	23.	35.	47.	12.	23.	47.	47.	4.
8.	15.	34.	6.	45.	27.	45.	8.	13.	16.	5.
9.	7.	7.	6.	5.	8.	5.	6.	5.	12.	5.
9.	12.	7.	4.	7.	7.	8.	5.	6.	11.	5.
9.	13.	11.	9.	7.	10.	19.	54.	51.	25.	5.
9.	11.	10.	6.	8.	7.	12.	8.	26.	8.	6.
10.	7.	7.	4.	5.	9.	10.	13.	15.	10.	6.
10.	8.	7.	6.	7.	14.	10.	15.	16.	11.	6.
10.	10.	9.	13.	12.	6.	19.	32.	8.	7.	6.
10.	4.	6.	11.	15.	17.	16.	8.	11.	5.	7.
11.	5.	3.	5.	4.	4.	7.	1.	10.	3.	7.
11.	5.	7.	8.	14.	2.	4.	9.	2.	6.	7.
11.	6.	5.	9.	8.	8.	7.	10.	7.	8.	7.
11.	13.	11.	18.	4.	15.	12.	8.	13.	4.	8.
12.	0.	4.	4.	2.	6.	7.	14.	6.	4.	8.
12.	2.	2.	6.	8.	5.	3.	6.	6.	5.	8.
12.	2.	0.	7.	3.	4.	5.	6.	11.	7.	8.
12.	4.	9.	5.	12.	18.	4.	2.	1.	0.	8.

Table F2.

August 8. Female.

Time	Ten replicates of spore density									
1.	59.	35.	47.	70.	47.	23.	35.	35.	23.	23.
1.	8.	12.	6.	17.	15.	13.	11.	24.	28.	18.
1.	23.	47.	94.	59.	35.	82.	23.	23.	12.	12.
1.	117.	106.	35.	35.	47.	35.	12.	47.	70.	23.
1.	15.	8.	19.	6.	40.	7.	5.	17.	27.	17.
1.	47.	47.	23.	47.	23.	47.	12.	47.	23.	23.
2.	94.	106.	82.	59.	59.	23.	47.	94.	35.	94.
2.	34.	38.	42.	38.	24.	29.	23.	18.	27.	52.
2.	59.	70.	106.	106.	59.	82.	70.	23.	35.	70.
2.	106.	70.	23.	82.	94.	94.	70.	35.	23.	23.
2.	47.	47.	35.	35.	47.	47.	35.	23.	23.	70.
2.	57.	48.	50.	15.	9.	72.	61.	37.	22.	31.
3.	82.	117.	106.	82.	94.	199.	35.	82.	117.	82.
3.	47.	82.	70.	47.	35.	47.	59.	47.	35.	59.
3.	11.	16.	16.	10.	8.	14.	21.	44.	778.	37.
3.	30.	33.	43.	82.	62.	66.	56.	44.	44.	46.
3.	60.	61.	65.	106.	80.	69.	83.	77.	73.	65.
3.	59.	70.	82.	70.	23.	70.	35.	47.	59.	70.
4.	70.	82.	70.	117.	82.	176.	211.	176.	70.	70.
4.	82.	50.	45.	52.	73.	132.	119.	142.	96.	54.
4.	164.	223.	94.	129.	94.	305.	422.	246.	176.	117.
4.	47.	70.	82.	82.	35.	94.	59.	47.	47.	47.
4.	94.	176.	164.	117.	141.	82.	70.	117.	47.	23.
4.	94.	47.	106.	82.	82.	47.	94.	82.	82.	23.
5.	117.	164.	82.	211.	152.	141.	223.	211.	70.	47.
5.	70.	82.	47.	47.	59.	23.	70.	23.	23.	94.
5.	235.	106.	106.	293.	223.	188.	211.	199.	199.	282.
5.	176.	282.	270.	70.	176.	82.	199.	188.	129.	82.
5.	106.	47.	59.	82.	164.	188.	211.	164.	106.	82.
5.	199.	158.	105.	146.	270.	158.	105.	223.	211.	270.
6.	59.	117.	82.	82.	82.	59.	35.	106.	129.	94.
6.	47.	59.	70.	47.	106.	82.	70.	82.	35.	47.
6.	293.	282.	152.	199.	282.	317.	106.	199.	141.	305.
6.	141.	199.	117.	141.	152.	129.	258.	188.	141.	129.
6.	59.	94.	152.	129.	188.	152.	129.	82.	94.	94.
6.	106.	47.	59.	82.	23.	106.	106.	82.	35.	70.

Time	Ten replicates of spore density									
7.	59.	35.	23.	23.	23.	23.	35.	12.	23.	47.
7.	18.	24.	24.	21.	17.	10.	6.	9.	12.	19.
7.	117.	94.	70.	129.	82.	35.	59.	70.	23.	141.
7.	141.	70.	106.	82.	164.	188.	211.	164.	106.	82.
7.	106.	94.	106.	129.	129.	70.	129.	106.	94.	82.
7.	106.	23.	59.	70.	59.	23.	35.	35.	35.	35.
8.	24.	19.	10.	29.	15.	20.	25.	23.	11.	8.
8.	10.	8.	11.	7.	14.	5.	6.	7.	6.	5.
8.	20.	18.	21.	10.	4.	9.	7.	8.	10.	15.
8.	42.	30.	24.	28.	5.	16.	27.	42.	61.	44.
8.	65.	73.	135.	88.	62.	73.	36.	78.	64.	107.
8.	25.	17.	8.	37.	9.	4.	10.	22.	15.	19.
9.	3.	3.	2.	5.	4.	2.	4.	2.	2.	4.
9.	8.	8.	4.	6.	10.	5.	10.	5.	4.	11.
9.	2.	2.	3.	2.	1.	3.	2.	1.	2.	3.
9.	27.	29.	28.	28.	42.	24.	8.	9.	12.	9.
9.	74.	45.	33.	23.	21.	19.	34.	14.	34.	32.
9.	3.	3.	4.	2.	3.	4.	4.	4.	4.	3.
10.	2.	3.	3.	1.	4.	2.	2.	4.	3.	2.
10.	7.	8.	4.	4.	5.	6.	8.	12.	9.	3.
10.	1.	3.	1.	0.	2.	2.	1.	1.	2.	1.
10.	21.	31.	5.	11.	15.	7.	9.	4.	60.	18.
10.	12.	14.	7.	54.	15.	9.	8.	5.	10.	4.
10.	2.	2.	3.	2.	4.	2.	2.	5.	3.	0.
11.	18.	8.	7.	6.	8.	5.	6.	7.	7.	6.
11.	4.	5.	3.	5.	3.	7.	4.	6.	8.	3.
11.	48.	27.	15.	54.	43.	47.	46.	44.	37.	10.
11.	12.	18.	14.	9.	7.	20.	23.	7.	17.	13.
11.	16.	41.	23.	19.	14.	35.	22.	20.	12.	20.
11.	2.	3.	0.	2.	0.	9.	4.	3.	2.	1.
12.	1.	2.	2.	1.	3.	2.	2.	6.	1.	0.
12.	2.	2.	2.	2.	1.	0.	2.	1.	2.	2.
12.	1.	0.	3.	1.	1.	0.	0.	0.	1.	1.
12.	0.	1.	4.	5.	7.	7.	8.	3.	3.	4.
12.	1.	2.	7.	9.	5.	9.	7.	5.	15.	2.
12.	2.	2.	3.	3.	5.	3.	2.	3.	2.	4.

Table F3.

August 17. Male.

Time	Ten replicates of spore density									
7.	35.	35.	35.	47.	82.	70.	70.	35.	47.	59.
7.	47.	35.	35.	47.	35.	23.	47.	59.	59.	47.
7.	35.	59.	59.	141.	35.	59.	47.	59.	47.	35.
7.	70.	82.	82.	47.	59.	59.	47.	141.	94.	59.
8.	82.	47.	82.	70.	70.	94.	94.	59.	82.	82.
8.	35.	35.	47.	35.	35.	35.	47.	35.	35.	47.
8.	35.	35.	82.	59.	35.	70.	117.	82.	164.	106.
8.	59.	106.	35.	59.	35.	59.	35.	35.	47.	47.
9.	59.	59.	82.	47.	47.	35.	70.	59.	59.	23.
9.	35.	47.	8.	13.	6.	10.	14.	19.	21.	25.
9.	35.	82.	59.	47.	82.	47.	59.	35.	59.	70.
9.	35.	82.	23.	35.	47.	70.	70.	23.	47.	47.
10.	94.	59.	35.	35.	70.	35.	47.	59.	47.	59.
10.	11.	7.	7.	6.	6.	11.	12.	10.	19.	20.
10.	47.	47.	35.	47.	35.	35.	47.	47.	35.	59.
10.	8.	10.	15.	30.	33.	16.	10.	8.	5.	5.
11.	9.	9.	7.	9.	11.	12.	15.	15.	16.	15.
11.	13.	23.	12.	29.	24.	23.	14.	11.	10.	3.
11.	5.	6.	4.	2.	4.	10.	106.	164.	141.	70.
11.	5.	3.	3.	3.	7.	6.	7.	4.	3.	3.
12.	4.	3.	9.	5.	4.	2.	6.	5.	4.	10.
12.	6.	7.	6.	3.	4.	6.	8.	6.	5.	4.
12.	4.	6.	3.	8.	2.	2.	3.	7.	2.	3.
12.	6.	3.	3.	4.	3.	4.	3.	3.	3.	3.

Time	Ten replicates of spore density									
1.	1.	2.	1.	1.	2.	3.	2.	1.	1.	3.
1.	5.	2.	2.	2.	1.	1.	1.	2.	4.	5.
1.	3.	3.	2.	2.	2.	3.	4.	3.	3.	2.
1.	1.	1.	1.	1.	2.	1.	1.	2.	1.	1.
2.	2.	3.	4.	3.	6.	4.	2.	2.	3.	3.
2.	7.	5.	10.	5.	6.	6.	6.	7.	4.	3.
2.	4.	9.	4.	21.	47.	47.	35.	94.	82.	47.
2.	10.	8.	4.	4.	15.	8.	5.	5.	7.	7.
3.	8.	6.	13.	13.	9.	4.	11.	7.	9.	6.
3.	59.	35.	23.	35.	35.	59.	35.	35.	35.	35.
3.	35.	47.	35.	35.	35.	47.	23.	47.	47.	35.
3.	1.	3.	3.	2.	5.	3.	5.	2.	7.	6.
4.	35.	82.	23.	35.	47.	70.	70.	23.	47.	37.
4.	47.	23.	23.	47.	23.	23.	47.	35.	47.	23.
4.	35.	35.	35.	47.	35.	47.	23.	45.	38.	68.
4.	35.	47.	35.	47.	59.	47.	47.	47.	59.	47.
5.	59.	59.	47.	47.	70.	70.	47.	35.	23.	35.
5.	47.	35.	47.	35.	47.	59.	82.	59.	35.	59.
5.	47.	35.	35.	23.	35.	23.	23.	35.	35.	23.
5.	94.	47.	59.	35.	59.	106.	35.	23.	59.	70.
6.	35.	47.	47.	47.	47.	35.	35.	47.	47.	70.
6.	47.	59.	35.	47.	70.	47.	47.	47.	70.	59.
6.	59.	47.	23.	35.	35.	35.	47.	35.	35.	59.
6.	47.	106.	106.	35.	94.	70.	82.	70.	59.	106.

Table F4.
August 17. Female.

Time	Ten replicates of spore density									
1.	3.	6.	3.	2.	2.	2.	4.	2.	5.	5.
1.	1.	3.	2.	1.	2.	1.	0.	0.	0.	0.
1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
1.	1.	2.	1.	6.	5.	2.	3.	4.	5.	4.
1.	1.	1.	2.	0.	0.	0.	0.	0.	0.	0.
1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
2.	6.	4.	6.	11.	10.	5.	7.	6.	19.	12.
2.	3.	4.	1.	1.	2.	1.	1.	1.	2.	3.
2.	1.	3.	1.	1.	1.	1.	2.	1.	1.	2.
2.	2.	1.	1.	4.	3.	2.	2.	7.	1.	7.
2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
2.	0.	0.	18.	0.	0.	0.	0.	0.	0.	0.
3.	14.	18.	13.	13.	13.	17.	23.	20.	15.	23.
3.	5.	4.	7.	8.	7.	6.	3.	6.	2.	3.
3.	6.	15.	33.	0.	12.	0.	0.	0.	0.	21.
3.	5.	1.	8.	6.	7.	8.	8.	6.	5.	5.
3.	1.	2.	1.	3.	1.	3.	1.	4.	4.	1.
3.	23.	0.	7.	0.	34.	0.	0.	0.	0.	0.
4.	94.	59.	82.	82.	59.	35.	35.	47.	35.	82.
4.	17.	5.	10.	21.	22.	8.	13.	13.	15.	13.
4.	35.	59.	35.	59.	70.	35.	23.	47.	35.	35.
4.	3.	334.	3.	4.	2.	3.	3.	5.	6.	7.
4.	7.	11.	5.	7.	4.	5.	3.	2.	8.	4.
4.	6.	7.	16.	14.	4.	10.	12.	6.	14.	12.
5.	129.	70.	152.	106.	117.	199.	188.	317.	340.	188.
5.	7.	5.	6.	8.	7.	9.	8.	5.	7.	8.
5.	35.	35.	35.	35.	47.	23.	59.	23.	35.	23.
5.	13.	111.	10.	97.	11.	10.	5.	7.	7.	66.
5.	5.	6.	3.	4.	2.	8.	10.	7.	3.	2.
5.	32.	18.	33.	14.	59.	42.	15.	34.	41.	57.
6.	70.	117.	129.	176.	35.	152.	94.	152.	94.	70.
6.	59.	35.	35.	47.	23.	59.	35.	35.	47.	70.
6.	82.	59.	23.	70.	70.	35.	94.	35.	47.	59.
6.	76.	129.	164.	76.	82.	59.	129.	82.	47.	70.
6.	94.	47.	129.	35.	59.	47.	35.	23.	25.	82.
6.	39.	28.	25.	21.	24.	36.	14.	11.	36.	54.

Time	Ten replicates of spore density									
7.	35.	47.	47.	70.	47.	23.	35.	47.	70.	82.
7.	47.	70.	59.	47.	70.	47.	35.	70.	47.	23.
7.	47.	199.	152.	35.	246.	23.	70.	100.	23.	35.
7.	211.	106.	59.	70.	70.	94.	23.	47.	35.	94.
7.	117.	59.	82.	47.	59.	82.	106.	82.	59.	59.
7.	15.	42.	47.	53.	20.	18.	38.	33.	41.	30.
8.	47.	47.	23.	59.	47.	70.	35.	59.	70.	47.
8.	30.	19.	23.	34.	49.	54.	60.	43.	25.	35.
8.	47.	59.	47.	35.	82.	94.	47.	59.	47.	82.
8.	72.	68.	99.	67.	43.	94.	45.	66.	64.	78.
8.	47.	70.	59.	70.	59.	82.	94.	47.	70.	94.
8.	13.	11.	15.	7.	11.	10.	17.	13.	27.	31.
9.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.
9.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.
9.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.
9.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.
9.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.
9.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.	-999.
10.	11.	9.	33.	17.	6.	15.	35.	38.	32.	45.
10.	21.	15.	16.	12.	22.	20.	27.	26.	24.	16.
10.	35.	23.	70.	82.	70.	23.	47.	59.	47.	70.
10.	35.	46.	55.	76.	45.	34.	75.	66.	33.	44.
10.	47.	47.	23.	35.	35.	82.	70.	82.	70.	23.
10.	15.	11.	20.	17.	13.	32.	14.	17.	22.	13.
11.	1.	1.	2.	1.	2.	6.	1.	1.	2.	2.
11.	9.	9.	7.	10.	7.	21.	14.	22.	21.	35.
11.	23.	35.	47.	47.	47.	35.	59.	59.	35.	35.
11.	6.	7.	4.	9.	12.	5.	6.	7.	8.	3.
11.	3.	2.	1.	1.	2.	1.	1.	0.	0.	0.
11.	5.	14.	17.	18.	12.	5.	5.	3.	9.	9.
12.	1.	1.	2.	1.	1.	4.	1.	2.	4.	1.
12.	1.	4.	2.	3.	2.	4.	1.	4.	4.	3.
12.	8.	8.	14.	8.	15.	23.	21.	27.	21.	17.
12.	2.	4.	0.	0.	4.	6.	2.	6.	8.	7.
12.	6.	2.	2.	3.	6.	6.	3.	5.	2.	3.
12.	6.	6.	4.	8.	5.	7.	4.	4.	7.	8.

Appendix G.

Appendix G. Spore production for various temperatures (Experiment 6).
CDDATEMPERATURESPORULATION (1X, 4F15.5)

Table G1.

°F	°C	Fly #	# Spores
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	1.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	2.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	3.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	4.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
40.00000	4.44444	5.00000	0.00000
50.00000	10.00000	1.00000	133333.00000
50.00000	10.00000	1.00000	233333.00000
50.00000	10.00000	1.00000	200000.00000
50.00000	10.00000	1.00000	300000.00000
50.00000	10.00000	1.00000	766667.00000
50.00000	10.00000	1.00000	666667.00000
50.00000	10.00000	1.00000	66667.00000
50.00000	10.00000	1.00000	133333.00000
50.00000	10.00000	1.00000	233333.00000
50.00000	10.00000	1.00000	100000.00000
50.00000	10.00000	2.00000	100000.00000
50.00000	10.00000	2.00000	166667.00000
50.00000	10.00000	2.00000	33333.00000
50.00000	10.00000	2.00000	100000.00000
50.00000	10.00000	2.00000	66667.00000
50.00000	10.00000	2.00000	33333.00000
50.00000	10.00000	2.00000	33333.00000
50.00000	10.00000	2.00000	66667.00000
50.00000	10.00000	2.00000	33333.00000
50.00000	10.00000	2.00000	33333.00000
50.00000	10.00000	3.00000	133333.00000
50.00000	10.00000	3.00000	66667.00000
50.00000	10.00000	3.00000	333333.00000
50.00000	10.00000	3.00000	200000.00000

Appendix G. (con.)

°F	°C	Fly #	# Spores
50.00000	10.00000	3.00000	166667.00000
50.00000	10.00000	3.00000	133333.00000
50.00000	10.00000	3.00000	66667.00000
50.00000	10.00000	3.00000	33333.00000
50.00000	10.00000	3.00000	100000.00000
50.00000	10.00000	3.00000	66667.00000
50.00000	10.00000	4.00000	166667.00000
50.00000	10.00000	4.00000	100000.00000
50.00000	10.00000	4.00000	33333.00000
50.00000	10.00000	4.00000	66667.00000
50.00000	10.00000	4.00000	200000.00000
50.00000	10.00000	4.00000	233333.00000
50.00000	10.00000	4.00000	133333.00000
50.00000	10.00000	4.00000	100000.00000
50.00000	10.00000	4.00000	266667.00000
50.00000	10.00000	4.00000	366667.00000
50.00000	10.00000	5.00000	66667.00000
50.00000	10.00000	5.00000	133333.00000
50.00000	10.00000	5.00000	100000.00000
50.00000	10.00000	5.00000	66667.00000
50.00000	10.00000	5.00000	366667.00000
50.00000	10.00000	5.00000	233333.00000
50.00000	10.00000	5.00000	33333.00000
50.00000	10.00000	5.00000	66667.00000
50.00000	10.00000	5.00000	133333.00000
50.00000	10.00000	5.00000	166667.00000
55.00000	12.77778	1.00000	642075.00000
55.00000	12.77778	1.00000	721050.00000
55.00000	12.77778	1.00000	626625.00000
55.00000	12.77778	1.00000	1012500.00000
55.00000	12.77778	1.00000	653925.00000
55.00000	12.77778	1.00000	773400.00000
55.00000	12.77778	1.00000	693375.00000
55.00000	12.77778	1.00000	813075.00000
55.00000	12.77778	1.00000	768975.00000
55.00000	12.77778	1.00000	789300.00000
55.00000	12.77778	2.00000	721050.00000
55.00000	12.77778	2.00000	1012500.00000
55.00000	12.77778	2.00000	773400.00000
55.00000	12.77778	2.00000	813075.00000
55.00000	12.77778	2.00000	789300.00000
55.00000	12.77778	2.00000	653925.00000
55.00000	12.77778	2.00000	819375.00000
55.00000	12.77778	2.00000	778950.00000

°F	°C	Fly #	# Spores
55.00000	12.77778	2.00000	626625.00000
55.00000	12.77778	2.00000	740550.00000
55.00000	12.77778	3.00000	626625.00000
55.00000	12.77778	3.00000	773400.00000
55.00000	12.77778	3.00000	768975.00000
55.00000	12.77778	3.00000	653925.00000
55.00000	12.77778	3.00000	897000.00000
55.00000	12.77778	3.00000	626625.00000
55.00000	12.77778	3.00000	750000.00000
55.00000	12.77778	3.00000	693375.00000
55.00000	12.77778	3.00000	819375.00000
55.00000	12.77778	3.00000	897000.00000
55.00000	12.77778	4.00000	1012500.00000
55.00000	12.77778	4.00000	813075.00000
55.00000	12.77778	4.00000	653925.00000
55.00000	12.77778	4.00000	778950.00000
55.00000	12.77778	4.00000	740550.00000
55.00000	12.77778	4.00000	693375.00000
55.00000	12.77778	4.00000	603000.00000
55.00000	12.77778	4.00000	768975.00000
55.00000	12.77778	4.00000	653775.00000
55.00000	12.77778	4.00000	642075.00000
55.00000	12.77778	5.00000	653925.00000
55.00000	12.77778	5.00000	789300.00000
55.00000	12.77778	5.00000	897000.00000
55.00000	12.77778	5.00000	740550.00000
55.00000	12.77778	5.00000	663750.00000
55.00000	12.77778	5.00000	897000.00000
55.00000	12.77778	5.00000	773400.00000
55.00000	12.77778	5.00000	642075.00000
55.00000	12.77778	5.00000	740550.00000
55.00000	12.77778	5.00000	663750.00000
60.00000	15.55556	1.00000	66667.00000
60.00000	15.55556	1.00000	100000.00000
60.00000	15.55556	1.00000	33333.00000
60.00000	15.55556	1.00000	33333.00000
60.00000	15.55556	1.00000	33333.00000
60.00000	15.55556	1.00000	33333.00000
60.00000	15.55556	1.00000	100000.00000
60.00000	15.55556	1.00000	66667.00000
60.00000	15.55556	1.00000	33333.00000
60.00000	15.55556	1.00000	66667.00000
60.00000	15.55556	2.00000	100000.00000
60.00000	15.55556	2.00000	33333.00000

Appendix G. (con.)

°F	°C	Fly #	# Spores
60.00000	15.55556	2.00000	33333.00000
60.00000	15.55556	2.00000	100000.00000
60.00000	15.55556	2.00000	33333.00000
60.00000	15.55556	2.00000	33333.00000
60.00000	15.55556	2.00000	133333.00000
60.00000	15.55556	2.00000	66667.00000
60.00000	15.55556	2.00000	33333.00000
60.00000	15.55556	2.00000	66667.00000
60.00000	15.55556	3.00000	2100000.00000
60.00000	15.55556	3.00000	900000.00000
60.00000	15.55556	3.00000	3000000.00000
60.00000	15.55556	3.00000	600000.00000
60.00000	15.55556	3.00000	4200000.00000
60.00000	15.55556	3.00000	5100000.00000
60.00000	15.55556	3.00000	1500000.00000
60.00000	15.55556	3.00000	2400000.00000
60.00000	15.55556	3.00000	3600000.00000
60.00000	15.55556	3.00000	900000.00000
60.00000	15.55556	4.00000	2400000.00000
60.00000	15.55556	4.00000	3600000.00000
60.00000	15.55556	4.00000	1800000.00000
60.00000	15.55556	4.00000	4800000.00000
60.00000	15.55556	4.00000	4500000.00000
60.00000	15.55556	4.00000	3300000.00000
60.00000	15.55556	4.00000	4500000.00000
60.00000	15.55556	4.00000	2400000.00000
60.00000	15.55556	4.00000	1500000.00000
60.00000	15.55556	4.00000	900000.00000
60.00000	15.55556	5.00000	600000.00000
60.00000	15.55556	5.00000	1200000.00000
60.00000	15.55556	5.00000	1500000.00000
60.00000	15.55556	5.00000	2100000.00000
60.00000	15.55556	5.00000	1800000.00000
60.00000	15.55556	5.00000	1200000.00000
60.00000	15.55556	5.00000	900000.00000
60.00000	15.55556	5.00000	1800000.00000
60.00000	15.55556	5.00000	1200000.00000
60.00000	15.55556	5.00000	2100000.00000
65.00000	18.33333	1.00000	943717.50000
65.00000	18.33333	1.00000	856845.00000
65.00000	18.33333	1.00000	960712.50000
65.00000	18.33333	1.00000	536250.00000
65.00000	18.33333	1.00000	930682.50000

°F	°C	Fly #	# Spores
65.00000	18.33333	1.00000	799260.00000
65.00000	18.33333	1.00000	887287.50000
65.00000	18.33333	1.00000	755617.50000
65.00000	18.33333	1.00000	804127.50000
65.00000	18.33333	1.00000	781770.00000
65.00000	18.33333	2.00000	856845.00000
65.00000	18.33333	2.00000	536250.00000
65.00000	18.33333	2.00000	799260.00000
65.00000	18.33333	2.00000	755617.50000
65.00000	18.33333	2.00000	781770.00000
65.00000	18.33333	2.00000	930682.50000
65.00000	18.33333	2.00000	748687.50000
65.00000	18.33333	2.00000	793155.00000
65.00000	18.33333	2.00000	960712.50000
65.00000	18.33333	2.00000	835395.00000
65.00000	18.33333	3.00000	960712.50000
65.00000	18.33333	3.00000	799260.00000
65.00000	18.33333	3.00000	804127.50000
65.00000	18.33333	3.00000	930682.50000
65.00000	18.33333	3.00000	663300.00000
65.00000	18.33333	3.00000	960712.50000
65.00000	18.33333	3.00000	825000.00000
65.00000	18.33333	3.00000	887287.50000
65.00000	18.33333	3.00000	748687.50000
65.00000	18.33333	3.00000	663300.00000
65.00000	18.33333	4.00000	536250.00000
65.00000	18.33333	4.00000	755617.50000
65.00000	18.33333	4.00000	930682.50000
65.00000	18.33333	4.00000	793155.00000
65.00000	18.33333	4.00000	835395.00000
65.00000	18.33333	4.00000	887287.50000
65.00000	18.33333	4.00000	986700.00000
65.00000	18.33333	4.00000	804127.50000
65.00000	18.33333	4.00000	930847.50000
65.00000	18.33333	4.00000	943717.50000
65.00000	18.33333	5.00000	930682.50000
65.00000	18.33333	5.00000	781770.00000
65.00000	18.33333	5.00000	663300.00000
65.00000	18.33333	5.00000	835395.00000
65.00000	18.33333	5.00000	919875.00000
65.00000	18.33333	5.00000	663300.00000
65.00000	18.33333	5.00000	799260.00000
65.00000	18.33333	5.00000	943717.50000

Appendix G. (con.)

°F	°C	Fly #	# Spores
65.00000	18.33333	5.00000	835395.00000
65.00000	18.33333	5.00000	919875.00000
70.00000	21.11111	1.00000	1500000.00000
70.00000	21.11111	1.00000	300000.00000
70.00000	21.11111	1.00000	900000.00000
70.00000	21.11111	1.00000	300000.00000
70.00000	21.11111	1.00000	900000.00000
70.00000	21.11111	1.00000	1500000.00000
70.00000	21.11111	1.00000	300000.00000
70.00000	21.11111	1.00000	1500000.00000
70.00000	21.11111	1.00000	600000.00000
70.00000	21.11111	1.00000	900000.00000
70.00000	21.11111	2.00000	600000.00000
70.00000	21.11111	2.00000	300000.00000
70.00000	21.11111	2.00000	900000.00000
70.00000	21.11111	2.00000	600000.00000
70.00000	21.11111	2.00000	600000.00000
70.00000	21.11111	2.00000	2700000.00000
70.00000	21.11111	2.00000	300000.00000
70.00000	21.11111	2.00000	900000.00000
70.00000	21.11111	2.00000	600000.00000
70.00000	21.11111	2.00000	300000.00000
70.00000	21.11111	3.00000	300000.00000
70.00000	21.11111	3.00000	600000.00000
70.00000	21.11111	3.00000	300000.00000
70.00000	21.11111	3.00000	900000.00000
70.00000	21.11111	3.00000	600000.00000
70.00000	21.11111	3.00000	900000.00000
70.00000	21.11111	3.00000	300000.00000
70.00000	21.11111	3.00000	600000.00000
70.00000	21.11111	3.00000	300000.00000
70.00000	21.11111	3.00000	300000.00000
70.00000	21.11111	4.00000	900000.00000
70.00000	21.11111	4.00000	600000.00000
70.00000	21.11111	4.00000	1200000.00000
70.00000	21.11111	4.00000	300000.00000
70.00000	21.11111	4.00000	300000.00000
70.00000	21.11111	4.00000	600000.00000
70.00000	21.11111	4.00000	2100000.00000
70.00000	21.11111	4.00000	300000.00000
70.00000	21.11111	4.00000	1200000.00000
70.00000	21.11111	4.00000	300000.00000

°F	°C	Fly #	# Spores
70.00000	21.11111	5.00000	133333.00000
70.00000	21.11111	5.00000	66667.00000
70.00000	21.11111	5.00000	200000.00000
70.00000	21.11111	5.00000	166667.00000
70.00000	21.11111	5.00000	866667.00000
70.00000	21.11111	5.00000	266667.00000
70.00000	21.11111	5.00000	333333.00000
70.00000	21.11111	5.00000	233333.00000
70.00000	21.11111	5.00000	300000.00000
70.00000	21.11111	5.00000	233333.00000
80.00000	26.66667	1.00000	66667.00000
80.00000	26.66667	1.00000	33333.00000
80.00000	26.66667	1.00000	100000.00000
80.00000	26.66667	1.00000	33333.00000
80.00000	26.66667	1.00000	100000.00000
80.00000	26.66667	1.00000	166667.00000
80.00000	26.66667	1.00000	33333.00000
80.00000	26.66667	1.00000	33333.00000
80.00000	26.66667	1.00000	33333.00000
80.00000	26.66667	1.00000	66667.00000
80.00000	26.66667	2.00000	33333.00000
80.00000	26.66667	2.00000	33333.00000
80.00000	26.66667	2.00000	66667.00000
80.00000	26.66667	2.00000	33333.00000
80.00000	26.66667	2.00000	166667.00000
80.00000	26.66667	2.00000	233333.00000
80.00000	26.66667	2.00000	100000.00000
80.00000	26.66667	2.00000	33333.00000
80.00000	26.66667	2.00000	33333.00000
80.00000	26.66667	2.00000	33333.00000
80.00000	26.66667	3.00000	133333.00000
80.00000	26.66667	3.00000	100000.00000
80.00000	26.66667	3.00000	33333.00000
80.00000	26.66667	3.00000	66667.00000
80.00000	26.66667	3.00000	300000.00000
80.00000	26.66667	3.00000	166667.00000
80.00000	26.66667	3.00000	33333.00000
80.00000	26.66667	3.00000	33333.00000
80.00000	26.66667	3.00000	33333.00000
80.00000	26.66667	4.00000	33333.00000
80.00000	26.66667	4.00000	33333.00000

Appendix G. (con.)

°F	°C	Fly #	# Spores
80.00000	26.66667	4.00000	100000.00000
80.00000	26.66667	4.00000	33333.00000
80.00000	26.66667	4.00000	266667.00000
80.00000	26.66667	4.00000	233333.00000
80.00000	26.66667	4.00000	66667.00000
80.00000	26.66667	4.00000	33333.00000
80.00000	26.66667	4.00000	33333.00000
80.00000	26.66667	4.00000	33333.00000
80.00000	26.66667	5.00000	66667.00000
80.00000	26.66667	5.00000	33333.00000
80.00000	26.66667	5.00000	66667.00000
80.00000	26.66667	5.00000	33333.00000
80.00000	26.66667	5.00000	233333.00000
80.00000	26.66667	5.00000	200000.00000
80.00000	26.66667	5.00000	33333.00000
80.00000	26.66667	5.00000	33333.00000
80.00000	26.66667	5.00000	66667.00000
80.00000	26.66667	5.00000	33333.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	1.00000	233333.00000
90.00000	32.22222	1.00000	166667.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	1.00000	66667.00000
90.00000	32.22222	1.00000	33333.00000
90.00000	32.22222	2.00000	33333.00000
90.00000	32.22222	2.00000	33333.00000
90.00000	32.22222	2.00000	66667.00000
90.00000	32.22222	2.00000	33333.00000
90.00000	32.22222	2.00000	166667.00000
90.00000	32.22222	2.00000	133333.00000

°F	°C	Fly #	# Spores
90.00000	32.22222	2.00000	33333.00000
90.00000	32.22222	2.00000	33333.00000
90.00000	32.22222	2.00000	33333.00000
90.00000	32.22222	2.00000	66667.00000
90.00000	32.22222	3.00000	33333.00000
90.00000	32.22222	3.00000	33333.00000
90.00000	32.22222	3.00000	133333.00000
90.00000	32.22222	3.00000	166667.00000
90.00000	32.22222	3.00000	333333.00000
90.00000	32.22222	3.00000	366667.00000
90.00000	32.22222	3.00000	66667.00000
90.00000	32.22222	3.00000	66667.00000
90.00000	32.22222	3.00000	33333.00000
90.00000	32.22222	3.00000	33333.00000
90.00000	32.22222	4.00000	33333.00000
90.00000	32.22222	4.00000	100000.00000
90.00000	32.22222	4.00000	33333.00000
90.00000	32.22222	4.00000	66667.00000
90.00000	32.22222	4.00000	166667.00000
90.00000	32.22222	4.00000	300000.00000
90.00000	32.22222	4.00000	100000.00000
90.00000	32.22222	4.00000	66667.00000
90.00000	32.22222	4.00000	66667.00000
90.00000	32.22222	4.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	200000.00000
90.00000	32.22222	5.00000	100000.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000
90.00000	32.22222	5.00000	33333.00000

Appendix H.

Spore germination data for various temperature and moisture conditions (See Experiment 8).

Moisture treatment 1=free moisture
Moisture treatment 2=100 relative humidity

CDDAFREEH2OGERMCOMPLETE
CDDA100RHGERMCOMPLETE
(1X, 4F10.5)

Table H1.

Moisture Treatment	°F	°C	Time	Proportion Germination
1.00000	40.00000	4.44444	3.00000	.01000
1.00000	40.00000	4.44444	3.00000	0.00000
1.00000	40.00000	4.44444	3.00000	0.00000
1.00000	40.00000	4.44444	3.00000	0.00000
1.00000	40.00000	4.44444	3.00000	0.00000
1.00000	40.00000	4.44444	6.00000	.14000
1.00000	40.00000	4.44444	6.00000	.01000
1.00000	40.00000	4.44444	6.00000	0.00000
1.00000	40.00000	4.44444	6.00000	.01000
1.00000	40.00000	4.44444	6.00000	.02000
1.00000	40.00000	4.44444	9.00000	0.00000
1.00000	40.00000	4.44444	9.00000	0.00000
1.00000	40.00000	4.44444	9.00000	.30000
1.00000	40.00000	4.44444	9.00000	0.00000
1.00000	40.00000	4.44444	9.00000	.01000
1.00000	40.00000	4.44444	12.00000	.24000
1.00000	40.00000	4.44444	12.00000	.24000
1.00000	40.00000	4.44444	12.00000	.24000
1.00000	40.00000	4.44444	12.00000	.24000
1.00000	40.00000	4.44444	12.00000	.24000
1.00000	50.00000	10.00000	3.00000	.05000
1.00000	50.00000	10.00000	3.00000	.16000
1.00000	50.00000	10.00000	3.00000	.06000
1.00000	50.00000	10.00000	3.00000	0.00000
1.00000	50.00000	10.00000	3.00000	0.00000
1.00000	50.00000	10.00000	6.00000	.06000
1.00000	50.00000	10.00000	6.00000	.01000
1.00000	50.00000	10.00000	6.00000	.26000
1.00000	50.00000	10.00000	6.00000	.12000
1.00000	50.00000	10.00000	6.00000	.10000
1.00000	50.00000	10.00000	9.00000	.04000
1.00000	50.00000	10.00000	9.00000	.15000
1.00000	50.00000	10.00000	9.00000	.37000
1.00000	50.00000	10.00000	9.00000	.07000
1.00000	50.00000	10.00000	9.00000	.05000
1.00000	50.00000	10.00000	12.00000	.33000
1.00000	50.00000	10.00000	12.00000	.45000
1.00000	50.00000	10.00000	12.00000	.50000
1.00000	50.00000	10.00000	12.00000	.33000
1.00000	50.00000	10.00000	12.00000	.44000
1.00000	60.00000	15.55556	3.00000	.07000
1.00000	60.00000	15.55556	3.00000	.11000
1.00000	60.00000	15.55556	3.00000	.13000
1.00000	60.00000	15.55556	3.00000	.17000

Moisture Treatment	°F	°C	Time	Proportion Germination
1.00000	60.00000	15.55556	3.00000	.25000
1.00000	60.00000	15.55556	6.00000	.15000
1.00000	60.00000	15.55556	6.00000	.32000
1.00000	60.00000	15.55556	6.00000	.22000
1.00000	60.00000	15.55556	6.00000	.54000
1.00000	60.00000	15.55556	6.00000	.10000
1.00000	60.00000	15.55556	9.00000	.12000
1.00000	60.00000	15.55556	9.00000	.50000
1.00000	60.00000	15.55556	9.00000	.18000
1.00000	60.00000	15.55556	9.00000	.33000
1.00000	60.00000	15.55556	9.00000	.04000
1.00000	60.00000	15.55556	12.00000	.67000
1.00000	60.00000	15.55556	12.00000	.76000
1.00000	60.00000	15.55556	12.00000	.59000
1.00000	60.00000	15.55556	12.00000	.58000
1.00000	60.00000	15.55556	12.00000	.80000
1.00000	70.00000	21.11111	3.00000	.16000
1.00000	70.00000	21.11111	3.00000	.12000
1.00000	70.00000	21.11111	3.00000	.04000
1.00000	70.00000	21.11111	3.00000	.03000
1.00000	70.00000	21.11111	3.00000	.17000
1.00000	70.00000	21.11111	3.00000	.32000
1.00000	70.00000	21.11111	6.00000	.21000
1.00000	70.00000	21.11111	6.00000	.28000
1.00000	70.00000	21.11111	6.00000	.19000
1.00000	70.00000	21.11111	6.00000	.13000
1.00000	70.00000	21.11111	6.00000	.44000
1.00000	70.00000	21.11111	6.00000	.25000
1.00000	70.00000	21.11111	9.00000	.61000
1.00000	70.00000	21.11111	9.00000	.07000
1.00000	70.00000	21.11111	9.00000	.58000
1.00000	70.00000	21.11111	9.00000	.22000
1.00000	70.00000	21.11111	9.00000	.16000
1.00000	70.00000	21.11111	9.00000	.39000
1.00000	70.00000	21.11111	12.00000	.86000
1.00000	70.00000	21.11111	12.00000	.67000
1.00000	70.00000	21.11111	12.00000	.75000
1.00000	70.00000	21.11111	12.00000	.95000
1.00000	70.00000	21.11111	12.00000	.79000
1.00000	70.00000	21.11111	12.00000	.72000
1.00000	80.00000	26.66667	3.00000	.03000
1.00000	80.00000	26.66667	3.00000	.01000
1.00000	80.00000	26.66667	3.00000	.11000
1.00000	80.00000	26.66667	3.00000	.19000

Moisture Treatment	°F	°C	Time	Proportion Germination
1.00000	80.00000	26.66667	3.00000	.02000
1.00000	80.00000	26.66667	3.00000	.06000
1.00000	80.00000	26.66667	6.00000	.40000
1.00000	80.00000	26.66667	6.00000	.15000
1.00000	80.00000	26.66667	6.00000	.23000
1.00000	80.00000	26.66667	6.00000	.10000
1.00000	80.00000	26.66667	6.00000	.04000
1.00000	80.00000	26.66667	6.00000	.10000
1.00000	80.00000	26.66667	9.00000	.14000
1.00000	80.00000	26.66667	9.00000	.38000
1.00000	80.00000	26.66667	9.00000	.32000
1.00000	80.00000	26.66667	9.00000	.56000
1.00000	80.00000	26.66667	9.00000	.36000
1.00000	80.00000	26.66667	9.00000	.30000
1.00000	80.00000	26.66667	12.00000	.84000
1.00000	80.00000	26.66667	12.00000	.93000
1.00000	80.00000	26.66667	12.00000	.55000
1.00000	80.00000	26.66667	12.00000	.70000
1.00000	80.00000	26.66667	12.00000	.67000
1.00000	80.00000	26.66667	12.00000	.86000
1.00000	90.00000	32.22222	3.00000	0.00000
1.00000	90.00000	32.22222	3.00000	0.00000
1.00000	90.00000	32.22222	3.00000	0.00000
1.00000	90.00000	32.22222	3.00000	0.00000
1.00000	90.00000	32.22222	3.00000	0.00000
1.00000	90.00000	32.22222	3.00000	0.00000
1.00000	90.00000	32.22222	6.00000	0.00000
1.00000	90.00000	32.22222	6.00000	0.00000
1.00000	90.00000	32.22222	6.00000	0.00000
1.00000	90.00000	32.22222	6.00000	0.00000
1.00000	90.00000	32.22222	6.00000	0.00000
1.00000	90.00000	32.22222	6.00000	0.00000
1.00000	90.00000	32.22222	9.00000	0.00000
1.00000	90.00000	32.22222	9.00000	0.00000
1.00000	90.00000	32.22222	9.00000	0.00000
1.00000	90.00000	32.22222	9.00000	.01000
1.00000	90.00000	32.22222	9.00000	0.00000
1.00000	90.00000	32.22222	9.00000	0.00000
1.00000	90.00000	32.22222	12.00000	0.00000
1.00000	90.00000	32.22222	12.00000	0.00000
1.00000	90.00000	32.22222	12.00000	0.00000
1.00000	90.00000	32.22222	12.00000	0.00000
1.00000	90.00000	32.22222	12.00000	0.00000
1.00000	90.00000	32.22222	12.00000	0.00000

Moisture Treatment	°F	°C	Time	Proportion Germination
2.00000	40.00000	4.44444	3.00000	0.00000
2.00000	40.00000	4.44444	3.00000	0.00000
2.00000	40.00000	4.44444	3.00000	0.00000
2.00000	40.00000	4.44444	3.00000	.02000
2.00000	40.00000	4.44444	3.00000	0.00000
2.00000	40.00000	4.44444	3.00000	0.00000
2.00000	40.00000	4.44444	3.00000	0.00000
2.00000	40.00000	4.44444	6.00000	0.00000
2.00000	40.00000	4.44444	6.00000	0.00000
2.00000	40.00000	4.44444	6.00000	0.00000
2.00000	40.00000	4.44444	6.00000	0.00000
2.00000	40.00000	4.44444	6.00000	0.00000
2.00000	40.00000	4.44444	6.00000	.01000
2.00000	40.00000	4.44444	6.00000	0.00000
2.00000	40.00000	4.44444	9.00000	.01000
2.00000	40.00000	4.44444	9.00000	0.00000
2.00000	40.00000	4.44444	9.00000	0.00000
2.00000	40.00000	4.44444	9.00000	.03000
2.00000	40.00000	4.44444	9.00000	.02000
2.00000	40.00000	4.44444	9.00000	0.00000
2.00000	40.00000	4.44444	9.00000	0.00000
2.00000	40.00000	4.44444	12.00000	.02000
2.00000	40.00000	4.44444	12.00000	.01000
2.00000	40.00000	4.44444	12.00000	.01000
2.00000	40.00000	4.44444	12.00000	.08000
2.00000	40.00000	4.44444	12.00000	.01000
2.00000	40.00000	4.44444	12.00000	.04000
2.00000	40.00000	4.44444	12.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	3.00000	0.00000
2.00000	50.00000	10.00000	6.00000	.01000
2.00000	50.00000	10.00000	6.00000	.01000
2.00000	50.00000	10.00000	6.00000	.02000
2.00000	50.00000	10.00000	6.00000	0.00000
2.00000	50.00000	10.00000	6.00000	.02000
2.00000	50.00000	10.00000	6.00000	.07000
2.00000	50.00000	10.00000	6.00000	.05000
2.00000	50.00000	10.00000	9.00000	.08000
2.00000	50.00000	10.00000	9.00000	.04000

Moisture Treatment	°F	°C	Time	Proportion Germination
2.00000	50.00000	10.00000	9.00000	.11000
2.00000	50.00000	10.00000	9.00000	.15000
2.00000	50.00000	10.00000	9.00000	.13000
2.00000	50.00000	10.00000	9.00000	.06000
2.00000	50.00000	10.00000	9.00000	.21000
2.00000	50.00000	10.00000	12.00000	.04000
2.00000	50.00000	10.00000	12.00000	.20000
2.00000	50.00000	10.00000	12.00000	.01000
2.00000	50.00000	10.00000	12.00000	.13000
2.00000	50.00000	10.00000	12.00000	.28000
2.00000	50.00000	10.00000	12.00000	.11000
2.00000	50.00000	10.00000	12.00000	.32000
2.00000	60.00000	15.55556	3.00000	0.00000
2.00000	60.00000	15.55556	3.00000	.01000
2.00000	60.00000	15.55556	3.00000	.03000
2.00000	60.00000	15.55556	3.00000	0.00000
2.00000	60.00000	15.55556	3.00000	0.00000
2.00000	60.00000	15.55556	3.00000	0.00000
2.00000	60.00000	15.55556	3.00000	.05000
2.00000	60.00000	15.55556	6.00000	.10000
2.00000	60.00000	15.55556	6.00000	.17000
2.00000	60.00000	15.55556	6.00000	.02000
2.00000	60.00000	15.55556	6.00000	.05000
2.00000	60.00000	15.55556	6.00000	.01000
2.00000	60.00000	15.55556	6.00000	.23000
2.00000	60.00000	15.55556	6.00000	.05000
2.00000	60.00000	15.55556	9.00000	.09000
2.00000	60.00000	15.55556	9.00000	.14000
2.00000	60.00000	15.55556	9.00000	.14000
2.00000	60.00000	15.55556	9.00000	.34000
2.00000	60.00000	15.55556	9.00000	.17000
2.00000	60.00000	15.55556	9.00000	.22000
2.00000	60.00000	15.55556	9.00000	.10000
2.00000	60.00000	15.55556	12.00000	.15000
2.00000	60.00000	15.55556	12.00000	.23000
2.00000	60.00000	15.55556	12.00000	.27000
2.00000	60.00000	15.55556	12.00000	.38000
2.00000	60.00000	15.55556	12.00000	.33000
2.00000	50.00000	15.55556	12.00000	.19000
2.00000	60.00000	15.55556	12.00000	.07000
2.00000	70.00000	21.11111	3.00000	0.00000
2.00000	70.00000	21.11111	3.00000	0.00000

Moisture Treatment	°F	°C	Time	Proportion Germination
2.00000	70.00000	21.11111	3.00000	0.00000
2.00000	70.00000	21.11111	3.00000	.01000
2.00000	70.00000	21.11111	3.00000	.20000
2.00000	70.00000	21.11111	3.00000	.02000
2.00000	70.00000	21.11111	3.00000	0.00000
2.00000	70.00000	21.11111	3.00000	0.00000
2.00000	70.00000	21.11111	3.00000	.01000
2.00000	70.00000	21.11111	3.00000	.04000
2.00000	70.00000	21.11111	6.00000	.01000
2.00000	70.00000	21.11111	6.00000	.10000
2.00000	70.00000	21.11111	6.00000	0.00000
2.00000	70.00000	21.11111	6.00000	.01000
2.00000	70.00000	21.11111	6.00000	.04000
2.00000	70.00000	21.11111	6.00000	.08000
2.00000	70.00000	21.11111	6.00000	.02000
2.00000	70.00000	21.11111	6.00000	0.00000
2.00000	70.00000	21.11111	6.00000	.02000
2.00000	70.00000	21.11111	6.00000	.01000
2.00000	70.00000	21.11111	9.00000	.12000
2.00000	70.00000	21.11111	9.00000	.10000
2.00000	70.00000	21.11111	9.00000	.07000
2.00000	70.00000	21.11111	9.00000	.23000
2.00000	70.00000	21.11111	9.00000	.11000
2.00000	70.00000	21.11111	9.00000	.26000
2.00000	70.00000	21.11111	9.00000	.14000
2.00000	70.00000	21.11111	9.00000	.12000
2.00000	70.00000	21.11111	9.00000	.18000
2.00000	70.00000	21.11111	9.00000	.12000
2.00000	70.00000	21.11111	12.00000	.40000
2.00000	70.00000	21.11111	12.00000	.19000
2.00000	70.00000	21.11111	12.00000	.12000
2.00000	70.00000	21.11111	12.00000	.08000
2.00000	70.00000	21.11111	12.00000	.16000
2.00000	70.00000	21.11111	12.00000	.21000
2.00000	70.00000	21.11111	12.00000	.14000
2.00000	70.00000	21.11111	12.00000	.20000
2.00000	70.00000	21.11111	12.00000	.12000
2.00000	70.00000	21.11111	12.00000	.19000
2.00000	80.00000	26.66667	3.00000	.03000
2.00000	80.00000	26.66667	3.00000	.02000
2.00000	80.00000	26.66667	3.00000	.09000
2.00000	80.00000	26.66667	3.00000	.02000

Moisture Treatment	°F	°C	Time	Proportion Germination
2.00000	80.00000	26.66667	3.00000	.25000
2.00000	80.00000	26.66667	3.00000	.16000
2.00000	80.00000	26.66667	3.00000	0.00000
2.00000	80.00000	26.66667	3.00000	0.00000
2.00000	80.00000	26.66667	3.00000	0.00000
2.00000	80.00000	26.66667	3.00000	0.00000
2.00000	80.00000	26.66667	6.00000	.02000
2.00000	80.00000	26.66667	6.00000	.11000
2.00000	80.00000	26.66667	6.00000	.20000
2.00000	80.00000	26.66667	6.00000	.13000
2.00000	80.00000	26.66667	6.00000	.15000
2.00000	80.00000	26.66667	6.00000	.21000
2.00000	80.00000	26.66667	6.00000	.23000
2.00000	80.00000	26.66667	6.00000	.32000
2.00000	80.00000	26.66667	6.00000	.27000
2.00000	80.00000	26.66667	6.00000	.11000
2.00000	80.00000	26.66667	9.00000	.31000
2.00000	80.00000	26.66667	9.00000	.38000
2.00000	80.00000	26.66667	9.00000	.37000
2.00000	80.00000	26.66667	9.00000	.10000
2.00000	80.00000	26.66667	9.00000	.35000
2.00000	80.00000	26.66667	9.00000	.15000
2.00000	80.00000	26.66667	9.00000	.08000
2.00000	80.00000	26.66667	9.00000	.03000
2.00000	80.00000	26.66667	9.00000	.12000
2.00000	80.00000	26.66667	9.00000	.45000
2.00000	80.00000	26.66667	12.00000	.15000
2.00000	80.00000	26.66667	12.00000	.40000
2.00000	80.00000	26.66667	12.00000	.44000
2.00000	80.00000	26.66667	12.00000	.29000
2.00000	80.00000	26.66667	12.00000	.27000
2.00000	80.00000	26.66667	12.00000	.30000
2.00000	80.00000	26.66667	12.00000	.14000
2.00000	80.00000	26.66667	12.00000	.23000
2.00000	80.00000	26.66667	12.00000	.15000
2.00000	80.00000	26.66667	12.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000

Moisture Treatment	°F	°C	Time	Proportion Germination
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	3.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	6.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	9.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000
2.00000	90.00000	32.22222	12.00000	0.00000

Appendix I.

Appendix I.

Spore germination data for various habitats (Experiment 9).

CDDAGERMFIELD2 (22F3.0)

Data coded as follows:

A-Day 1=6-16-80 2=7-16-80 3=7-23-80 4=8-21-80

B-Time 1=6:00a.m. 2=8:00a.m. 3=10:00a.m. 4=12:00p.m. 5=6:00p.m.

C-Carrots, ground level, evaluated at time t

D-Carrots, ground level, evaluated at time t+6 hours

E-Carrots, mid canopy, evaluated at time t

F-Carrots, mid canopy, evaluated at time t+6 hours

G-Carrots, top of canopy, evaluated at time t

H-Carrots, top of canopy, evaluated at time t+6 hours

I-Border, ground level, evaluated at time t

J-Border, ground level, evaluated at time t+6 hours

K-Border, mid canopy, evaluated at time t

L-Border, mid canopy, evaluated at time t+6 hours

M-Border, top of canopy, evaluated at time t

N-Border, top of canopy, evaluated at time t+6 hours

O-Onions ground level, evaluated at time t

P-Onions, ground level, evaluated at time t+6 hours

Q-Onions, mid canopy, evaluated at time t

R-Onions, mid canopy, evaluated at time t+6 hours

S-Onions, top of canopy, evaluated at time t

T-Onions, top of canopy, evaluated at time t+6 hours

U-Control, evaluated at time t

V-Control, evaluated at time t+6 hours

-9 = no detectible spores (spores fragmented)

Table II.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
1.	1.	27.	90.	23.	62.	17.	87.	31.	71.	[illegible]											
1.	1.	29.	76.	17.	77.	28.	71.	47.	73.	61.	62.	36.	73.	27.	70.	21.	69.	13.	71.	49.	71.
1.	1.	16.	71.	16.	77.	37.	69.	39.	76.	37.	83.	23.	77.	23.	62.	4.	70.	14.	71.	71.	92.
1.	1.	9.	84.	27.	92.	21.	79.	27.	60.	68.	85.	12.	80.	31.	81.	17.	87.	26.	83.	38.	86.
1.	1.	22.	81.	35.	83.	19.	91.	42.	69.	53.	71.	27.	71.	11.	79.	31.	82.	5.	87.	52.	74.
1.	2.	26.	72.	31.	81.	21.	71.	61.	83.	64.	71.	43.	73.	31.	58.	23.	71.	19.	72.	71.	79.
1.	2.	31.	73.	19.	82.	27.	68.	73.	91.	67.	86.	49.	64.	27.	62.	19.	77.	13.	68.	64.	83.
1.	2.	37.	81.	27.	87.	33.	83.	49.	87.	50.	57.	37.	89.	33.	84.	29.	68.	27.	58.	49.	92.
1.	2.	17.	63.	24.	91.	16.	77.	57.	71.	19.	93.	28.	76.	19.	83.	31.	64.	24.	67.	72.	70.
1.	2.	23.	92.	21.	59.	19.	91.	64.	73.	38.	77.	42.	83.	12.	87.	16.	58.	30.	82.	54.	84.
1.	3.	33.	61.	21.	50.	17.	31.	72.	81.	68.	72.	51.	71.	13.	24.	34.	36.	17.	39.	83.	87.
1.	3.	26.	54.	17.	41.	41.	18.	71.	83.	76.	82.	42.	76.	27.	41.	12.	42.	38.	27.	87.	93.
1.	3.	6.	43.	16.	37.	12.	12.	68.	62.	79.	93.	49.	68.	19.	38.	23.	41.	31.	48.	68.	71.
1.	3.	27.	37.	31.	32.	17.	41.	83.	92.	82.	71.	37.	51.	31.	37.	37.	23.	23.	53.	71.	64.
1.	3.	17.	41.	7.	29.	25.	23.	75.	81.	71.	86.	27.	43.	33.	41.	7.	19.	22.	12.	69.	92.
1.	4.	-9.	-9.	-9.	-9.	-9.	-9.	79.	81.	73.	81.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	93.	82.
1.	4.	-9.	-9.	-9.	-9.	-9.	-9.	81.	78.	71.	73.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	87.	77.
1.	4.	41.	37.	-9.	-9.	-9.	-9.	73.	78.	79.	72.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	81.	76.
1.	4.	22.	54.	-9.	-9.	-9.	-9.	66.	73.	81.	71.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	87.	89.
1.	4.	19.	41.	-9.	-9.	-9.	-9.	72.	69.	70.	64.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	70.	89.
1.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	71.	71.
1.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	78.	68.
1.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	92.	86.
1.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	83.	89.
1.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	89.	93.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
2.	1.	27.	87.	36.	51.	42.	71.	31.	71.	43.	70.	31.	71.	6.	64.	11.	69.	16.	71.	67.	82.
2.	1.	49.	50.	27.	54.	13.	76.	37.	73.	33.	76.	37.	83.	27.	53.	10.	71.	37.	68.	54.	76.
2.	1.	35.	51.	51.	61.	23.	81.	28.	48.	47.	68.	24.	58.	34.	71.	31.	54.	22.	64.	49.	69.
2.	1.	46.	73.	39.	73.	32.	39.	42.	59.	37.	91.	39.	69.	24.	68.	36.	49.	31.	50.	72.	73.
2.	1.	41.	76.	38.	85.	19.	59.	50.	66.	27.	85.	46.	71.	26.	71.	23.	63.	27.	42.	38.	58.
2.	2.	51.	68.	39.	71.	37.	65.	43.	50.	41.	37.	31.	43.	14.	20.	36.	18.	34.	27.	76.	77.
2.	2.	63.	74.	49.	76.	47.	79.	21.	31.	48.	41.	37.	36.	26.	13.	9.	12.	30.	36.	81.	71.
2.	2.	54.	59.	52.	73.	39.	77.	37.	36.	27.	36.	27.	28.	19.	22.	23.	26.	23.	12.	64.	62.
2.	2.	40.	83.	37.	71.	32.	81.	38.	41.	28.	46.	37.	24.	31.	24.	31.	36.	26.	27.	70.	83.
2.	2.	47.	91.	43.	84.	28.	68.	48.	38.	32.	20.	41.	36.	21.	17.	17.	28.	11.	20.	69.	77.
2.	3.	74.	81.	76.	81.	39.	81.	42.	41.	31.	41.	42.	36.	34.	17.	14.	36.	23.	36.	71.	84.
2.	3.	67.	65.	81.	73.	56.	70.	21.	43.	38.	23.	38.	41.	39.	28.	37.	28.	30.	34.	77.	71.
2.	3.	59.	73.	64.	76.	65.	64.	37.	20.	26.	37.	50.	42.	10.	14.	21.	31.	17.	8.	87.	92.
2.	3.	81.	76.	73.	59.	43.	78.	34.	17.	24.	31.	31.	28.	7.	26.	13.	41.	18.	27.	67.	68.
2.	3.	93.	84.	58.	89.	71.	69.	26.	31.	37.	18.	28.	16.	21.	19.	32.	12.	29.	12.	91.	76.
2.	4.	83.	84.	82.	83.	-9.	-9.	21.	24.	27.	24.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	90.	82.
2.	4.	76.	71.	65.	79.	-9.	-9.	31.	27.	42.	28.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	73.	81.
2.	4.	91.	68.	73.	58.	-9.	-9.	37.	21.	23.	36.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	84.	73.
2.	4.	72.	74.	92.	61.	-9.	-9.	31.	20.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	86.	96.
2.	4.	83.	93.	53.	91.	-9.	-9.	26.	40.	33.	39.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	89.	67.
2.	5.	76.	81.	49.	78.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	84.	87.
2.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	87.	91.
2.	5.	83.	91.	81.	72.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	81.	73.
2.	5.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	70.	86.
2.	5.	71.	68.	73.	79.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	76.	87.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
3.	1.	33.	96.	47.	87.	26.	74.	47.	85.	62.	84.	37.	86.	13.	68.	16.	71.	21.	87.	64.	90.
3.	1.	57.	62.	51.	86.	31.	68.	59.	77.	47.	73.	29.	98.	10.	74.	37.	74.	12.	74.	71.	83.
3.	1.	46.	74.	32.	91.	17.	83.	54.	68.	28.	92.	17.	74.	27.	77.	11.	68.	17.	86.	39.	91.
3.	1.	51.	83.	61.	69.	28.	64.	31.	90.	43.	81.	33.	68.	5.	93.	23.	91.	8.	61.	54.	73.
3.	1.	63.	70.	37.	73.	19.	76.	27.	83.	45.	83.	12.	90.	17.	97.	12.	87.	6.	93.	62.	79.
3.	2.	72.	84.	83.	79.	43.	73.	81.	83.	73.	96.	23.	78.	17.	71.	14.	82.	26.	87.	79.	76.
3.	2.	77.	90.	81.	87.	37.	79.	60.	87.	64.	81.	37.	69.	32.	68.	23.	73.	24.	81.	63.	85.
3.	2.	69.	79.	61.	91.	19.	81.	73.	96.	47.	87.	46.	77.	14.	93.	31.	91.	19.	92.	71.	96.
3.	2.	54.	76.	73.	87.	28.	86.	82.	72.	54.	70.	12.	93.	21.	81.	18.	71.	14.	94.	86.	74.
3.	2.	76.	97.	58.	71.	14.	69.	59.	91.	61.	78.	28.	84.	19.	78.	29.	86.	11.	73.	59.	81.
3.	3.	77.	84.	62.	83.	46.	62.	84.	83.	74.	93.	43.	44.	23.	69.	17.	21.	29.	43.	93.	84.
3.	3.	81.	81.	54.	86.	46.	41.	86.	92.	72.	87.	14.	64.	27.	72.	24.	34.	31.	57.	87.	73.
3.	3.	84.	93.	78.	92.	51.	38.	83.	72.	63.	84.	31.	37.	31.	71.	38.	12.	17.	20.	71.	96.
3.	3.	82.	71.	77.	73.	13.	17.	71.	83.	81.	87.	29.	23.	17.	58.	16.	36.	14.	38.	64.	81.
3.	3.	63.	70.	71.	69.	31.	82.	68.	97.	87.	71.	23.	38.	19.	47.	7.	19.	26.	47.	85.	86.
3.	4.	84.	71.	76.	62.	-9.	-9.	84.	92.	71.	81.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	83.	93.
3.	4.	73.	87.	72.	93.	-9.	-9.	68.	78.	81.	84.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	78.	76.
3.	4.	64.	84.	83.	84.	-9.	-9.	93.	84.	76.	76.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	69.	84.
3.	4.	91.	87.	69.	87.	-9.	-9.	77.	81.	71.	69.	-9.	-9.	-9.	-9.	37.	43.	16.	-9.	92.	79.
3.	4.	81.	74.	81.	81.	-9.	-9.	67.	70.	73.	93.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	92.	98.
3.	5.	82.	86.	92.	87.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	83.	79.
3.	5.	81.	89.	83.	81.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	92.	84.
3.	5.	73.	71.	76.	70.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	71.	93.
3.	5.	79.	72.	81.	93.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	73.	90.
3.	5.	74.	79.	68.	81.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	79.	86.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
4.	1.	45.	62.	39.	80.	34.	64.	56.	74.	44.	71.	37.	81.	11.	49.	13.	71.	12.	73.	51.	84.
4.	1.	42.	73.	61.	71.	37.	73.	39.	81.	51.	68.	39.	87.	36.	64.	28.	70.	14.	84.	48.	71.
4.	1.	59.	84.	52.	76.	46.	58.	42.	64.	62.	72.	42.	71.	22.	71.	33.	89.	31.	76.	47.	70.
4.	1.	66.	58.	43.	64.	41.	72.	51.	79.	43.	76.	49.	68.	17.	54.	4.	88.	27.	72.	58.	74.
4.	1.	40.	70.	49.	73.	42.	81.	41.	71.	54.	67.	37.	54.	28.	39.	41.	64.	16.	68.	64.	91.
4.	2.	73.	84.	58.	76.	46.	71.	76.	61.	49.	91.	49.	81.	37.	41.	23.	32.	31.	73.	67.	87.
4.	2.	64.	91.	66.	86.	39.	77.	74.	68.	58.	73.	42.	92.	21.	67.	31.	81.	36.	61.	83.	83.
4.	2.	80.	87.	64.	93.	42.	83.	68.	91.	71.	69.	61.	58.	8.	68.	16.	47.	21.	62.	59.	92.
4.	2.	58.	87.	72.	71.	49.	91.	40.	76.	63.	81.	53.	74.	13.	71.	24.	78.	24.	51.	71.	71.
4.	2.	41.	81.	49.	68.	37.	34.	51.	83.	63.	82.	37.	81.	26.	75.	29.	50.	40.	68.	73.	78.
4.	3.	81.	86.	73.	89.	47.	54.	79.	87.	68.	91.	64.	71.	31.	40.	34.	32.	11.	31.	87.	73.
4.	3.	82.	71.	79.	93.	51.	60.	64.	83.	72.	87.	47.	43.	13.	31.	14.	36.	17.	10.	91.	84.
4.	3.	64.	93.	72.	92.	37.	38.	82.	86.	81.	86.	39.	44.	24.	6.	31.	3.	21.	7.	92.	87.
4.	3.	73.	91.	86.	87.	27.	47.	81.	81.	78.	93.	66.	39.	17.	14.	20.	18.	19.	29.	73.	82.
4.	3.	76.	82.	89.	69.	39.	23.	59.	71.	71.	74.	47.	51.	23.	21.	13.	7.	24.	16.	86.	91.
4.	4.	81.	73.	69.	92.	-9.	-9.	81.	81.	83.	91.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	81.	93.
4.	4.	70.	83.	79.	83.	-9.	-9.	71.	93.	91.	74.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	87.	71.
4.	4.	68.	94.	73.	71.	-9.	-9.	68.	81.	71.	70.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	87.	74.
4.	4.	77.	80.	81.	69.	-9.	-9.	72.	70.	64.	83.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	94.	87.
4.	4.	79.	89.	71.	77.	-9.	-9.	77.	68.	83.	87.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	82.	82.
4.	5.	76.	77.	86.	90.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	73.	83.
4.	5.	83.	69.	70.	71.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	86.	67.
4.	5.	91.	87.	64.	69.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	79.	91.
4.	5.	72.	91.	81.	87.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	93.	91.
4.	5.	80.	88.	84.	82.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	-9.	79.	73.

Appendix J.

Appendix J. Host-pathogen interaction data (Experiment 10). CDDAEMUSCAEINFECTIONTIME (1X, 5F10.4)

Table J1.

Exposure Treatment	Number Infected	Total Number	Proportion Infected	Arcsin Infection
1.0000	64.0000	85.0000	.7530	60.1989
1.0000	50.0000	73.0000	.6850	55.8578
1.0000	51.0000	64.0000	.7970	63.2207
2.0000	5.0000	51.0000	.0980	18.2431
2.0000	14.0000	97.0000	.1440	22.3011
2.0000	21.0000	93.0000	.2260	28.3851
3.0000	34.0000	79.0000	.4300	40.9761
3.0000	39.0000	64.0000	.6090	51.2958
3.0000	47.0000	93.0000	.5050	45.2865
4.0000	33.0000	65.0000	.5080	45.4584
4.0000	42.0000	70.0000	.6000	50.7685
4.0000	48.0000	81.0000	.5900	50.1849
5.0000	17.0000	42.0000	.4050	39.5236
5.0000	24.0000	53.0000	.4530	42.3031
5.0000	39.0000	51.0000	.7650	61.0027
6.0000	5.0000	80.0000	.0625	14.4775
6.0000	0.0000	76.0000	0.0000	0.0000
6.0000	1.0000	72.0000	.0140	6.7952

Appendix K.

Temperature data and Degree Day Accumulation (base 4.4°C) for Grant, Michigan. 1977-1979.

TABLE 1.

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
4/ 1/78	4.5	45	44
4/ 2/78	4.5	34	25
4/ 3/78	5.2	43	31
4/ 4/78	8.9	51	31
4/ 5/78	14.2	56	27
4/ 6/78	17.7	49	36
4/ 7/78	25.0	57	36
4/ 8/78	27.0	47	31
4/ 9/78	27.2	41	28
4/10/78	33.5	59	24
4/11/78	36.5	48	36
4/12/78	43.2	59	27
4/13/78	44.6	44	37
4/14/78	46.6	47	30
4/15/78	47.7	45	26
4/16/78	52.5	56	21
4/17/78	57.4	56	21
4/18/78	59.3	45	38
4/19/78	69.8	60	41
4/20/78	71.8	45	38
4/21/78	77.7	56	31
4/22/78	83.3	57	25
4/23/78	87.4	50	37
4/24/78	99.4	63	41
4/25/78	109.6	65	32
4/26/78	122.7	69	36
4/27/78	134.4	69	30
4/28/78	145.3	68	28
4/29/78	158.9	71	34
4/30/78	163.0	53	27
5/ 1/78	168.2	56	25
5/ 2/78	176.3	60	33
5/ 3/78	187.6	66	35
5/ 4/78	195.1	55	40
5/ 5/78	199.0	49	38
5/ 6/78	208.0	62	33
5/ 7/78	220.0	61	43
5/ 8/78	235.5	64	47
5/ 9/78	246.0	55	46
5/10/78	261.0	66	44
5/11/78	278.0	68	46
5/12/78	298.0	64	56
5/13/78	319.5	66	57
5/14/78	335.0	59	52
5/15/78	354.0	64	54
5/16/78	373.0	65	53
5/17/78	393.0	77	43
5/18/78	419.0	81	51
5/19/78	442.5	81	46
5/20/78	470.0	74	61
5/21/78	482.1	65	39
5/22/78	496.5	71	37
5/23/78	516.5	76	44
5/24/78	541.0	83	46
5/25/78	565.0	83	45
5/26/78	595.5	86	55
5/27/78	628.0	88	57
5/28/78	661.5	90	57
5/29/78	697.5	90	62
5/30/78	726.0	80	57
5/31/78	753.5	79	56
6/ 1/78	784.0	82	59
6/ 2/78	803.0	68	50
6/ 3/78	815.6	68	36
6/ 4/78	834.1	75	42
6/ 5/78	851.1	73	41
6/ 6/78	874.1	81	45
6/ 7/78	902.1	79	57
6/ 8/78	919.6	71	44
6/ 9/78	936.6	72	42
6/10/78	958.1	78	45
6/11/78	991.6	85	62
6/12/78	1014.6	66	60
6/13/78	1026.1	64	39
6/14/78	1034.3	61	31
6/15/78	1059.8	79	52
6/16/78	1084.3	74	55
6/17/78	1110.8	72	61
6/18/78	1136.3	76	55
6/19/78	1161.3	79	51

TABLE 1. CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
6/20/78	1189.8	83	54
6/21/78	1212.8	70	56
6/22/78	1231.3	75	42
6/23/78	1250.8	74	45
6/24/78	1276.3	82	49
6/25/78	1305.8	74	65
6/26/78	1337.3	79	64
6/27/78	1371.8	83	66
6/28/78	1401.8	85	55
6/29/78	1432.3	86	55
6/30/78	1462.8	84	57
7/ 1/78	1482.3	62	57
7/ 2/78	1504.3	64	60
7/ 3/78	1530.3	74	58
7/ 4/78	1555.3	82	48
7/ 5/78	1582.8	82	53
7/ 6/78	1615.8	86	60
7/ 7/78	1649.8	83	65
7/ 8/78	1678.3	75	62
7/ 9/78	1702.8	80	49
7/10/78	1722.3	70	49
7/11/78	1739.3	73	41
7/12/78	1759.3	79	41
7/13/78	1792.3	81	65
7/14/78	1819.8	82	53
7/15/78	1848.3	84	53
7/16/78	1871.3	79	47
7/17/78	1895.3	82	46
7/18/78	1927.8	82	63
7/19/78	1965.3	85	70
7/20/78	2003.8	91	66
7/21/78	2037.8	82	66
7/22/78	2073.3	85	66
7/23/78	2100.3	75	59
7/24/78	2125.3	82	48
7/25/78	2152.3	81	53
7/26/78	2180.8	77	60
7/27/78	2211.8	78	64
7/28/78	2228.9	75	39
7/29/78	2252.9	74	54
7/30/78	2272.9	71	49
7/31/78	2293.4	77	44
8/ 1/78	2319.9	81	52
8/ 2/78	2344.9	78	52
8/ 3/78	2367.4	75	50
8/ 4/78	2383.9	73	40
8/ 5/78	2401.9	76	40
8/ 6/78	2427.4	85	46
8/ 7/78	2456.9	83	56
8/ 8/78	2484.4	83	52
8/ 9/78	2514.4	82	58
8/10/78	2536.4	79	45
8/11/78	2559.4	80	46
8/12/78	2590.4	84	58
8/13/78	2622.4	88	56
8/14/78	2656.4	90	58
8/15/78	2692.4	89	63
8/16/78	2723.9	78	65
8/17/78	2756.4	85	60
8/18/78	2786.4	79	61
8/19/78	2815.4	71	67
8/20/78	2835.9	75	46
8/21/78	2859.9	82	46
8/22/78	2888.4	85	52
8/23/78	2919.9	85	58
8/24/78	2953.9	85	63
8/25/78	2977.4	72	55
8/26/78	3007.4	78	62
8/27/78	3036.4	74	64
8/28/78	3068.4	78	66
8/29/78	3097.4	77	61
8/30/78	3122.4	78	52
8/31/78	3144.9	76	49
9/ 1/78	3168.9	80	48
9/ 2/78	3197.4	79	58
9/ 3/78	3225.4	74	62
9/ 4/78	3246.4	77	45
9/ 5/78	3275.4	86	52
9/ 6/78	3305.9	84	57
9/ 7/78	3338.9	88	58

TABLE 1 . CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
9/ 8/78	3373.9	89	61
9/ 9/78	3402.4	75	62
9/10/78	3437.9	90	61
9/11/78	3472.9	88	62
9/12/78	3495.4	63	62
9/13/78	3512.9	63	52
9/14/78	3534.4	72	51
9/15/78	3555.4	73	49
9/16/78	3577.4	75	49
9/17/78	3600.9	69	58
9/18/78	3626.4	75	56
9/19/78	3654.4	81	55
9/20/78	3683.9	82	57
9/21/78	3700.9	61	53
9/22/78	3713.4	64	41
9/23/78	3725.2	67	35
9/24/78	3743.2	74	42
9/25/78	3755.7	64	41
9/26/78	3769.1	69	37
9/27/78	3786.1	62	52
9/28/78	3796.0	65	30
9/29/78	3806.2	62	38
9/30/78	3825.2	65	53
10/ 1/78	3841.7	62	51
10/ 2/78	3855.9	70	38
10/ 3/78	3869.9	65	43
10/ 4/78	3880.4	61	40
10/ 5/78	3894.4	62	46
10/ 6/78	3902.4	50	46
10/ 7/78	3905.1	47	37
10/ 8/78	3908.3	49	34
10/ 9/78	3916.3	61	30
10/10/78	3928.0	68	32
10/11/78	3941.5	62	45
10/12/78	3955.5	60	48
10/13/78	3961.6	55	35
10/14/78	3962.8	44	35
10/15/78	3970.3	58	35
10/16/78	3975.4	54	32
10/17/78	3980.2	55	25
10/18/78	3988.8	58	39
10/19/78	3995.3	56	35
10/20/78	4000.1	54	29
10/21/78	4014.7	70	39
10/22/78	4029.2	68	41
10/23/78	4035.2	49	43
10/24/78	4038.5	52	22
10/25/78	4044.0	55	31
10/26/78	4048.0	48	40
10/27/78	4054.0	56	32
10/28/78	4056.6	49	28
10/29/78	4058.7	48	24
10/30/78	4070.3	66	36
10/31/78	4078.8	60	35

TABLE 2 .

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
4/ 1/79	0.0	38	32
4/ 2/79	0.0	36	30
4/ 3/79	2.7	50	24
4/ 4/79	2.7	40	33
4/ 5/79	4.0	45	30
4/ 6/79	4.0	28	15
4/ 7/79	4.0	38	14
4/ 8/79	4.0	32	30
4/ 9/79	4.9	44	28
4/10/79	7.3	50	18
4/11/79	7.9	43	28
4/12/79	22.7	73	35
4/13/79	30.7	54	42
4/14/79	33.9	49	34
4/15/79	37.3	48	38
4/16/79	44.1	55	38

TABLE 2 . CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
4/17/79	51.5	61	26
4/18/79	60.7	65	26
4/19/79	71.1	68	25
4/20/79	84.7	73	30
4/21/79	99.2	58	51
4/22/79	110.0	67	30
4/23/79	125.5	75	34
4/24/79	140.0	67	42
4/25/79	161.5	65	58
4/26/79	169.5	52	44
4/27/79	175.4	56	31
4/28/79	175.8	42	34
4/29/79	179.3	52	24
4/30/79	180.5	44	35
5/ 1/79	186.1	56	29
5/ 2/79	201.6	69	42
5/ 3/79	210.6	53	45
5/ 4/79	215.2	53	31
5/ 5/79	219.1	53	24
5/ 6/79	238.1	70	48
5/ 7/79	263.1	80	50
5/ 8/79	296.6	86	61
5/ 9/79	331.1	83	66
5/10/79	364.6	84	63
5/11/79	392.6	71	65
5/12/79	398.4	53	38
5/13/79	407.8	64	30
5/14/79	423.8	67	45
5/15/79	433.9	63	36
5/16/79	444.8	68	28
5/17/79	459.0	70	38
5/18/79	486.5	82	53
5/19/79	508.5	70	54
5/20/79	522.1	70	36
5/21/79	534.1	62	42
5/22/79	544.7	67	29
5/23/79	560.7	65	47
5/24/79	571.7	59	43
5/25/79	583.9	66	38
5/26/79	596.4	63	42
5/27/79	607.9	60	43
5/28/79	619.4	59	44
5/29/79	634.2	74	33
5/30/79	649.2	64	46
5/31/79	675.2	79	53
6/ 1/79	696.7	66	57
6/ 2/79	713.4	75	38
6/ 3/79	737.9	81	48
6/ 4/79	762.9	80	50
6/ 5/79	787.9	77	53
6/ 6/79	816.4	83	54
6/ 7/79	848.9	80	65
6/ 8/79	882.9	84	64
6/ 9/79	914.4	75	68
6/10/79	945.4	74	68
6/11/79	963.9	73	44
6/12/79	979.2	73	37
6/13/79	996.4	76	38
6/14/79	1023.9	84	51
6/15/79	1057.4	85	62
6/16/79	1090.9	87	60
6/17/79	1117.9	68	66
6/18/79	1141.4	74	53
6/19/79	1164.9	81	46
6/20/79	1192.9	78	58
6/21/79	1224.9	79	65
6/22/79	1246.4	68	55
6/23/79	1259.4	64	42
6/24/79	1276.9	73	42
6/25/79	1292.5	74	36
6/26/79	1313.0	79	42
6/27/79	1342.0	81	57
6/28/79	1369.0	82	52
6/29/79	1397.0	76	60
6/30/79	1423.5	75	58
7/ 1/79	1441.5	62	54
7/ 2/79	1466.0	79	50
7/ 3/79	1488.0	76	48
7/ 4/79	1514.0	76	56
7/ 5/79	1530.2	74	38
7/ 6/79	1548.0	78	37
7/ 7/79	1569.5	81	42
7/ 8/79	1594.0	80	49
7/ 9/79	1624.0	84	56
7/10/79	1654.5	85	56
7/11/79	1687.5	85	61
7/12/79	1722.5	89	61
7/13/79	1758.5	89	63
7/14/79	1794.0	84	67

TABLE 2 . CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
7/15/79	1830.0	88	64
7/16/79	1857.5	82	53
7/17/79	1881.5	76	52
7/18/79	1901.5	80	40
7/19/79	1924.0	84	41
7/20/79	1948.5	86	43
7/21/79	1976.5	86	50
7/22/79	2007.0	86	55
7/23/79	2039.5	89	56
7/24/79	2071.0	79	64
7/25/79	2104.0	76	70
7/26/79	2132.0	79	57
7/27/79	2161.0	87	51
7/28/79	2193.0	83	61
7/29/79	2220.5	85	50
7/30/79	2249.5	82	56
7/31/79	2281.5	80	64
8/ 1/79	2309.0	74	61
8/ 2/79	2337.5	81	56
8/ 3/79	2366.5	81	57
8/ 4/79	2397.0	82	59
8/ 5/79	2426.0	82	56
8/ 6/79	2452.0	79	53
8/ 7/79	2486.5	88	61
8/ 8/79	2516.5	78	62
8/ 9/79	2543.0	80	53
8/10/79	2573.5	76	65
8/11/79	2591.0	71	44
8/12/79	2606.8	73	38
8/13/79	2628.8	70	54
8/14/79	2644.3	63	48
8/15/79	2660.8	70	43
8/16/79	2674.6	73	31
8/17/79	2691.1	63	50
8/18/79	2716.6	76	55
8/19/79	2742.1	77	54
8/20/79	2768.1	72	60
8/21/79	2794.6	79	54
8/22/79	2821.6	76	58
8/23/79	2853.1	79	64
8/24/79	2879.1	69	63
8/25/79	2902.1	72	54
8/26/79	2923.1	78	44
8/27/79	2941.6	65	52
8/28/79	2969.6	74	62
8/29/79	2999.6	78	62
8/30/79	3030.1	83	58
8/31/79	3060.6	83	58
9/ 1/79	3090.6	80	60
9/ 2/79	3123.6	79	67
9/ 3/79	3149.6	78	54
9/ 4/79	3176.6	78	56
9/ 5/79	3204.1	83	52
9/ 6/79	3232.1	82	54
9/ 7/79	3247.6	59	52
9/ 8/79	3257.5	64	33
9/ 9/79	3272.1	70	39
9/10/79	3297.6	73	58
9/11/79	3320.1	75	50
9/12/79	3350.1	84	56
9/13/79	3377.6	71	64
9/14/79	3394.1	64	49
9/15/79	3405.5	66	35
9/16/79	3423.1	77	38
9/17/79	3442.6	77	42
9/18/79	3467.6	76	54
9/19/79	3477.0	65	27
9/20/79	3493.7	75	38
9/21/79	3513.7	68	52
9/22/79	3524.1	67	28
9/23/79	3534.9	67	30
9/24/79	3550.1	72	38
9/25/79	3566.6	73	40
9/26/79	3584.3	79	35
9/27/79	3604.4	81	39
9/28/79	3624.9	80	41
9/29/79	3652.4	83	52
9/30/79	3676.9	77	52
10/ 1/79	3691.2	74	31
10/ 2/79	3710.2	64	54
10/ 3/79	3723.2	62	44
10/ 4/79	3731.2	60	33
10/ 5/79	3738.3	59	30
10/ 6/79	3747.3	55	43
10/ 7/79	3752.8	51	40

TABLE 2 . CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
10/ 8/79	3758.1	54	33
10/ 9/79	3763.4	52	38
10/10/79	3766.4	49	32
10/11/79	3767.4	44	32
10/12/79	3770.3	47	38
10/13/79	3772.0	45	36
10/14/79	3774.4	49	25
10/15/79	3784.4	64	33
10/16/79	3790.5	55	35
10/17/79	3805.5	60	50
10/18/79	3818.0	60	45
10/19/79	3838.5	66	55
10/20/79	3860.5	70	54
10/21/79	3890.0	73	66
10/22/79	3920.5	75	66
10/23/79	3924.0	45	42
10/24/79	3925.7	45	36
10/25/79	3925.7	38	33
10/26/79	3926.7	44	32
10/27/79	3929.8	50	29
10/28/79	3935.8	51	41
10/29/79	3940.7	55	26
10/30/79	3947.5	57	34
10/31/79	3964.5	72	42

TABLE 3.

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
4/ 1/80	2.1	48	26
4/ 2/80	10.9	61	34
4/ 3/80	11.0	41	33
4/ 4/80	12.4	45	32
4/ 5/80	18.7	57	31
4/ 6/80	28.9	64	34
4/ 7/80	41.4	59	46
4/ 8/80	54.4	59	47
4/ 9/80	55.0	42	38
4/10/80	55.0	38	32
4/11/80	56.2	44	35
4/12/80	56.7	42	36
4/13/80	57.9	45	28
4/14/80	57.9	37	28
4/15/80	58.3	42	32
4/16/80	60.0	47	24
4/17/80	63.5	52	24
4/18/80	63.5	37	36
4/19/80	76.4	68	37
4/20/80	90.9	74	32
4/21/80	106.9	72	40
4/22/80	133.9	84	50
4/23/80	141.5	56	39
4/24/80	141.6	41	26
4/25/80	145.4	52	27
4/26/80	151.4	54	37
4/27/80	159.4	55	41
4/28/80	167.4	55	41
4/29/80	175.4	53	43
4/30/80	186.9	58	45
5/ 1/80	203.9	68	46
5/ 2/80	220.0	73	39
5/ 3/80	240.5	82	39
5/ 4/80	262.5	84	40
5/ 5/80	285.5	83	43
5/ 6/80	298.1	68	36
5/ 7/80	302.1	51	33
5/ 8/80	306.0	52	29
5/ 9/80	312.7	57	33
5/10/80	326.4	69	38

TABLE 3 CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
5/11/80	344.4	67	49
5/12/80	360.4	70	42
5/13/80	376.4	63	49
5/14/80	384.0	59	33
5/15/80	393.2	62	34
5/16/80	404.8	68	32
5/17/80	418.3	61	46
5/18/80	437.3	64	54
5/19/80	458.3	75	47
5/20/80	478.3	75	45
5/21/80	498.0	83	35
5/22/80	521.0	85	41
5/23/80	546.0	85	45
5/24/80	580.0	84	64
5/25/80	608.0	82	54
5/26/80	625.0	77	36
5/27/80	645.0	80	40
5/28/80	670.0	80	50
5/29/80	695.5	73	58
5/30/80	723.5	79	57
5/31/80	747.5	71	57
6/ 1/80	760.0	58	47
6/ 2/80	782.5	73	52
6/ 3/80	806.5	73	55
6/ 4/80	823.5	74	40
6/ 5/80	841.0	71	44
6/ 6/80	867.5	78	55
6/ 7/80	895.0	79	56
6/ 8/80	905.0	58	42
6/ 9/80	917.0	64	40
6/10/80	924.0	59	29
6/11/80	937.1	72	30
6/12/80	955.2	77	39
6/13/80	976.7	80	43
6/14/80	1005.2	81	56
6/15/80	1026.7	63	60
6/16/80	1041.2	69	40
6/17/80	1054.5	71	33
6/18/80	1078.0	77	50
6/19/80	1094.0	57	55
6/20/80	1110.2	74	38
6/21/80	1132.7	78	47
6/22/80	1161.7	82	56
6/23/80	1192.2	87	54
6/24/80	1225.7	88	59
6/25/80	1259.2	88	59
6/26/80	1296.7	89	66
6/27/80	1324.7	80	56
6/28/80	1354.7	84	56
6/29/80	1382.7	76	60
6/30/80	1407.7	75	55
7/ 1/80	1433.7	83	49
7/ 2/80	1461.2	81	54
7/ 3/80	1486.2	87	43
7/ 4/80	1516.7	85	56
7/ 5/80	1550.7	94	64
7/ 6/80	1574.2	79	48
7/ 7/80	1606.2	88	56
7/ 8/80	1638.2	85	59
7/ 9/80	1665.7	83	52
7/10/80	1696.7	89	53
7/11/80	1735.7	93	65
7/12/80	1772.2	85	68
7/13/80	1805.7	89	58
7/14/80	1843.7	94	62
7/15/80	1882.7	86	72
7/16/80	1915.2	86	59
7/17/80	1947.2	80	64
7/18/80	1975.7	86	51
7/19/80	2014.7	92	66
7/20/80	2057.7	96	70
7/21/80	2089.2	75	68
7/22/80	2119.7	79	62
7/23/80	2145.7	80	52
7/24/80	2170.2	82	47
7/25/80	2199.2	86	52
7/26/80	2228.2	72	66
7/27/80	2257.2	76	62
7/28/80	2292.2	83	67
7/29/80	2323.2	82	60
7/30/80	2345.7	76	49
7/31/80	2376.7	84	58
8/ 1/80	2411.2	87	62
8/ 2/80	2438.2	75	59
8/ 3/80	2468.7	83	58
8/ 4/80	2495.2	86	47
8/ 5/80	2525.2	83	57
8/ 6/80	2556.7	87	56
8/ 7/80	2593.2	87	66

TABLE 3. CONTINUED

DATE	ACC. DEGDAY	MAX TEMP	MIN TEMP
8/ 8/80	2627.7	86	63
8/ 9/80	2662.7	84	66
8/10/80	2697.7	84	66
8/11/80	2724.7	73	61
8/12/80	2751.2	76	57
8/13/80	2771.2	72	48
8/14/80	2800.2	81	57
8/15/80	2823.2	76	50
8/16/80	2841.2	74	42
8/17/80	2865.7	67	62
8/18/80	2897.7	81	63
8/19/80	2925.2	86	49
8/20/80	2956.7	86	57
8/21/80	2990.2	81	66
8/22/80	3016.7	81	52
8/23/80	3042.7	87	45
8/24/80	3068.2	84	47
8/25/80	3096.2	75	61
8/26/80	3129.7	85	62
8/27/80	3163.2	87	60
8/28/80	3197.7	84	65
8/29/80	3234.7	89	65
8/30/80	3268.2	82	65
8/31/80	3298.7	74	67
9/ 1/80	3327.7	74	64
9/ 2/80	3358.7	76	66
9/ 3/80	3383.2	80	49
9/ 4/80	3410.2	82	52
9/ 5/80	3432.7	78	47
9/ 6/80	3457.7	80	50
9/ 7/80	3483.7	81	51
9/ 8/80	3512.2	84	53
9/ 9/80	3534.7	71	54
9/10/80	3549.2	70	39
9/11/80	3566.7	73	42
9/12/80	3584.2	65	50
9/13/80	3614.2	81	59
9/14/80	3641.2	74	60
9/15/80	3658.7	62	53
9/16/80	3676.7	64	52
9/17/80	3690.2	61	46
9/18/80	3702.9	68	36
9/19/80	3719.9	72	42
9/20/80	3747.4	75	60
9/21/80	3776.9	75	64
9/22/80	3795.4	69	48
9/23/80	3806.4	61	41
9/24/80	3817.8	65	37
9/25/80	3831.8	66	42
9/26/80	3838.8	56	37
9/27/80	3849.0	64	34
9/28/80	3862.5	63	44
9/29/80	3880.5	73	43
9/30/80	3900.0	76	43
10/ 1/80	3920.5	73	48
10/ 2/80	3933.5	64	42
10/ 3/80	3936.1	46	39
10/ 4/80	3937.6	45	34
10/ 5/80	3941.1	49	36
10/ 6/80	3947.4	57	31
10/ 7/80	3957.6	66	29
10/ 8/80	3962.2	53	32
10/ 9/80	3969.3	59	30
10/10/80	3979.5	64	34
10/11/80	3988.0	49	48
10/12/80	3994.5	53	40
10/13/80	4002.2	60	31
10/14/80	4002.6	42	33
10/15/80	4005.9	49	35
10/16/80	4017.9	63	41
10/17/80	4034.9	67	47
10/18/80	4042.9	50	46
10/19/80	4049.9	52	42
10/20/80	4053.9	48	40
10/21/80	4057.9	50	36
10/22/80	4061.4	52	25
10/23/80	4068.0	55	37
10/24/80	4077.9	62	37
10/25/80	4079.9	43	41
10/26/80	4079.9	39	36
10/27/80	4080.0	41	28
10/28/80	4080.1	41	25
10/29/80	4081.3	46	16
10/30/80	4083.5	49	19
10/31/80	4088.8	52	38

Appendix L.

Computer Source Code for *E. muscae*, OM and SCM Simulation Program.

```
      PROGRAM DRIVE(INPUT,OUTPUT,TAPE1,TAPE2,TAPE3,TAPE4)
C*********************************************
C VARIABLES USED :   DRIVE
C
C  BASE - BASE TEMPERATURE, BELOW WHICH NO D-DAYS ACCUMULATE
C  CUMDD - CUMULATIVE D-DAYS
C  DMAG - NUMBER OF DISEASED DEAD ONION MAGGOT ADULTS
C  DT - TIME INCREMENT
C  FRMDD - DEGREE DAYS
C  HOUR - (PI)/12, USED IN TEMPERATURE SINE WAVE
C  HRANG - DAILY TEMPERATURE RANGE
C  HTIME - TIME OF DAY, 0-24
C  IDAY - JULIAN DAY
C  IDT - NUMBER OF DT'S IN ONE DAY
C  LX - PARAMETER, 0=GO THROUGH INITIALIZATION,
C       1=SKIP INITIALIZATION
C  NDAY - NUMBER OF DAYS PROGRAM RUNS
C  OM - INITIAL ONION MAGGOT PUPAE COUNT
C  PINFCT - PERCENT INFECTION
C  PSUM - EMERGENCE RATE
C  PUPA1 - INITIAL SEED CORN MAGGOT COUNT, 1ST GENERATION
C  PUPA2 - INITIAL SEED CORN MAGGOT COUNT, 2ND GENERATION
C  SCSTOR - NUMBER OF SEED CORN MAGGOT ADULTS
C  SCUMDD - SOIL CUMULATIVE D-DAYS
C  SQ1 - NUMBER OF LIVING DISEASED ONION MAGGOT ADULTS
C  SQ2 - NUMBER OF LIVING DISEASED PRE-OVIPOSITIONAL
C        ONION MAGGOT ADULTS
C  STEMP - SOIL TEMPERATURE
C  STRG - ARRAY OF NUMBERS OF ONION MAGGOTS IN EACH LIFE STAGE
C  TEMP - TEMPERATURE IN EACH DT
C  THETA - ARGUMENT OF SINE FUCTION ; (HTIME-9)*HOUR
C  TMAX - MAXIMUM DAILY TEMPERATURE
C  TMIN - MINIMUM DAILY TEMPERATURE
C  TOTAL - TOTAL NUMBER OF ADULT ONION MAGGOTS
C  Z1 - NUMBER OF HOURS IN ONE DT
C*********************************************
C
C*********************************************
C SUBROUTINES CALLED :   DRIVE
C
C  DEGDAY - COMPUTES NUMBER OF DEGREE DAYS ACCUMULATED PER DAY
C  SCMAG - COMPUTES SEED CORN MAGGOT ADULT EMERGENCE
C          AND DEVELOPMENT
C  ENTMOP - COMPUTES ENTOMOPHTHORA DISEASE DEVELOPMENT
C  MAGGOT - COMPUTES ONION MAGGOT DEVELOPMENT FOR
C           EACH LIFE STAGE
C  ATEMP - READS AIR TEMPERATURE FROM TAPE1
C  STEMP - READS SOIL TEMPERATURE FROM TAPE2
C  FNL - TABLE LOOK-UP FUNCTION
C*********************************************
```

```
      DIMENSION STRG(6),STEMP(13),IDAYSP(20),IFDAY(20)
      COMMON/PASS1/TEMP,LX,DT,EGGT
      COMMON/PASS2/HTIME,DMAG,FAREA,BAREA
      COMMON/PASS3/STRG,SQ1,SQ2
      COMMON/PASS6/SCSTOR
      COMMON/PASS7/OM,OWPUPA,STMP,PSUM
      COMMON/PASS8/PUPA1,PUPA2,CUMDD,ISPMORT
      COMMON/PRPARM/OMPR,SCMPR,ENTPR
      COMMON/FUNG/IFMORT
      INTEGER OMPR,SCMPR,ENTPR
C *************************************************************
      DATA BASE/4.44/,LX/0/
      REWIND 1
      REWIND 2
      REWIND 3
      REWIND 4
      REWIND 5
C *************************************************************
C *************************************************************
C
C PROGRAM INITIALIZATION
      DO 77 I=1,20
      IFDAY(I)=0
77    IDAYSP(I)=0
C
      PRINT*,"WHAT IS THE TIME INCREMENT,DT ?"
      READ*,DT
      PRINT*,"WHAT IS THE INITIAL PUPAE COUNT ?"
      READ*,OM
      OM=OM/DT
      PRINT*,"WHAT IS THE SEED CORN MAGGOT DENSITY?"
      PRINT*,"GENERATION 1?"
      READ*,PUPA1
      PRINT*,"GENERATION 2?"
      READ*,PUPA2
      PRINT*,"WHAT IS THE FIELD AREA (M2)?"
      READ*,FAREA
      PRINT*,"WHAT IS THE BORDER AREA (M2)?"
      READ*,BAREA
      PRINT*,"ENTER NUMBER OF DAYS TO SPRAY WITH INSECTICIDE-"
      READ*,ISPRAY
      DO 66 I=1,ISPRAY
      PRINT*,"ENTER JULIAN DATE FOR SPRAY-",I
66    READ*,IDAYSP(I)
      ISPMORT=0
      IZ=1
      PRINT*,"ENTER NUMBER OF DAYS TO SPRAY WITH FUNGICIDE-"
      READ*,IFUNG
      DO 99 I=1,IFUNG
      PRINT*,"ENTER JULIAN DATE FOR SPRAY-",I
```

```
99      READ*,IFDAY(1)
        IFMORT=0
        IFZ=1
C
C ***********************************************************
        OMPR=0
        SCMPR=0
        ENTPR=0
C
C TIME SETTING
C
        Z1=DT*24.
        IDT=INT(1./DT+.005)
        HOUR=(22./7.)/12.
        CUMDD=0.
        SCUMDD=0.
        PRINT*,"HOW MANY DAYS SHALL IT RUN?"
        READ*,NDAYS
        FRMDD=0.
C
C ***********************************************************
C
C MAIN DAY LOOP
C
        DO 1000 L=1,NDAYS
        HTIME=0.
        PSUM=0.
C
C WEATHER INPUT AND CENTIGRADE CONVERSION WITH DDAY CALC.
        CALL ATEMP(IDAY,TMIN,TMAX,TMEAN,HRANG)
        CALL SSTEMP(IIDAY,STEMP,LX)
        CALL DEGDAY(TMAX,TMIN,BASE,FRMDD)
        IF(IDAY.NE.IDAYSP(IZ))GO TO 88
        IZ=IZ+1
        ISPMORT=1
88      CONTINUE
        IF(IDAY.NE.IFDAY(IFZ))GO TO 97
        IFZ=IFZ+1
        IFMORT=1
97      CONTINUE
C
C WITHIN DAY LOOP  J=1,IDT
        DO 900 J=1,IDT
C
C       INSTANTANEOUS TEMPERATURE AND DEVELOPMENT ESTIMATES
        CUMDD=CUMDD+FRMDD*DT
        HTIME=HTIME+Z1
        THETA=(HTIME-9.)*HOUR
        TEMP=TMEAN+HRANG*SIN(THETA)
        STMP=FNL(STEMP,0.,2.,13,HTIME)
```

```
      CTIME=HTIME-1/2*Z1
      STP=FNL(STEMP,0.,2.,13,CTIME)
      IF (STP.GT.BASE) SFRMDD=(STP-BASE)*DT
      IF (STP.LE.BASE) SFRMDD=.00001
      SCUMDD=SCUMDD+SFRMDD
      CALL MAGGOT
      CALL SCMAG
      CALL ENTMOP
      ISPMORT=0
      LX=1
900   CONTINUE
      TOTAL=STRG(2)+STRG(1)+SQ1+SQ2
      PINFCT=(SQ1+SQ2)/TOTAL
      IF(TOTAL.LE.0)PINFCT=0.
      WRITE (3,100) IDAY,CUMDD,STRG(5),STRG(4),STRG(3),STRG(2),
     +STRG(1),SQ1,SQ2,DMAG,SCSTOR
100   FORMAT (1X,15,10(2X,F9.1))
      WRITE (4,110) IDAY,CUMDD,PSUM,TOTAL,PINFCT
110   FORMAT (1X,15,4(2X,F10.3))
1000  CONTINUE
      OWPUPA=OWPUPA+STRG(4)+STRG(3)
      PRINT*,"OVERWINTERING PUPAE=",OWPUPA
      PRINT*,"THIRD EGGS EGGS LAID=",EGGT
      END
C
C
C
C ***********************************************************
C **********************SUBROUTINES**************************
C ***********************************************************
C
      SUBROUTINE DEVDEL(VIN,VOUT,R,STRG,DEL,DELP,DT,K,STORE)
C
C          VIN - UNLAGGED INPUT VARIABLE
C          VOUT - LAGGED OUTPUT VARIABLE
C          R - ARRAY OF INTERMEDIATE RATES
C          STRG - TOTAL IN STORAGE
C          DEL - MEAN DELAY
C          DELP - PREVIOUS MEAN DELAY
C          DT - TIME INCREMENT
C          K - NUMBER OF STAGES IN PROCESS
C          STORE - ARRAY OF INTERMEDIATE STORAGE
C
      DIMENSION R(K),STORE(K)
      FK=FLOAT(K)
      A=DT*FK/DEL
      V=VIN
      DELD=(DEL-DELP)/(DT*FK)
      DELP=DEL
      DO 10 I=1,K
```

```
      DR=R(1)
      R(1)=DR+A*(V-DR*(1.+DELD))
      V=DR
10    CONTINUE
      VOUT=R(K)
      STRG=0.
      DO 20 I=1,K
      STORE(I)=R(I)*DEL/FK
      STRG=STRG+STORE(I)
20    CONTINUE
      RETURN
      END
C
C
C
C
C
C **************************************************************
C
      SUBROUTINE DELAY(TEMP,DEL,A,B)
C
C          TEMP - TEMERATURE AT TIME OF EVALUATION
C          DEL - ARRAY OF DELAY RATES FOR ALL STAGES
C          A - A COEFFICIENTS FOR ALL STAGES
C          B - B COEFFICIENTS FOR ALL STAGES
C
      REAL A(6), B(6), DEL(5)
      IF (TEMP .LE. 4.44) DEL(1)=100
      IF (TEMP .GT. 4.44) DEL(1)=A(1)+B(1)/TEMP
      DO 10 I=2,3
      IF (TEMP .LE. 4.44) DEL(I)=100
      IF (TEMP .GT. 4.44) DEL(I)=A(I)*(TEMP**B(I))
10    CONTINUE
      DO 20 I=4,5
      IF (TEMP .LE. 4.44) DEL(I)=100
      IF (TEMP .GT. 4.44) DEL(I)=A(I)+B(I)/TEMP
20    CONTINUE
      RETURN
      END
C
C
C
C
C
C **************************************************************
      SUBROUTINE DEGDAY(XMAX,XMIN,BASE,XHEAT)
C
C XMAX - MAXIMIM TEMPERATURE
C XMIN - MINIMUM TEMPERATURE
C BASE - BASE TEMPERATURE, BELOW WHICH NO D-DAYS ACCUMULATE
```

```
C  XHEAT - D-DAYS
C
      DATA TPIE/6.283185308/, HPIE/1.570796327/
      IF (XMAX .GT. BASE) GOTO 10
      XHEAT=.00001
      RETURN
10    CONTINUE
      Z=XMAX-XMIN
      XM=XMAX+XMIN
      IF (XMIN .LT. BASE) GOTO 20
      XHEAT=XM/2.-BASE
      IF (XHEAT .GT. 0.) GOTO 30
      XHEAT=.00001
30    RETURN
20    CONTINUE
      TBASE=BASE*2.
      A=ASIN((TBASE-XM)/Z)
      XHEAT=(2.*COS(A)-(TBASE-XM)*(HPIE-A))/TPIE
      IF (XHEAT .GT. 0.) GOTO 40
      XHEAT=.00001
40    RETURN
      END
C
C
C*************************************************************
C
      SUBROUTINE MAGGOT
C*****************************************
C VARIABLES USED :    MAGGOT
C
C  A - ARRAY OF "A" COEFFICIENTS FOR ALL STAGES OF OM
C  B - ARRAY OF "B" COEFFICIENTS FOR ALL STAGES OF OM
C  BASE - BASE TEMPERATURE, BELOW WHICH NO D-DAYS ACCUMULATE
C  DEGGS - #OF EGGS PRODUCED BY DISEASED OM
C  DEL - ARRAY OF MEAN DELAY VALUES FOR ALL STAGES OF OM
C  DT - TIME INCREMENT
C  FEC - FECUNDITY RATE FOR HEALTHY ADULT OM
C  KS - NUMBER OF STAGES IN OVERWINTERING DELAY PROCESS
C  LX - PARAMETER ; 0=GO THROUGH INITIALIZATION,
C       1=SKIP INITIALIZATION
C  OM - INITIAL PUPAE COUNT FOR OM
C  OMOUT - ARRAY OF LAGGED OUTPUTS FOR EACH LIFE STAGE
C  PREVDEL - PREVIOUS MEAN DELAY VALUE
C  PUPAE - NUMBER OF OVERWINTERING PUPAE IN DELAY PROCESS
C  RATES - ARRAY OF INTERMEDIATE RATES FOR EACH LIFE
C          STAGE OF OM
C  SADULTS - NUMBER OF ADULTS LEAVING OVERWINTERING DELAY
C  SDEL - MEAN DELAY VALUE FOR OVERWINTERING PUPAE
C  SPDEL - PREVIOUS MEAN DELAY VALUE FOR OVERWINTERING PUPAE
C  SQ1 - NUMBER OF LIVING DISEASED ADULTS
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C   SQ2 - NUMBER OF LIVING DISEASED PREOVIPOSITIONAL ADULTS
C   SRATES - ARRAY OF INTERMEDIATE RATES FOR
C            OVERWINTERING PUPAE
C   STORE - ARRAY OF INTERMEDIATE STORAGE FOR EACH LIFE STAGE
C   STRG - NUMBER OF INDIVIDUALS IN EACH LIFE STAGE
C   SURVIVE - ARRAY OF SURVIVAL RATES FOR EACH LIFE STAGE
C   TEMP - TEMPERATURE AT EACH DT
C*****************************************
C
C*****************************************
C SUBROUTINES CALLED :     MAGGOT
C   DELAY - COMPUTES MEAN DELAY VALUES FOR EACH LIFESTAGE OF
C           OM BASED ON TEMP
C   DEVDEL - TIME-VARYING DISTRIBUTED DELAY
C*****************************************
      REAL A(6),B(6),OMOUT(6),RATES(20,5),STRG(6),DEL(5),
     +SURVIVE(5),PREVDEL(5),SRATES(20),STORE(20),ARG(4),VAL
     +(4),VAL2(4)
      COMMON/PASS1/TEMP,LX,DT,EGGT
      COMMON/PASS3/STRG,SQ1,SQ2
      COMMON/PASS4/RATES,DEL,DEGGS,OMOUT,SURADT
      COMMON/PASS7/OM,OWPUPA,STMP,PSUM
      COMMON/PASS8/PUPA1,PUPA2,CUMDD,ISPMORT
      COMMON/PRPARM/OMPR,SCMPR,ENTPR
      INTEGER OMPR,SCMPR,ENTPR
      DATA A/-37.6,899.9,1167.4,-4.41,-1.85,3820./
      DATA B/1475.2,-1.6,-1.4,478.7,112.4,-1.8/,BASE/4.44/
      DATA SURVIVE/1.,1.,1.,1.,1./
      DATA ARG/10.,15.56,26.67,32.22/
      DATA VAL1/-.0607,-.2157,-.2727,-.62262/
      DATA VAL2/-.0058,-.028,-.0672,-.1095/
C
C PROGRAM INITIALIZATION
      IF(LX.GT.0)GO TO 810
C
C     OVERWINTERING PUPAE
      OWPUPA=0.
      DO 60 I=1,20
      STORE(I)=0.
60    SRATES(I)=0.
      SADULTS=PUPAE=0.
      KS=20
      SPDEL=100.
      SDEL=0.
      SQ1=0.
C
C     ONION MAGGOT EGGS-ADULTS
      DEGGS=0.
      FEC=6.
      EGGT=0.
```

```
      OMOUT(6)=0.
      STRG(6)=0.
      DO 1 I=1,5
      PREVDEL(I)=100.
      DEL(I)=0.
      STRG(I)=0.
      OMOUT(I)=0.
1     CONTINUE
      DO 10 II=1,5
      DO 10 I=1,20
10    RATES(I,II)=0.
810   CONTINUE
C
C INSTANTANEOUS DEVELOPMENTAL ESTIMATES
      CALL DELAY(TEMP,DEL,A,B)
      CALL OWDEL(STMP,A(3),B(3),DEL(3))
C
      EGGT=EGGT+DT*OMOUT(6)
C ONION MAGGOT DELAYS, EGGS-ADULTS AND OW PUPAE
      DO 800 I=1,5
      CALL DEVDEL(OMOUT(I+1),OMOUT(I),RATES(1,I),STRG(I),
     +DEL(I),PREVDEL(I),DT,KS,STORE)
      OMOUT(I)=OMOUT(I)*SURVIVE(I)
800   CONTINUE
C COMPUTE SURVIVAL
      TSUR1=TABLE(VAL1,ARG,TEMP,4)
      TSUR2=TABLE(VAL2,ARG,TEMP,4)
      SUREGG=AMIN1(EXP(TSUR1*DT),1.)
      SRPUPA=AMIN1(EXP(TSUR2*DT),1.)
      SURADT=SRPUPA
      IF (TEMP.GE.31.1) SURADT=.9
      IF(ISPMORT.EQ.1)SURADT=SURADT*.7
      DO 1000 I=1,20
      RATES(I,5)=RATES(I,5)*SUREGG
      RATES(I,4)=RATES(I,4)*SRPUPA
      RATES(I,2)=RATES(I,2)*SURADT
      RATES(I,1)=RATES(I,1)*SURADT
1000  CONTINUE
      CALL DEVDEL(OM,SADULTS,SRATES(1),PUPAE,DEL(3),SPDEL,
     +DT,KS,STORE)
      OMOUT(3)=OMOUT(3)+SADULTS
      PSUM=PSUM+OMOUT(3)
      OM=0.
      OMOUT(6)=DT*(STRG(1)*FEC+DEGGS)
      IF(CUMDD.LT.2000) GO TO 820
      OWPUPA=OWPUPA+DT*OMOUT(3)
      OMOUT(3)=0.
820   RETURN
      END
      SUBROUTINE ENTMOP
C*****************************************
```

```
C VARIABLES USED :    ENTMOP
C
C C - ARRAY OF FECUNDITY RATES FOR DISEASED OM
C DEGGS - # OF EGGS PRODUCED BY DISEASED OM
C DEL - ARRAY OF MEAN DELAY VALUES FOR OM
C DELSC - MEAN DELAY VALUE FOR SEED CORN MAGGOT
C DELT2 - MEAN DELAY VALUE FOR ENTOMOTHPHORA
C DEL1A - ARRAY OF DELAY VALUES OF OM ADULTS FOR 2-D DELAY
C DEL1B - ARRAY OF DELAY VALUES OF OM PREOVIPOSITIONAL
C         ADULTS FOR 2-D DELAY
C DEL2 - ARRAY OF DELAY VALUES ON ENTOMOTHPHORA FOR 2-D DELAY
C DMAG - NUMBER OF DEAD DISEASED OM
C DSC - NUMBER OF DEAD DISEASED SEED CORN MAGGOTS
C DT - TIME INCREMENT
C HTIME - TIME OF DAY, Ø-24
C INFSC - ARRAY OF INFECTED SEED CORN MAGGOTS
C INFT - INFECTION RATE
C K - NUMBER OF STAGES IN 2-D DELAY PROCESS (LEFT TO RIGHT)
C KZ - NUMBER OF STAGES IN 2-D DELAY PROCESS (TOP TO BOTTOM)
C LX - PARAMETER ; Ø= GO THROUGH INITIALIZATION PROCESS,
C      1= SKIP INITIALIZATION
C NUMBER - TOTAL NUMBER OF SCM AND OM ADULTS
C OB1 - ARRAY OF DISEASED OM ADULTS LEAVING 2-D DELAY,
C       OUT BOTTOM
C OB2 - ARRAY OF DISEASED PREOVIPOSITIONAL OM ADULTS LEAVING
C       2-D DELAY, OUT BOTTOM
C OR1 - ARRAY OF DISEASED OM ADULTS LEAVING 2-D DELAY,
C       OUT RIGHT
C OR2 - ARRAY OF DISEASED PREOVIPOSITIONAL OM ADULTS LEAVING
C       2-D DELAY, OUT RIGHT
C OUTB1 - NUMBER OF DISEASED DEAD OM ADULTS LEAVING 2-D DELAY
C OUTB2 - NUMBER OF DISEASED DEAD PREOVIPOSITIONAL OM ADULTS
C         LEAVING 2-D DELAY
C OUTR1 - NUMBER OF LIVING DISEASED OM ADULTS LEAVING
C OUTR2 - NUMBER OF LIVING DISEASED PREOVIPOSITIONAL OM
C         ADULTS LEAVING
C QDUM1 - TEMPORARY STORAGE FOR 2-D DELAY, OM ADULTS
C QDUM2 - TEMPORARY STORAGE FOR 2-D DELAY, PREOVIPOSITIONAL
C         OM ADULTS
C Q1 - ARRAY OF INTERMEDIATE STORAGE FOR DISEASED OM ADULTS
C Q2 - ARRAY OF INTERMEDIATE STORAGE FOR DISEASED
C      PREOVIPOSITIONAL OM ADULTS
C RATES - ARRAY OF INTERMEDIATE RATES FOR HEALTHY OM
C SCRATE - ARRAY OF INTERMEDIATE RATES FOR HEALTHY SCM
C SCSTOR - NUMBER OF SCM ADULTS
C SPORES - TOTAL NUMBER OF SPORES
C SQ1 - NUMBER OF LIVING DISEASED OM ADULTS
C SQ2 - NUMBER OF LIVING PREOVIPOSITIONAL OM ADULTS
C STRG - NUMBER OF HEALTHY INDIVIDUALS IN EACH LIFE
C        STAGE OF OM
```

```
C TEMP - TEMPERATURE AT EACH DT
C TRIN1 - INPUT ARRAY DISEASED ADULTS FOR 2-D DELAY
C TRIN2 - INPUT ARRAY OF DISEASED PREOVIPOSITIONAL ADULTS
C         FOR 2-D ARRAY
C TSTOR1 - ARRAY OF INFECTED OM ADULTS FOR INPUT IN TO 2-D
C          DELAY
C TSTOR2 - ARRAY OF INFECTED PREOVIPOSITIONAL OM ADULTS
C          FOR 2-D DELAY
C*****************************************
C
C*****************************************
C SUBROUTINES USED :     ENTMOP
C INFECT - COMPUTES INFECTION RATE
C DELAY2 - COMPUTES DELT2-MEAN DELAY VALUE FOR ENTOMOTHPHORA
C DEL2D - TWO DIMENSIONAL TIME-VARYING DISTRIBUTED
C         DELAY PROCESS
C*****************************************
      REAL RATES(20,5),DEL(5),STRG(6),TSTOR1(20),TRIN1(20,20)
     +TRIN2(20,20),DEL1A(20,20),DEL2(20,20),DEL1B(20,20),
     +Q2(20,20),QDUM1(20),QDUM2(20),OR1(20),OR2(20),OB1(20),
     +TSTOR2(20),INFT,INFSC(20),SCRATE(20),C(20),TQ1(20),
     +Q1(20,20),OB2(20),OMOUT(6)
      REAL INFSTG,INFSTO(20),DSCRAT(20)
      COMMON/PASS1/TEMP,LX,DT,EGGT
      COMMON/PASS2/HTIME,DMAG,FAREA,BAREA
      COMMON/PASS3/STRG,SQ1,SQ2
      COMMON/PASS4/RATES,DEL,DEGGS,OMOUT,SURADT
      COMMON/PASS5/SC,SCRATE,DELSC,SCINF
      COMMON/PASS6/SCSTOR
      COMMON/PASS8/PUPA1,PUPA2,CUMDD,ISPMORT
      COMMON/PRPARM/OMPR,SCMPR,ENTPR
      INTEGER OMPR,SCMPR,ENTPR
      DATA C/0.,0.,0.,0.,0.,0.,.06,.06,.06,1.8,1.8,1.8,
     +2.7,2.7,2.7,2.7,2.7,2.7,2.7,2.7/
C PROGRAM INITIALIZATION
      K=20
      K2=20
      IF (LX.GT.0) GO TO 100
      DO 3 I=1,K
      DO 2 J=1,K2
      TRIN1(I,J)=0.
      TRIN2(I,J)=0.
      DEL1A(I,J)=100.
      DEL1B(I,J)=100.
      DEL2(I,J)=100.
      Q1(I,J)=0.
      Q2(I,J)=0.
2     CONTINUE
3     CONTINUE
      OUTR1=0.
      DELT=100.
```

```
      INFSTG=0.
      OUTB1=0.
      OUTR2=0.
      OUTB2=0.
      SQ1=0.
      SQ2=0.
      K2=20
      DMAG=0.
      DSC=0.
      SCINF=0.
      INFT=0.
      DO 4 I=1,20
      OR1(I)=0.
      OR2(I)=0.
      OB1(I)=0.
      OB2(I)=0.
      QDUM1(I)=0.
      QDUM2(I)=0.
      DSCRAT(I)=0.
      INFSC(I)=0.
      INFSTO(I)=0.
4     CONTINUE
100   CONTINUE
C *****************************************************************
C COMPUTE INFECTION DELAYS
C *****************************************************************
      NUMBER=STRG(1)+STRG(2)+SQ1+SQ2+SCSTOR
C COMPUTE INFECTION RATE
      DFLIES=DSC+DMAG
      CALL INFECT2(DFLIES,HTIME,TEMP,CUMDD,LX,BAREA,FAREA,DT,
     +INFT)
      FK=FLOAT(K)
C COMPUTE NUMBER OF ADULTS INFECTED
      DO 10 J=1,K
      TSTOR1(J)=INFT*RATES(J,1)
      TRIN1(1,J)=TSTOR1(J)*DEL(1)/FK
      RATES(J,1)=RATES(J,1)-TSTOR1(J)
      TSTOR2(J)=INFT*RATES(J,2)
      TRIN2(1,J)=TSTOR2(J)*DEL(2)/FK
      RATES(J,2)=RATES(J,2)-TSTOR2(J)
10    CONTINUE
      TRIN1(1,1)=OR2(1)+TRIN1(1,1)
      DO 20 J=2,K2
      TRIN1(J,1)=OR2(J)
20    CONTINUE
C COMPUTE NUMBER OF SC ADULTS INFECTED
      DSC=0.
      DO 25 I=1,20
      INFSC(I)=INFT*SCRATE(I)
      SCRATE(I)=SCRATE(I)-INFSC(I)
```

```
      DSCRAT(I)=DSCRAT(I)+INFSC(I)
25    CONTINUE
      SCINF=SCINF/DT
C COMPUTE NUMBER OF INFECTED OM AT EMERGENCE
      AZYINF=.1*DT
      IF (CUMDD.GT.1500.) AZYINF=.3*DT
      TOMOUT=AZYINF*OMOUT(3)
      OMOUT(3)=OMOUT(3)-TOMOUT
      TRIN2(1,1)=TRIN2(1,1)+TOMOUT*DEL(3)/FK
C COMPUTE DELAY RATE FOR ENTOMOP.
      CALL DELAY2(TEMP,DELT2)
      DO 40 I=1,20
      DO 30 J=1,20
      DEL1A(I,J)=K/DEL(1)
      DEL1B(I,J)=K/DEL(2)
      DEL2(I,J)=K2/DELT2
      Q1(I,J)=Q1(I,J)*SURADT
      Q2(I,J)=Q2(I,J)*SURADT
30    CONTINUE
40    CONTINUE
C ENTOMOP. INFECTION DELAYS
      CALL DEVDEL(SCINF,DSC,INFSC,INFSTG,DELT2,DELT,
     +DT,K,INFSTO)
      CALL DEL2D(TRIN1,OUTR1,OUTB1,DEL1A,DEL2,Q1,SQ1,DT,K,K2,
     +QDUM1,OR1,OB1)
      CALL DEL2D(TRIN2,OUTR2,OUTB2,DEL1B,DEL2,Q2,SQ2,DT,K,K2,
     +QDUM2,OR2,OB2)
      DMAG=OUTB1+OUTB2
C COMPUTE # OF EGGS PRODUCED BY DISEASED OM--DEGGS
      DEGGS=0.
      DO 60 I=1,20
      TQ1(I)=0.
      DO 50 J=1,20
      TQ1(I)=TQ1(I)+Q1(I,J)/DT
50    CONTINUE
      DEGGS=DEGGS+C(I)*TQ1(I)
60    CONTINUE
      RETURN
      END
      SUBROUTINE SCMAG
C*****************************************
C VARIABLES USED :   SCMAG
C
C AOUT - LAGGEDD OUTPUT FOR SEED CORN MAGGOT DELAY
C CUMDD - CUMULATIVE DEGREE DAYS
C DELSC - MEAN DELAY VALUE FOR SEED CORN MAGGOT
C DT - TIME INCREMENT
C EMERGE - NUMBER OF EMERGED SCM TO ENTER ADULT DELAY
C LX - PARAMETER ; 0 = GO THROUGH INITIALIZATION,
C      1 = SKIP INITIALIZATION
C MEAN - CUMDD AT AT 50 EMERGENCE FOR GEN1 AND GEN2
```

```
C         OF SEED CORN MAGGOT
C PDEV - PERCENT EMERGENCE OF SCM POPULATION
C PREDEV - PREVIOUS CUMULATIVE PERCENT EMERGENCE
C PREVDELSC - PREVIOUS MEAN DELAY VALUE
C PROB - CUMULATIVE PERCENT EMERGENCE
C PUPA1 - NUMBER OF SCM IN 1ST GENERATION
C PUPA2 - NUMBER OF SCM IN 2ND GENERATION
C SCRATE - ARRAY OF INTERMEDIATE RATES FOR SCM DELAY
C SCSTOR - NUMBER OF SCM ADULTS
C SIGMA - STANDARD DEVIATION WITH RESPECT TO MEAN
C TEMP - TEMPERATURE AT EACH DT
C Z - INPUT FOR NORMAL DISTRIBUTION USED TO COMPUTE PROB
C**********************************************
C
C**********************************************
C SUBROUTINES CALLED :    SCMAG
C DELAY3 - COMPUTES DELSC; MEAN DELAY VALUE; ACCORDING
C          TO TEMP
C DEVDEL - TIME-VARYING DISTRIBUTED DELAY
C NORMAL - COMPUTES PROB USING CURRENT VALUE OF Z
C**********************************************
      DIMENSION SCRATE(20),PROB(2),STORE(20),XMEAN(2),SIGMA(2)
      DIMENSION PREDEV(2),Z(2),PDEV(2)
      COMMON/PASS1/TEMP,LX,DT,EGGT
      COMMON/PASS5/SC,SCRATE,DELSC,SCINF
      COMMON/PASS6/SCSTOR
      COMMON/PASS8/PUPA1,PUPA2,CUMDD,ISPMORT
      COMMON/PRPARM/OMPR,SCMPR,ENTPR
      INTEGER OMPR,SCMPR,ENTPR
      DATA XMEAN(1)/202.78/,XMEAN(2)/1511.11/,SIGMA(1)/77.78/,
     +SIGMA(2)/138.89/,K/20/
C PROGRAM INITIALIZATION
      IF (LX.GT.0)GO TO 100
      PROB(1)=PROB(2)=0.
      PREVDEL=100.
      DELSC=0.
      AOUT=0.
      DO 5 I=1,20
      SCRATE(I)=0.
      STORE(I)=0.
5     CONTINUE
100   CONTINUE
C COMPUTE SC ADULT EMERGENCE
      DO 10 I=1,2
      PREDEV(I)=PROB(I)
      Z(I)=(CUMDD-XMEAN(I))/SIGMA(I)
      CALL NORMAL(Z(I),PROB(I),DEN)
      PDEV(I)=PROB(I)-PREDEV(I)
10    CONTINUE
      EMERGE=(PDEV(1)*PUPA1+PDEV(2)*PUPA2)/DT
```

```
C COMPUTE INFECTION BY ENT AT EMERGENCE
      TSCINF=.25*DT*EMERGE
      EMERGE=EMERGE-TSCINF
      SCINF=TSCINF*DT
C APPLICATION OF SPRAY MORTALITY
      IF(ISPMORT.NE.1)GO TO 1000
      DO 6 IS=1,20
6     SCRATE(IS)=SCRATE(IS)*.2
C COMPUTE SC ADULT DELAY
1000  CALL DELAY3(TEMP,DELSC)
      CALL DEVDEL(EMERGE,AOUT,SCRATE,SCSTOR,DELSC,PREVDEL,
     +DT,K,STORE)
      RETURN
      END
      SUBROUTINE NORMAL(X,P,D)
C
C
C  COMPUTES Y=P(X)=PROBABILITY THAT THE RANDOM VARIABLE
C DISTRIBUTED NORMALLY (0,1) IS LESS THAN OR EQUAL TO X.
C THE ORDINATE OF THE NORMAL DENSITY AT X, IS ALSO COMPUTED.
C
C
C*********************************************
C VARIABLES USED :     NORMAL
C
C X - INPUT SCALAR FOR WHICH P(X) IS COMPUTED
C P - OUTPUT PROBABILITY
C D - OUTPUT DENSITY
C*********************************************
      AX=ABS(X)
      T=1.0/(1.0+.2316419*AX)
      D=0.3989423*EXP(-X*X/2.0)
      P=1.0-D*T*((((1.330274*T-1.821256)*T+1.781478)*T-
     +0.3565638)*T+0.3193815)
      IF (X) 1,2,2
1     P=1.0-P
2     RETURN
      END
      SUBROUTINE DELAY3(TEMP,DEL)
C*********************************************
C VARIABLES USED :    DELAY3
C
C TEMP - TEMPERATURE AT EACH DT
C A - "A" COEFFICIENT FOR SEED CORN MAGGOT
C B - "B" COEFFICIENT FOR SEED CORN MAGGOT
C DEL - MEAN DELAY VALUE
C*********************************************
      A=-37.602
      B=1475.231
      IF (TEMP.LE.4.44) DEL=100.
```

```
      IF (TEMP.GT.4.44) DEL=A+B/TEMP
      RETURN
      END
      SUBROUTINE DELAY2(TEMP,DEL2)
C*********************************************
C VARIABLES USED :     DELAY2
C
C TEMP - TEMPERATURE AT EACH DT
C A - "A" FOR ENT
C B - "B" FOR ENT
C DELZ - MEAN DELAY VALUE FOR ENT
C*********************************************
      A=-.02518
      B=153.55
      IF (TEMP.LE.4.44) DEL2=100.
      IF (TEMP.GT.4.44) DEL2=A+B/TEMP
      RETURN
      END
      SUBROUTINE DEL2D(TRIN,OUTR,OUTB,DEL1,DEL2,Q,SQ,DT,K1,
C*********************************************
C VARIABLES USED :    DEL2D
C
C DEL1 - MEAN DELAY VALUE FOR LEFT - RIGHT FLOW
C DEL2 - MEAN DELAY VALUE FOR TOP - BOTTOM FLOW
C K1 - NUMBER OF DELAY STAGES, LEFT - RIGHT
C K2 - NUMBER OF DELAY STAGES, TOP - BOTTOM
C OB1 - ARRAY OF OUTPUT, OUT BOTTOM
C OR1 - ARRAY OF OUTPUT, OUT RIGHT
C OUTB - OUTPUT OF STAGE K2, BOTTOMMOST STAGE
C OUTR - OUTPUT OF STAGE K1, RIGHTMOST STAGE
C Q - ARRAY OF K1 * K2 STORAGES IN DELAY PROCESS
C RIL - RATE IN LEFT
C RIT - RATE IN TOP
C ROB- RATE OUT BOTTOM
C ROR - RATE OUT RIGHT
C SQ - SUM OF ALL STORAGES IN THE DELAY PROCESS
C TRIN - K1 BY K2 ARRAY OF INPUTS TO THE K1 * K2 STAGES
C*********************************************
     +K2,QDUM,OR1,OB1)
      DIMENSION TRIN(K1,K2),Q(K1,K2),DEL1(K1,K2),DEL2(K1,K2)
     +,QDUM(K2),OR1(20),OB1(20)
      OUTR=OUTB=0.
      SQ=0.
      DO 80 II=1,K1
      DO 70 JJ=1,K2
      ROR=DEL1(II,JJ)*Q(II,JJ)
      OUTR1=0.
      IF (II.EQ.K1) OUTR1=ROR
      IF (II.EQ.K1) OR1(JJ)=OUTR1
      ROB=DEL2(II,JJ)*Q(II,JJ)
```

```
      OUTB1=0.
      IF (JJ.EQ.K2) OUTB1=ROB
      IF (JJ.EQ.K2) OB1(I1)=OUTB1
      R1L=0.
      IF (I1.NE.1) R1L=DEL1(I1-1,JJ)*QDUM(JJ)
      RIT=0.
      IF (JJ.NE.1) RIT=DEL2(I1,JJ-1)*QDUM(JJ-1)
      QDUM(JJ)=Q(I1,JJ)
      Q(I1,JJ)=Q(I1,JJ)+DT*(TRIN(I1,JJ)+R1L+RIT-ROR-ROB)
      OUTR=OUTR+OUTR1
      OUTB=OUTB+OUTB1
      SQ=SQ+Q(I1,JJ)/DT
70    CONTINUE
80    CONTINUE
      RETURN
      END
      SUBROUTINE INFECT(NUMBER,SPORES,INFT,HTIME)
      REAL INFT
      INFT=.01
      RETURN
      END
      SUBROUTINE ATEMP(IDAY,TMIN,TMAX,TMEAN,HRANG)
C*************************************************************
C VARIABLES USED:     ATEMP
C  IDAY - JULIAN DAY
C  TMIN - MINIMUM TEMPERATURE
C  TMAX - MAXIMUM TEMPERATURE
C  TMEAN - MEAN TEMPERATURE
C  HRANG - TEMPERATURE RANGE
C*************************************************************
      READ(1,50) IDAY,TMAX,TMIN
50    FORMAT(1X,5X,I3,2(5X,F3.0))
      TMAX=(TMAX-32.)*5./9.
      TMIN=(TMIN-32.)*5./9.
      TMEAN=(TMAX+TMIN)/2.
      HRANG=(TMAX-TMIN)/2.
      RETURN
      END
      SUBROUTINE SSTEMP(I1DAY,STEMP,LX)
C*************************************************************
C VARIABLES USED:        STEMP
C  I1DAY - JULIAN DAY
C  STEMP - SOIL TEMPERATURE
C*************************************************************
      DIMENSION STEMP(13),DAY(13)
      IF (LX.GT.0) GO TO 100
      DO 10 I=1,13
      READ (2,50) STEMP(I)
      STEMP(I)=(STEMP(I)-32.)*5./9.
10    CONTINUE
```

```
      GO TO 30
100   CONTINUE
      STEMP(1)=STEMP(13)
      DO 20 I=2,13
      READ (2,50) STEMP(I)
      STEMP(I)=(STEMP(I)-32.)*5./9.
20    CONTINUE
30    CONTINUE
50    FORMAT(F2.0)
      RETURN
      END
      FUNCTION FNL(DVAL,XS,DX,N,X)
C TABLE LOOK-UP FUNCTION : GIVES Y-VALUE FOR ANY X-VALUE
C INPUT,  GIVEN POINTS ON A CURVE (DVAL).
C
C  VARIABLES :   FNL
C
C DVAL - ARRAY CONTAINING Y-VALUES
C XS - FIRST X-VALUE
C DX - INCREMENT IN X-VALUES
C N - NUMBER OF POINTS
C X - X-VALUE INPUT
C
      DIMENSION DVAL(1)
      IF (X-XS) 10,10,5
5     IF (X-XS-N*DX) 20,15,15
10    FNL=DVAL(1)
      GOTO 25
15    FNL=DVAL(N+1)
      GOTO 25
20    XD=X-XS
      I=1.0+XD/DX
      FNL=(XD-FLOAT(I-1)*DX)*(DVAL(I+1)-DVAL(I))/DX+DVAL(I)
25    RETURN
      END
      SUBROUTINE OWDEL(STMP,A,B,SDEL)
C*****************************************************
C VARIABLES USED:          OWDEL
C  STMP - SOIL TEMPERATURE
C  A - A COEFFICIENT FOR PUPAE
C  B - B COEFFICIENT FOR PUPAE
C  SDEL - DELAY RATE FOR PUPAE
C*****************************************************
      IF (STMP.LE.4.44) SDEL=100.
      IF (STMP.GT.4.44) SDEL=A*(STMP**B)
      RETURN
      END
      FUNCTION TABLE(VAL,ARG,DUMMY,K)
C
C ***************************************************
```

```
C ***********************************************************
C VARIABLES USED:          TABLE
C
C VAL - ARRAY OF Y-VALUES
C ARG - ARRAY OF X-VALUES
C DUMMY - X-VALUE INPUT
C K - DIMENSION OF VAL AND ARG
C ***********************************************************
C
C THIS FUNCTION COMPUTES THE Y VALUE FOR ANY X VALUE GIVEN.
C THE ELEMENTS OF THE ARGUMENT ARRAY DO NOT HAVE TO BE
C EQUALLY SPACED AND THIS FUNCTION DOES NOT ESTRAPOLATE
C BEYOND THE END POINTS.
C ***********************************************************
C ***********************************************************
      DIMENSION VAL(1),ARG(1)
      DUM=AMAX1(AMIN1(DUMMY,ARG(K)),ARG(1))
      DO 1 I=2,K
      IF (DUM.GT.ARG(1)) GO  TO 1
      TABLE=(DUM-ARG(I-1))*(VAL(I)-VAL(I-1))/
     +(ARG(I)-ARG(I-1))+VAL(I-1)
      RETURN
1     CONTINUE
      RETURN
      END
      SUBROUTINE INFECT2(DFLIES,HTIME,TEMP,CUMDD,LX,BAREA,
     +FATEA,DT,INFT)
C ***********************************************************
C VARIABLES USED:              INFECT2
C DFLIES - NUMBER OF DEAD DISEASED FLIES
C HTIME - TIME OF DAY IN HOURS
C TEMP - TEMPERATURE
C CUMDD - CUMULATIVE DEGREE DAYS
C LX - PARAMETER PASSED FOR INITIALIZATION
C BAREA - BORDER AREA
C FAREA - FIELD AREA
C DT - TIME INCREMENT
C SUMFLY - # OF DEAD FLIES IN ONE DAY
C TOTCAD - TOTAL NUMBER OF CADAVERS PER DAY
C CADM2 - NUMBER OF CADAVERS PER METER SQUARED
C SPORE - SPORES PER DT
C TOTAL - TOTAL NUMBER OF SPORES
C XLOAD - HABITAT LOADING
C INFT - INFECTION RATE
C ***********************************************************
C SUBROUTINES CALLED:
C NORMAL
C TABLE - TABLE LOOK UP FUNCTION
C ***********************************************************
C ***********************************************************
      DIMENSION VAL(21),ARG(21)
```

```
      COMMON/FUNG/IFMORT
      REAL INFT
      DATA XMTEMP/16.5/,XSTEMP/3.878/,XMTIME/5.85/,XSTIME/2.032/
      DATA VAL/.001,.05,.1,.15,.2,.25,.3,.35,.4,.45,.5,.55,.6,
     +.65,.7,.75,.8,.85,.9,.95,.99/
      DATA ARG/0.,3.36,3.72,3.96,4.16,4.33,4.48,4.61,4.75,4.87,
     +5.00,5.13,5.25,5.39,5.52,5.67,5.84,6.04,6.28,6.64,7.33/
C PROGRAM INITIALIZATION
      IF (LX.GT.0) GO TO 10
      SUMFLY=0.
      Y=24*DT+19.
      Z=24*DT+7.
      CADM2=0.
      TOTCAD=0.
      POLD=0.
      TOTAL=0.
C COMPUTE SUM OF FLIES DAILY
10    SUMFLY=SUMFLY+DFLIES
      IF (HTIME.GT.19..AND.HTIME.LT.Y) TOTCAD=SUMFLY
      IF (HTIME.GT.19..AND.HTIME.LT.Y) SUMFLY=0.
      CADM2=TOTCAD/BAREA
C COMPUTE NUMBER OF SPORES PER FLY
      XZ=(TEMP-XMTEMP)/XSTEMP
      CALL NORMAL(XZ,P,D)
      SPORE=D*3500000.
      IF (HTIME.GT.7..AND.HTIME.LT.19.) GO TO 100
      XI=HTIME-19.
      IF (HTIME.LT.19.) XI=HTIME+5.
      XZ=(XI-XMTIME)/XSTIME
      CALL NORMAL(XZ,P,D)
      WEIGHT=P-POLD
      WEIGHT=ABS(WEIGHT)
      POLD=P
      SPORE=SPORE*WEIGHT
      TOTAL=TOTAL+SPORE
C COMPUTE INFECTION RATE WHEN IT=1
100   IT=0
      IF (HTIME.GT.7..AND.HTIME.LT.Z) IT=1
      IF (IT.EQ.0) GO TO 200
      TSPORE=TOTAL*CADM2
      TOTAL=0.
      IF (TSPORE.LE.0.) TSPORE=.1
      TSPORE=TSPORE/1000000.
      PMORT=4.86+2.029*(ALOG10(TSPORE))
      PERINF=TABLE(VAL,ARG,PMORT,21)
      XLOAD=30.
      IF (CUMDD.GT.361.) XLOAD=44.55-.0403*CUMDD
      IF (CUMDD.GT.1055.) XLOAD=2.
      IF (CUMDD.GT.1805.) XLOAD=-850.2+.472*CUMDD
      IF (CUMDD.GT.2055.) XLOAD=120.
```

```
      TBAREA=XLOAD*BAREA
      INFT=TBAREA/(FAREA+TBAREA)*PERINF
C  APPLICATION OF FUNGICIDE MORTALITY TO GERMINATING SPORES
      IF(IFMORT.GT.1)INFT=0.
      IF(IFMORT.EQ.3)IFMORT=0
      IF(IFMORT.EQ.2)IFMORT=3
      IF(IFMORT.EQ.1)IFMORT=2
      WRITE (5,500) CUMDD,INFT,PERINF,CADM2,TSPORE
500   FORMAT(1X,5(2X,F10.4))
      GO TO 300
200   INFT=0.
300   RETURN
      END
```