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EFFECTS OF DENSITY AND HOST PLANT TYPE ON FECUNDITY AND SURVIVAL OF *DELIA RADICUM* (BOUCHÉ), *D. ANTIQUA* (MEIGEN) AND *D. PLATURA* (MEIGEN) (DIPTERA: ANTHOMYIIDAE).

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November, 1992

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ISBN 0-315-87854-1

Canada

SHORT TITLE

Fecundity and Survival of the Cabbage,
Onion and Seed Corn Maggots.

CHRISTINE M. NORONHA

ABSTRACT

Christine M. Noronha

EFFECTS OF DENSITY AND HOST PLANT TYPE ON FECUNDITY AND SURVIVAL OF *DELIA RADICUM* (BOUCHÉ), *D. ANTIQUA* (MEIGEN) AND *D. PLATURA* (MEIGEN) (DIPTERA: ANTHOMYIIDAE).

The effects of intraspecific and interspecific competition, host plant, and prior host plant experience on fecundity, rate of oviposition and mortality of adults and larval survival of *Delia radicum* Bouché (Cabbage Maggot (CM)), *D. antiqua* Meigen (Onion Maggot (OM)), and *D. platura* Meigen (Seed Corn Maggot (SCM)), were studied on cabbage, onion and bean plants.

An optimum density for maximum fecundity per female was observed when the four experimental densities were compared. This optimum density was higher on host than on non-host plants. CM females were host specific and did not oviposit on non-host plants. Rates of oviposition and mortality over a 30-day period were calculated for each density. The rate of oviposition was slower at higher densities on host plants for CM, OM and SCM. The rate of mortality increased at the highest density for CM (cabbage), OM (bean) and SCM (cabbage), but remained unaffected for OM on onion and cabbage and for SCM on onion and bean, when densities were compared. For OM, a delay in the rate of oviposition and mortality on cabbage (non-host plant) when compared with onion (host plant), suggests that cabbage was not as readily accepted as an oviposition site. Interspecific competition experiments at six density ratio's of SCM:OM indicated increased fecundity, or an increase in the rate of oviposition for OM, at the lower densities when single and mixed species were compared. For SCM no effects on fecundity were recorded, but the rate of oviposition was slower and rate of mortality faster at the lowest density in the presence of OM. Similar studies with SCM and CM showed no such effects of competition.

Host plant exposure of SCM females during the pre-oviposition period resulted in a delay in initial acceptance of subsequent host plants as oviposition sites. This happened only when females were exposed to a secondary host during the pre-oviposition period. Once oviposition began, host discrimination ceased and a switch in oviposition sites to the preferred host did not alter the rate of oviposition. In CM, the rate of larval development increased at density 6 (optimum density). Above this density a decrease in the rate of development and a significant reduction in pupal weight was observed. Time required for fly emergence was not affected by increasing larval densities.

RÉSUMÉ

Christine M. Noronha

EFFETS DE DENSITÉ ET DE PLANTE HôTE SUR LA FÉCONDITÉ ET LA SURVIE DE *DELIA RADICUM* (BOUCHÉ), *D. ANTIQUA* (MEIGEN) AND *D. PLATURA* (MEIGEN) (DIPTERA: ANTHOMYIIDAE).

Les effets de la competition intraspecifique et interspecifique, de la plante hôte et d'une pré-exposition à la plante hôte avant la ponte, sur la fécondité, la proportion des pontes ainsi que la mortalité des stades adultes et larvaires chez *Delia radicum* Bouché (mouche du chou (CM)), *D. antiqua* Meigen (mouche de l'oignon (OM)) et de *D. platura* Meigen (mouche des légumineuses (SCM)) furent étudiés sur le chou, l'oignon et l'haricot.

Lorsque quatre densités furent comparées, nous avons observé une densité optimale pour une valeur maximale de la fécondité par femelle. Cette densité était plus élevée chez les plantes hòtes. Les femelles CM étaient spécifiques à leur hôtes et ne pondaient pas sur les autres plantes. Pour chaque densité, les taux de pontes et de mortalité ont été calculés sur une période de 30 jours. Sur les plantes hôtes et chez CM, OM et SCM, les taux des pontes étaient plus lents aux densités plus élevées. A la densité la plus élevée, le taux de mortalité augmentait pour CM (chou), OM (haricot) et SCM (chou), mais n'était pas affectée chez OM sur l'oignon et le chou ainsi que chez SCM sur l'oignon et l'haricot. Chez OM, nous avons noté un délai dans les taux de ponte et de mortalité sur le chou (plante dont il n'est pas l'hôte) comparativement à l'oignon (plante hôte), suggérant que le chou ne serait pas vraiment accepté comme site de ponte. Les expériences sur la compétition interspécifique furent réalisées avec six rapports de densité différents SCM:OM; comparativement aux résultats individuels, nous avons obtenu une augmentation de la fécondité, ou une augmentation dans le taux des pontes chez OM aux densités les moins élevées. Aucun effet sur la fécondité n'a été observé chez SCM, toutefois le taux de ponte fut plus lent et celui de la

mortalité plus rapide, à la densité la moins élevée en présence d'OM. Des travaux similaires chez SCM et CM n'ont pas démontré de tels effets sur la compétition.

En exposant les femelles SCM à la plante hôte durant une période précédant la ponte, nous avons noté un délai dans l'acceptation initiale des plantes hôtes subséquents comme site de ponte. Ceci fut observé seulement lorsque les femelles sont exposées aux hôtes secondaires durant la période précédent la ponte. Une fois la ponte commencée, la discrimination pour l'hôte cesse et le changement de site de ponte vers l'hôte préférentiel n'a pas altéré le taux de ponte. Chez CM, le taux du développement larvaire augmente à une densité de 6 (densité optimale). Alors qu'à une densité superieur à celle-ci on a observé une diminution dans le taux du développement ainsi qu'une réduction significative du poids des pupes. L'augmentation de la densité larvaire n'a pas eut d'effet sur le temps requis pour l'émergence des mouches.

To my parents Gabriel and Agusta Noronha.

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ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. Stuart B. Hill and co-supervisors Dr. Guy Boivin and Dr. Charles Vincent (Agriculture Canada Research Station St-Jean-sur-Richelieu) for all their help and advice throughout this project.

My technicians, Gerry Grant, Marusia Davidova and Mary Matheson deserve a special thanks for their untiring assistance in the tedious task of extracting and counting eggs.

Thanks go to Dr David Gordon, Dr. Jeanette O'Hara-Hines (Dept of Mathematics, University of Waterloo), Peter Alvo, and Dr. M Fanous (Macdonald College, McGill University) for all their statistical advice and helpful discussions, and to Jay Whistlecraft (Agriculture Canada Research Station London Ontario) for discussions on rearing techniques, and providing pupae of *D. platura*.

Thanks also to Pierre Langlois for providing valuable assistance and advice on the technical aspects of this research, to Ann Grainger for maintaining the incubators and to Janet Taylor, Diane King and Marie Kubecki for their secreterial support.

My special thanks to Tanya Searle and Danica Baines for all their support, encouragement and good humour, Susan Johnson for all her help and proofreading this thesis, Robert Paul for helping with the drawings, Dr. Barry Jewell for proofreading, Mai Huynh for checking the references, Martin Nadeau and Adla Halwani for translating the abstract. Luciano Germani for taking the pictures.

My sincere thanks to Dr. Manfred Rau for being very understanding and giving me time off from work to complete this thesis.

I am grateful to the Government of Pakistan for awarding me a post graduate scholarship for five years, and to the Conseil des recherches en pêche et agro-alimentaire du Québec for providing research funding for two years.

Many thanks to my family in Canada especially James, Louisa and Noel Noronha, for all their support.

Last but not least, I would like to thank my family especially my parents Gabriel and Agusta Noronha for their continuous love, and encouragement.

ORIGINAL CONTRIBUTIONS

1. First study on intraspecific competition among the Cabbage Maggot, Onion Maggot, and Seed Corn Maggot for an oviposition site.

2. First study on the effects of population density on acceptance of non-host plants as oviposition sites for Cabbage Maggot and Onion Maggot.

3. First study on interspecific competition between Cabbage Maggot and Seed Corn Maggot, and between Onion Maggot and Seed Corn Maggot on adult fecundity, survival and rate of egg deposition.

4. First study on the effects of pre-oviposition host plant exposure of Seed Corn Maggot adults on the subsequent acceptance of other hosts as oviposition sites.

5. First study on intraspecific larval competition of Cabbage Maggot.

IMPORTANT CONTRIBUTIONS TO KNOWLEDGE GAINED FROM THIS STUDY

1. The discovery of an Allee effect of density, i.e., the presence of an optimum density for maximum fecundity, demonstrating a group effect in relation to fecundity for the three anthomyiid species: Cabbage Maggot, Onion Maggot and Seed Corn Maggot.

2. A demonstration that Cabbage Maggot is highly host specific, and will not accept other plants as oviposition sites. Onion Maggot is not as host specific and will lay its full complement of eggs on a non-host plant, if given no other choice. This acceptance is also host restricted as the females retained their eggs for a longer period of time in the presence of non-host plant cabbage. This indicates that females, confronted with such a situation in the field, will disperse in search of a more appropriate host.

3. Although found in the field together, Cabbage Maggot and Seed Corn Maggot do not compete for oviposition sites. However, Onion Maggot and Seed Corn Maggot, depending on adult ratios, will compete and may displace one another.

4. Pre-ovipositon exposure of SCM females to secondary hosts results in discrimination at the initial encounter with a potential host.

5. The Cabbage Maggot larvae have an optimum density for faster development, above and below which rate of development is slower. A decrease in weight of the pupae also results at densities above this optimum.

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INTRODUCTION

In nature, organisms do not lead an isolated existence; rather, they are in constant interaction with their environment, food sources, and other organisms of the same and different species. A knowledge of the effects of these interactions on the behaviour, physiology, food preference, survival and reproduction of insect pests can help us design more effective monitoring and control programs for such species.

The Cabbage Maggot (CM) (*Delia (=Hylemya) radicum* Bouché), and Onion Maggot (OM) (*D. antiqua* Meigen) are major pests on crucifers and *Allium* spp. respectively, whereas the Seed Corn Maggot (SCM) (*D. platura* Meigen), is a generalist that feeds on a wide range of plant families including Liliaceae, Gramineae, Solanaceae, Leguminosae, Cruciferae, Cucurbitaceae, with beans being the preferred host (Miller and McClanahan 1960, Ristich 1950). The economic importance of these three species is well known to vegetable growers in many regions of the world. In some years, heavy infestation may result in the destruction of 90% of crops, such as cabbage, cauliflower, onion, and bean. The adults are attracted mainly by host plant odours, CM to isothiocyanates, OM to n-dipropyl disulphide, and SCM to the odour of germinating seeds and soil organic matter (Barlow 1965, Dindonis and Miller 1980, 1981a, Hawkes et al. 1978, Matsumoto and Thorsteinson 1968a, 1968b, Nair et al. 1973, Nottingham 1988, Nottingham and Coaker 1985, Ristich 1950). In addition, colour, shape and size of the plant, and microorganisms in the soil and those associated with the host plant also attract ovipositing females (Dindonis and Miller 1980, 1981a, Eckenrode et al. 1975a, Hough-Goldstein and Bassler 1988). Decomposer microorganisms provide nourishment for the larvae, either directly or by breaking down the substrate making the metabolites available for larval assimilation (Eckenrode et al. 1975a, Eymann and Friend 1985a,b).

Since the larvae of CM, OM, and SCM are not very mobile, optimal placement of eggs by the female is important for survival. Thus, ovipositing females are attracted to and aggregate on plants that are highly suitable for larval survival, which may explain their patchy distribution in the field (Harcourt 1967, Whitfield et al. 1985). In fact, Havukkala and Miller (1987), Hough-Goldstein et al. (1987), and Yathom (1970), have reported that females are attracted to sites occupied by other ovipositing females and lay more eggs on such sites.

Aggregations in areas of high attractiveness could result, however, in resource limitations, and increased intraspecific competition. As density within these aggregations increases, fecundity of the females may decrease (Fujita 1954, Jones and Finch 1987, MacLagan and Dunn 1936, Park 1932, Pearl 1932), or increase, because of a group effect, which has been recorded in *Drosophila melanogaster* (Diptera: Drosophilidae), and *Tribolium confusum* (Coleoptera: Tenebrionidae) (Allee 1965, MacLagan 1932). Increased oviposition may affect larval survival, larval, pupal, and adult weight, and change the developmental rate of the different stages (Beaver 1973, Craig et al. 1990, Gilpin 1974, Quiring and McNeil 1984, Wasti et al. 1975)

These three amthomyiid species are very closely related, they have similar feeding behaviour and share resources. SCM larvae, being generalists, are often found feeding in the same roots as OM and CM larvae (Miles 1952, 1955). In addition, environmental thresholds among these three species for egg laying and adult activity have been found to be very similar. Thus, it is possible that resource overlap may occur and lead to interspecific competition for oviposition sites. Such interspecific competition among phytophagous insects is considered to be rare, mainly because such insects are usually much less abundant than their host plants, and complete resource overlap between the species, thought to be essential for competition, does not occur (Lawton and Strong Jr. 1981, Strong Jr. 1984). Janzen (1973) believes, however, that because all parts of a plant are connected, any species feeding on any part are automatically competing with all other species on that plant. Interspecific competition studies with CM and the other species feeding on the same host have shown that the presence of frass of the garden pebble moth, *Evergestis forficalis* (Lepidoptera: Pyralidae), deterred CM adults from ovipositing on that plant. This occurred in spite of the fact that CM feeds on the roots of the plant, whereas, the garden pebble moth feeds on the aerial parts of the plant (Jones and Finch 1987). Such findings support Janzen's (1973) view. In addition to competition, the experiences of an individual during its lifetime may affect subsequent host plant choice and fecundity (Courtney and Kibota 1990, Papaj and Prokopy 1989). SCM, a generalist, does not require the presence of host plant material for egg maturation, although prior exposure to a particular host plant may affect the rate of acceptance of subsequent encountered hosts (Weston and Miller 1987).

Numerous studies have been conducted on CM, OM and SCM. However, none have examined the effects of interaction among and between these species on oviposition and survival on host and non-host plants. The purpose of this study was to examine these effects, as well as the consequences of prior exposure on oviposition, and host acceptance by adults of these three species.

NOTATION AND STYLE

The notation and style conventions followed in this thesis were those given in the CBE style manual 1978, and published by the Entomological society of America. The references cited in the text are by both authors where there are only two authors, or by first author where there are three or more authors, and are arranged in alphabetical order in the reference section.

CHAPTER 1

LITERATURE REVIEW

HISTORY AND DISTRIBUTION

The Cabbage Maggot (CM) (*Delia (=Hylemya) radicum* Bouché), Onion Maggot (OM) (*D. antiqua* Meigen), and Seed Corn Maggot (SCM) (*D. platura* Meigen), are well known pests throughout the world. They were accidentally introduced from Europe into North America in the mid-1800's (Gibson and Treherne 1916). CM is restricted to the temperate holarctic region (de Wilde 1947, Schoene 1916). It was first reported from the U.S.A. in 1835 (Slingerland 1894). In Canada, Couper (1875) reported a fly, which was probably CM, damaging cabbage plants in the district of Montreal. However, it was not until Fletcher (1885) reported the destruction, by this maggot, of 25 to 75% of Canada's cauliflower crop that its economic importance was established.

OM, originally considered to be a palaearctic species, is now found throughout the world. Its main host, the onion, was introduced to the U.S.A. from Europe in the 17th century. By the 1800's the fly was well established throughout North America (Ellington 1963). OM was first reported from Massachusetts by Harris in 1852. In Canada, Couper (1875) was the first to report severe damage by this fly to onions in the fields around Montreal.

SCM has a world-wide distribution. It was first reported in Canada in 1849 in Martin Falls, Ontario, and in the province of Nova Scotia (Gibson and Treherne 1916). However, it was not until Jack (1885) observed severe maggot damage to golden wax bean crops in Chateauguay, Quebec, that its economic importance was realised.

These three species presently occur throughout Canada, and cause severe economic damage to their host plants.

DESCRIPTION OF DEVELOPMENTAL STAGES.

The cabbage maggot, onion maggot and seed corn maggot are very similar in appearance at all four developmental stages. A general description of each of these stages, is given below. Specific differences are listed in Table 1.

EGGS.

The eggs of these three species share basic characteristics. They are white, elongate, with one side convex and the other concave. The posterior end is blunt, and the anterior end is tapering with a thick rim around the micropylar end. The surface of the chorion is ridged forming a pattern on the surface that is characteristic for each species. Two raised ridges, forming a groove, extend along the length of the egg. The length of this groove differs between the species (Table 1) (Coaker and Finch 1971, de Wilde 1947, Ellis and Eckenrode 1979, Gibson and Treherne 1916, Hartman and Southern 1988, Mann 1945, Miles 1952, 1953, 1955, Reid 1940, Smith 1922, Varis 1967, Workman Jr. 1958).

LARVAE:

The larvae are legless maggots with a blunt posterior and a tapering anterior end. The head is greatly reduced, with prominent mandibular hooks that are capable of rasping the root tissue. A short distance behind the head are fan-shaped prothoracic spiracles, each bearing processes that vary in number between the species. At the caudal end, on the eighth abdominal segment, are fleshy tubercles, the largest pair being nearest the centre. Also visible are two raised reddish brown spiracles. The three species can be distinguished by the arrangement and number of the caudal tubercles. The three larval stages can be easily distinguished from each other by the size of the mouth hooks, and the number of stigmata per abdominal stigmatophore (Caesar 1922, Gibson and Treherne 1916, Loosjes 1976, Miles 1950a, b, 1952, 1958, Reid 1940, Workman Jr. 1958).

PUPAE

The pupae are generally similar in shape and form. They are sub-elliptical with a smooth surface, and their colour varies from yellowish brown to dark reddish brown. Because the pupa is formed by the contraction of the outer skin of the mature larva, it retains the distinguishing characteristics of the larva, including the hardened tubercles on the eighth abdominal segment, which is used for identification of the species. Pupal size varies between species (de Wilde 1947, Gibson and Treherne 1916, Loosjes 1976, Reid 1940, Varis 1967, Workman Jr. 1958)

TABLE 1. A list of taxonomic characters used to identify the Cabbage Maggot (CM), Onion Maggot (OM), and Seed Corn Maggot (SCM).

Developmental Stage	Cabbage Maggot (CM)	Onion Maggot (OM)	Seed Corn Maggot (SCM)
Eggs			
Length (mm)	0.93-1.02	1.12-1.23	0.9-0.95
Width (mm)	0.31-0.50	0.5	0.3-0.32
Chorion	Longitudinally ridged	Finely reticulated	Reticulated with elongate hexagons
Groove	Along entire length	Along one fourth to half its length	Along one fifth its length
Micropyle	Deeply sunken	Barely recessed	Barely recessed
Larvae (full grown)			
Length (mm)	8	9-10	5-7
Caudal tubercles	12 pairs, central pair bifurcated at tip.	8 pairs, central pair not bifurcated	8 pairs, central pair not bifurcated
Anterior spiracles	11-13	10-13	5-8
Pupae			
Length (mm)	5.5-5.6	5-7	4-5
Adults			
Length (mm)	5.6	6-7	5
Pre-alar thoracic bristle	> half length of adjacent bristle	Half length of adjacent bristle	< half length of adjacent bristle
Hind tibia	No bristles	No bristles	A row of bristles
Hind femur	Dense cluster of bristles	No bristles	No bristles

(Brooks 1951, Caesar 1922, Coaker and Finch 1971, de Wilde 1947, Ellis and Eckenrode 1979, Gibson and Treherne 1916, Hartman and Southern 1988, Loosjes 1976, Mann 1945, Miles 1950a, b, 1952, 1953, 1955, 1958, Reid 1940, Smith 1922, Varis 1967, Workman Jr. 1958).

ADULTS :

The adults of these three species superficially resemble the common house fly, being slightly smaller and less robust. The body is slender, the abdomen is more tapered than in the house fly, and more cone shaped towards the posterior end. When at rest, the wings are placed one over the other on the back, with the angle of divergence being smaller than in the house fly. The body is covered with bristles. The eyes of the males are holoptic, and those of the females are dichoptic (Brooks 1951, Caesar 1922, Ellis and Eckenrode 1979, Gibson and Treherne 1916, Miles 1953).

BIOLOGY

LIFE CYCLE

Adults of CM, OM and SCM emerge from the soil in spring from overwintered pupae (Coaker and Finch 1971, Higley and Pedigo 1984b). The date of spring emergence depends on weather conditions and soil temperature. Number of degree-days required for spring emergence is 174 to 200 DD for CM, 103 DD for OM, and 190 DD for SCM above the thresholds of 4.5, 5.5, and 3.9°C respectively (Coaker and Wright 1963, Eckenrode and Chapman 1972, Eckenrode et al. 1975b, Funderburk et al. 1984, Higley and Pedigo 1984b, Liu et al. 1982, Nair and McEwen 1975, Sanborn et al. 1982). Adults generally emerge during the night or early morning, when the temperature is low, probably to avoid desiccation. On emerging, the adults begin feeding on immediate sources of nectar and pollen of surrounding weeds. The proteins and carbohydrates obtained are essential for sexual maturation in both males and females (Baker and Stewart 1928, Niemczyk 1964). Males generally emerge before females and are ready to mate after three to five days. Females emerge later than the males and require more time to become receptive to mating (Collier and Finch 1985, Theunissen 1973). A post-emergence period of 6 to 8 days for CM, 10 to 12 days for OM, and 5 to 7 days for SCM is required before oviposition begins (Coaker and Finch 1971, Reid 1940, Workman Jr. 1958).

The eggs are generally laid in cracks in the soil around the base of host plants. However, when the weather is cool and moist and the probability of desiccation is low, eggs may also be laid on the leaves and stem of the plant. Under these conditions such sites provide faster and easier points of entry for the young maggots (Gibson and Treherne 1916, Miles 1958). The eggs hatch within three days, depending on weather conditions. At optimum temperatures of 20°-25° C, average hatching time is 2.5 days for CM, two to three days for OM, and two days for SCM (Caesar 1922, Ellis and Eckenrode 1979, Miles 1950a,b, Sanborn et al. 1982, Throne and Eckenrode 1985, 1986).

Upon hatching, the maggots immediately seek out and enter the roots of the host plant and begin feeding on the internal tissues. Root damage can be so extensive that the plant may wilt and finally die. Although these maggots are mainly confined to the roots, where they do most of their damage, they are occasionally found feeding in the stem and midribs or fleshly leaf stalks (Coaker and Finch 1971, Gibson and Treherne 1916). The highest percentages of crop loss occur in the spring when the plants are small. Seedlings are killed, however, before the maggots can complete their development. In OM the larvae may move from one seedling to another until development is complete. Destruction by OM of as many as eight onion seedlings by a single maggot, before it matures, has been reported (Ellington 1963, Gibson and Treherne 1916, Hough 1981). Although CM is able to move similar distances to those reported for OM, damage of more than one plant by a single larva has not been reported. No data are available for SCM. Later in the season when the plants are older and well established they can survive more severe attacks, and can also support a higher number of larvae. Coaker (1970) showed in the U.K. that brussel sprouts suffer few second and third generation attacks. However, even if a plant survives, maggot feeding can result in deformed and stunted plants. In some seasons, as much as 75 to 90% of a cabbage, onion or bean crop can be destroyed by these maggots (Forbes and King 1957, Hawley 1922, Rawlins and Gonzalez 1966).

The development of the three larval instars varies from 21 to 28 days in CM, and 14 to 21 days in OM and SCM. Fully developed third instar larvae cease feeding, leave the root and pupate in the soil, 10 to 12 cm from the root, at an average depth of 5 to 10 cm, or 23 cm in overwintering generations (Foott 1954, Gibson and Treherne 1916, Reid 1940, Workman Jr. 1958). The larva may also pupate in the tissue of the root in which it was feeding. The pupal stage lasts from 10 to 15 days in the summer, provided that there is no pupal aestivation as a result of exceedingly high temperatures (above 30°C) (Funderburk et al. 1984, Higley and Pedigo 1984b, Missonnier 1960, 1963).

Number of generations per season depends on prevailing climatic conditions. In CM this varies from one in Northern USSR to five in parts of USA (Brooks 1951, Carlson et al. 1947). In southwestern Quebec there are three complete generations with a partial fourth for CM, two complete generations with a partial third for OM , and three generations for SCM (Armstrong 1924, Boivin and Benoit 1987, Perron and Lafrance 1961).

Since weather conditions and temperature have an effect on adult longevity, fecundity, egg hatch, larval duration and adult emergence, an increase or decrease in developmental time at any stage of the life cycle can occur. This variability in developmental rate results in considerable overlap of generations in the field. Thus, flies of two different generations may be found in a field at the same time (Miles 1953, 1955).

In the fall, with the approach of colder temperatures and shorter daylengths, the larvae of the last generation leave the host and move into the soil to overwinter as diapausing pupae (Miles 1955, Read 1965). In spring, with the warmer temperatures and longer daylengths, the adults emerge.

HOST PLANTS AND NATURE OF DAMAGE

CM, OM and SCM cause direct as well as indirect damage to their host plants. Direct damage is caused by the maggot feeding on the root tissue which may result in wilting, deformation or death of the plant. The maggots can also transmit, or provide a port for entry of disease organisms such as club root and root rot (Ellis and Eckenrode 1979, Wheatly 1971). The nature of direct damage caused by each of these three species is described in the following section.

Cabbage Maggot (CM)

CM is a primary pest of cruciferous plants such as rutabagas, kohlrabi, radish, broccoli, turnip, rape, cauliflower, brussel sprouts, cabbage, black mustard, wild mustard, tumble mustard, jointed charlock, and hares-ear mustard (Brittain 1927, Liu and Butts 1982). The flies are attracted to the secondary plant chemicals (eg. glucosinolates and isothiocynates) that are present in all members of this family (Städler 1978). Attractiveness to isothiocyanates has been extensively studied (Finch 1978, Finch and Ackley 1977, Hawkes 1975, Hawkes et al. 1978, Mellor and Woodsman 1935, Nair et al. 1973, Nottingham 1988, Nottingham and Coaker 1985). The presence of CM larvae on non-cruciferous plants, such as beans, beets and celery, has been recorded only by Chittenden (cited in Gibson and Treherne 1916), although this may have been a misidentification.

On hatching, the maggots seek out and enter the roots and feed on the internal tissue. This feeding activity may cause the leaves of the plant to wilt, become discoloured and eventually fall off. The first generation flies lay most of their eggs on the hypocotyl, the larvae feeding more on the hypocotyl than on the root itself (Asyakin and Ivanova 1987, Hardman and Ellis 1978). In cabbage and cauliflower, the maggots feed in the tap root and tunnel up and down near the surface. In this case, the presence of a few maggots does not destroy the plant. On plants such as radish and turnip, however, the tunnelling of one or two maggots is sufficient to either destroy the root bulb or make it unmarketable (Caesar 1922). The extent of plant injury depends on the number of maggots in the root and on the age of the plant. Damage is greatest in spring when the plants are small and most susceptible to destruction. Older and larger plants can support a higher number of maggots without showing apparent signs of attack and they can recover faster. Gibson and Treherne (1916) found 127 maggots in a single root of a cauliflower plant. Survival of maggots and attractiveness of plants to ovipositing flies decreases with age (Ellis and Eckenrode 1979, Ellis et al. 1979, 1980, Freuler 1978, Swailes 1958). This decrease in attractiveness may be because the root tissue becomes tougher with age, and more difficult for young larvae to enter. Severe attacks can result in 90% of brassica plants being killed, and sometimes losses to edible parts alone may be as large as 60% (Forbes and King 1957, Strickland 1965).

Onion Maggot (OM)

OM is specific to the genus *Allium* (Hough 1981), its host specificity being associated with the presence of certain sulphur compounds that are present in this genus (Matsumoto 1970, Matsumoto and Thorsteinson 1968a, b, Soni and Finch 1977). Although the preferred host is onions, (*A. cepa* (L.)), garlic, leeks and bunching onions are also attacked, although fewer larvae mature on these hosts (Hammond 1924). Survival on non-host plants, such as radish, turnips, tulip bulbs and lettuce, has also been reported (Smith 1922, Workman Jr. 1958).

Eggs are laid around the base of the plant or in the axils of the leaves. On hatching, the young larvae tunnel through the sheath until they reach the young forming bulb where they feed, often reducing it to a rotting mass. Early in the season, when the plants are young and unable to recover quickly, damage can be severe. The larvae generally move from one seedling to another, each larva destroying as many as eight seedlings (Dustan 1933, Ellington 1963, Hough 1981). These larvae are capable of moving large distances: 7 to 12 day old maggots have been found to cover a distance of 25 cm within 24 h (Kendall 1932). Damage caused by larval feeding can occur at any stage of the growth of a plant. However, as plants mature they become more resistant to maggot attack and less attractive to ovipositing females. This may be the reason why plants with flaccid growth are generally preferred as oviposition sites over plants with pronounced growth (Finch et al. 1986, Gray 1924). The number of maggots that can survive on a single bulb depends on its size. As many as 67 larvae of all stages and 12 puparia have been reported from a single bulb (Gibson and Treherne 1916). Although larger plants may survive maggot attacks, rotting or deformation of the injured bulb may occur, thus reducing the value of the crop (Dustan 1933). In addition to seedlings, transplants and sets sown in the spring are also susceptible to maggot attack.

Attacks on plants are not confined to the growing season, but they may also continue after harvest. Generally in Ontario, but not in Quebec, when bulbs are harvested they are placed in piles in the field to dry. The cuts and bruises sustained during this process increases their attractiveness to ovipositing females of the last generation. In addition to the direct damage by feeding maggots within these piles, an ideal environment is created for subsequent decay during storage. The common practice of discing unharvested bulbs into the soil in fall provides a major source of food for the overwintering population, and should be avoided (Eckenrode 1988, Eckenrode and Nyrop 1986, Finch and Eckenrode 1985).

Seed Corn Maggot (SCM)

SCM is a generalist, feeding on a wide variety of crops including beans, peas, corn, turnips, cabbage, radish, onions, beets, seed potato, hedge mustard, soybeans, tobacco, cucurbits, cereals, alfalfa, buckwheat, pepper, and spinach (Gibson and Treherne 1916, Miller and McClanahan 1960, Reid 1940). Although mature plants are attacked, some experiments have demonstrated a preference for sprouting and germinating seedlings (Funderburk and Pedigo 1983, Hammond 1984, Higley and Pedigo 1984b). In addition to feeding on living plant material, the larvae are also saprophytic, feeding on decaying organic matter.

On hatching, the maggot bores between the cotyledons of the seed in the soil and feeds on the leaflets of the plumule and on the bud of the growing tip. After the plumule has been destroyed completely, the maggots enter the cotyledons and begin feeding on the internal tissue. Up to four maggots have been found within a single seed. When the seedlings emerge from the soil, the maggots are generally carried above the ground inside the cotyledons. As soon as the cotyledons dry, the maggots leave them and enter the stem near the roots, or burrow through the stem from the cotyledons down towards the root (Gibson and Treherne 1916, Hawley 1922). Hawley (1922) found 75% of a field of beans damaged in this way. Sometimes, only the leaf tissue, not the growing tip, is destroyed. In this case, the plant may survive but the first two leaves are usually deformed.

MATING AND OVIPOSITION

Cabbage Maggot (CM)

On emergence, CM adults must feed before becoming receptive to mating (Caesar 1922, Coaker and Finch 1967, 1973, Finch and Coaker 1969, Hawkes 1972b, Miles 1953). Males reach sexual maturity after two days and continue to mate throughout their lives. Swailes (1961) found no relationship between age and fertility of males. Before females can mate they require a three day post-emergence maturation period, during which they feed and their eggs develop. Most females begin mating four to five days after emergence and mate only once (Coaker and Finch 1967, Finch 1974a, b, Swailes 1961). Although mating is not necessary for ovogenesis, it is required for egg laying. Unmated females will retain their eggs, which are eventually resorbed. Since females mate only once, increasing or decreasing the ratio of males to females in rearing cages does not affect total egg production or egg hatch (Missonnier and Stengel 1966).

Females become receptive to the odour of the secondary plant substances of their host plant seven to nine days after emergence, and oviposition generally begins as soon as the host plant is found and accepted (Brittain 1927, Caesar 1922, Coaker and Finch 1971, 1973, de Wilde 1947, Finch 1974a, Foott 1954, Gibson and Treherne 1916, Hawkes 1972a, b, Schoene 1916, Smith 1927, Varis 1967). When such substances are detected, gravid females leave the adjacent vegetation and field borders, where they feed and move towards the odour source. It generally takes only a few hours between odour detection to egg deposition. However, in the absence of a suitable host, fecundity decreases and eventually the follicles may be resorbed (Coaker and Finch 1973, Hawkes 1972b, Missonnier and Stengel 1966). Such females generally live longer and, if host plants are finally encountered, they lay fewer eggs. Egg viability decreases as the age of the female increases (Finch 1974b).

CM feed only on crucifers. Gravid females are attracted to glucosinolates and their volatile derivatives (mustard oils and isothiocyanates) present in crucifers (Nair et al. 1976, Städler 1978). However, although all crucifers are thought to contain glucosinolates, only some elicit oviposition, which suggests that a preference exists for certain specific glucosinulates (Nair et al. 1973, 1976, Traynier 1967a, b). Finch, (1978) isolated 11 chemicals attractive to CM adults in wild and cultivated crucifers. He suggested that one or more of these may be involved in attraction and host plant selection by the CM. Wind tunnel studies have shown that on perceiving a suitable host plant odour, gravid females begin flying up-wind towards the attractive odour source. Females generally stay within the odour plume when flying upwind. However, if the odour is lost, the female will turn around, fly downwind a short distance, circle, reenter the plume, and once again fly upwind (Hawkes 1975, Hawkes et al. 1978, Nottingham 1988, Nottingham and Coaker 1985). These flies can travel large distances in search of a suitable host plant. Females show a greater tendency to disperse than males (Nair and McEwen 1974).

In addition to chemicals, visual stimuli are also used to find suitable hosts. In fact, the final choice of landing site within a host patch apparently involves only visual cues (Abu Yaman 1960, Prokopy et al. 1983a, b, Traynier 1965). Prokopy et al. (1983b) observed that females can orientate towards host plants at a distance of 40 to 60 cm using only a visual stimulus such as leaf colour. Females also use leaf colour to differentiate between host plant cultivars, yellow leaves being more attractive than green ones. In addition to colour, structure also affects host plant selection, horizontal dimensions being more attractive than vertical ones (Abu Yaman 1960). Visual stimulation is not necessary for egg development (Dapsis and Ferro 1983, Hawkes and Coaker 1979, Prokopy et al. 1983a).

The presence of microorganisms on host plant material also plays a major role in attraction and rate of development for OM and SCM, and a similar response has been observed for CM (Doane and Chapman 1964, Eckenrode et al. 1975a, Ellis et al. 1982).

Finding and landing on a suitable host plant alone does not elicit oviposition. The female generally follows a specific behaviour pattern before a plant is accepted for oviposition (Zohren 1968). Upon landing on a potential host, the female carries out "leaf blade runs" using the leaf rim for guidance. Following these runs, the female then seeks out the midrib on the underside of the leaf and runs down the petiole and stem. It is believed that stem runs are performed to detect the chemical nature of the plant, as receptor cells that are sensitive to sinigrin have been identified in the tarsal sensory hairs (Städler 1978). On reaching the ground, the female generally moves onto the soil around the base of the stem. She changes her orientation continuously, occasionally climbing up the stem for a short distance before returning to the soil. By this time, the ovipositor has been extended and is moved in a whip like fashion. The substrate is examined repeatedly by probing with the ovipositor. The probing is interrupted for additional climbing. Before eggs are laid, the ovipositor is inserted into the soil and the female uses her hind legs to rake soil particles around the ovipositor before laying some eggs. On completion, the whole chain of behaviour is reinitiated, beginning with the leaf surface runs. Eggs are laid either singly or in groups, sometimes as many as 30 in a batch (Gibson and Treherne 1916, Matthewman and Harcourt 1972). The eggs are deposited near the host plant, usually within 2.5 to 5 cm of the stem, or around the base of the stem itself. Oviposition is generally cyclic with egg laying occurring at approximately three to five day intervals, the intervening time being devoted mainly to feeding (Coaker and Finch 1967, Hawkes 1972b,c, Swailes 1961). Oviposition is also affected by weather conditions and has been found to be highest on calm warm sunny days (up to 20°C) (Miles 1951a, 1958).

In the laboratory, mated females can live for 22 to 29 days, and lay approximately 100 to 200 eggs. Mated males have a shorter life span and live approximately 19 days (Brittain 1927, Caesar 1922, Miles 1951b, Swailes 1958, Vodinskaya 1928).

Onion Maggot (OM)

As with CM females, OM females must feed after emergence for oogenesis to take place and to become receptive to mating. Males generally emerge before females and are ready to mate after three to five days (Theunissen 1973). Males are polygamous, alternating mating with feeding, and mate throughout their lives. Females become receptive to mating five to six days after emerging and mate only once (Martin and McEwen 1982, McEwen et al. 1973, Theunissen 1973, Vernon 1979). Size of males does not affect mating and fertilization, but female size is positively correlated with egg production (Robinson and Zurlini 1981). In cages, because females mate only once, the number of males present does not affect egg production (Missonnier and Stengel 1966, Robinson and Zurlini 1981).

After a pre-oviposition period of 7 to 10 days, the females are ready to oviposit and respond to suitable host plant odours (Eyer 1922, Martin and McEwen 1982, McEwen et al. 1981, Theunissen 1973). Like CM, adult males and females of OM are both attracted to onions, which may offer a source of nutrition for the adults (Dindonis and Miller 1980, Loosjes 1976). They observed adults of both sexes feeding on onion juice in the field. The flies are chiefly attracted to the sulphur compounds associated with *Allium* spp. N-dipropyl disulphide has been found to be the main chemical constituent of onions that attracts the flies and stimulates females to oviposit (Dindonis and Miller 1980, 1981b, Matsumoto and Thorsteinson 1968a,b, Pierce et al. 1978, Vernon et al. 1981). Dindonis and Miller (1980) observed, in the field, that flies could perceive host plant chemicals from a distance of up to several meters. They would fly upwind, in a series of short flights, directly towards the onion source. Martinson et al. (1988) found that these flies were capable of flying long distances. They trapped large numbers of flies in non-host vegetation up to 1.5 km from overwintering sites during their first flight.

In addition to host plant chemicals, OM shows a distinct attraction to the presence of microorganisms, both in the soil and on the plant. Damaged and diseased onions are generally preferred over healthy plants, although healthy plants are also accepted as oviposition sites (Dindonis and Miller 1980, Ellis et al. 1979a, Miller et al. 1984, Perron 1972, Perron and LeRoux 1962). Hausmann and Miller (1989) studied the oviposition preference of OM in relation to host plant damage. Females were allowed to oviposit on undamaged, lightly damaged, moderately damaged, and severely damaged plants, the extent of damage being quantified by allowing 20 late second instar larvae to feed on the plants for varying lengths of time. They observed that females preferentially oviposited and successfully colonized 90 to 100% of onion plants with slight to moderate damage, as compared with 15 to 20% of healthy and severely damaged plants. Larval survival was also found to be higher on slightly to moderately damaged bulbs. This indicates that although the presence of microorganisms is important in host selection, the extent of microbial colonization and activity is also critical. Dindonis and Miller (1981a) observed a similar increase in trap catches as the chopped onion bait began to decay. Peak activity was observed on day three to five when the extent of decay was moderate, but numbers declined as the decaying process continued.

Microorganisms involved in the rotting process probably cause the release of specific sulphur compounds from the onion plant that have a synergistic effect when combined with other attractants and oviposition stimulants (Dindonis and Miller 1980, 1981a, Hough 1981). This effect of microorganisms was further verified when garlic and garlic-onion mixtures did not produce the same response, probably because of the antimicrobial properties of garlic. Ellis et al. (1979a) found that seedlings grown in a sterile medium did not elicit oviposition stimulation.

Although the presence of microbes is stimulatory, it is not essential. Studies show that microbial volatiles alone are not stimulatory, and healthy seedlings on their own can elicit a response comparable to that of decomposing seedlings (Dindonis and Miller 1980, 1981a, Hausmann and Miller 1989, Hough 1981, Hough et al. 1981, Ishikawa et al. 1983, 1987). Hough et al. (1981) found that *Pseudomonas* spp. enhanced oviposition, but, other organisms may also be involved. These microorganisms have a nutritional value, as the larvae have been found to develop faster in the presence of bacterial contamination (Eymann and Friend 1985a, b, Friend et al. 1959b,, Schneider et al. 1983). Chemical stimuli are important in host finding, but, plant shape and colour (hues, saturation and intensity) all play an important role in the final selection within a host plant patch. Gravid OM females, when exposed to surrogate stems of different shapes, were found to prefer narrow vertical cylinders (4mm in diameter) as oviposition sites as compared to any other shape (Harris and Miller 1984). Thus, plant odour, structure and colour all play a role in oviposition stimulation. Although these three stimuli can elicit an oviposition response separately, maximal response is obtained when all three stimuli are combined.

On reaching a host plant, a gravid female will run up and down the stem a number of times. During these runs the ovipositor is moved from side to side. The fly eventually runs right down the stem to the soil, and walks on the ground, continuously probing it with the ovipositor. If a suitable place is found, the female will lay a batch of eggs. The female will then search for another host plant and repeat the procedure (Harris and Miller 1983, Mowry et al. 1989). This sequence of behaviour is repeated every time a batch of eggs is laid and appears to be important in the final act of ovipositing. The number of females alighting on stems, the stem runs, soil probing, and the number of eggs laid are all positively correlated with one another (Harris and Miller 1983). It is believed that during this procedure the fly is actually testing the suitability of the plant as a potential food source for its offspring, and the suitability of the soil as an oviposition site.

Oviposition is influenced by weather and soil properties, including particle size, soil moisture and temperature (Keller and Miller 1990). Most eggs are generally laid in crevices in the soil near the base of the plant. Later in the season (end of August and September, when the weather is cool) they are also laid on the stems and axils of leaves. OM shows a cyclic oviposition behaviour, heavy laying occurring once every two days, and becoming less frequent as the flies age (Vernon 1979). Egg production is highest between days 10 to 15, after which oviposition decreases.

OM females demonstrate an aggregative behaviour during the oviposition period. Females tend to oviposit on plants occupied by other ovipositing females on them. Sometimes two or three females may be seen ovipositing at the same time, and aggressive behaviour towards each other has also been observed (Harris and Miller 1983, Havukkala and Miller 1987).

Host plant attractiveness is associated with growth rate and phenology. Vigorously growing plants are more attractive, especially during the bulb formation stage, as compared with small seedlings (Gray 1924, Harris et al. 1987). Labeyrie (1957) and Perron (1972) observed maximum oviposition during the period of maximal vegetative growth of the plant. Females also tend to aggregate in areas where seedling growth is dense (Workman Jr. 1958). The uneven distribution of infestation in the field may partly be explained by this preference for vigorously growing plants that become attractive at different times during the season (Harcourt 1967).

Average longevity for males and females is 50 days and 70 days respectively at 20-28°C (Vernon and Borden 1979). Female fecundity may range from 200 to 760 eggs per female under laboratory conditions (Hammond 1924, Perron 1972). However, in the field, oviposition was considerably lower, being 24 to 58 eggs per female (Allen and Askew 1970, Perron et al. 1953, Vernon 1979). This decrease in the field may be because of the influences of diet and weather conditions.

Seed Corn Maggot (SCM)

Flies of this species, like the CM and OM, feed immediately after emergence and before mating. Mating is believed to occur in swarms. Miller and McClanahan (1960) observed large swarms of males hovering at a number of sites. However, mating within these swarms was not observed. Males are polygamous, but females are monogamous. Thus, increasing the ratio of males to females in cages does not increase female fecundity (Hough-Goldstein et al. 1987).

After a period of five to seven days, females become receptive to host odour (Higley and Pedigo 1984a, Reid 1940). This response may occur before the female is ready to oviposit. In this case the female spends time inspecting the site before ovipositing (McLeod 1964). This species is both polyphagous and saprophagous. It responds to the odour of decaying organic matter, a wide variety of germinating seeds, seedlings, and to freshly cultivated soil (Barlow 1965, Ristich 1950). As with OM, microorganisms also play a role in attraction of SCM. These microorganisms growing on organic matter produce metabolites that stimulate oviposition in SCM. Hough-Goldstein and Bassler (1988) confirmed the stimulatory effect of microorganisms when they found that females preferentially selected sites, and oviposited, in beakers that contained bacterial cultures in the sand, even if contact with the bacteria was not possible. The females stayed longer and laid more eggs on the inoculated substrate. Studies by Eckenrode et al. (1975a) also showed that sterile germinating seeds were not stimulatory. Thus, oviposition site selection may be influenced by volatiles released by microbial activity. Hough-Golgstein and Bassler (1988) observed that although females would lay eggs on moist sand alone, or in the presence of an olfactory stimuli, the presence of exposed peas on the soil surface increased the number of eggs laid. Attraction of females to freshly cultivated soil is believed to be in response to changes in the moisture and heat holding capacity of the soil that creates a number of suitable micro-habitats for oviposition (Miles 1950a, Miller and McClanahan 1960, Reid 1940, Dethier 1963) . Above ground structures play little or no role in stimulating oviposition in SCM females, and site selection by females is based largely on the organic nature of the site, organic soils being most preferred (Barlow 1965, Weston and Miller 1987).

Although the microbes themselves probably do not nourish the flies directly, they are able to convert a range of organic substrates into metabolites that are more readily assimilated by the larvae (Huff 1928, Leach 1931, Nair and McEwen 1973). Although prior damage by other insects renders a potential host plant more suitable for growth and development of SCM, it is not a prerequisite for attack.

The continuous presence of host plants is not necessary for oogenesis, vitellogenesis and oviposition. However, it has been found that during the oviposition period, the presence of lima beans in oviposition cups increased egg production and decreased the time between emergence and first egg deposition (Weston and Miller 1987, 1989)

. Although the flies are attracted to decaying organic matter, germinating seeds and seedlings are particularly favoured. The stage of seed development has been found to affect oviposition attraction and stimulation (Ibrahim and Hower Jr. 1979, Ristich 1950, Yu et al. 1975). Ibrahim and Hower Jr. (1979) found that in a choice situation, significantly more eggs were laid adjacent to newly emerging or emerged seedlings than to germinating seeds. However, when the choice was removed, the response was similar for both situations.

SCM females also tend to aggregate in the field. The exact reason for aggregation is not known, but an increase in oviposition in such aggregated populations has been observed. This suggests that this species demonstrates the presence of a group effect on fecundity (Hough-Goldstein et al. 1987, Yathom 1970), as found in the present study.

Once an oviposition site is found, eggs are generally deposited beneath the soil surface in cracks and crevices, or directly on the seedlings or seeds, either singly or in groups of up to 10 eggs per cluster (Miles 1958). One female may lay up to 150 eggs during her lifetime. Longevity of parous females is 28 to 42 days depending on the temperature.

INTRASPECIFIC COMPETITION.

Competition between individuals occurs when a resource is in short supply, and it increases in intensity as density of the population increases. Fecundity and mortality rate of competing insect species are commonly affected by competition. Pearl and Parker (1922) were the first to report an effect of competition on fecundity: during their studies on the fruit fly, *Drosophila melanogaster* (Diptera: Drosophilidae), they observed a decrease in fecundity as population density increased. However, because they recorded number of surviving imagoes and not number of eggs laid, conclusions about effects on fecundity can only be tentative. Pearl (1932) repeated these experiments, and this time recorded the number of eggs laid per female per day and obtained the same results. A similar response of fecundity to crowding was observed in *Rhizopertha dominica* (Coleoptera:

Bostrichidae) (Crombie 1942). The curve obtained from this type of response was later termed a "Drosophila Type" curve by Fujita (1954).

Crombie (1942) and Park (1932) suggested that this decrease in fecundity with increasing density may be related to higher physical interference and interruption of copulation, resting and oviposition. Crombie (1942) found no effect of copulation frequency on total fecundity in adults of *Rhizopertha dominica*. Thus, in *R. dominica*, collision interference, and interference of rest, feeding and oviposition, may be the cause for decreased fecundity. In *Setophilus oryzae* (Coleoptera: Curculionidae), however, density was found to affect copulation frequency and aggressiveness, which in turn affected fecundity (MacLagan and Dunn 1936). Therefore, mutual interference and the availability of oviposition sites can affect fecundity. Ishida (1952), by simultaneously varying the density of the weevil *Callosobruchus chinensis* (Coleoptera: Curculionidae) and the number of oviposition sites in his experiments, confirmed that these two factors can independently affect fecundity. Thus, in a "Drosophila Type" curve, the intensity of the effects increases as the population density increases. A response differing from the "Drosophila response" was reported by Allee (1931) when he analyzed Chapman's (1928) results with *Tribolium confusum* (Coleoptera: Tenebrionidae). He observed that the highest rate of increase in the population occurred at the second lowest and not the lowest density of females. In other words an optimum density exists, above and below which the negative effects of density are greatest, and a response to undercrowding is apparent. MacLagan (1932) confirmed the existence of this type of curve in his study on

Tribolium confusum. Fujita (1954) named this response an "Allee Type" curve. Park (1932) suggested that this effect may be caused by a higher rate of collision of females and males resulting in increased copulation and recopulation, and a higher fecundity up to an optimum density. Any further increase in density may result in interference and a decrease in fecundity. "Allee" type responses to crowding have subsequently been found in several species of beetles and flies (Nuorteva 1954, Rich 1956, Richards 1947).

The "Drosophila" and "Allee" type curves are not peculiar to a species, and either type may occur within a species depending on the environment and population density at the time fecundity is measured. Kirchner (1939), working with *Dixippus morosus* (Coleoptera: Curculionidae) and three different universe sizes, obtained an "Allee" type curve in the largest universe, and a "Drosophila" type curve in the smallest. Nakamura (1967), however, obtained a different species response. In his study on two weevil species of *Callosobruchus*, he observed that *C. chenensis* exhibited a Drosophila type curve and *C. rhodesianus* (Coleoptera: Curculionidae) an "Allee" type curve. Thus, response to crowding may vary both between species and within species. In a study of the azuki bean weevil, yet another type of curve that was intermediate between the "Drosophila" and "Allee" types was obtained (Utida 1941). Crowding of these weevils resulted in competition for oviposition sites, which in turn affected egg production. Population density does not always affect the fecundity of competing individuals within a population. Karandinos and Axtell (1972) reported that in *Hippelates pusio* (Diptera: Chloropidae), the rate of oviposition was not affected by density, nor was oviposition inhibited by the close proximity of other females or eggs in the oviposition cups. Density may also affect feeding activity of individuals. Strong Jr. (1984) found that Hispine species show an inverse density dependent response. Both species in his study, *Cephaloleia consanguinea* and *C. perplexa* (Coleoptera: Hispinidae), ate more leaf scrolls per individual at a higher than at a lower density.

The longevity of competing individuals is often affected by crowding. Ishida (1952) reported that density affected adult longevity of males and females differently. He found that as density increased, male longevity decreased, whereas female longevity increased. This happened, however, only if oviposition sites were restricted and females were forced to retain their eggs. In LeCato and Pienkowski's (1972) study of alfalfa weevils, *Hypera postica* (Coleoptera: Curculionidae), longevity of males was not significantly affected by density, whereas female longevity responded negatively to density, i.e., longevity decreased with increasing density. He observed that the overall life span of the females increased in the absence of males. This may be because of the interference and constant mating pressure by the males. On the other hand, males lived slightly longer in the presence of females. Decreased longevity with increased population density has been recorded in certain beetles, including *Trogoderma spp.* (Coleoptera: Dermestidae), in *Drosophila spp.*, and in certain solitary grasshoppers (Davis 1945, Pearl et al. 1927, Smith 1970).

INTERSPECIFIC COMPETITION:

Species that are closely related phylogenetically and ecologically, and that share the same resources, either compete or coexist. Ayala (1972) classified interspecific competition into two types: "Qualified" and "Unqualified". "Qualified competition" occurs when one species restricts the growth of the other species less than its own growth, and "Unqualified competition" when each species restricts the growth of the other species as much as or more than its own growth. The population dynamics of a species sharing a resource is determined by its ability to exploit the resource that is essential for growth, or to increase its reproductive potential (Ayala 1972). Under such circumstances, two species can coexist, even if one species is more efficient at exploiting the shared resource, so long as the other species has a higher individual fecundity (Ayala 1972, DeBach 1966). Ayala (1970, 1972) found that the fruit flies *Drosophila serrata* and *Drosophila nebulosa* (Diptera: Drosophilidae) coexisted for 25 generations at fairly constant frequencies, although unqualified competition existed. Sometimes two species may coexist only because species A has an advantage over species B at one stage of its life cycle and is at a disadvantage at another stage. Factors that may contribute to species displacement include changes in physical conditions, environmental modifications by the competing species, cannibalism, predation, active interferences (e.g., inhibition of mating, feeding or oviposition), disease, parasitism and genetic drift (DeBach 1966).

The initial frequency of a competing species is important in the colonization of a habitat. A species that is an effective competitor in a situation where initial frequencies are equal may be a weak competitor when its initial frequency is lower than that of the other species. One reason may be because of the difficulty of finding a mate. Thus, the relative frequency of the competitor is the factor that determines the result of competition (Narise 1965). Ayala (1971), using mixed populations of *D. willistoni* and *D. pseudoobscura* (Diptera: Drosophilidae) at frequencies of 20%, 50%, and 80%, found that if the initial frequency of *D. pseudoobscura* is 80%, the frequency would drop to 72% in one week. On the other hand, if the initial frequency was 20%, it would increase to 25% after a week. In single species cultures, the number of flies produced was higher than in mixed cultures. Thus, competition is probably a major population control factor in mixed populations. Frequency dependence may also lead to a stable coexistence of the two competing species. Similarly, populations of *D. melanogaster* and *D. simulans* (Diptera: Drosophilidae) increased as the relative frequency of their parents increased (Narise 1965). Not only initial frequency of a species within a mixed population affects its ability to coexist, but environmental conditions also play an important role. Ayala (1972) found that at temperatures of 25°C, *Drosophila serrata* is eliminated in three to four generations by *D. nebulosa*, whereas at lower temperatures they coexist for many generations. Thus it appears that in certain species can co-exist because of the ability to increase or decrease their population to a density at which the detrimental effects on each other is minimized. This is achieved by increased fecundity, prolonged longevity, suppression of competitor populations, or effective utilization of environmental conditions.

Interspecific competition is unlikely to occur in phytophagous insects, according to Lawton and Strong Jr. (1981), Price (1983) and Strong Jr. et al. (1984). These authors argue that these species are too rare in comparison to their food resource, and that natural enemies and environmental conditions usually keep their populations at levels low enough to avoid any chance of competition. This conclusion has been supported by numerous studies in which no effect of interspecific competition has been found (Rathcke 1976, Ross 1957, Strong Jr. 1982, 1984, Strong Jr. et al. 1984). However, McClure and Price (1975) reported the existence of competition between tree feeding species of leafhoppers (Cicadellidae). Similar results were reported by Stiling (1980) with other species of leafhoppers, and by Darlington (1974) with a gall wasp (Cynipidae).

The quality and physiology of a potential host plant plays an important role in host selection by an insect. Environmental and genetic variation among host plants result in plants of different quality and attraction to insects. Plants that are best suited to support the progeny of competing species generally exhibit a patchy distribution in a field, and this becomes an important limiting factor for the species sharing that resource. This results in interspecific competition. Fritz et al. (1986) found in their study of four species of willow sawflies that host plant phenotype played a more important role in the population dynamics of these species than did interspecific competition.

INSECT - HOST PLANT ASSOCIATIONS

Host plant selection and placement of eggs by females is crucial for survival, especially for species in which the larvae are immobile and are not capable of moving any distance to sample a potential food source. In herbivorous insects, host selection and avoidance is guided by a complex combination of physical and chemical stimuli. Colour, shape and host plant odour play an important role in initial orientation towards a potential food source. On arrival, plant texture and chemical stimulants are responsible for the acceptance or rejection of the plant. For example, the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae), is attracted to the yellow hues of foliage for feeding and resting, and to the form of the fruit for mating and oviposition (Prokopy and Owens 1983). Female spruce budworms will readily lay their eggs on paper models of conifer twigs, whereas in nature they are laid on needles of conifers (Städler 1974, Wilson 1963). The onion maggot is attracted to and will lay eggs on cylindrical objects (Harris and Miller 1984). Plant chemicals play an important role in long-range orientation and oviposition stimulation. The importance of host plant chemicals in oviposition site selection by insects is well demonstrated by the butterfly *Pieris (=Antogeia) brassicae* (Lepidoptera: Pieridae). Females can be stimulated to lay their eggs on green paper treated with sinigrin, or on bean plants cultured in a solution of glucosinulates (David and Gardiner 1962, Ma and Schoonhoven 1973). Research to better understand the relationship of insects to their host plants, has been conducted with a number of insects such as the oriental fruit fly, cherry fruit fly, onion fly, cabbage fly, carrot fly, and colorado potato beetle (Guerin and Städler 1982, Howlett 1915, Levinson 1977, Matsumoto 1970, Visser and Nielsen 1977).

Polyphagous species are stimulated to lay eggs by non-specific cues, such as moisture, sugar, and amino acids, whereas specialists usually respond to specific secondary plant substances. A specialist will accept or reject a plant on the basis of the presence or absence of a certain chemical stimulant. For a generalist, choice of a host is governed by the absence of deterrents (Renwick 1983). In addition to colour, shape and chemicals, the effect of environmental factors such as drought, temperature, disease and other stress factors, as well as physiological stage of the plant, also play a role in acceptance of a plant as an oviposition site. Host preference of *Heliothis zea* (Lepidoptera: Noctuidae) has been found to change as the plant host matures (Stadelbacher 1980). Thus, the presence of specific chemicals may offer protection from one insect pest, but may increase the risk of invasion by other insects (Renwick 1983).

Although insects have the sensory capabilities of accepting or rejecting a plant, host detection is very important in selection. The distance of a suitable host plant patch from a nectar source is one factor that can affect acceptance. Singer (1971, 1982) reported that when the host plant sites of *Euphydryas editha* (Lepidoptera: Nymphalidae) are not as abundant, or are further away from a nectar source, the probability of accepting secondarily preferred hosts as an oviposition site is higher. Occasionally, plants entirely inappropriate for larval survival are accepted. For example, *A. cardamines* (L.) (Lepidoptera: Pieridae) oviposited relatively more eggs on plants that could not support larval development as compared with plants capable of supporting survival and development (Courtney 1981). In a no-choice situation, plants that only weakly stimulated oviposition were also accepted (Courtney and Courtney 1982).

Dethier (1982) has proposed a model of host plant acceptance. According to this model, an insect under normal conditions will only accept the most preferred host plant for oviposition or food. However, if the insect is deprived of its preferred host, after a certain period of time, the balance begins to move in the opposite direction and eventually marginally acceptable plants are chosen for oviposition and feeding. Sometimes completely unsuitable plants may also be accepted. A mechanical analog of this rolling fulcrum model has been presented by Miller and Strickler (1984). Females of *E. editha* become increasingly polyphagous with time if not allowed to oviposit. However, after ovipositing a cluster of eggs, no plant is accepted, but after a period of several hours the number of acceptable hosts increase (Singer 1982). Thus, the threshold for acceptance or rejection varies depending on the nutritional and reproductive state of the insect. The tendency to change from monophagy to polyphagy also depends on the rate at which the fulcrum moves, and also on the movement capabilities of the insect (Miller and Strickler 1984). Generally, the host plant range for larval survival is much larger than that for ovipositing females (Thompson 1988a, b).

Although a number of insects show the rolling fulcrum capabilities in host plant selection, there are some exceptions to the rule. Females of an *Oncopsis* sp. (Homoperta: Cicadellidae) are reported to be highly discriminating in their selection of host plants on which to oviposit. When females were isolated with unsuitable hosts they died without laying their eggs (Claridge et al. 1977). Thus, host plant selection by insects is a complex process and differs from species to species.

LEARNING BEHAVIOUR

Among herbivorous insects that learn to discriminate between host species, conditioning could influence response to a resource in two ways. A first experience with a particular resource could increase the likelihood of its subsequent discovery and acceptance. Conditioning also may reduce the chances of subsequent discovery and acceptance of alternate hosts. True learning has been demonstrated in bees, wasps, butterflies, flies, and leafhoppers (Jaenike 1983, Mark 1982, Prokopy et al. 1982a, Rausher 1983, Rausher and Odendall 1987, Traynier 1984, Vinson et al. 1977).

Studies in the laboratory (Jaenike 1983, Jermy et al. 1968, Prokopy et al. 1982a, 1986), and in the field (Prokopy et al. 1982b), have indicated that prior exposure to a particular resource as a larva or adult may influence a female's tendency to search for and oviposit on that particular host type.

Papaj and Prokopy (1989) listed three criteria by which learning behaviour can be specified: 1) the individual's behaviour changes in a repeatable way as a result of experience, 2) the behaviour changes gradually with repeated experience, often following a so called learning curve, and 3) the changes in behaviour following the experience wanes in the absence of the continuous presence of that host.

In polyphagous species, the adaptive advantage of learning is not as apparent as in oligophagous species (Prokopy et al. 1984). If present, however, it could play a role in enhancing the foraging efficiency of the species. Such behaviour could be advantageous if it predisposes an adult to return to the host plant on which the larvae had been feeding, thereby, increasing the survival chances of the larvae of host specific species. Renwick (1983) states that a specialist will accept or reject a plant based on the presence or absence of certain chemicals, whereas, a generalist's choice is based on the absence of deterrents. Thus, learning is not dependent on the prior exposure of the adult to the host plant. Encounter rates with various resources provide information about the environment. Since optimal oviposition depends on the frequencies of encounters, learning could provide valuable information in the host selection process.

In some cases, learning may be age dependent, host preference being more easily modified in younger than in older insects. Such behaviour has been demonstrated in ants, wasps and stick insects (Cassidy 1978, Wardle and Borden 1985).

Learning may also cause a reversal in the rank order of preference. Adults of *Rhagoletis pomonella* (Diptera: Tephritidae) are more likely to oviposit on fruit types with which they have had previous experience, even if it is not their preferred host (Papaj and Prokopy 1988). Similar preference for low ranking hosts as a result of previous experience was observed also in *Drosophila melanogaster* (Diptera: Drosophilidae) (Jaenike 1983).

CHAPTER 2

PRELIMINARY EXPERIMENTS

INTRODUCTION

CM and OM are thought to be host specific, feeding only on their respective host plants (Crucifers and *Allium spp.*). However, they have been reported feeding on non-host plant material (Gibson and Treherne 1916, Smith 1922, Workman 1958). In addition, they have also been caught in traps set out for other species, for example, CM has been found in traps set out to monitor OM populations, and vice versa (Boivin and Vincent pers. comm.) These findings raised the following questions about these species.

1). Would CM and OM oviposit on non-host plants in a no-choice situation ?

2). Would CM and OM oviposit on non-host plants in a choice situation ?

3). Can larvae survive on non-host plant tissue ?

4). Would CM and OM adults oviposit in the presence of SCM and vice versa ?

5). Could the eggs of these three species be extracted from the ovipositing medium (sand) and placed on plants for larval studies, without any loss or damage as a result of handling ?

To answer these questions, preliminary experiments were conducted: methods and results are given below.

EXPERIMENTAL METHODS AND OBSERVATIONS

1) Oviposition on non-host plants in a no-choice situation.

CM and OM females were tested on non-host plant species. Oviposition by OM on several non-host plants has been reported by Workman (1958). Ten adult females of CM and OM were placed in separate cages (30 x 30 x 20 cm) and provided with food and water. An oviposition container with a bean plant and moist sand was provided as the oviposition site. The container was replaced every three days. The eggs were extracted and counted using the technique described in Chapter 3. In some insects it has been shown that prolonged host plant deprivation leads to non-host plant acceptance during oviposition (Dethier 1982, Miller and Stickler 1984). The experiment was carried out for 15 days to determine if acceptance of the host plant for oviposition would increase over time. Parallel experiments were conducted with OM females using cabbage seedlings as oviposition sites, and with CM females using onion seedlings (non-host species) as oviposition sites.

In these no-choice experiments, OM females laid 75 and 94 eggs on cabbage and bean respectively, whereas CM females did not lay eggs on onion or bean (eggs were laid on either the floor or the sides of the cage).

2. Oviposition on non-host plants in a choice situation.

Based on the above results, OM females were provided simultaneously with onion, bean and cabbage plants as oviposition sites. Ten OM females were placed in a cage (60 X 30 X 30 cm) with food and water. The cages were kept in a well aerated insectary to minimize the possibility that the odours of each of the three plants would contaminate the air above the other plants. The experiment was replicated five times, and the plants placed randomly in the cages. Eggs were collected every three days. OM females laid their eggs on all of the three plant species provided, although fewer eggs were laid on cabbage plants. After 10 days, this experiment was terminated as the flies died as a result of high temperatures (32-35°C) and low R.H., which persisted for a week that year. Data collected by this date (78 eggs on onion, 65 on bean, and 57 on cabbage) were enough to ascertain that OM females will lay eggs on non-host plants, even in a choice situation.

3. Survival of OM larvae on non-host plant material.

Next, an experiment was designed to find out if OM larvae can survive on non-host plant tissues. Approximately 15 first-instar larvae (hatched in a Petri dish) were placed on a piece of rutabaga. The larvae were allowed to feed on the rutabaga for 21 days. After this time, the soil was sifted to extract pupae. Sixty-six percent of the larvae placed on the rutabaga reached the pupal stage. The pupae were then placed in an incubator to check for fly emergence. Larval survival and fly emergence from larvae fed non-host plant material has been reported for this species (Workman 1958). In my experiment, however, no flies emerged.

4. Oviposition occurrence when pairs of species (SCM + CM, and SCM + OM) were provided with a single host species.

The larvae of SCM have been observed feeding, along with CM and OM, on cabbage and onion plants (Miles 1955, 1952). Ten females of SCM and OM, and SCM and CM were placed in cages in incubators at 16:8 (L:D) 21 ± 1°C, and 70% RH., with food and water, and each provided with an onion and cabbage plant respectively as an oviposition site. These plants were replaced with fresh plants on day three. The number of eggs laid by each species of fly (25 SCM and 36 OM on onion, 37 SCM and 26 CM on cabbage) was counted to determine if they would oviposit in the presence of the other species, and if the different eggs could be identified. Based on the number of eggs laid by the different species, no mutual interference of oviposition was detected.

5. Larval survival on host and non-host plants.

At the outset of this project, I had intended to study intraspecific and interspecific competition between both adults and larvae of these three anthomyiid species on host and non-host plants. Various methods of egg and larval extraction, and transfer onto experimental plants, were used to increase larval survival of CM, OM and SCM on their primary host plants (cabbage, onion and bean) respectively. In the first trial the eggs were transferred onto the soil adjacent to the stem of the host plant with a camel hair brush (size 00). Eggs from the same batch were washed onto a filter paper; this was placed in a Petri dish, and kept in an incubator to check egg viability. Emerging larvae were allowed to feed on the host plant and were recovered after

21 days. A mean of 87% recovery was obtained with CM larvae. With OM and SCM larvae, however, few plants were damaged and larval survival was very low in comparison to the high egg viability. Because it was suspected that the eggs had been damaged by the brush, the experiment was repeated using a different method of egg transfer. The eggs were picked up, while they were floating on water, with a Pasteur pipette and placed around the base of the host plant. Although Hausmann and Miller (1989) have successfully completed such egg transfers, my method was unsuccessful, and resulted in only 5 to 10% larval survival. Damaging the plant prior to transferring the eggs did not increase larval survival, and using first instar larvae instead of eggs also failed to increase survival. Consequently further competition studies with OM and SCM larvae were abandoned.

Results obtained from these experiments revealed the following:

1. The Cabbage Maggot (CM) do not lay eggs on non-host plant species in a choice or no-choice situation.
2. The Onion Maggot (OM) do accept cabbage and bean (non-host plants) as oviposition sites in choice and no-choice situations.
3. Transferred as larvae, OM larvae do feed and survive on non-host plant materials.
4. CM, and OM do lay eggs in the presence of SCM adults and eggs, and vice versa.
5. Extraction and placement of CM eggs on three-leaf stage cabbage plants resulted in high pupal recovery; however, no success was achieved with OM and SCM eggs. Thus, further studies using this technique for OM

and SCM were abandoned.

Based on these preliminary experiments the following topics were selected for further study:

1. Effects of intraspecific competition on fecundity, rate of oviposition and female mortality on host and non-host plants (CM on cabbage, and OM and SCM on cabbage, onion and bean) (Chapter 4).
2. Effects of interspecific competition on fecundity, rate of oviposition and female mortality on selected host plants. (CM and SCM on cabbage, and OM and SCM on onion) (Chapter 5).
3. Intraspecific larval competition on host plants (CM on cabbage) (Chapter 7).

CHAPTER 3

MATERIALS AND METHODS

INSECT REARING

Pupae of CM and OM were obtained from the Agriculture Canada Research Station at St-Jean-sur-Richelieu, Quebec. SCM pupae were obtained from the Agriculture Canada Research Station in London, Ontario. All three species were reared in the laboratory for the duration of this study, using the methods described by Tolman et al. (1980) and Whistlecraft et al. (1980 a, b).

Larvae and adults were kept in controlled environment chambers at 20 ± 1°C, 16:8 (L:D), and 70-75% R.H. Adults of CM, OM, and SCM were maintained in cages (30 x 30 x 20 cm) composed of a wooden base and frame, with three sides and the top covered with tergal^{R}, and the fourth side having a tergal^{R} sleeve for access (Fig. 1A). Food for the flies was formulated from soya flour, brewer's yeast, and yeast hydrolysate in a 1 : 1 : 1 ratio and provided on filter paper in a Petri dish. A nylon mesh was used to cover the food to prevent adults from sticking to the yeast hydrolysate. Each cage was also provided with two 10 ml vials, with a hole cut in the cap through which a dental wick protruded, containing water and a 10% honey solution respectively. The food, honey solution and water were changed weekly and dead flies were removed. To maintain the culture, every 14 days, new pupae were placed in moist sand in containers which were put in cages for adult emergence.

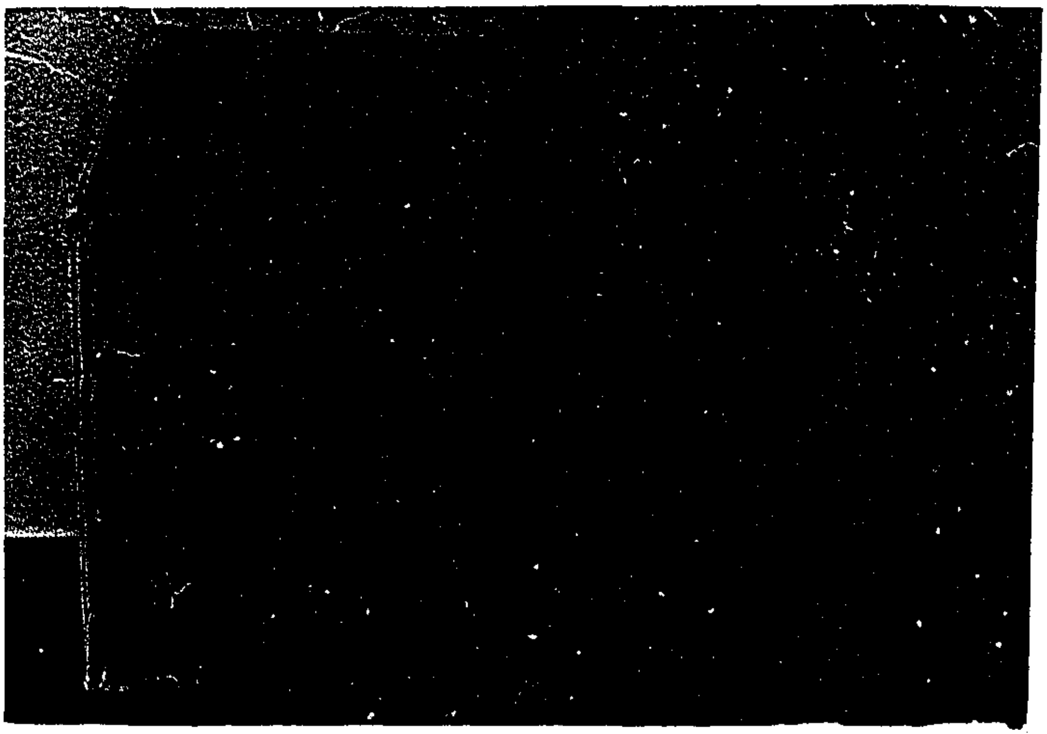
An oviposition site was provided that consisted of two 250 g plastic containers stacked on top of each other (Fig. 1B). The lower container was filled with 50 ml of water, and the upper container with the appropriate ovipositing medium. To keep the ovipositing medium moist, a small hole (1.5 cm in diameter) was cut in the bottom of the upper container through which a dental wick was inserted into the water below. The upper container was replaced every third day, and the ovipositing medium containing eggs was transferred to a plastic box (20 x 15 cm) and placed in the incubator.

The larvae were reared at 20 ± 1°C, 16:8 (L:D), and 70-75% R.H. Food for the larvae was provided every seven days until pupation. Pupae were extracted from the soil and stored in moist sand at 4°C until further use. Pupae of all three species can be stored in this way for 108 days, after which time the rate of adult emergence begins to decline (Ticheler, 1971). Differences in rearing method used for each of the three species is given below.

Cabbage Maggot : The ovipositing medium was sand with a piece of rutabaga (ca. 5 x 5 x 4 cm) placed on the surface as an oviposition stimulant. Eggs were laid around the rutabaga in the sand. On hatching, the larvae fed on the piece of rutabaga, a fresh piece being added every seventh day. Pupae were extracted from the soil, as well as the few that pupated inside the rutabaga, after approximately 21 days.

Onion Maggot: The ovipositing medium was sand with an onion half (ca. 8 cm in diameter) on top as the oviposition stimulant. The females laid their eggs in the soil around the onion and sometimes on the onion itself. On hatching, the larvae burrowed into the onion bulb and began feeding. Fresh food (onion halves) was added to the larval container every seventh day. Pupae were extracted from the soil after approximately 21 days.

Figure 1. Apparatus used in rearing, Cage (A), Oviposition container (B)




B

Seed Corn Maggot: For SCM, a mixture of sand and muck soil was used, mainly because larval survival was higher in a mixture compared to sand alone. This may be because microorganisms associated with organic soil provide nourishment for the developing larvae by breaking down soil organic matter (Barlow 1965, Nair and McEwen 1973, Weston and Miller 1987). Instead of the diet mixture recommended by Whistlecraft et al. (1980a), pre-soaked lima beans mixed into the soil were used for oviposition and as larval food. This was because the fungal growth that developed on the former resulted in high larval mortality. Every third day fresh lima beans were added to the larval container. The pupae were extracted from the soil after approximately 14 days.

PLANT GROWTH.

The same host cultivars were used throughout the study: cabbage (Stone Head cv.), onion (Canada Maple cv.) and bean (Gold Rush cv.). Plants were grown in growth chambers under constant conditions of 16:8 (L:D), and 25:18°C (day:night). A mix of coarse grade vermiculite, horticultural peat and pasteurized top soil, in a 1:1:2 ratio, was used as the planting medium. The plants were watered every two days and fertilizer (20:20:20 (N.P.K)) (0.10 g / 100 ml) was added to the pots every 14 days. Seeds of all three crop plants were first germinated in a Petri dish to ensure both viability and consistency of plant age. Planting trays of six cells per cube were used. Plants used for all oviposition experiments were at the same physiological age (third to fourth true-leaf stage for cabbage and onion, and second true-leaf stage for bean). Plants at the sixth true-leaf stage were used for larval studies.

SAMPLING TECHNIQUES

Extraction

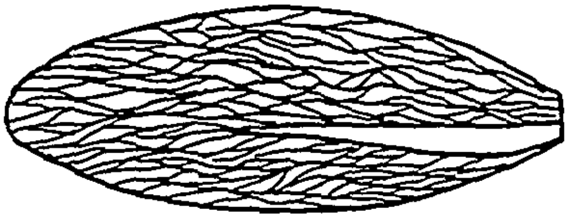
Eggs were extracted from the ovipositing medium (sand) by floatation on water. The medium was placed in a 1000 ml beaker. This was then filled with distilled water and stirred with a glass rod. The eggs floated to the surface and the water was poured through a hand sieve (60 mesh/ cm). The beaker was again filled with water and any remaining eggs were washed out. Preliminary trials showed that seven washes provided optimal (99%) egg recovery. Eggs were extracted immediately after their removal from the cage. The collected eggs were washed from the sieve into a vial, and stored in water at room temperature until the next day for counting. Structural differences in the eggs of the three species are given in Fig. 2.

Counting

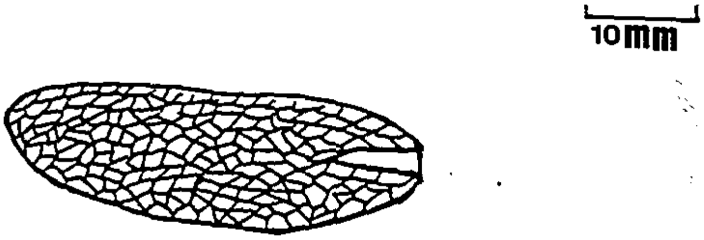
A 20 cm^2 black cloth with a grid stitched with white thread was used to count the eggs. The cloth was placed in a Buchner funnel and the collected eggs were poured onto it. The Buchner funnel was attached to a 2000 ml flask that was connected to a vacuum pump. About 100 ml ofwater was poured into the funnel and the pump was turned on . This procedure ensured that the eggs were distributed over the grid. This cloth was then removed and all of the eggs counted at 10 x 25 magnification, under a stereoscopic microscope (Fig. 3).

Figure 2. Structural differences in the egg surface of Cabbage Maggot (A), Onion Maggot (B), and Seed Corn Maggot (C).

A



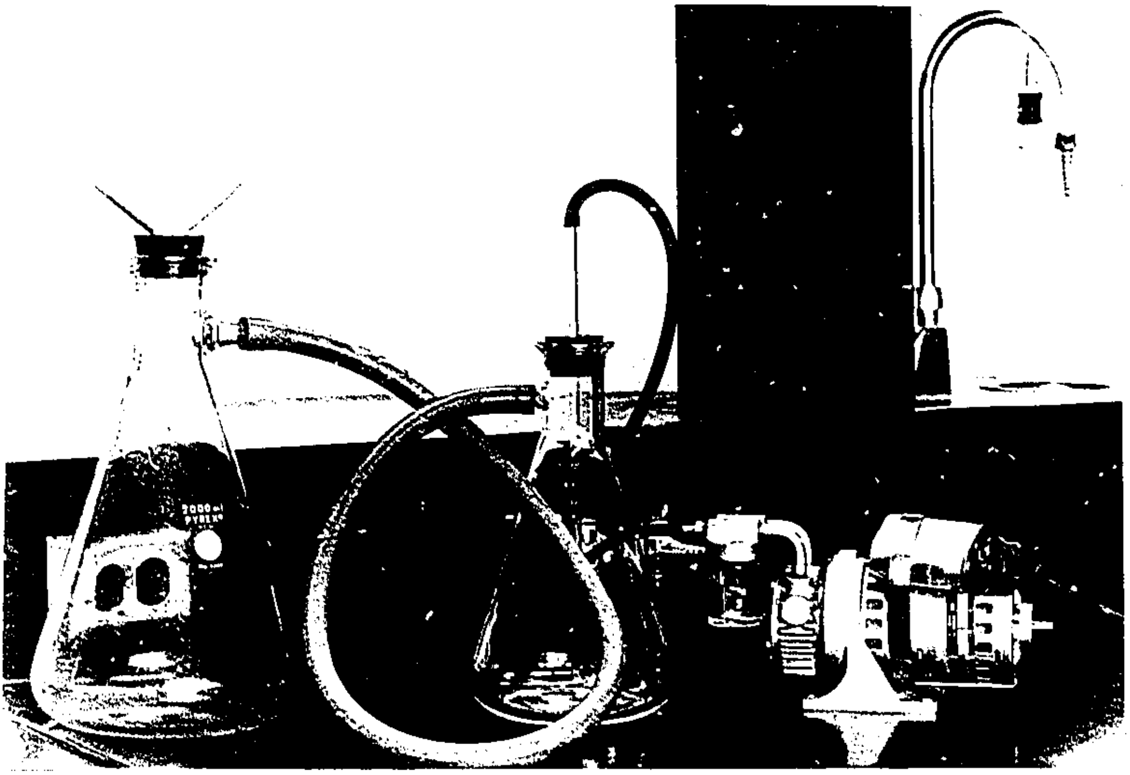
B



C

20 X 25

Figure 3. Apparatus used for sampling and counting eggs


2000 ml
PYREX

STATISTICAL ANALYSIS:

All fecundity data were analyzed using the following statistical procedures. Total number of eggs laid on each sampling day was divided by the number of females alive on that day, to give number of eggs laid per female per day. These data were used in all statistical analyses. All data were transformed using square root transformations. Total number of eggs laid per female per density was subjected to Analysis of Variance (ANOVA), significance being recorded at the $\alpha = 0.05$ level (Sokal and Rohlf, 1981; SAS Users Manual, 1985 p. 449). Means were compared using "Tukeys" Studentized Range Test (Sokal and Rohlf, 1981). The cumulative number of eggs laid per female per density, for each replicate over the 30-day experimental period was calculated. These numbers were then subjected to probit analysis, to estimate the time (days) to reach 50% oviposition: (OT_{50}) (rate of oviposition), and time to reach 50% mortality: (LT_{50}), (rate of mortality) (SAS Users Manual, 1985, p. 640). Overlapping fiducial limits were calculated at $p=0.05$ level of significance. For larval intraspecific studies, the mean pupal weight was calculated by dividing the total pupal weight in each replicate by the number of larvae that pupated. An analysis of variance was performed on these numbers, significance being recorded at 0.05 level. Survival of larvae and days to pupate were analyzed in the same way.

CHAPTER 4

EFFECT OF INTRASPECIFIC OVIPOSITION COMPETITION ON FECUNDITY AND SURVIVAL OF CABBAGE MAGGOT, ONION MAGGOT AND SEED CORN MAGGOT ON CABBAGE, ONION, AND BEAN PLANTS.

INTRODUCTION

Individuals of the same species have very similar requirements for survival, growth, and reproduction. As population density increases, the combined demand for a resource may exceed its immediate supply. Under such conditions, intraspecific competition for this limited resource may reduce survival, growth, fecundity and rate of reproduction. The intensity of these effects would be expected to increase as density of the population increases. Three anthomyiid species were selected to study the effects of density on reproductive behaviour under controlled laboratory conditions.

Cabbage Maggot (CM) and Onion Maggot (OM) are primary pests of crucifer and *Allium* spp. respectively (Brittain 1927, Gibson and Treherne 1916, Workman Jr. 1958). The Seed Corn Maggot (SCM) is a generalist that feeds on a wide variety of plants including crucifers and *Allium* spp. (Miller and McClanahan 1960, Reid 1940).

CM and OM are mainly attracted to the secondary plant chemicals (glucosinolates and n-dipropyl disulphide) released by their respective host plants (cabbage and onion). SCM is attracted to odours associated with both the decomposing organic matter in soil, and germinating seeds (Barlow 1965, Finch 1978, Hawkes 1975, Matsumoto and Thorsteinson 1968a, 1968b, Ristich 1950). For these three species, in addition to secondary plant compounds, the physiological age of the plant (younger plants are generally preferred to older ones), and microorganisms in the soil and on damaged plants increase the attractiveness of the site for oviposition. Attraction to these sites may explain the aggregative or clustered population distribution of adults and larvae in the field (Havukkala and Miller 1987, Yathom 1970).

Such a behaviour could result in resource limitations within these aggregations leading to competition for oviposition sites among gravid females. Competition between individuals increases in intensity as density of the population increases, which in turn may affect fecundity and mortality of the competing species, as has been found in Drosophila (MacLagan and Dunn 1936, Park 1932), *Cephaloleia consanguinea* and *C. perplexa* (Coleoptera: Hispinidae) (Strong Jr. 1984).

The purpose of the present study was 1) to examine the effects of female population density of CM, OM and SCM on fecundity, rate of oviposition, and female mortality, when these flies were competing for an oviposition site and, 2) to observe the effects of density on fecundity in the presence of non-host plant species.

MATERIALS AND METHODS

INSECT REARING

CM, OM, and SCM were reared continuously throughout the experiment within controlled environmental chambers at 21 ± 1°C, 16:8 (L:D) and 70-75% R.H., as described in Chapter 3.

PLANT GROWTH

Cabbage, onion and bean plants were grown in the laboratory in growth chambers at 16:8 (L:D) and 25:18°C (day:night). For all experiments described in this chapter, third to fourth true-leaf stage cabbage, and onion plants and second-true-leaf stage bean plants were used. Further details are provided in Chapter 3.

EXPERIMENTAL PROCEDURES

The experimental method employed was generally similar for all three species. CM was tested with cabbage, OM and SCM were each tested with cabbage, onion and bean plants.

The required number of pupae were removed from storage, and placed in moist sand in a 250 ml plastic container within a cage, and flies were allowed to emerge over two days following the first female emergence. Care was taken to use only pupae that had pupated within the same seven day period. The pupae were mixed before putting them into an emergence cage to ensure randomness. The adults were provided with food (brewers yeast, soya flour, and yeast hydrolysate), water and honey solution and were kept in the cage for three (SCM) or four (CM and OM) days, corresponding to their respective rates of development. They were then sexed and placed in new cages (30 x 30 x 20 cm) at densities of 5, 10, 20, and 40 females, with equal numbers of males to ensure that all females would be mated. Since the focus of this study was fecundity and female survival, all subsequent references to density refer only to female density. Each cage was supplied with food, water and 10% honey solution, and an oviposition container. The latter consisted of a plastic container (250 ml) with a large hole (2 cm in diameter) in the centre and a smaller hole (1.8 cm in diameter) towards the edge, cut in the lid (Fig. 4). Water (50 ml) was placed in the lower container and a dental wick was inserted through the smaller hole in the lid into the water below. A cube from the planting tray containing a single plant was placed in the container. The aerial parts of the plant were passed through the larger hole in the lid. Sand was then put on top of the lid, 1.3 cm deep, surrounding the plant, as the ovipositing medium. The cages were placed in a walk-in incubator set at 21 ± 1°C, 70 - 75% R.H, and 16:8 (L:D), in a randomized complete block design. Each density was replicated four times. The experiment lasted 30 days, and during this time the oviposition dish was replaced every second day. Eggs were collected and counted using the method described in Chapter 3. Number of dead females was recorded every sample day.

STATISTICAL ANALYSIS

All data were analyzed using the procedure described in Chapter 3. For each species, fecundity, and the rate of oviposition and mortality, measured as days to reach 50% oviposition (OT_{50}) per female, and days to reach 50% mortality (LT_{50}) were compared between four female densities (5, 10, 20, and 40), as well as between the three host plants (cabbage, onion and bean). Significant differences in (OT_{50}) and (LT_{50}) between densities were found when fiducial limits did not overlap.

Figure 4. Oviposition container used for all experiments.


HONEY
MIEL

RESULTS

A. INTRASPECIFIC OVIPOSITION COMPETITION IN THE CABBAGE MAGGOT.

On cabbage plants. a significant effect of density on fecundity per CM female was observed (ANOVA, F= 3.90, $df_{9,3}$, $p < 0.05$). Fecundity per female was significantly lower at density 5 compared with densities 10, 20 and 40. Although no significant differences between densities 10, 20 and 40 were observed, there was a gradual decline in fecundity as density increased (Fig.5). The time required to reach 50% egg deposition (OT_{50}) showed a reduction in the rate of oviposition as density increased from 5 to 10, with no further change with increasing density. Thus, it appears that females lay their eggs at a slower rate at higher densities (Table 2). Adult density was observed to have an effect on rate of mortality of females, the LT_{50} (time to 50% mortality) at density 5 being significantly slower than at 20 and 40, and at density 40 being significantly faster compared with densities 5, 10, and 20. No differences between densities 5 and 10, or between 10 and 20 were observed (Table 3). The pattern of oviposition and mortality over the experimental duration (30 days) for the four densities shows a sharp rise in the cumulative number of eggs laid per female between days 10 to 14 at density 5 compared with densities 10, 20 and 40. A similar sharp increase in mortality between days 12 to 20 at density 5 was recorded. No sudden changes in oviposition trend was recorded for densities 10, 20 and 40 (Fig. 6,7).

B. INTRASPECIFIC OVIPOSITION COMPETITION IN THE ONION MAGGOT.

Fecundity of OM females was studied on all three plant species. On onions (host plant) a significant effect of density on fecundity per female was recorded (ANOVA, F= 26.23, $df_{9,3}$, $p < 0.05$). As density of flies increased, fecundity per female also increased, although there was no significant difference between densities 10 and 20 (Fig. 8A). A harmful effect of density on rate of oviposition was observed, the rate (OT_{50}) being significantly faster at densities 5 and 10 compared with 20 and 40 (Table 2). Density had no significant effect on rate of female mortality (LT_{50}) (Table 3).

On beans (non-host plant), total fecundity per female was significantly affected by density (ANOVA, F= 10.45, $df_{9,3}$, $p < 0.05$). A significantly higher number of eggs was laid at density 5 than at densities 10, 20 and 40 (Fig. 8B). Rate of oviposition (OT_{50}) was significantly slower at densities 5 and 20, compared with 10 and 40 (Table 2). LT_{50} was also significantly slower at density 5 and faster at density 40 when compared with each other and density 10 and 20, but no difference between densities 10 and 20 were detected (Table 3).

On cabbage (non-host plant) a significant effect of density on fecundity per female was recorded (ANOVA, F= 4.58, $df_{9,3}$, $p < 0.05$). Fecundity per female at density 10 was significantly higher than at densities 5, 20, and 40. No significant difference in fecundity between densities 5, 20 and 40 was observed (Fig. 8C). No significant difference in rate of oviposition (OT_{50}) with increasing density was observed (Table 2). Rate of mortality (LT_{50}) also showed no significant difference with change in density (Table 3).

The highest fecundity on host plant (onion) was reached at density 40, while, on non-host plants, it was reached at density 5 (bean), and 10 (cabbage). A smooth increase in the cumulative percent eggs laid per female per day on onions and beans, at all four densities, during the experimental duration (30 days) was observed. On cabbage, although considerably slower as compared with bean and onion, a stepwise pattern of increase in cumulative percent eggs laid per female per day can be detected (Figures 9 A, B, C). This pattern may indicate the non-preference of cabbage as an oviposition site. The trend in mortality over 30 days shows a sharp increase in cumulative percent mortality at density 5 between days 18 and 20 on onion, an increase up to day 14 on bean, after which it stabilized, and no sudden increase on cabbage (Fig. 10 A, B, C).

C. INTRASPECIFIC OVIPOSITION COMPETITION IN THE SEED CORN MAGGOT

With onion plants, a significant effect of density on fecundity per female was observed (ANOVA, F= 4.77, $df_{9,3}$, $p < 0.05$). Fecundity was highest at density 10, and no significant differences were found between the other densities (Fig. 11A). The rate of oviposition (OT_{50}) was faster at density 5, and slower at density 20, when compared with each other and with densities 10 and 40: no significant difference between densities 10 and 40 was observed (Table 2). A significant difference in LT_{50} between densities 10 and 5, 20 and 40 was observed (Table 3).

On beans, fecundity was significantly affected by density (ANOVA, F= 13.45, $df_{9,3}$, $p < 0.05$). Fecundity per female was higher at densities 20 and 40 than at 5 and 10 (Fig. 11B). A slower rate of oviposition

(OT_{50}) at densities 20 and 40 was also observed when compared with 5 and 10 (Table 2). No difference was recorded between densities 5 and 10 or between 20 and 40. The LT_{50} was significantly slower at density 10 (Table 3).

On cabbage plants, a significant effect of fecundity per female was recorded (ANOVA, F= 4.61, $df_{9,3}$, $p < 0.05$). Fecundity was highest at density 5, and no significant difference was found between either densities 10 and 20, or 20 and 40 (Fig. 11C). The OT_{50} was significantly faster at density 5 compared with the other densities (Table 2). The rate of mortality (LT_{50}) was significantly slower at density 5, compared with 10, 20 and 40. No difference between the latter three densities was recorded (Table 3).

The oviposition trend over the sampling period is shown in Figure 12 (A,B,C). On bean and cabbage, the cumulative percent eggs per sampling day showed a gradual increase over time. On onion, however, a sharp increase in the cumulative percent eggs laid was observed between days 4 and 12 at density 5, compared with densities 10, 20 and 40. The trend in mortality over time did not change on bean, cabbage and onions (Fig. 13 A, B, C)

DISCUSSION

These results show that in a closed ecosystem there is an optimum adult density for maximum fecundity in CM, OM, and SCM. This optimum density was higher on host plants compared with non-host plants. CM was found to be most selective, ovipositing only on cabbage: OM and SCM accepted all host and non-host plants as oviposition sites. The rate of oviposition was reduced at higher densities on host plants when all four densities were compared. Rate of oviposition by OM was considerably slower on non-host plants (cabbage and bean) when compared with the host plant (onion). A similar delay in rate of mortality on cabbage was also recorded. The rate of oviposition in SCM was slower at higher densities, but the rate of mortality was slower at lower densities on cabbage and bean plants.

The existence of such an increase in fecundity up to an optimum adult population density, above which a decrease in fecundity occurs, is termed an "Allee" type response (Allee 1928; Pearl 1932). Such a response in an organism may be an adaptation to certain nutritional, physiological and behaviourial requirements of individuals within a population. For example, an increase in adult density may lead to increased mating, which may stimulate oviposition (Gerber 1973); or host plants may be conditioned by larval feeding, thereby increasing the availability of essential nutrients, which in turn results in aggregation of adults and increased oviposition stimulation. Field studies with the mosquito, *Culex tarsalis* (Diptera: Culicidae), show that the topographical features of the surrounding area can also play a role in oviposition site selection and aggregation of females (Laurence and Samarawickrema 1970).

Aggregative behaviour has been recorded in CM, OM and SCM adults (Harcourt 1967, Mukerji 1969, Nair and McEwen 1975). In such aggregations, the close proximity of other ovipositing females, and the presence of eggs in the ovipositing cups, does not inhibit oviposition.

Harris and Miller (1983) and Havukkala and Miller (1987) have reported that OM females readily oviposited on plants that already had other ovipositing females on them. The flies showed no apparent aggressive behaviour towards one another. These authors observed that two or three OM females sometimes oviposit at the same time. Such behaviour has also been demonstrated with *Hippelates pusico* (Loew) (Diptera: Chloropidae) (Karandinos and Axtell 1972). The physiological state of the host plant can also play a role in this aggregative behaviour, resulting in increased oviposition (Harcourt 1967, Nair and McEwen 1975, Swailes 1958). Aggregations, in some insects, can stimulate oviposition. SCM females have been observed to aggregate in the field, at which times increased oviposition has been recorded (Hough-Goldstein et al. 1987; Yathom 1970). A similar increase in oviposition as density increased was recorded in all three species in this study.

Increased oviposition as density of females increases may be beneficial to larval survival by conditioning of the host. Larval feeding in these three species is largely responsible for providing an entrance route for microorganisms, which in turn comprise a source of nourishment for the larvae, which consequently develop and mature faster in their presence (Eymann and Friend 1985a, Friend et al. 1959b, Schneider et al. 1983). All of these species are attracted to odours associated with the soil microorganisms that are responsible for the rotting of the host tissue (Dindonis and Miller 1980, 1981a, Hausmann and Miller 1989, Hough 1981, Hough-Goldstein and Bassler 1988). Thus, aggregation of females on a plant may lead to a higher number of eggs laid, increased larval feeding, increased microbial activity (conditioning of the host tissue), faster larval development, and a shorter exposure time of the larvae to enemy organisms. In the moth *Cactoblastis cactorum* (Lepidoptera : Pterophoridae), clumping of egg sticks is considered to be an altruistic behaviour that is beneficial to the group, similarly, aggregation in the cabbage aphid *Brevicoryne brassicae* (Homoptera: Aphididae) increases survival (Monro 1967, Way and Cammell 1970). In the mosquito, *Culex tarsalis* (Diptera: Culicidae), females are stimulated by the presence of egg rafts of other females, and *Mansonia uniformis* (Diptera: Culicidae) often lay eggs on leaves that already carry eggs of other females (Laurence and Samarawickrema 1970). In the latter species, it was found that the more a leaf had been used, the more likely it was that ovipositing females would choose that leaf to aggregate and oviposit on. It may be that the number of eggs indicates the suitability of the oviposition site for maximum progeny survival. This may explain why an increase in oviposition as density increased was recorded in my experiments.

Another reason for increased oviposition stimulation may be the presence of an oviposition pheromone, which becomes repellent at high concentrations (high female densities) and less stimulating at lower concentrations (lower female densities). This would explain the presence of an optimum density for maximum fecundity. The rate of oviposition per female, in this study, shows a delay at higher densities of 20, and 40 for all three species on their respective host plants (CM on cabbage, OM and onion, and SCM on bean). Coupland (1991) reported aggregations of *Simulium reptans* (Diptera: Simullidae) at main oviposition sites. These females laid eggs faster in areas with freshly laid eggs, however, egg laying took longer once the eggs were older. Davies (1957) has postulated the presence of a pheromone that acts as an attractant and hastens egg deposition. Thus, the possibility of such a pheromone in CM, OM and SCM remains to be investigated.

At high densities, decrease in fecundity may also be because of disturbance of the females during oviposition. CM and OM exhibit a specific pre-oviposition behaviour during which the females run along the stem of the host plant and then on the ground, probing the soil repeatedly with the ovipositor before egg deposition (Harris and Miller 1983, Zohren 1968). At lower densities, lack of stimulation by other ovipositing females, may cause a decrease in fecundity.

Aggregation resulting in increased fecundity with increasing population density up to an optimum has also been observed in the weevil *Callosobruchus maculatus* (Coleoptera: Bruchidae) on cowpea seeds, the mosquito *Culex tarsalis* (Diptera: Culicidae), the midge *Hippelates pusio* (Diptera: Chloropidae), and the confused flour beetle *Tribolium confusum* (Coleoptera: Tenebrionidae) (El Sawaf, 1956; Karandinos and Axtell 1972, Kirchna 1939, Nuorteva 1954, Rich 1956, Richards 1947).

Oviposition by OM was also tested with two non-host plants in the present study. Although OM is considered to be host specific, feeding only on plants of *Allium* spp., a number of reports have indicated its presence on non-host plants (Smith 1922, Workman Jr. 1958). In my preliminary experiments (Chapter 2), OM females were found to oviposit on both cabbage and bean plants. However, intraspecific competition studies with OM showed that the optimal fly density for oviposition was lower on the non-host species than on the host species (onion). Rate of oviposition and mortality data for non-host plants, in comparison with onion, indicate that the flies retain their eggs until a suitable host is found, this phenomenon occurring especially in the presence of the non-host plant cabbage. SCM, being a generalist, accepted all three host plants. However, the optimum density for oviposition differed from one host to the next, being higher on onions and lower on beans. Thus, type of host plant and fly density can both affect fecundity. In OM the rate of oviposition was significantly slower on cabbage and beans (non-host plants), indicating that females in a natural environment may leave the area for a more suitable oviposition site.

CM, unlike OM, did not accept any other host plant as an oviposition site. When certain insects (Coleoptera, Lepidoptera, Homoptera) are confined with plants that are not related to their host plants, they may cease to oviposit, and they retain their eggs (Andres and Angalet 1963, Claridge et al. 1977, Courtney and Courtney 1982, Singer 1971, 1982). In contrast, some insects, like OM, when confined with a non-host plant in a no-choice situation, will lay high numbers of eggs on plants that are highly unsuitable for larval development (Singer 1982). Courtney (1981) found that the butterfly *Anthocharis cardamines* (Lepidoptera: Pieridae) laid relatively more eggs on plants that cannot support larval development than on plants that could support survival and development, in a choice situation. In a no-choice situation, plants that only weakly stimulated oviposition were accepted.

The acceptance of non-host plants by OM females, in the present experiments, can be explained on the basis of the rolling fulcrum theory (Dethier 1982, Miller and Strickler 1984). According to this theory, an insect under normal conditions will only accept the most preferred host plant for oviposition and feeding. However, if the insect is deprived of its preferred host, after a certain period of time, the balance of acceptance begins to move in the opposite direction, and eventually marginally acceptable plants are chosen for oviposition and feeding. Even completely unsuitable plants may be accepted by some species. A similar shift in acceptance of oviposition sites was observed in OM females. Deprived of their own host, these females accepted beans and cabbage (non-host plants) as oviposition sites. This acceptance was considerably delayed, however, suggesting that the physiological state of the females determined the acceptance of these non-host plants (Fig. 11 A,B,C). CM females, on the other hand, did not show such a shift in acceptance, and died before laying eggs, confirming its extreme host plant specificity. SCM, being a generalist, accepted all three host plants as oviposition sites, although the optimal density was different on each host.

Density dependent mortality has been found to be common in a number of insects (Ishida 1952, LeCato and Pienkowski 1972). In the present study, the rate of female mortality increased with density for CM and OM ovipositing on cabbage and onions respectively. The stress caused by disturbance and interference at high population densities during oviposition is most likely to be the main factor causing mortality. However, on non-host plants, OM mortality was considerably slower on cabbage, but on beans, although it was slower when compared with onions, the rate of mortality increased with an increase in fly density. This corresponds with the data for oviposition; thus, egg retention, as occurs on non-host plants, may result in increased longevity, as has been found in some other species. SCM did not show any effect of density on mortality, irrespective of the host plant. Ishida (1952) reported that as density increased, female longevity of the azuki bean weevil also increased. This happened, however, only if oviposition sites were restricted and females were forced to retain their eggs. In LeCato and Pienkowski's (1972) study of the alfalfa weevil *Hypera postica* (Coleoptera: Curculionidae), female longevity responded negatively to insect density, i.e., longevity decreased with increasing density. Decrease in longevity with crowding has been recorded in certain beetles, *Trogoderma spp.* (Coleoptera: Dermestidae), *Drosophila spp.* (Diptera, Drosophilidae), and certain solitary grasshoppers (Orthoptera: Acrididae) (Davis 1945, Pearl et al. 1927, Smith 1970). In the present study it appeared that the availability of a suitable host also played a role in the rate of female mortality.

Thus, from the present study it can be concluded that on host plants there is an optimum density for maximum fecundity per female CM, OM and SCM. CM is very host specific, females will not oviposit on non-host plants and shifts in oviposition behaviour, even under stressful conditions, do not occur; although low numbers of CM adults have been trapped in fields of non-host plants (G. Boivin and C. Vincent pers. com.), whereas OM females will. However, the delay in the rate of oviposition in OM on non-host plants indicates that, given a choice females will search for a more suitable host. SCM, on the other hand, will oviposit on all three host plants.

This information can be useful in interpreting monitoring data, and when relating fly population density to the amount of damage expected. The presence of CM and OM in onion and cabbage fields respectively may not be economically important, however, further studies with OM on non-host plants are recommended, as I found that OM larvae can survive on non-host plant material. The presence of SCM in a cabbage, onion or bean field, on the other hand, should be considered important, and the correct monitoring and identifying procedure is necessary for accurate predictions of crop damage. The use of a highly attractive trap crop could prove quite beneficial, as the females will tend to aggregate on the trap crop and lay most of their eggs on these crops.

Figure 5. Total number of eggs laid per female Cabbage Maggot (CM) per density on cabbage plants. Densities with the same letter are not significantly different at $\alpha = 0.05$ (Tukey's test).

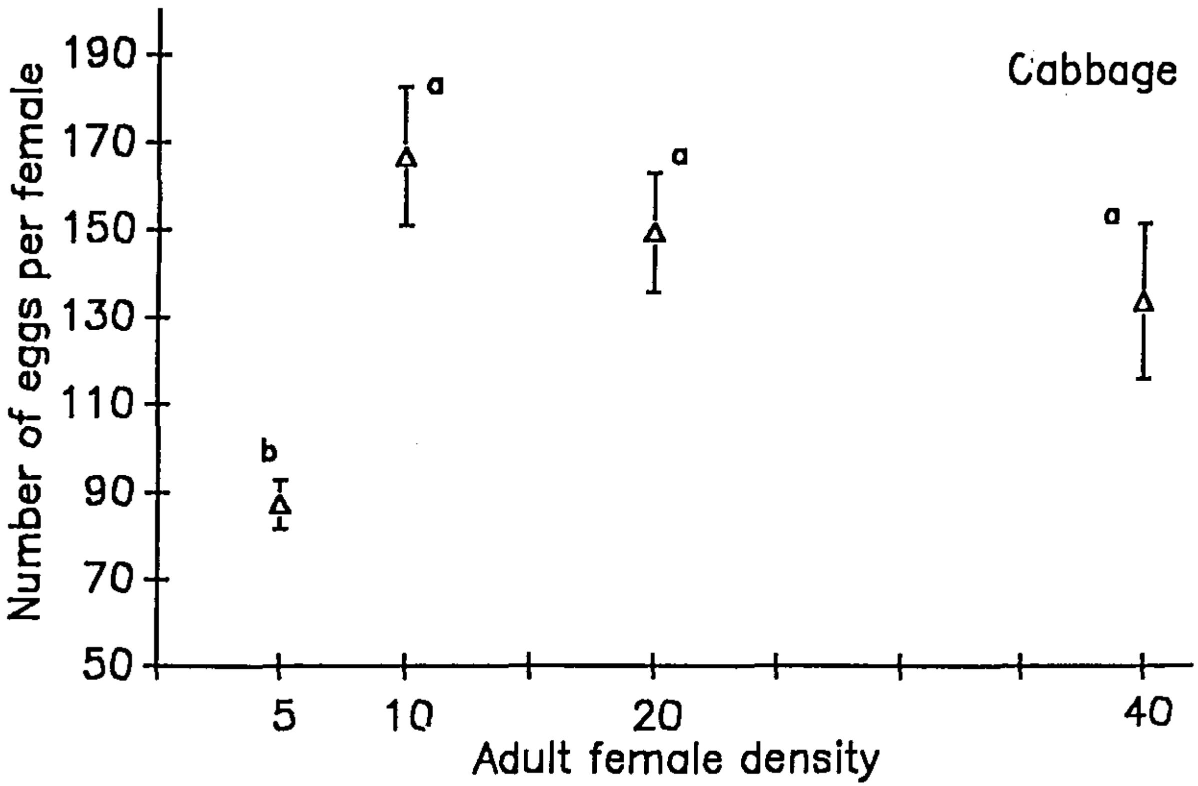
Cabbage
Number of eggs per female
190
170
150
130
110
90
70
50
Adult female density
5
10
20
40
a
a
a
b

Figure 6. Cumulative percentage of eggs laid per female Cabbage Maggot (CM) per density on cabbage plants.

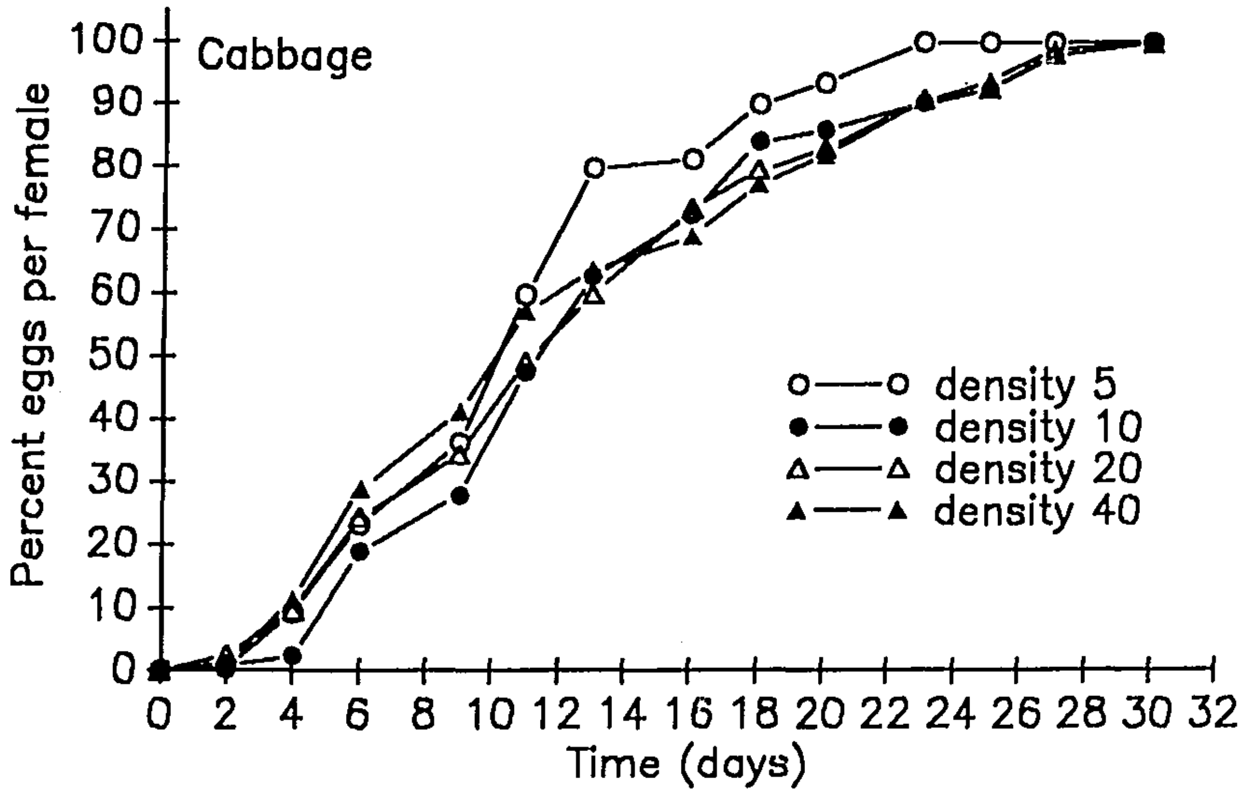

Cabbage
Percent eggs per female
0
10
20
30
40
50
60
70
80
90
100
Time (days)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
density 5
density 10
density 20
density 40

Figure 7. Cumulative percentage of female Cabbage Maggot (CM) mortality per density on cabbage plants.

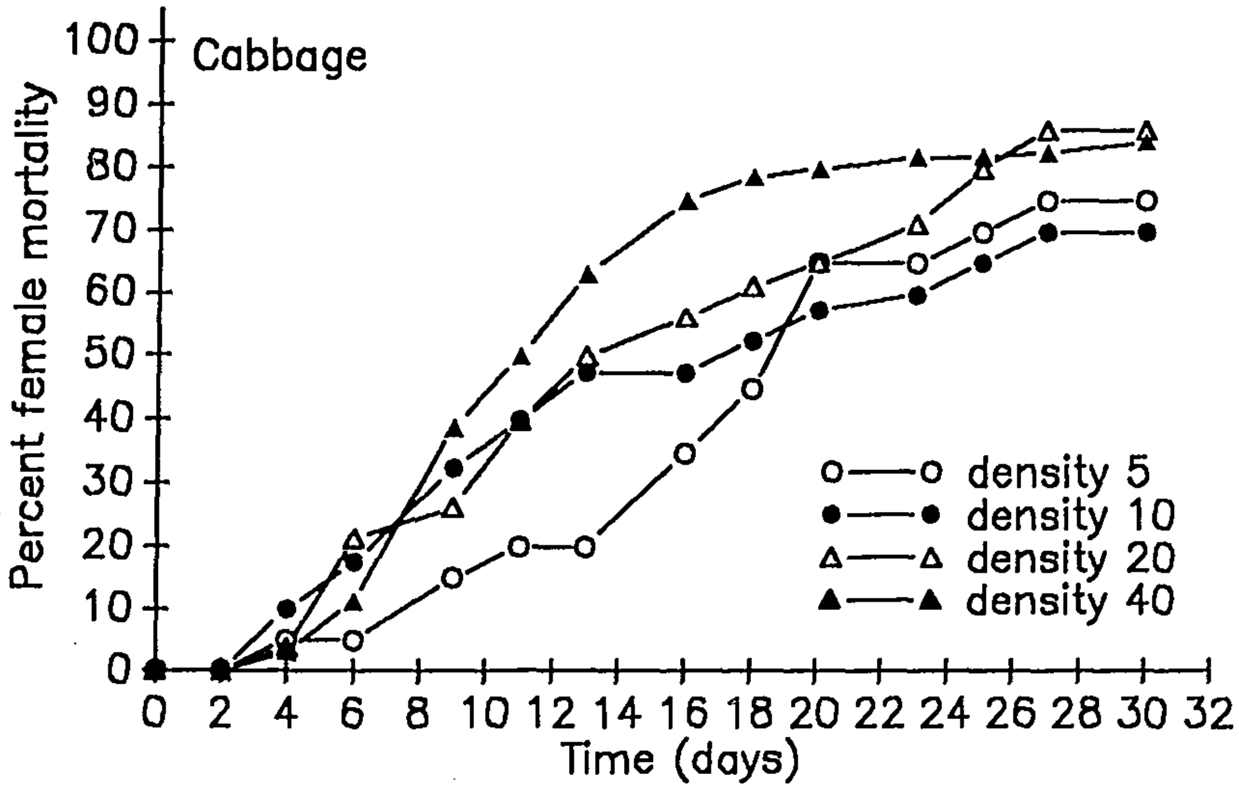

Cabbage
Percent female mortality
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
Time (days)
o——o density 5
●——● density 10
Δ——Δ density 20
▲——▲ density 40

Figure 8. Total number of eggs laid per female Onion Maggot (OM) per density on onion (A), bean (B), and cabbage (C) plants. Densities with the same letter are not significantly different at $\alpha = 0.05$ (Tukey's test).

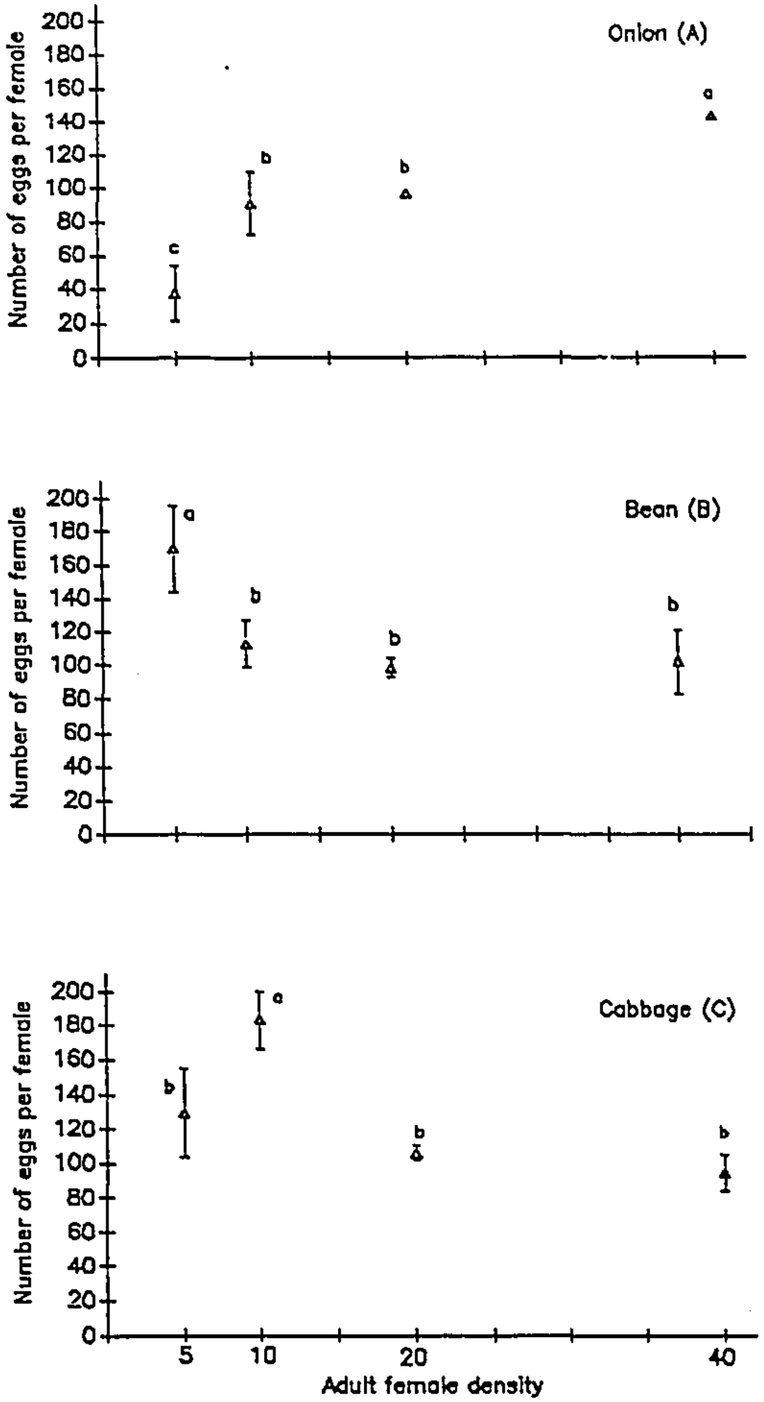

Onion (A)
Bean (B)
Cabbage (C)
Number of eggs per female
0
20
40
60
80
100
120
140
160
180
200
a
b
c
5
10
20
40
Adult female density

Figure 9. Cumulative percentage of eggs laid per female Onion Maggot (OM) per density on onion **(A)**, bean **(B)**, and cabbage **(C)** plants.

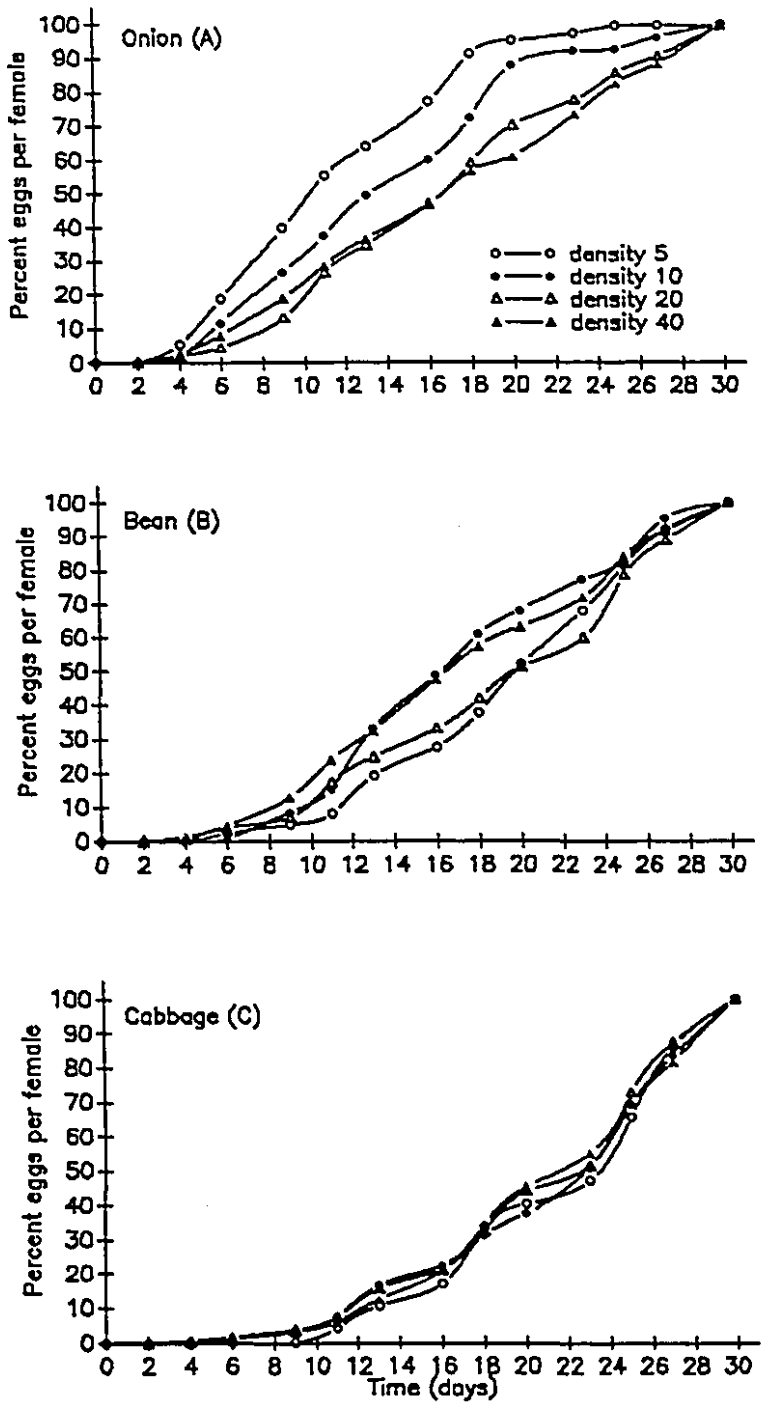

Onion (A)
Bean (B)
Cabbage (C)
Percent eggs per female
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Time (days)
density 5
density 10
density 20
density 40

Figure 10. Cumulative percentage of female Onion Maggot (OM) mortality per density on onion (A), bean (B), and cabbage (C) plants.

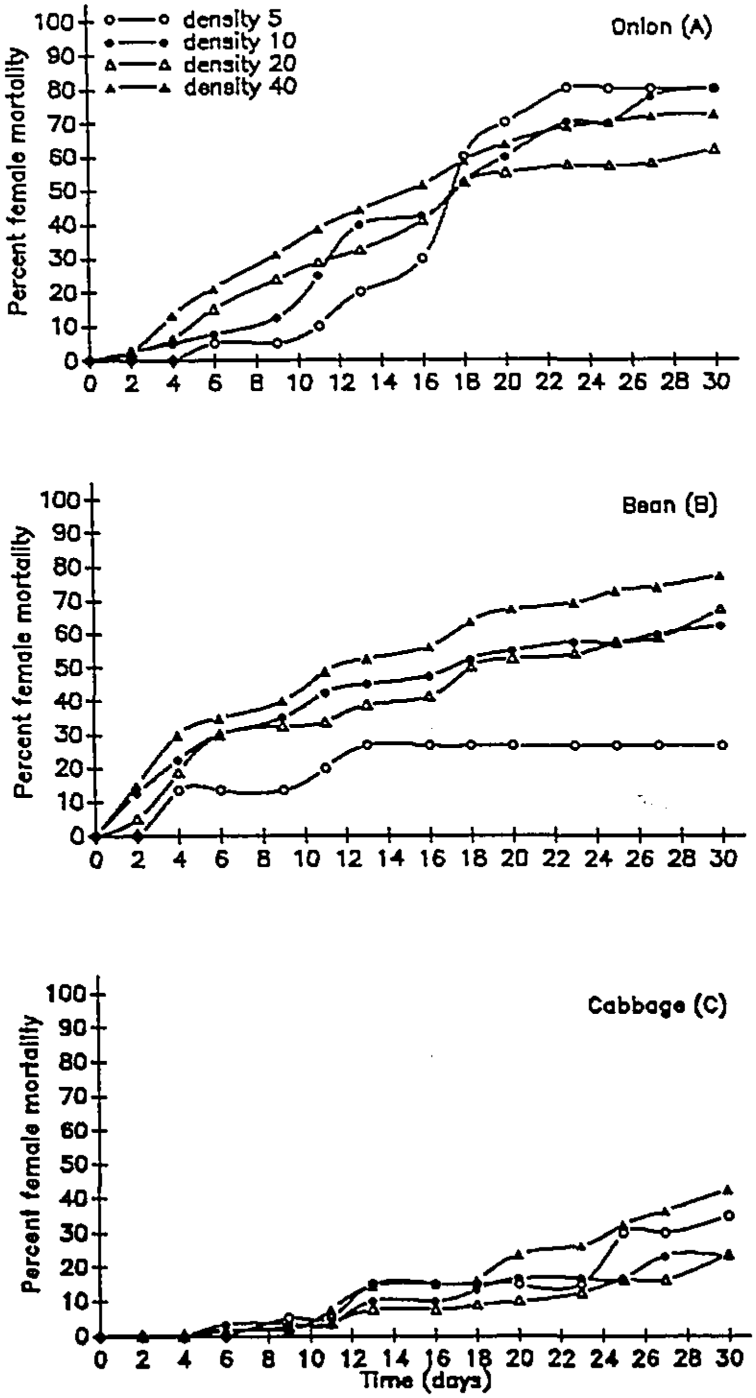

density 5
density 10
density 20
density 40
Onion (A)
Bean (B)
Cabbage (C)
Percent female mortality
0
10
20
30
40
50
60
70
80
90
100
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
Time (days)

TABLE 2. Estimated number of days required to reach 50 % oviposition (OT_{50}) by Cabbage Maggot (CM), Onion Maggot (OM) and Seed Corn Maggot (SCM) on cabbage, onion and bean plants, along with fiducial limits and slope of the line ($\alpha = 0.05$).

Insect Species	Host Plant	Adult Density	Days to 50% Oviposition	95% Fiducial Limits Upper	Lower	Slope
CM	Cabbage	5	10.5	9.9	11.1	0.18
		10	12.8	11.6	13.9	0.15
		20	12.6	11.7	13.4	0.13
		40	12.6	11.7	13.6	0.12
OM	Onion	5	12.9	12.4	13.8	0.17
		10	13.3	12.6	13.8	0.15
		20	16.3	15.6	17.0	0.14
		40	16.8	15.9	17.7	0.14
OM	Bean	5	19.4	19.1	19.8	0.17
		10	17.1	16.3	18.0	0.16
		20	18.9	18.3	19.6	0.14
		40	17.1	16.4	17.7	0.15
OM	Cabbage	5	22.2	21.2	23.8	0.17
		10	21.3	20.3	22.4	0.14
		20	20.6	19.7	21.7	0.15
		40	20.8	20.2	21.5	0.15
SCM	Onion	5	6.9	6.1	7.6	0.26
		10	10.2	9.7	10.7	0.20
		20	12.6	11.8	13.4	0.15
		40	10.5	9.7	11.3	0.14
SCM	Bean	5	9.7	9.0	10.3	0.14
		10	8.1	7.5	9.7	0.17
		20	11.9	11.2	12.5	0.12
		40	11.1	10.5	11.6	0.12
SCM	Cabbage	5	10.0	8.9	11.5	0.14
		10	12.7	11.9	13.5	0.15
		20	13.7	12.8	14.8	0.15
		40	12.7	11.8	13.6	0.14

TABLE 3. Estimated number of days required to reach 50 % mortality (LT_{50}) by Cabbage Maggot (CM), Onion Maggot (OM) and Seed Corn Maggot (SCM) on cabbage, onion and bean plants, along with fiducial limits and slope of the line ($\alpha = 0.05$).

Insect Species	Host Plant	Adult Density	Days to 50% Mortality	95% Fiducial Limits		
				Upper	Lower	Slope
CM	Cabbage	5	20.3	18.2	21.5	0.10
		10	18.6	17.4	20.2	0.07
		20	16.5	15.2	17.1	0.09
		40	11.3	8.6	13.4	0.08
OM	Onion	5	19.1	16.1	22.7	0.08
		10	19.2	16.1	23.5	0.09
		20	18.6	16.8	20.6	0.06
		40	17.4	15.0	20.1	0.07
OM	Bean	5	55.8	37.2	66.0	0.03
		10	19.0	17.5	22.2	0.04
		20	20.3	18.7	22.1	0.05
		40	13.6	12.2	15.1	0.05
OM	Cabbage	5	34.4	29.5	44.8	0.06
		10	33.1	29.9	38.0	0.07
		20	42.4	37.5	50.9	0.05
		40	31.2	28.4	45.0	0.07
SCM	Onion	5	10.7	8.8	12.9	0.07
		10	16.1	13.2	19.1	0.06
		20	14.2	11.8	16.3	0.07
		40	14.5	12.1	16.8	0.06
SCM	Bean	5	14.0	11.6	16.1	0.08
		10	24.6	21.9	28.4	0.05
		20	13.5	12.4	14.6	0.05
		40	12.0	10.2	13.6	0.07
SCM	Cabbage	5	23.6	21.2	25.7	0.06
		10	19.1	17.5	20.9	0.08
		20	17.4	15.7	19.5	0.08
		40	20.0	19.2	20.9	0.07

Figure 11. Total number of eggs laid per female Seed Corn Maggot (SCM) per density on onion (A), bean (B), and cabbage (C) plants. Densities with the same letter are not significantly different at $\alpha = 0.05$ (Tukey's test).

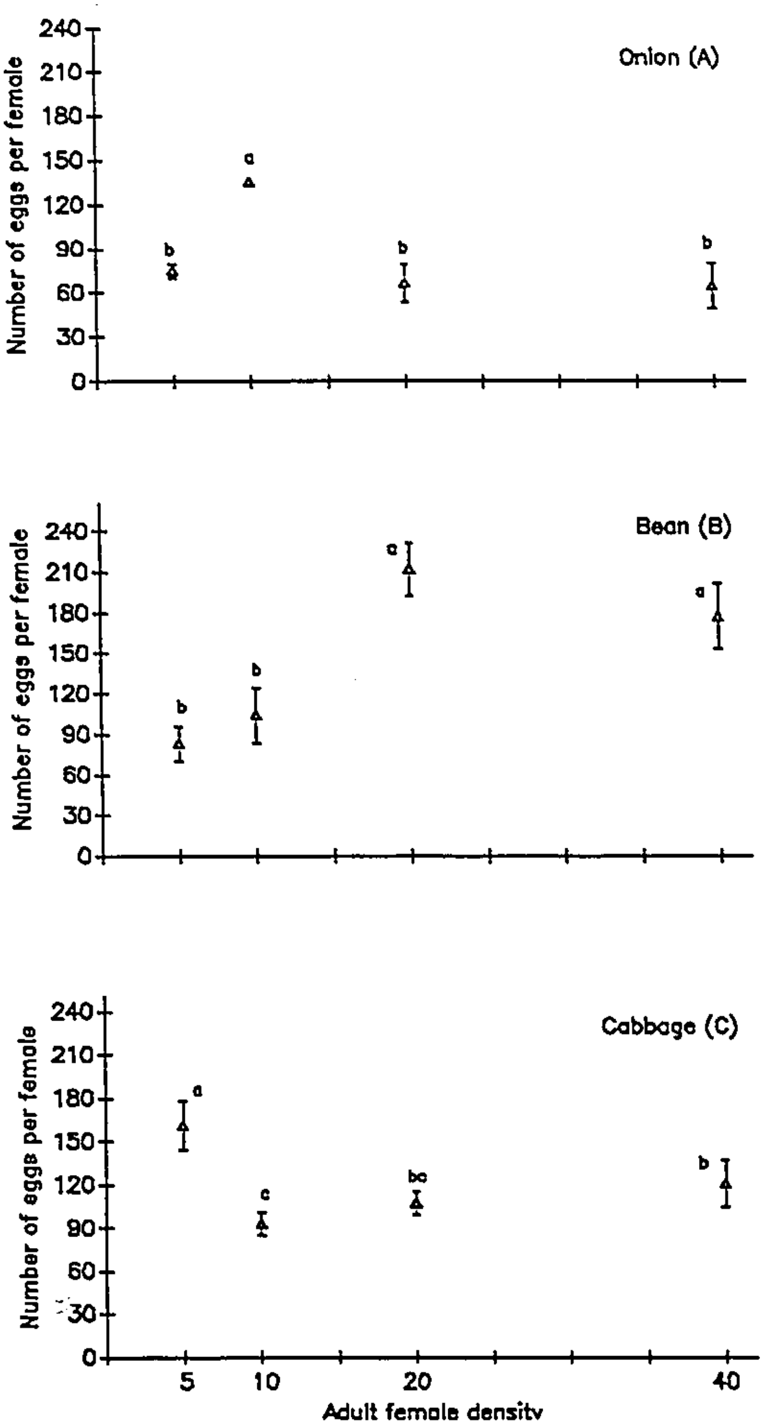

Onion (A)
Number of eggs per female
240
210
180
150
120
90
60
30
0
a
b
b
b
Bean (B)
Number of eggs per female
240
210
180
150
120
90
60
30
0
b
b
a
a
Cabbage (C)
Number of eggs per female
240
210
180
150
120
90
60
30
0
a
c
bc
b
5
10
20
40
Adult female density

Figure 12. Cumulative percentage of eggs laid per female Seed Corn Maggot (SCM) per density on onion **(A)**, bean **(B)**, and cabbage **(C)** plants.

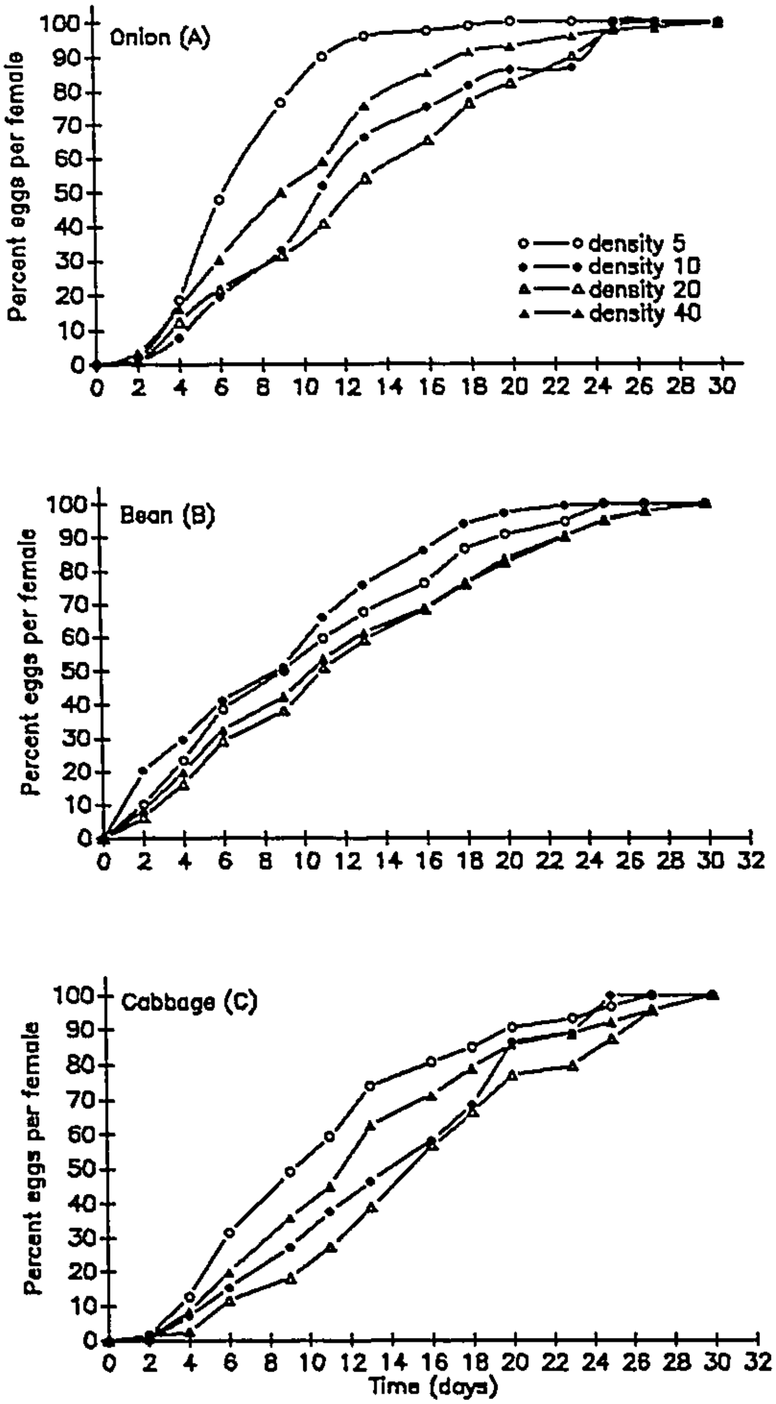
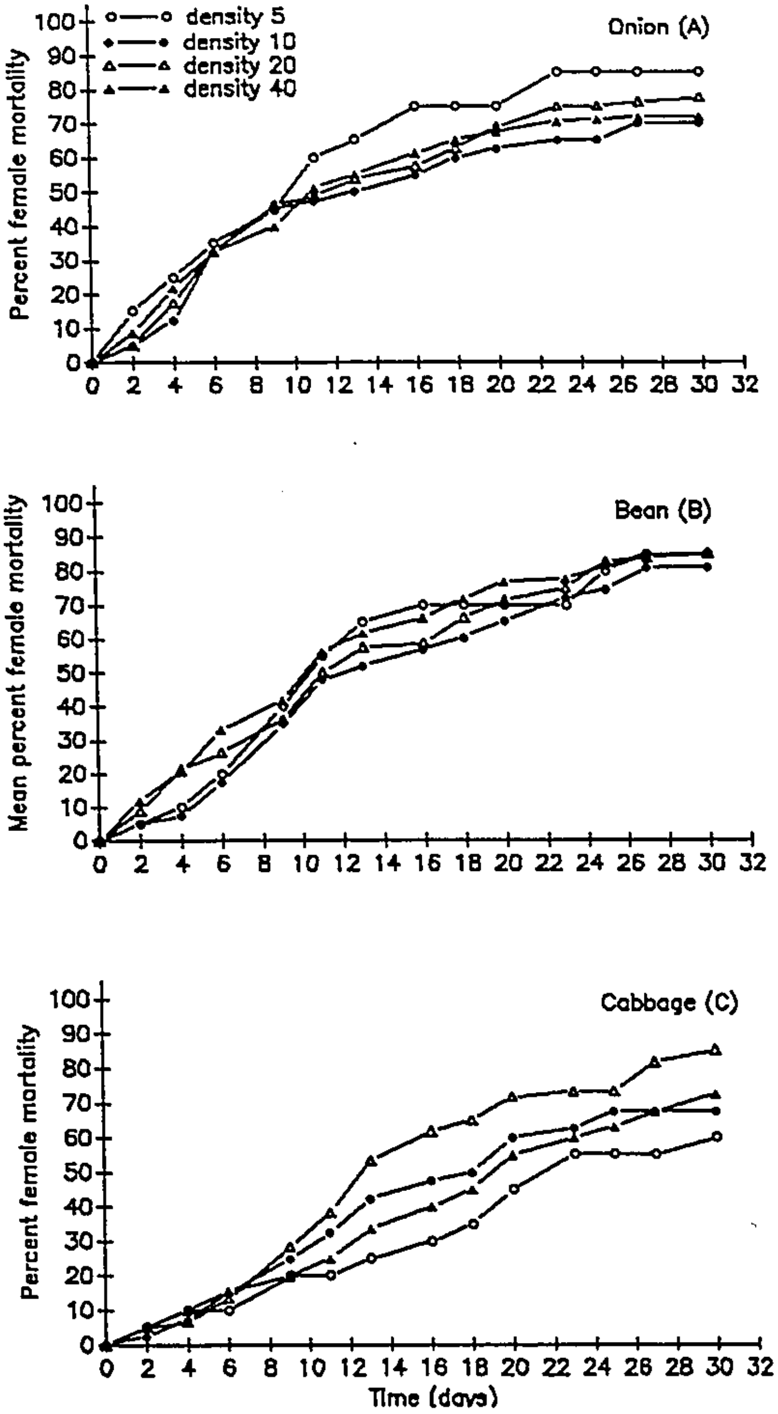

Onion (A)
Percent eggs per female
100
90
80
70
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
○—○ density 5
●—● density 10
▲—△ density 20
▲—▲ density 40
Bean (B)
Percent eggs per female
100
90
80
70
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Cabbage (C)
Percent eggs per female
100
90
80
70
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Time (days)

Figure 13. Cumulative percentage of female Seed Corn Maggot (SCM) mortality per density on onion (A), bean (B), and cabbage (C) plants.



○—○ density 5
●—● density 10
△—△ density 20
▲—▲ density 40
Onion (A)
Percent female mortality
0
10
20
30
40
50
60
70
80
90
100
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Bean (B)
Mean percent female mortality
0
10
20
30
40
50
60
70
80
90
100
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Cabbage (C)
Percent female mortality
0
10
20
30
40
50
60
70
80
90
100
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Time (days)

CHAPTER 5

INTERSPECIFIC COMPETITION FOR OVIPOSITION SITES BETWEEN SEED CORN MAGGOT AND ONION MAGGOT, AND SEED CORN MAGGOT AND CABBAGE MAGGOT.

INTRODUCTION

The relative abundance of plants is dynamic. The landscape is a mosaic of plant patches of different types, ages, structures, concentrations of secondary compounds and physical properties. For an insect in nature, patches of highly attractive and suitable host plants may be rare (Thompson 1982, 1985). When two or more species share the same resource, they either compete with each other for the best host that can support their progeny, or coexist. The intensity of their competition depends on the extent of resource overlap that exists between the species; if they coexist, it may be because one or more species is able to use additional resources so that the shared resource does not become limiting, thus avoiding competition (Ayala 1970). Although most phytophagous insect species share resources, competition between such species has rarely been observed (Futuyma and Gould 1979, Harrison 1964, Lawton 1982, McClure 1974, Redfern and Cameron 1978). This may be because either population densities of herbivorous insects lie below the level at which competition normally takes place, or because the species have sufficiently different niches and resource requirements (Harrison 1964, Pipkin et al. 1966). Janzen (1973) argues that because all parts of a plant are connected, a species feeding on one part will indirectly be competing with all of the other species on that plant.

The three *Delia* species, *Delia radicum* (Bouché) (Cabbage Maggot (CM)), *D. antiqua* (Meig.) (Onion Maggot (OM)), and *D. platura* (Meig.)

(Seed Corn Maggot (SCM)), used in this study are very closely related (Griffiths 1986, Harris et al. 1986). There is not only a similarity in placement of eggs and in threshold temperatures for adult activity, but the larvae of SCM have also been found feeding in the same root as CM and OM (Harcourt 1967, Miles 1952, 1953, 1955). Interspecific competition between gravid females of these species for sites best suited for larval survival may play an important role in the population dynamics of these species.

Based on the above information, a study was conducted under controlled environmental conditions in the laboratory to determine if the presence of different adult female densities of SCM would affect the fecundity, rate of oviposition and survival of OM and CM, and whether OM and CM flies might affect these factors in SCM.

MATERIALS AND METHODS

Since field studies have reported only the presence of SCM with OM and CM on the latter two species host plant, only these combinations of species were tested.

INSECT REARING

CM, OM and SCM were reared in the laboratory under constant conditions, as described in Chapter 3.

PLANT GROWTH

The plants used in this study were grown in growth chambers in the laboratory. Details are given in Chapter 3.

EXPERIMENTAL PROCEDURE

Experiment 1. Pupae of OM and SCM that had pupated within the same five-day period, were placed in separate cages and adults were allowed to emerge over a two-day period. These adults were provided with food and water, and maintained at 21°±1°C, 16:8 (L:D) and 70-75% RH in an incubator, until use. For this study, five-day-old SCM flies, and seven-day-old OM flies were used. Differently aged adults were used because the females of these two species mature at different rates (Higley and Pedigo 1984a, Martin and McEwen 1982). In the field, on emerging from pupae, the adults generally feed and mate in the hedgerows or field borders, and only move into the field and search for a host when they are ready to lay eggs (Coaker and Finch 1971). If competition for oviposition sites does occur it would take place at this time. Thus, females that were ready to oviposit were used for these experiments. Adults of OM (seven-days-old) and SCM (five-days-old) were sexed and placed in a cage (30 x 30 x 20 cm) at mixed densities of 20:0, 16:4, 12:8, 8:12, 4:16, and 0:20 (OM:SCM) with 20:0 and 0:20 (OM:SCM) being the control or single species condition. A 1♀:1♂ sex ratio was used for each species. The experiment was conducted in a randomized complete block design, in a walk-in incubator, under similar environmental conditions as listed above. There were four replicates per density. An onion plant (third to fourth-true-leaf stage) was used as the oviposition site. The oviposition container was similar to the one used in the intraspecific experiments (Chapter 4). The eggs were collected every three days, over a 30-day period, using the collecting procedure described in Chapter 3. On each sampling day any dead flies were removed, sexed and identified.

Experiment 2. This was similar to Experiment 1, except that the OM flies were replaced with seven-day-old CM flies, and cabbage plants (third to fourth-true-leaf stage) were used as the oviposition site.

EGG IDENTIFICATION

The eggs were identified and counted under a stereoscopic microscope at 20 X 25 magnification. Before starting these experiments, a known number of eggs of two of the species were mixed and identified. This procedure was repeated 8 to 10 times until 99% accuracy was achieved, thus preventing errors caused by mis-identification. The eggs of these three species are very similar in appearance, differing only in the pattern of ridges on the surface of the chorion. Great care had to be taken when counting and identifying the eggs, especially those of OM and SCM. The chorion of CM eggs are longitudinally ridged with two more prominent ridges forming a groove that extends the length of the egg. The eggs of SCM and OM are similar, the chorion being finely reticulate in appearance. However, the "cells" on OM eggs are more elongate than those on SCM eggs. The groove on the eggs of SCM and OM extends upto 1/5, and 1/2 the length of the egg respectively (Gibson & Treherne 1916, Hartman and Southern 1988, Miles 1952, 1953, 1955, Varis 1967) (Fig. 3). Owing to the large number of adults required to provide a sufficient number of females of the two species of the same age, and the limited capacity of the rearing facility, no more than four replicates could be set up for each experiment.

STATISTICAL ANALYSIS

The procedure used to analyze the data was similar to that described in Chapter 3. In this study, the fecundity, time to reach 50 % oviposition (OT_{50}), and time to reach 50% mortality (LT_{50}), for the 30-day experimental duration, under mixed species conditions was compared with the results of the single species condition. The rate of oviposition and mortality was determined by the number of days required to reach 50% oviposition or mortality, and significance was found when non-overlapping fiducial limits were observed.

RESULTS

A. *SCM : OM Combination.*

A significant difference in the fecundity per female was recorded (ANOVA, F=3.28, $df=_{27,4}$, $P < 0.05$). SCM showed no difference in the fecundity per female under mixed and single species conditions, irrespective of the initial number of adults of either species that was present (Fig. 14). In OM, a significantly higher number of eggs were laid at population density 4. The time required to reach 50% oviposition for each species under single and mixed species conditions was found to be significantly slower for SCM at population density 4 and accelerated for OM at population density 8 (Table 4A). The rate of mortality (time to reach 50 % mortality) was accelerated at density 4 for SCM, and slower for OM at density 8 (Table 4B).

B. *SCM :CM Combination*

SCM and CM showed no significant difference in fecundity per female under single and mixed species conditions (ANOVA, F= 1.53, $df_{27,4}$, P>0.05) (Fig. 17). When compared with single species conditions, no significant difference in the time to reach 50 % oviposition was observed under mixed conditions for SCM and CM (Table 5A). No significant difference in the rate of mortality was recorded under single and mixed species conditions for both SCM and CM (Table 5B).

DISCUSSION

Results obtained from this study show that interspecific competition between SCM and OM for oviposition sites affects the total fecundity of OM females at the lowest density 4; however, the rate of oviposition was significantly accelerated and mortality was slower at density 8 compared with the other combinations. In SCM, fecundity of females was not affected at any ratio combination, but the rate of oviposition was slower and mortality accelerated at density 4. Competition between SCM and CM adults exhibited no such effects.

Thus, it appears that OM females when placed in a no-choice situation will compensate for low population densities by increasing fecundity or the rate of oviposition. Such increase in clutch size to maximize fitness has been observed in *Trichogramma evanescens* (Waage 1986, Waage and Ming 1984). In addition to increased oviposition, the rate of mortality is also reduced. Thus, a female that lives longer may either lay eggs at a faster rate, or it may retain its eggs. In some insects, when oviposition sites are restricted and females are forced to retain their eggs, longevity of the female increases, as has been reported for the azuki bean weevil (Ishida 1952).

In SCM, on the other hand, a decrease in the rate of oviposition and increase in mortality in mixed species populations may indicate that SCM females are more susceptible to stress as a result of competition. Under natural field conditions, both SCM and OM females, when confronted with such a situation, may leave the site in search of another. This may be the reason why, in the field, SCM larvae are always found in lower numbers compared with CM and OM larvae (Miles 1952, 1955, Reid 1940). In addition, because SCM has the advantage of being a generalist, it may more easily switch from one host to another (this is discussed more extensively in Chapter 6) (Barlow 1965, Hough-Goldstein and Bassler 1988, Ristich 1950).

Interactions among species can also lead to disturbance, interference, behavioural avoidance and emigration. In SCM and OM, when higher densities of the other species were present, disturbance during stem runs, or other stresses on females ready to lay eggs on a plant, may be the reason for increased mortality and slower oviposition. Thus, competition among these species in the field may not result in a direct effect, such as increased mortality or decreased fecundity, but may result primarily in the emigration of adults. Such effects have been found in *Copestlum roraima* (Diptera), *Cephaloleia neglecta* (Coleoptera: Cephaloidae) and *Xenarescus monocerus* (Coleoptera: Chrysomelidae) (Seifert and Seifert 1979a, b)

The lack of competition between SCM and CM supports the view that phytophagous insect species, in general, are the least likely group to exhibit interspecific competition (Harrison 1964, Pipkin et al. 1966, Rathcke 1976). However, there is evidence of interspecific competition between CM and the beetles, aphids and lepidoptera feeding on crucifers (Finch and Jones 1987). These authors found that if the eggs or frass of these competitors of CM were present on the host plant, either the fecundity of CM was reduced or the host plant was rejected. This was observed, even though these competitors feed on the aerial parts of the plant, whereas CM feeds on the root tissue.

Sometimes, however, the detection of competition depends on the symptom used to detect it. Moon (1980), when studying competition in face fly larvae, found from survival data that competition occurred when densities exceeded two larvae per g of dung; however, stunting, which is also affected by density, occurred when density exceeded one larvae per g of dung. The present study shows that competition does not affect fecundity, rate of oviposition or mortality of CM or SCM, but it may affect adult displacement, larval mortality, growth rate, and adult weight, which were not examined in the present study.

There can be several reasons why SCM and CM adults do not compete for an oviposition site. The immatures of each species may survive better in the presence of the other species. Both CM and SCM are attracted, and stimulated to oviposit, by odours associated with microorganisms in the soil that are responsible for the rotting of host tissues. These microbes provide nourishment for the larvae, either directly or by breaking down the organic substances, thereby making it more readily available for larval consumption (Dindonis and Miller 1980, Eckenrode et al. 1975a, Ellis at al. 1979, Friend et al. 1959a, Hausmann and Miller 1989). Since larval feeding and boring into the root tissues provides an entrance route for these microorganisms, the presence of eggs may be used as an indicator for the choice of a site with potential optimal conditioning of the host tissues (Havukkala and Miller 1987, Hough-Goldstein et al., 1987; Yathom, 1970). In addition, the capability of the larvae of SCM and CM to use microorganisms as an additional food resource may render competition unnecessary. In this case, the host plant tissues would be less likely to be limiting and therefore a cause of competition. Such use of microorganisms that grow on the frass of other insects, as an additional food source, has been recorded in larvae of the family Chloropidae (Diptera) in birch bracket fungus (*Polyporus betulinus*) (Bulliard), which grows on dead trees (Pielou 1967).

Competition would also be avoided because of SCM's saprophagous capabilities, whereas CM and OM need fresh host plant tissues to develop. Consequently, the egg laying sites of SCM may be chosen at random, and as a result, the offspring of SCM and CM will be less likely to affect one another. In such cases, individuals are neither attracted to or rejected by sites on which other individuals are present, and they would not compete.

Thus, the physiological differences and capabilities of exploiting sufficiently different alternate food sources, by these two species, may be the reason why they do not compete. Harris et al. (1986), using electrophoresis, found that the CM is not as closely related to SCM and OM, as are the latter two species to each other.

The results obtained in the present study provide us with a better understanding of the relationship that may occur between CM, OM, and SCM. As mentioned earlier CM females are deterred from ovipositing on plants containing the frass of the cabbage butterfly (Finch and Jones 1987). In this study no such deterrent effect between SCM and CM and SCM and OM was observed on cabbage and onion plants respectively. Thus, monitoring the population density of both SCM and CM in a cabbage field should be considered. OM demonstrates increased fecundity and rate of oviposition when present at lower densities mixed species densities when mixed single species conditions are compared. SCM exhibits a delay in the rate of oviposition, and an increase in the rate of mortality at lower mixed species densities when mixed and single species conditions are compared. There is a possibility that if given the choice, a female of OM or SCM in such a situations will emigrate from the area. If trap crops are being used as part of a control program in an agricultural system, such behaviour may result in the fly species with the higher population density displacing the other species into the main field. Further studies in this area are required to determine if this is the case in the field. Since these flies are very similar in appearance, a definite identification should be made when attributing damage, and when selecting appropriate control techniques.

Figure 14. Total number of eggs laid per female Seed Corn Maggot (SCM) and Onion Maggot (OM), on onion, under single and mixed species conditions. Bars with the same letter are not significantly different ($\alpha = 0.05$) (Tukey's test).

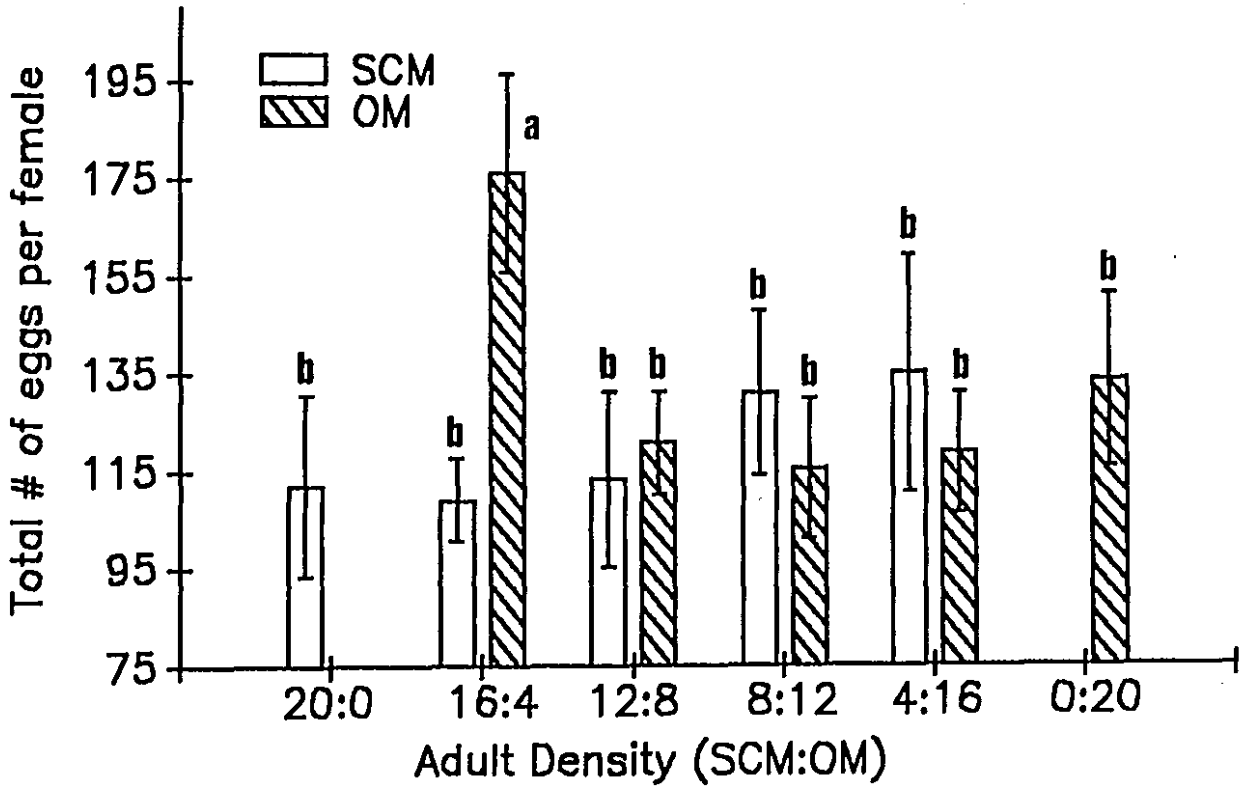

SCM
OM
a
b
195
175
155
135
115
95
75
Total # of eggs per female
20:0
16:4
12:8
8:12
4:16
0:20
Adult Density (SCM:OM)

Figure 15. Total number of eggs laid per female Seed Corn Maggot (SCM), and Cabbage Maggot (CM), on cabbage, under single and mixed species conditions. Bars with the same letter are not significantly different ($\alpha = 0.05$) (Tukey's Test)

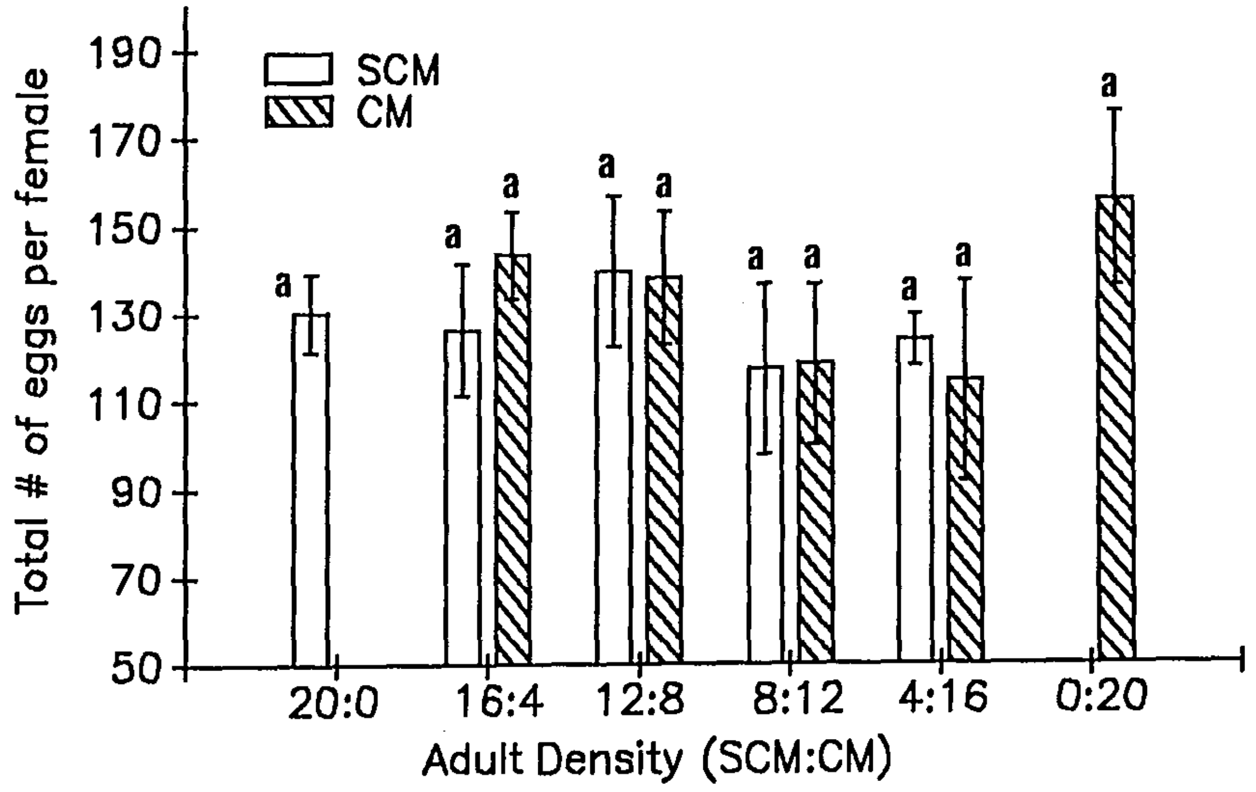

SCM
CM
Total # of eggs per female
190
170
150
130
110
90
70
50
a
a
a
a
a
a
a
a
a
a
a
20:0
16:4
12:8
8:12
4:16
0:20
Adult Density (SCM:CM)

TABLE 4. Estimated number of days to reach 50% oviposition (OT_{50}), and mortality (LT_{50}) ,by Seed Corn Maggot (SCM) and Onion Maggot (OM) females under mixed species condition.Also given are the fiducial limits and slope (α =0.05).

A.

Insect Species	Female density	Time (days)to 50% oviposition OT_{50}	95% Fiducial limits		
			Lower	Upper	Slope
SCM	20	13.9	13.4	14.5	2.54
	16	12.8	12.3	13.8	3.61
	12	14.5	13.6	15.2	3.41
	8	14.2	13.1	15.3	3.32
	4	17.3	16.7	17.8	2.04
OM	20	18.2	17.3	19.4	2.68
	16	17.6	17.5	18.3	2.45
	12	18.6	17.8	19.5	2.65
	8	14.7	14.3	15.5	2.75
	4	18.4	17.6	19.3	2.64

B.

Insect Species	Female density	Time (days) to 50% mortality LT_{50}	95% Fiducial limits		
			Lower	Upper	Slope
SCM	20	26.3	22.2	31.1	3.33
	12	25.4	20.3	34.6	3.80
	12	19.5	15.2	24.4	3.95
	8	27.7	21.6	31.0	3.55
	4	11.3	9.4	14.1	3.72
OM	20	19.5	17.2	22.3	3.74
	16	19.9	16.6	24.2	3.87
	12	21.5	18.7	24.5	3.19
	8	37.5	27.2	84.3	3.39
	4	23.0	19.3	24.4	3.31

Table 5. Estimated number of days to reach 50% oviposition (OT_{50}) and 50% mortality (LT_{50}), by Seed Corn Maggot (SCM) and Cabbage Maggot (CM) on cabbage under single and mixed species conditions. Also given are the fiducial limits and slope ($\alpha = 0.05$).

A.

Insect Species	Female density	Time (days) to 50% oviposition OT_{50}	95% Fiducial limits Lower	Upper	Slope
SCM	20	11.5	10.4	11.8	3.15
	16	12.6	11.5	13.4	3.36
	12	12.3	11.4	12.8	3.10
	8	13.3	11.2	13.4	2.93
	4	11.4	10.5	12.6	3.02
CM	20	10.4	9.3	11.8	3.48
	16	9.6	8.1	10.5	4.04
	12	10.2	9.5	11.6	3.56
	8	11.0	9.7	12.3	3.14
	4	10.8	10.3	11.4	3.70

B.

Insect Species	Female density	Time (days)to 50% mortality LT_{50}	95% Fiducial limits Lower	Upper	Slope
SCM	20	23.8	20.6	27.4	3.34
	16	23.6	20.5	28.0	3.36
	12	25.8	23.7	27.2	3.40
	8	31.7	25.3	41.5	3.62
	4	18.6	15.4	25.3	3.95
CM	20	20.2	17.6	23.4	3.46
	16	23.5	20.0	27.5	3.17
	12	24.9	20.3	33.1	3.61
	8	26.8	20.6	33.4	3.62
	4	18.4	13.2	21.5	3.62

CHAPTER 6

EFFECTS OF EXPOSURE DURING THE PRE-OVIPOSITION PERIOD OF SEED CORN MAGGOT ADULTS, TO BEAN, ONION AND CABBAGE PLANTS ON THE SUBSEQUENT ACCEPTANCE OF THESE PLANTS AS OVIPOSITION SITES.

INTRODUCTION

Numerous studies on phytophagous insects, including certain wasps (Vinson et al. 1977, Wardal and Borden 1985,), beetles (Mark 1982, Rausher 1983), butterflies (Rausher and Odendall 1987, Traynier 1986) and flies (Jaenike 1982, Prokopy et al. 1982a,b, 1986), have shown that prior experience to a particular host type may increase the frequency with which the insects subsequently detect, land on, and oviposit on that particular host (Jaenike 1983, Papaj and Prokopy 1986, Papaj and Rausher 1983, Traynier 1984).

SCM is a polyphagous and saprophagous species that feeds on a wide range of host plant types. The adults are attracted to odours from microorganisms that are decomposing organic matter in the soil and to germinating seedlings (Barlow 1965, Ristich 1950). SCM does not require the continuous presence of a suitable host for oogenesis, vitellogenesis, or oviposition. They will actually lay eggs on freshly turned soil that is devoid of plants. However, the presence of, and contact with, suitable host plant material is stimulatory, increasing egg production and reducing the time to first egg deposition (Hough-Goldstein and Bassler 1988, Weston and Miller 1987). Thus, the fecundity of SCM adults can be influenced by the quality of the host plant material that is present during the oviposition period.

It has been found that prior experience with a host plant conditions a female, influencing its search mode ultimately governing oviposition site selection (Cooley et al. 1986, Jaenike 1986, Prokopy et al. 1986). Such conditioning was observed in the apple maggot fly, where early experience with a host plant determined acceptance or rejection of an oviposition site in future encounters (Papaj and Prokopy 1986). Although polyphagous species, like SCM, may be thought to accept most plant species, it has been found that polyphagous species habituate to a host species more often than herbivores with more restricted diets (Jermy 1987). Habituation to a particular host in these species may increase the efficiency of host finding in an individual (Prokopy et al. 1986).

The purpose of the present study was to determine if prior experience with one host during the pre-oviposition period will affect host plant selection by ovipositing females; and the degree to which SCM adults are able to change host plants after the initial oviposition has taken place.

MATERIALS AND METHODS

INSECT REARING

The insects were reared according to the methods described in Chapter 3.

PLANT GROWTH

The plants to be tested, onion, cabbage and bean, were reared using the procedure described in Chapter 3.

EXPERIMENTAL PROCEDURE

In order to determine the effects of prior exposure of SCM females on acceptance of host plants as oviposition sites, the number of eggs laid on each host that was presented was recorded every two days.

Initial acceptance was estimated by the number of eggs laid after the first two days of egg laying after pre-oviposition exposure. All adults were obtained from puparia formed by larvae that were reared on lima beans. The adults of both sexes were provided with food (see Chapter 3) and maintained in a cage (30 x 30 x 20 cm) at 20 ± 1°C, 16:8 (L:D) photoperiod and 70-75% R.H. for a five-day pre-oviposition period following the first female emergence. During this period, the flies were exposed to a second-true-leaf-stage bean, or a third-true-leaf-stage onion or cabbage plant, that had been placed in the cage on day one. No eggs were deposited during this pre-oviposition exposure duration on any plant. On the fifth day, the adults were sexed and placed in separate cages at densities of 10:10 ♀:♂ per cage. Each cage was provided with adult food, water and one of the three host plants (bean, onion, or cabbage) being tested (Chapter 3). These plants were changed every second day, the host plant species remaining the same for six days. On the sixth day the host plants in the cages were replaced by bean plants, which were also changed every second day. The reason for switching to beans is because this host is considered to be the preferred host of SCM. I wanted to see if after ovipositing on onion and cabbage SCM would readily switch to ovipositing on bean. Eggs were sampled every two days over a period of 12 days.

To prevent the mixing of host plant odour, cages with the same host species were placed in the same incubator. The conditions in the incubators were monitored and maintained at similar levels throughout the experiment. The eggs were collected, and counted, using the technique described in Chapter 3. Number of dead flies were recorded every sampling day.

STATISTICAL ANALYSIS

The data obtained were analyzed using the procedure described in Chapter 3. The mean number of eggs laid per female per sample day were subjected to an analysis of variance, and Tukey's multiple range test, to determine the acceptance of the plant as a suitable host. Fecundity, rate of mortality (LT_{50}), and rate of oviposition (OT_{50}) on the three host species used in each experiment were compared. The rate of oviposition (OT_{50}) and mortality (LT_{50}) were estimated by the number of days required to reach 50% oviposition or 50% mortality respectively. Overlapping fiducial limits between densities lacked significance.

RESULTS

SCM ADULTS EXPOSED TO BEANS DURING THE PRE-OVIPOSITION PERIOD.

Exposure of SCM adults to bean plants during the pre-oviposition period did not significantly affect the number of eggs laid by day 2 (ANOVA $F=2.68$, $df_{15,2}$, $P>0.05$). This indicated that the initial acceptance of onion and cabbage as oviposition sites is not influenced by prior exposure to beans during the pre-oviposition period. The percentage of eggs laid per female by day two of the oviposition period on bean, onion and cabbage was 21, 20 and 17% respectively (Fig.16). No significant difference in the number of eggs laid on day 8 after switching to beans was recorded (ANOVA $F=0.07$, $df_{15,2}$, $p>0.92$). The females, after laying for six days on onion and cabbage, accepted bean as the oviposition site without any change in the rate of egg laying on day 8. Comparisons of fiducial limits revealed no significant difference in the time to reach 50 % oviposition. Thus, all three plants were accepted at the same rate (Table 6). No change in time to reach 50% female mortality (LT_{50}) was observed (Table 7). The trend in mortality over the 12 day duration was higher on beans from day 6 to 12 (Fig. 19).

SCM ADULTS EXPOSED TO ONION DURING THE PRE-OVIPOSITION PERIOD.

When SCM adults were exposed to onion during the pre-oviposition period, a significant difference between host plants in the mean number of eggs laid by day two was recorded (ANOVA F=3.70, $df_{15,2}$, $P< 0.05$). A significantly lower percentage of eggs was laid on cabbage compared with onion and bean (4, 22, and 22% respectively). It appears that the rank order of initial preference of host plants for oviposition was onion, bean and cabbage. With continued exposure to cabbage, conditioning to this host plant occurred. This resulted in a sharp increase in the number of eggs laid, and by day four no difference in the number of eggs laid was recorded (Fig.17). No significant difference in the number of eggs laid on day 8 was observed (ANOVA F=2.67, $df_{15,2}$, $p>.06$). Thus, switching to bean plants in cages that had onion and cabbage plants as the oviposition sites did not affect host plant acceptance. Time to reach 50% oviposition (OT_{50}) was significantly faster on beans (preferred host) compared with cabbage and onion (Table 6). The rate of mortality (LT_{50}) was not significantly different (Table 7). The trend in mortality over the experimental duration did not show any sudden increase or decrease (Fig. 20).

SCM ADULTS EXPOSED TO CABBAGE DURING THE PRE-OVIPOSITION PERIOD.

A significant difference in the number of eggs laid per plant per female by day two of the oviposition period was observed (ANOVA F=27.86, $df_{15,2}$, P< 0.05). Comparisons of the number of eggs on the three hosts reveals an initial delay in the acceptance of the onion plants compared with beans and cabbage. The percentage of eggs was 11, 28, and 28% on onion, cabbage and beans respectively (Fig. 18). Conditioning as a result of continued presence of onion occurred, and by day four number of eggs laid was comparable to that for bean and cabbage plants. No significant effect in the number of eggs laid on day 8 was recorded (ANOVA F=2.95, $df_{15,2}$, p>0.08). Thus, switching to bean plants, after oviposition had started on cabbage and onion, did not affect oviposition A significant reduction in the rate of oviposition OT_{50} on onion was observed when SCM females were initially provided cabbage (Table 6). No significant difference in the rate of mortality was observed (Table 7). The rate of mortality did not change over time (Fig. 21).

DISCUSSION

The results obtained in the present laboratory study indicate that initial acceptance by SCM of a particular plant species for oviposition is affected by host plant exposure during the pre-oviposition period. The rank order of host plant preference changes according to the host type to which the adult was initially exposed during the pre-oviposition period.

During the present study it was observed that modifications in host acceptance differed with different host plant exposure. When

SCM adults were exposed to either one of the two secondary hosts, onion or cabbage, during the pre-oviposition period, initial acceptance of the other secondary host was delayed. The females appear to be able to differentiate between the two hosts. No significant difference in the number of eggs laid on bean (preferred host) by females exposed to different pre-oviposition hosts was observed. However, the rate of oviposition was accelerated on beans when the flies had prior exposure to onion, and was slower on onion when they had prior exposure to cabbage (Table 6). When the adults had prior exposure to beans, no discrimination between the three hosts used was observed, and the numbers of eggs laid were similar. Hough-Goldstein (1985) reported that prior egg laying exposures did not alter oviposition preference in oviposition site selection of SCM, when host plant seeds were used as the oviposition stimulant, however, when females were allowed to oviposit on a less preferred host the subsequent introduction of a preferred host resulted in increased oviposition. This indicates that a preferred host plant is accepted for oviposition irrespective of prior-exposure. Hoffmann (1988) obtained similar results with *Drosophila melanogaster* (Diptera: Drosophilidae), in which alteration of host preference occurred in some, but not all, host plant exposure cases. Papaj and Prokopy (1988) and Jaenike (1983) reported that exposure to a low ranking (secondary) host does not alter acceptance of the higher ranked (primary) host.

Conditioning of an insect to a particular host, results from continuous exposure to that host and depends on the frequency of encounters. When SCM had prior exposure to the secondary hosts cabbage and onion, the continuous exposure to these less preferred hosts resulted in host plant conditioning, and finally SCM females accepted these plants at the same rate as the preferred host. Conditioning as a result of continued exposure is known to occur in other insects. In fact, some insects have been conditioned to lay eggs on plants that are completely unsuitable for larval survival (Singer 1971, 1982). Such conditioning to host plants with prolonged exposure has been demonstrated in the cabbage butterfly, *Pieris (=Antogia) rapae* (Lepidoptera: Pieridae) (Traynier 1984). Prior experience was found to influence the first five landings on the alternate host, but as landings continued, an even distribution of acceptance on preferred and alternate hosts, was observed. Thus, with continued exposure, the effects of prior experience are obliterated, and eventually the adult accept the other host.

Although the adaptive advantage of learning to reject or accept a host plant in polyphagous species does not seem as important as in oligophagous species, it would be expected to enhance the efficiency of host finding by such individuals. The expected disadvantage would be a reduction in the chances of finding additional alternate hosts (Prokopy et al 1986). Such changes in host plant preference, as a result of previous experience of the individuals, has been demonstrated in a range of polyphagous and oligophagous species: pierid butterflies (Lepidoptera: Pieridae) (Lewis and Lipani 1988), leaf beetles (Coleoptera: Chrysomelidae) (Mark 1982), fruit flies (Diptera: Drosophilidae) (Hoffmann 1988), and the apple maggot, *Rhagoletis pomonella* (Diptera: Trypetidae) (Papaj and Prokopy 1986), as a result of first experience, may increase the chances of discovery and acceptance of a similar suitable host.

Prior experience may influence the search pattern of individuals, and encounters with other suitable hosts could also result in a switch in preference. In a polyphagous species like SCM, in which the larvae can survive on a variety of hosts, such a switch would not take very long. In SCM, the attraction to non-host plant stimulants, such as the organic matter in the soil, may have a greater influence on oviposition site selection. However, the final choice of oviposition site may be decided only after the female lands. Once oviposition begins, a switch to another host, in this case the preferred host bean, resulted in no change in numbers of eggs laid. Thus, it appears that the females do not need to be conditioned to a particular host. Rausher and Odendall (1987) found that the butterfly *Battus philenor* (Lepidoptera: Papilionidae) switches hosts for oviposition a number of times. This butterfly has two seasonal host searching behaviours. Early in the season the adults search for a broad leaf host, and later in the season for a narrow leaf host. These individuals can be trained to search for one host or the other. The switch in hosts occurs primarily after the female alights on and oviposit on the host species, even if it is not the species it was currently searching for. Thus, it appears that physical contact may change the host preference of a species.

This lack of discrimination in SCM once oviposition begins suggests that, in addition to conditioning, the degree of discrimination between host plant types may be age dependent in this species. Such age dependent host plant acceptance or discrimination has been observed in other insect species. Changes in the degree of preference with the age of the female has been reported in ants, where previous experience affects habitat selection more in young ants than in older ones (Jaisson, 1980). In newly emerged parasitic wasps, oviposition behaviour is more affected by previous experience than in older wasps (Wardel and Borden 1985). A similar difference in feeding preference has been observed in stick insects (Cassidy 1978).

When the pattern of oviposition in the three experiments (Fig. 16, 17, 18) are compared, it can be seen that the frequency of oviposition, although not significantly different, is always highest on the host plant to which the adults were exposed during the pre-oviposition period. Thus, prior experience may change the rank order of host preference. This has also been found in the apple maggot, *Rhagoletis pomonella* (Diptera: Trypetidae), and the fruit fly, *Drosophila melanogaster* (Diptera: Drosophilidae) (Jaenike 1983, Papaj and Prokopy 1989).

Thus, in the present study I found that ovipositing SCM flies do show initial discrimination between hosts, and that this is based on prior exposure. This discrimination only occurs during the initial stages of the search for a suitable host plant, when the SCM adults are exposed to their secondary hosts, onion and cabbage plants. Continued exposure resulted in conditioning to the less preferred host after which all suitable hosts were accepted. The pattern of the rank order of preference changed in response to prior exposure. Pre-oviposition experience may change the rate of oviposition in this species.

Figure 16. Cumulative percentage of eggs laid per female Seed Corn Maggot (SCM) per sampling day for females exposed to bean during the pre-oviposition period and subsequently provided with bean (O---O) (n=57.25), onion (•----•) (n=51.73), and cabbage (▲----▲) (n=49.03), as the oviposition site for six days, and then switched to bean for another six days. ----- represents switch from onion and cabbage to bean plants from day 6 to 12.

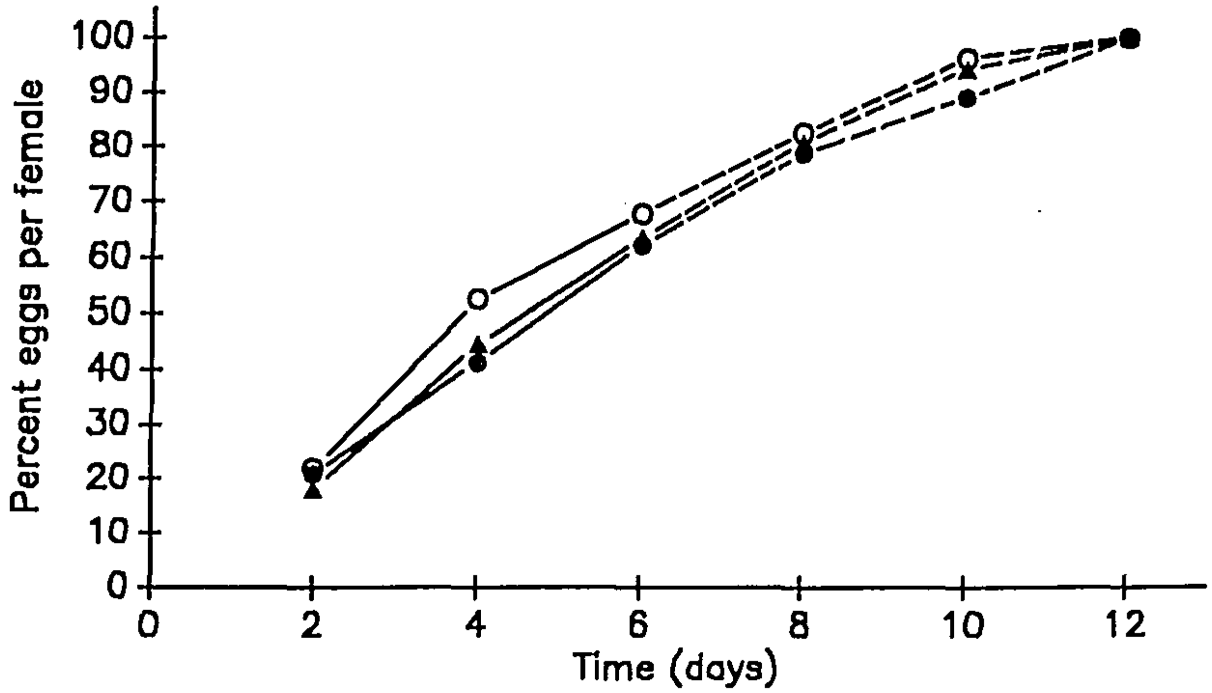

Percent eggs per female
0
10
20
30
40
50
60
70
80
90
100
Time (days)
0
2
4
6
8
10
12

Figure 17. Cumulative percentage of eggs laid per female Seed Corn Maggot (SCM) per sampling day for females exposed to onion during the pre-oviposition period and subsequently provided with bean (O---O) (n=38.78), onion (•----•) (n=43.50), and cabbage (▲----▲) (n=30.23), as the oviposition site for another six days, and then switched to bean from another six days. ----- represents switch from onion and cabbage to bean plants from day 6 to 12.

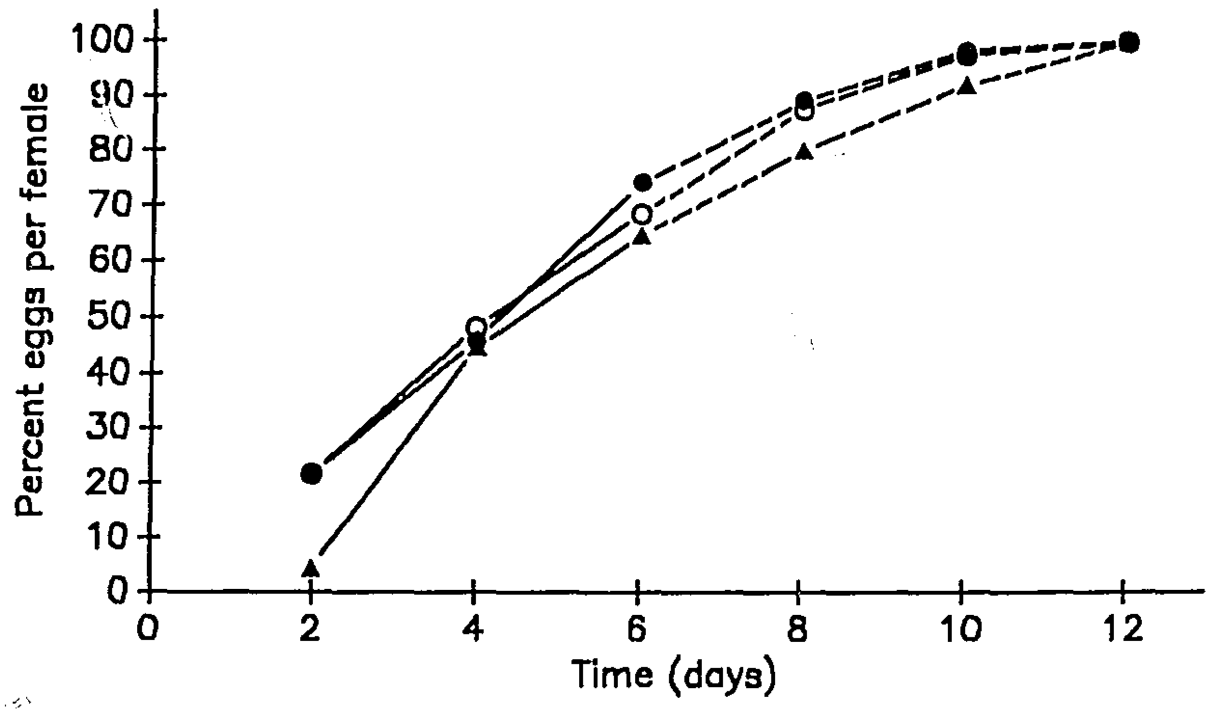

Percent eggs per female
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
Time (days)

Figure 18. Cumulative percentage of eggs laid per female Seed Corn Maggot (SCM) per sampling day for females exposed to cabbage during the pre-oviposition period and subsequently provided with bean (O---O) (n=25.15), onion (•---•) (n=17.15), and cabbage (▲-----▲) (n=27.23), as the oviposition site for another six days, and then switched to bean from another six days. ----- represents switch from onion and cabbage to bean plants from day 6 to 12.

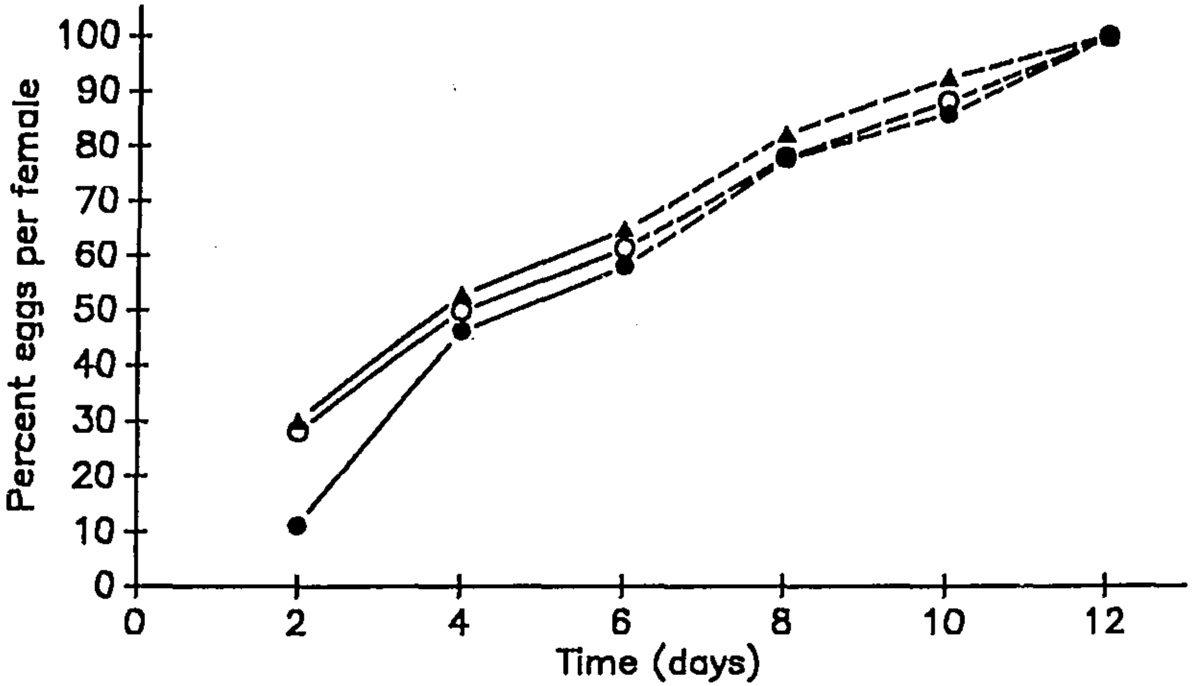

Percent eggs per female
0
10
20
30
40
50
60
70
80
90
100
Time (days)
0
2
4
6
8
10
12

Figure 19. Cumulative percentage mortality per female Seed Corn Maggot (SCM) per sampling day for females exposed to bean during the pre-oviposition period and subsequently provided with bean (O---O), onion (•---•), and cabbage (▲----▲), as the oviposition site for six days, and then switched to bean for another six days. ----- represents switch from onion and cabbage to bean plants from day 6 to 12.

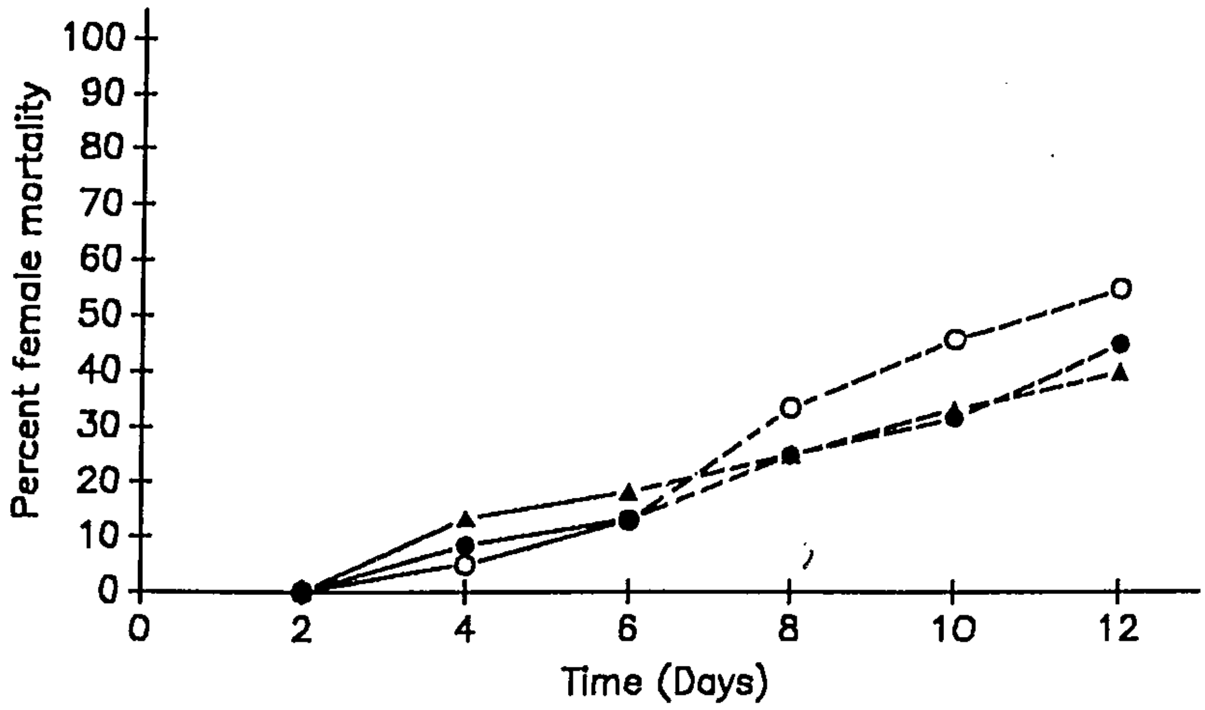

Percent female mortality
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
Time (Days)

Figure 20. Cumulative percentage mortality per female Seed Corn Maggot (SCM) per sampling day for females exposed to onion during the pre-oviposition period and subsequently provided with bean (O---O), onion (●----●), and cabbage (▲-----▲), as the oviposition site for another six days, and then switched to bean from another six days. ----- represents switch from onion and cabbage to bean plants from day 6 to 12.

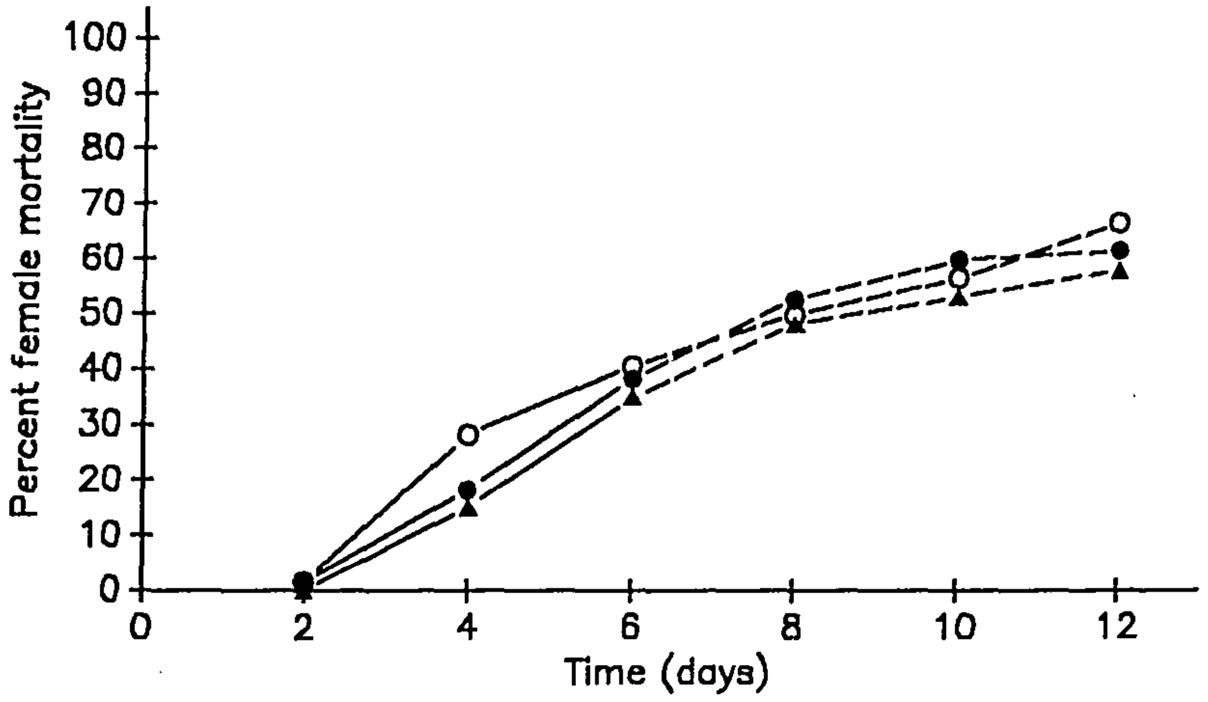

Percent female mortality
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
Time (days)

Figure 21. Cumulative percentage mortality per female Seed Corn Maggot (SCM) per sampling day for females exposed to cabbage during the pre-oviposition period and subsequently provided with bean (O---O), onion (•----•), and cabbage (▲-----▲), as the oviposition site for another six days, and then switched to bean from another six days. ----- represents switch from onion and cabbage to bean plants from day 6 to 12.

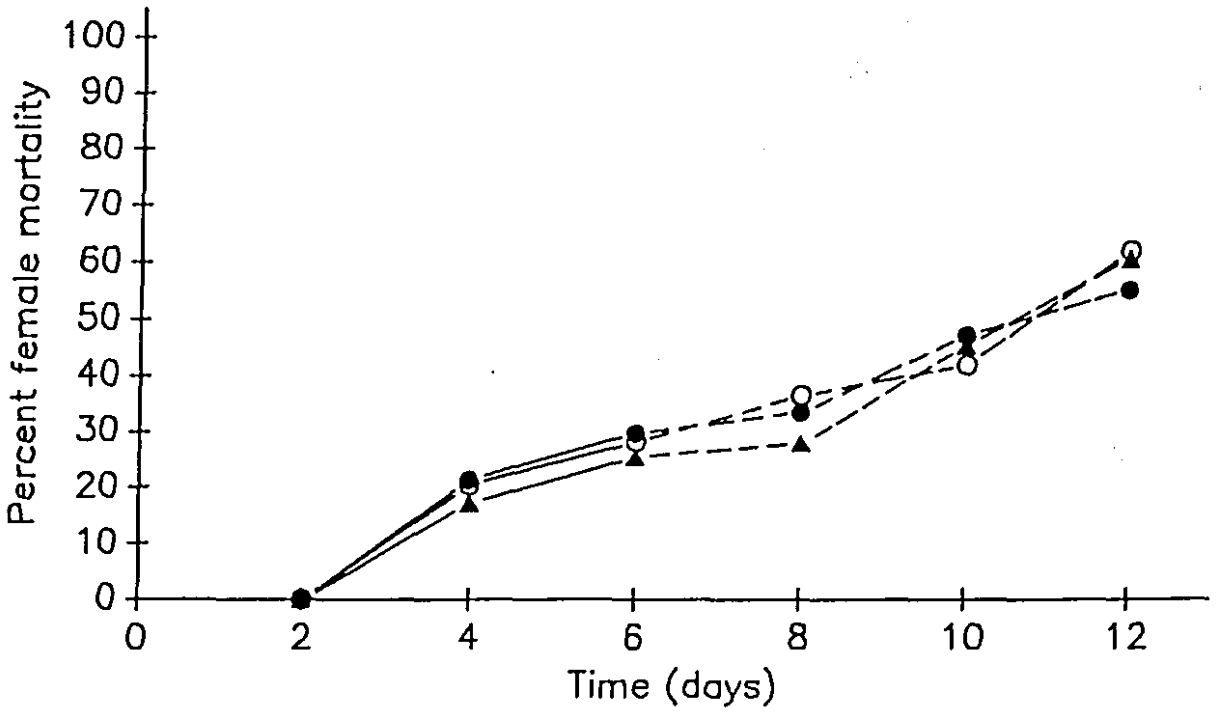

Percent female mortality
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
Time (days)

TABLE 6. Estimated results of the time to reach 50% oviposition (OT_{50}) of Seed Corn Maggot (SCM) on bean, onion and cabbage from days one to six and switched to bean for another six days, when exposed to one of these hosts during the pre-oviposition period.

Preoviposition Exposure	Test plant exposure days 1-6	6-12	Time (days) to 50% oviposition (OT_{50})	95% Fiducial limits Lower	Upper	Slope
bean	bean	bean	5.3	4.2	6.2	2.81
	onion	bean	5.2	4.2	5.4	2.79
	cabbage	bean	6.3	5.0	7.6	3.27
onion	bean	bean	5.1	4.5	5.4	3.12
	onion	bean	6.2	5.7	7.2	3.49
	cabbage	bean	6.6	5.6	7.3	4.23
cabbage	bean	bean	4.3	3.8	5.0	3.14
	onion	bean	6.4	5.5	7.1	3.12
	cabbage	bean	4.3	4.0	5.1	3.36

TABLE 7. Estimated number of days to reach 50% mortality (LT_{50}) of Seed Corn Maggot (SCM) on beans, onion and cabbage from days one to six and switched to bean for another six days, when exposed to one of these hosts during the pre-oviposition period.

Preoviposition Exposure	Test plant exposure days 1-6	6-12	Time (days)to 50% mortality (LT_{50})	95% Fiducial limits Lower	Upper	Slope
bean	bean	bean	10.3	9.9	13.6	2.81
	onion	bean	10.7	10.2	13.8	2.79
	cabbage	bean	11.6	11.0	14.3	3.27
onion	bean	bean	9.3	7.9	10.5	3.12
	onion	bean	8.7	7.5	9.7	3.49
	cabbage	bean	9.6	8.2	10.1	4.23
cabbage	bean	bean	9.8	9.3	10.4	3.14
	onion	bean	10.3	8.5	10.7	3.12
	cabbage	bean	9.9	8.3	11.6	3.36

CHAPTER 7

EFFECTS OF INTRASPECIFIC COMPETITION ON LARVAL MORTALITY, PUPAL WEIGHT, AND DEVELOPMENTAL RATE OF THE CABBAGE MAGGOT (CM).

INTRODUCTION

The population dynamics of an insect, may depend on the ability of the immatures to compete for a limited resource. Effects of larval competition may be experienced during the larval stage (reduced weight, increased mortality, and developmental rate), or the adult stage (smaller, less fecund individuals), both affecting the population density of the next generation. Numerous studies on insects that live within their food supply have shown similar results (Beaver 1973, Bøggild and Keiding 1958, Miller 1964, Moon 1980, Quiring and McNeil 1984, Valiela 1969). An increase in the population density of the insect does not always affect density negatively. In some insects, such as *Drosophila melanogaster* (Diptera: Drosophilidae), increased population density resulted in increased weight of pupae and adults (Miller 1964). Similarly, Valiela (1969) found that face flies had a lower pupal weight and a higher mortality rate at low densities. Such increase in weight as density increases is generally linked to necrophagy in these groups.

Larvae of the cabbage maggot (CM), *Delia radicum*, feed in the roots of plants of the family Cruciferae. The overwintering adults emerge in the spring and lay their eggs around the base of young plants. On hatching, the first instar larvae bore into the root tissue and begin feeding. The larvae pass through three larval instars inside the root before pupating in the surrounding soil (Coaker and Finch 1971, Hughes and Slater 1959). Young larvae leave the root in search of another host only when population densities are very high (especially in young plants). CM larvae searching for a new host are capable of moving a distance of up to 10 cm (Coaker 1966). Under such conditions mortality from desiccation and predation is very high. Because the large roots of more mature plants are capable of sustaining higher larval populations, few larvae probably leave such hosts. Gibson and Treherne (1916) reported finding 123 larvae of different ages feeding within a single mature cauliflower root.

The natural mortality during the first generation is generally over 95%. Most losses occur between the egg and first larval stage and between the pupal and adult stages (Hughes and Slater 1959). No mortality from predation was recorded in subsequent larval stages, and the only density-dependent mortality was caused by the death of the host (Hughes and Slater 1959, and Hughes and Mitchell 1960).

The purpose of the present study was to determine the effects of larval population density on mortality, rate of development, and weight of the pupae when feeding on a sixth-true-leaf stage cabbage plant.

MATERIALS AND METHODS

INSECT REARING

The cabbage maggots were reared in the laboratory using the method described in Chapter 3.

PLANT GROWTH

Cabbage plants were grown in the laboratory in a growth chamber at 16:8 (L:D), 80-90% R.H, and 20:18 ±1°C (day:night). A mixture of soil, peat and vermiculite was used as the growing medium. The seeds were sown in 7.5 cm pots. Fertilizer 20:20:20 (N.P.K.) was added at the time of sowing, and every second week at the time of watering (0.1 mg / 100 ml water). After approximately six weeks, when the plants had reached the sixth-true-leaf stage, they were inoculated with eggs.

EXPERIMENTAL PROCEDURE

Freshly laid CM eggs were obtained from laboratory reared females. These eggs were extracted from the oviposition containers, using the method described in Chapter 3. The eggs were washed into a Petri dish, picked up, using a pasteur pipette, and placed at random around the base of a cabbage plant, in a 7.5 cm diameter plastic pot. Five different densities of 2, 4, 6, 8, and 10 eggs per plant, with 10 replicates each were set up. The remaining eggs were counted and placed on filter paper in a petri dish, and kept in an incubator at 21 ± 1°C, to check for viability. The experimental pots were placed in a growth chamber at 16:8 (L:D), 20:18 ± 1°C (day: night) and 80-85% R.H. in a randomized complete block design. Pots were watered every second day and fertilizer (20:20:20) (0.1 g per 100 ml of water) was added every two weeks. To determine the effects of population density on developmental rate, plants were checked for pupae at three different dates. After 17 days the soil was removed from the pots and any pupae that were present were collected. Care was taken not to damage the plants as they were replanted. The pots were then returned to the growth chamber for another four days. After this 21-day period, the soil was once again sieved for pupae. Under normal conditions, most larvae pupate within 21 days. However, in this present experiment not all the larvae were recovered by this time. Thus, the plants were once again replanted and returned to the growth chamber to allow any remaining larvae to pupate. On day 24 the plants were removed, "late" pupae were collected from the soil. The plant roots were then dissected but no larvae were found inside them. All pupae were weighed 24 hours after collection, because newly formed pupae are heavier during the first few hours of pupation, and the exact time of pupation for each pupa was not known. The pupae were then placed in sand in an incubator at 21±1 °C, and the number of days to adult emergence was recorded.

STATISTICAL ANALYSIS

The number of pupae found at each density, and the days required per replicate per density for adult emergence was recorded. The weight of each pupa was recorded, totalled and divided by the number of larvae that pupated for each replicate. These data were then subjected to an analysis of variance, and the means compared using "Tukey's" Studentized Range Test at α=0.05 level.

RESULTS

Mortality was significantly affected by increasing egg density (F=16.54, $df_{9,4}$, $p< 0.01$). Mortality was 15% at the lowest density and 52% at the highest density. No significant differences were recorded between densities 4, 6 and 8, or 8 and 10. An increase in density from 2 to 4 resulted in a 28% increase in mortality. However, the mortality difference between densities 4 and 10 was only 9% (Table 8).

Results show a significant difference in pupal weights as population density increases (F=7.94, $df_{9,4}$, P<0.01). No difference was recorded between densities 2,4 and 6, or densities 4, 6, and 8. However, as population density increased, the number of pupae having weights below 10 mg increased from 0 at density 2, to 31% at density 10 (Table 8).

Increased density resulted in a significant acceleration in the rate of development at density 6, but a further increase in density to 10 caused a delay in developmental rate (F = 10.15, $df_{9,4}$, $p < 0.01$). At the lower densities (2 and 4) at 21°C, rate of development was 21 days, which is the expected time required for pupation under the conditions of the experiment (Whistlecraft et al. 1980b). No differences were recorded between densities 2, 4, and 8, or 8 and 10 (Table 8).

The number of days required for adult emergence were not affected by larval density. However, pupae below 6 mg obtained at higher densities, did not emerge.

DISCUSSION

Competition among CM larvae for a limited food source resulted in reduced weight, increased mortality and a change in development rate. The mechanisms involved may include "interference", in which one individual either directly (aggression, cannibalism) or indirectly (producing poisons, or physiologically altering the medium) harms a competitor, and "exploitation", in which each individual has access to a reduced portion of the resource relative to its ability to exploit the resource in competition with other individuals.

Although mortality clearly increased (by 28%) with an increase in larval population density from 2 to 4, the increase from density 4 to 10 was much smaller (9%), and was not significant. With *Drosophila melanogaster* (Diptera: Drosophilidae), Gilpin (1974) found that with an increase in population density there was a reduction in emergence, even though food was not limiting. He postulated that direct aggression by larger individuals and poisoning of the food medium were the most likely explanations. In the face fly *Musca autumnails* (Diptera: Muscidae), the burrowing larvae can change the moisture and nutrient status of a dung pat, thereby making it unsuitable for other larvae (Moon 1980).

During the course of this present study I spent 3 hours on 8 occasions observing, in the laboratory, the behaviour of the larvae towards each other in a Petri dish. The larvae were not aggressive or cannibalistic towards each other, even if starved for 24 hours. It is unlikely, therefore, that these behaviours were responsible for the increased mortality and decreased pupal weights that were recorded. It is more likely that a mechanism involving the conditioning of the food source may be responsible. On hatching, the CM maggots seek out and enter the root of the host plant and begin feeding on the internal tissues. They are mainly confined to the roots, where they do most of the damage (Coaker and Finch 1971). The rate of larval feeding, and the type of food accumulated and carried over from the larval stage, governs the behaviour of the adults and the success of the next generation (Coaker and Finch 1973). It is this larval feeding that conditions (i.e, increases microbial activity within) the root tissues, and surrounding soil. At the appropriate microbial population density, these microorganisms can provide essential nutrients for the larvae. A correct balance of feeding rate and microbial breakdown of the root tissue is essential for the production of large pupae, which in turn become large highly fecund flies (Doane and Chapman 1964, Finch and Coaker 1969). The high increase in mortality between larval densities 2 and 4 may be because of insufficient microbial activity for use as an additional food source, together with competition and increased nutritional needs of the larvae. An overgrowth of microorganisms may result in the accumulation of toxins that inhibit larval development, as was observed at higher densities 8 and 10. On the other hand, the extra microbial activity may provide the larvae with an alternative, though less nourishing, source of food than the host plant. This may account for a slower increase in mortality between densities 4, 6, 8, and 10 when compared with 2 and 4. Increased mortality from desiccation and predation can also result from the immature larvae leaving the root in search of food. Coaker (1966) found that at high population densities some larvae leave the root and move up to 10 cm from the host.

At larval densities of 8 and 10, an increase in interaction, together with the faster depletion of the host (the host plant was completely destroyed by the end of the experiment), may be responsible for reduced pupal weight. Wasti et al. (1975) found, however, that pupal weight in house flies decreased as density increased from 20 and 60 larvae /g manure and no such effect was observed between densities 10 and 20 or 60 and 100. Possibly the supply of food was adequate at densities 10 and 20, and perhaps microbial food substituted for this at density 60 and 100. The negative effects of competition were only experienced between densities 20 and 60.

Many insects have a minimal weight range below which mortality occurs. Beaver (1973) found in his study on *Sarcophaga* spp. (Diptera : Sarcophagidae) that mortality varied little with density until a minimum size limit was reached. Consequently, effects of larval competition are more easily seen in terms of pupal weight than in larval mortality. In the present study, pupal weight decreased and mortality increased with an increase in larval population density. Larval population density may also affect the rate of development of the different stages. This may be increased or decreased depending on the species and the population density. In the present study, 10% of the larvae at density 6 showed accelerated development (17 days), and 12 and 20% of the larvae at densities 8 and 10, respectively, exhibited decrease development (22 and 24 days). With minimal competition, most CM larvae pupated within 21 days. Thus, it appears that at density 6, with respect to rate of development, an optimum balance between host tissues and nutrients that were provided by microbial activity may have been achieved. In species such as CM, in which eggs are laid in small groups, moderate crowding may result in accelerated development (Peters and Barbosa 1977)

Although no effects of larval population density on the time required for adult emergence were detected, it was noted that 10% of the pupae weighing less than 10 mg, (most of which occurred at densities 8 and 10), did not emerge.

Thus, larval competition reduces the weight of pupae, which in turn results in small adults that are likely to exhibit reduced fecundity. This may partly explain the commonly observed drop in field population densities between the first and second generations. Overwintered first generation flies are generally larger and more fecund than subsequent generations (Finch and Coaker 1969, Hughes and Mitchell 1960). Also, because the plants on which the large first generation adults oviposit are very small, resource depletion would be likely to be experienced quickly, resulting in reduced larval survival, smaller pupae and smaller second generation adults with low fecundity.

In a study of natural mortality of CM in the field, Hughes and Slater (1959) found that over 95% of the first generation generally died during development. Key factors were predation and parasitism of the egg and pupal stages, and plant death comprised the only density-dependent mortality factor for the larvae. Older and larger plants, later in the season, were capable of supporting larger populations of maggots, which in turn produced larger pupae and adults. Gibson and Treherne (1916) reported finding 123 maggots within a single cauliflower root. Thus, competition may have both a direct (reduced weight, increased mortality) and an indirect effect (reduced fecundity of females as a result of low body weight, and reduced population density of the next generation) on the population dynamics of this species.

In conclusion, with an increase in cabbage maggot population density, larval mortality increased and pupal weight decreased. At the highest population density it took longer to pupate, but the length of the pupal stage was unaffected.

TABLE 8. Effects of intraspecific competition for food on development of the Cabbage Maggot (CM) larvae.

Egg density	Mean % larval mortality	Ave. pupal wt. mg	% Pupae wt. below 10 mg	Days to pupation	Days from egg to adult emergence
2	15 a	15.73 a	0	21 a	12-14
4	43 b	13.48 ab	0	21 a	11-13
6	38 b	13.62 ab	0	17 b	12-15
8	45 bc	12.69 b	18	22 ac	12-15
10	52 c	11.09 c	31	24 c	11-14

Means with the same letter are not significantly different $p>0.05$

GENERAL DISCUSSION AND CONCLUSIONS

Fecundity, rate of egg deposition, and survival of an insect are affected by food availability, environmental conditions, competition among and between species for a limited resource, and prior experience with host plants. Oviposition site selection is critical for survival in most insects. This is especially the case where adult and larval feeding habitats are different, and where the larvae are not very mobile. In such cases, survival depends on the correct placement of eggs by the female. In insects, choice of a host plant for oviposition is influenced by a number of factors including its physical, physiological, and nutritive properties, egg load of the female, and female survival rate (Myers 1985, Scriber 1984).

Competition among herbivores is considered to occur only infrequently because it is assumed that plant resources are homogenous, abundant and are rarely limiting (Hairston et al. 1960, Price 1983). Under natural conditions, however, all plants are not alike. Environmental and genetic variation among host plants creates plant patches that differ in quality and attractiveness to insects (Thompson 1988b). As a result of these patch dynamics, phytophagous insects are confronted with a spectrum of quality differences among their plant hosts, only some of which are likely to be highly suitable for larval development (Jenzen 1985). Depending on the number of suitable plant patches available, and the characteristics of the insect population, ovipositing females will compete for, and demonstrate optimal oviposition behaviour on, these preferred plants. This behaviour could result in competition among and between species that share the same resource for the best sites that can support their progeny (Thompson 1985). Another long-held assumption is that competition occurs only at very high herbivore densities. However, taking into account the patch dynamics theory, it would seem that competition could occur at any population density if all of the high quality hosts are occupied, and not just when all of the hosts are occupied. This may explain Craig et al.'s (1990) finding of a decrease in fitness of individual sawflies, even at low densities.

In the present study I found that CM, OM, and SCM adults demonstrated an increase in fecundity as population density increased up to an optimum on both host and non-host plants. This optimum was higher on host plants when compared with non-host plants. Such an increase in fecundity up to an optimum population density above and below which individual fecundity is lower is termed an "Allee" effect (Allee 1928, El-Sawaf 1956, Karandinos and Axtell 1972, Laurence and Samarawickrema 1970, Pearl 1932). In addition to fecundity, the rate of oviposition was slower at lower densities.

The "decision" by a female to oviposit is based on the need to maximize fitness by allocating the optimum number of progeny per host (Waage 1986, Waage and Ming 1984, Wajnberg et al. 1989). Such behaviour has been well documented in parasitoids (Waage and Ming 1984, Wajnberg et al. 1989). CM, OM, and SCM adults are attracted to, and stimulated to oviposit, by odours associated with microorganisms responsible for the rotting of host tissue. These microbes provide nourishment for the larvae, either directly or by breaking down the substrate and making it more readily available for larval assimilation, thereby increasing larval survival (Eckenrode et al. 1975a, Ellis at al 1979, Friend et al. 1959a,b). The population density of gravid females on a plant, and the number of eggs laid on it, may indicate the level of microbial activity on that plant. This information may be used by an ovipositing female when "deciding" whether to maximize or minimize its clutch size. Judd and Borden (1992) found that insect eggs are contaminated with microorganisms by the females during laying.

In some species, increased clutch size has been associated with aggregative behaviour. One reason why insects aggregate is to overcome host defence and, in some cases, conditioning of the host may take place making it more attractive to ovipositing females. In some phytophagous insects, such as CM, OM, and SCM, the development of saprophagous microorganisms on the host as a result of larval feeding, could increase the attractiveness of such hosts to these insects and result in increased oviposition. However, after a certain optimum density, maximizing fitness by increased clutch size may not be beneficial. Increased fecundity at high densities may result in faster host tissue depletion and reduced progeny survival. Most parasitoids, exhibit a decline in individual fitness with increase in clutch size, although there is evidence of an "Allee" effect in some species. In these latter parasitoids, very small broods often fail entirely because of their inability to overcome host defense (Ikawo and Okabe 1985). Thus at lower than optimum densities, the lack of oviposition stimulation, together with reduced conditioning of the host, may reduce fecundity per female. Charnov and Skinner (1984) found that intraspecific competition between adult *Trichogamma* spp. may result in a larger clutch size being allocated to host species on which fitness is lower. OM females, in the present study, oviposited on non-host plants. Thus, availability of resources, as well as the physical state of an individual, determines its clutch size.

CM, OM and SCM are all more attracted to damaged than undamaged plants, larval survival being higher in the former because of the presence of saprophagous microorganisms. Females of these species aggregate in such areas and are stimulated to lay more eggs (Dindonis and Miller 1980, Hausmann and Miller 1989). OM females are also more attracted to plants that already bear eggs or to plants with ovipositing females on them. Sometimes two or three females can be seen ovipositing on the same onion plant, showing no aggressive behaviour to one another (Harris and Miller 1983, Havukkala and Miller 1987, Hough-Goldstein et al. 1987, Yathom 1970). This habit may contribute to the presence of an optimum density, above and below which oviposition decreases, as was observed in the present study. Another stimulatory factor may also be the presence of a pheromone on the eggs. This pheromone, whose concentration may depend on the number of eggs laid, may be stimulatory, and hence attract other individuals to lay more eggs. However, at higher concentrations it may become a repellent. Judd and Borden (1992) confirmed the presence of a pheromone laid down during oviposition on the egg of the onion fly. According to this study it appears that microorganisms transmitted with the eggs may be involved in this attraction and oviposition stimulation. Such a behaviour would be beneficial for the larvae, as the microorganisms can aid in the entrance of the first instar larvae into the root system. These microorganisms are responsible for the decomposition of the host tissue, which becomes more accessible to the newly hatched larvae. In addition, these microbes provide nourishment for the larvae.

A decrease in fecundity above an optimum density may occur because of the detrimental effects of overcrowding. These effects include higher collision interference and interruptions of rest and oviposition, and chemical changes in the resource that deter other individuals, or reduce their fecundity (Prokopy et al. 1984). The unique pre-oviposition behaviour of these anthomyiid flies would make them particularly susceptible to overcrowding. The females alighting on a potential plant first perform stem walks, and eventually move to the soil surface, where they probe the soil repeatedly with their ovipositor before laying a batch of eggs (Miller and Harris 1983; Miller and McClanahan 1960, Zohren 1968). Their well developed tarsal receptors enable the females to evaluate the suitability of the host during these runs (Städler 1978). Disturbance during this behaviour may result in retention or resorption of eggs, and increased adult mortality as a result of associated stress.

In addition, at population densities above the optimum level, resource depletion might prevent the larvae from maturing enough to pupate. Under such conditions, to continue feeding, the larvae might have to move to another host plant. Seven to 12 day old larvae of OM have been observed to travel a distance of 25 cm within 24 h (Kendall

1932). However, during this movement, the larvae are vulnerable to desiccation and predation. Because of this, maximizing oviposition can be detrimental to progeny survival and population densities below the optimum may not provide the ideal biotic environment for larval development.

In the present study, CM larvae demonstrated the presence of an optimum density for development above which this was prolonged. Although survival decreased with increasing population density, the larval weight was maintained until population density was very high. The use of microorganisms as an alternate food source would explain the maintenance of high pupal weights. This polyphagous ability is beneficial for the species because if the weight of the larvae decrease then the subsequent adults will be small and less fecund, and this will result in a decrease in population density in the next generation. In the field, however, Hughes and Slater (1959), and Hughes and Mitchell (1960) reported that larval mortality was very low, even at high adult population densities. The use of microbes as a food source may be responsible for the larvae not having to leave the food source and risk dying as a result of exposure to enemies and desiccation. Wasti et al. (1975) found that pupal weight decreased between densities 20 and 60 larvae, but not between densities 10 and 20 or 60 and 100. This lack of a decrease in pupal weight at higher densities may be the result of a favourable balance between the plant food resource and the microorganisms.

Thus, to summarise, at densities below optimum, the biotic environment is not at its optimum level to stimulate oviposition, and at densities above optimum, disturbance of females during feeding, oviposition, pheromone concentration, and increased rate of resource depletion, may be responsible for decreased oviposition, and increased larval mortality.

In some insects, however, a non-host plant is never accepted, even if the individuals are isolated with the plant for extended periods in a no-choice situation (Claridge et al. 1977). CM females used in the present study were found to be host specific, and would not lay eggs on non-host plants. In the present study, OM females accepted cabbage and beans (non-hosts) as oviposition sites and, although an optimum population density was observed with both of these plants, this optimum level was lower on non-host plants as compared with host plants. Thus, female population density and host type can affect fecundity. In addition, a delay in both the rate of oviposition and mortality on cabbage, a non-host plant, was recorded. Courtney (1981) and Singer (1982) observed that in a no-choice situation, most insects will accept a plant that under normal circumstances only weakly stimulates oviposition, or is completely unsuitable for larval survival under normal conditions (Singer, 1971; 1982; Courtney 1981). According to the rolling fulcrum model, an insect under normal conditions will only accept the most preferred host plant for oviposition or food. If, however, an insect is deprived of its preferred host, after a certain time, the balance of host preference begins to change, and eventually marginally acceptable plants are chosen for oviposition (Miller and Strickler 1984). Most so-called oligophagous species are able to survive on a number of alternate hosts, which may include completely unrelated plants (Thompson 1988a). Although, OM is considered to be host specific, larvae were found to survive on cabbage, beans and various other plants (Workman 1958).

Thus, CM, OM and SCM demonstrate the presence of an optimum density for maximum fecundity. This optimum density is higher on host plants as compared with non-host plants. CM is host specific and accepts only its host plant cabbage as an oviposition site. OM and SCM accept all three hosts as oviposition sites, but rate of oviposition is delayed for OM on non-host plants in a no-choice situation.

In addition to intraspecific competition for the best possible site, an individual also has to compete with organisms of other species sharing the same resource. It is generally believed that interspecific competition depends on the extent of resource overlap between species. According to Janzen (1973), however, because all parts of a plant are connected, a species feeding on one part is automatically competing with all other species on that plant. This concept is supported by the results of a study on competition between CM and certain beetles, aphids and Lepidoptera on crucifers (Finch and Jones 1987). The fecundity of CM females decreased in the presence of these other groups, even though they fed on different parts of the plant. In fact, the presence of frass or eggs on the plant was sufficient to deter CM females from ovipositing on these plants. Thus, it appears that complete overlap of resources between species is not essential for interspecific competition to occur. CM and SCM larvae are often found feeding in the same root, but in the present study no effect of such competition was observed.

The population dynamics of a species that shares a resource is determined by its ability to obtain enough of that resource to complete its growth, and eventually reproduce. In CM, OM, and SCM, the attraction to and use of microorganisms as a supplementary or alternate food source by competing larvae may act as an additional resource, which decreases the effects of competition for host plant material. Another possible reason for coexistence of CM and SCM is that the immatures may survive better in the presence of the other species. This agrees with Pielou's (1967) reason for lack of competition as each species can draw on additional resources so that the coexisting species are not limited by the shared resource. In such a situation the larvae of one species may break down the host defences, and the other species contributes by conditioning the host tissue. SCM larvae can survive on only decaying organic matter and microbes in the soil, whereas OM and CM require the host plant tissue in addition to the microbes to increase development rate, and escape predators. Thus, the extent of competition depends on the ability of an individual to exploit an additional resource. In this case the offspring of the two species will not affect each other (Ayala, 1970; 1972; Pielou 1967).

In my study on interspecific competition the results show that in OM:SCM combinations, the ratio of the species affected the rate of oviposition, mortality and fecundity, but these factors were not affected in SCM: CM combinations. There are a number of reasons why frequency affects the outcome of competition. These include difficulty in finding a mate when numbers are low, disturbance during feeding, oviposition, and rest, and greater aggressive behaviour, higher fecundity, and development rate in one of the species (Ishida 1952, Ross

1957, Seifert and Seifert 1979a, b). In the present study, under controlled environmental conditions, disturbance, or aggressive behaviour, were the most likely reasons for OM and SCM competing.

Phytophagous insect species rarely exhibit competition, although they often show considerable overlap in their habitat and resource use (Lawton and Strong Jr. 1981, Price 1983, and Strong Jr. 1984). It is generally believed that these species are too rare in comparison to their resource, and that natural enemies and environmental conditions usually keep their populations at levels low enough to avoid any chance of competition (Harrison 1964, Pipkin et al. 1966). Sometimes, the detection of competition depends on the symptoms used to detect it. Moon (1974), using survival data of face fly larvae, found that competition occurred when densities exceeded two larvae per g of fresh dung, but stunting, which could result in higher mortality during the pupal stage, or reduce adult fecundity, occurred when the density exceeded one larva per g of fresh dung.

Thus, to summarise, interspecific competition can be avoided, as it was in CM and SCM, by the use of additional resources by the immatures, better survival in the presence of the other species, and by the random selection of oviposition sites. In the case of OM and SCM, however, OM females compensated for low numbers, in a no-choice situation, by increasing fecundity, rate of oviposition and delaying mortality at lower densities. SCM, on the other hand, exhibited negative effects of competition at low densities by decreasing the rate of oviposition and increasing mortality. Under field conditions, such situations may result in the females emigrating to another area.

In addition to competition, the experience that an individual accumulates over its lifetime may influence host acceptance by that individual. Past encounters with potential host plants are known to affect detection, preference and selection of hosts in future encounters. An excellent and extensive review of insect learning is given by Papaj and Prokopy (1989). Adult experience of hosts may be one of the most important factors resulting in differences between individual insects within the same population. Experience may, in any one situation, modify ranking or specificity or both of these factors (Papaj and Rausher 1983). Such modification in specificity is most common in Phasmatoidea, Lepidoptera and Diptera (Cassidy 1978, Hoffmann 1988, Jaenike 1983, 1988, Singer 1982, 1983).

Studies in the laboratory (Jaenike 1983, Jermy 1987, Prokopy et al. 1982a, 1986), and in the field (Prokopy et al. 1982b), have indicated that prior exposure to a particular resource as a larva or adult may influence a female's tendency to search for, and oviposit on, that particular host type.

SCM is a polyphagous species feeding on a wide range of host plants (beans being the preferred host). Results of the present study show that prior experience to some, but not all, host plants during the pre-oviposition period influenced the initial acceptance of other hosts. The preferred host of SCM (beans) was always accepted irrespective of the host species to which the individuals were initially exposed. Host discrimination occurred only when the females were presented with a secondary host plant (onions and cabbage). When SCM adults were exposed to onions during the pre-oviposition period, an initial delay in acceptance of cabbage was observed, and when exposed to cabbage, an initial delay in acceptance of onions was observed. A change in the rate of oviposition on onion and beans when exposed to the secondary hosts onion and cabbage was also observed. Papaj and Prokopy (1988) reported that exposure to a low ranking host results in acceptance of the higher ranked host, but not vice versa.

Since encounter rates with various resources provide information about the environment, optimal oviposition would be expected to depend on the frequencies of encounters, and learning would provide valuable information in the host selection process. The continued presence of a plant may condition a female to accept that host. In the present study, I found that the continued presence of the host plants, though not accepted by SCM females at the initial encounter, were eventually accepted at the same rate as the primary host. This finding corresponds with one of the criteria used to determine learning behaviour, i.e., the behaviour changes gradually with repeated experience, often following a so called learning curve, and the changes in behaviour following an experience wanes in the absence of the continuous presence of that host (Papaj and Prokopy 1986). In the butterfly *Pieris rapae* (Lepidoptera: Pieridae), prior experience influenced the first five subsequent landings, but after that the females soon lost their ability to discriminate between hosts (Traynier 1984). Thus, with continued exposure to one plant, individuals can be conditioned to accept another host.

A switch in host plant type once oviposition had begun did not appear to disrupt oviposition, or change acceptance. This suggests that, in addition to conditioning, learning may be also be age dependent, host preference being more easily modified in younger than in older insects. Such age dependent learning behaviour has been demonstrated in ants, wasps and stick insects (Cassidy 1978, Jaisson 1980, Wardle and Borden 1985). Thus, in my study, learning to discriminate only occurred during the initial stages of host plant choice.

From the present study it can be concluded that ovipositing females of CM, OM, and SCM aggregate, and fecundity in these aggregations increase as density increases up to a threshold level, above which fecundity decreases. In CM, OM, and SCM, rate of oviposition was accelerated at higher densities and survival was significantly affected by density. OM females laid eggs on non-host plants in a no-choice situation, whereas CM females did not do this, but rather died before ovipositing. OM larvae were found to be able to survive to pupation on non-host plant tissue.

SCM and CM did not compete for oviposition sites, but rather coexisted. In the case of mixed populations of SCM and OM, fecundity, rate of oviposition and survival were all affected by the frequency of the other species in the cage. SCM females were found to learn by prior experience during the initial oviposition or host finding period. Once oviposition had started, the females did not distinguish between host plants. Mortality increased with increasing larval population density. I also recorded a reduction in pupal weight and prolonged developmental rate at high densities, and a reduction in developmental rate at an optimum density (6).

Practical Implications Of This Study

This study has improved our understanding of the oviposition behaviour and host plant choice of the three anthomyiid flies, Cabbage Maggot (CM), Onion Maggot (OM), and Seed Corn Maggot (SCM). Although the aggregative nature of these flies was known, as well as the fact that they commonly occur together in the field, the effects of population density in these aggregations on the fecundity of individuals, and on oviposition by females of the other species, were not known.

The knowledge obtained by this study can be used to interpret monitoring data. Although densities used in the intraspecific study would never be reached in the field, except for maybe the lower densities, aggregations of adults in an area could result in increased oviposition stimulation. This increased oviposition should be taken into consideration when relating population densities to the amount of damage expected. Since adult aggregations result in increased oviposition, highly attractive trap crops (susceptible cultivars) could be established to attract these females. Controls such as insecticide applications and the release of suitable predators and parasites in these trap crops might be used to kill most of the population. A strict monitoring procedure should be followed throughout the season.

One of the reasons for carrying out this project was to determine if CM and OM would accept non-host plants as oviposition sites, and if so what was its importance. This study shows that CM is very host specific, accepting only cabbage plants (host) as the oviposition site.

OM, on the other hand, oviposited on non-host plants, and the larvae survived to pupation on these plants. Thus, the presence of, or monitoring for CM, in a non-host field may not be necessary, but further field studies are required to establish the importance of OM on non-host plants.

OM and SCM, and CM and SCM, do not deter each other from ovipositing on the same plant. Thus, monitoring of adults in onion and cabbage fields, respectively, is important for applying an effective control strategy. Because these three species are very similar in appearance, correct identification of the species is very important, and failure to make such identifications may lead to inefficient control strategies.

SCM is a generalist and feeds on all three plants. Since selection of host plant species in SCM is only initially affected by prior exposure to a host, switching to other host species occurs easily. Continued exposure to a host will result in acceptance of that host plant. Thus, at the beginning of the flight period, the crop in which the females emerged may be in danger of being attacked. However, because SCM is polyphagous, subsequent generations may attack a different species.

FUTURE RESEARCH

Future research on these three species should be directed towards establishing the presence or absence of an oviposition pheromone for all three species. Judd and Borden (1992) recently discovered the presence of an oviposition pheromone in OM that attracts other ovipositing adults and stimulates aggregation and oviposition. The presence of an optimum density for maximum fecundity, in my experiments, supports the presence of such a pheromone, but it also suggests that at higher concentrations, when population densities increase, the pheromone may become a repellent. Such a repellent effect as concentration of the pheromone increases may explain why in my experiments fecundity decreased above the optimum population density. The presence of such a pheromone would be useful in various pest management strategies.

Since OM females have been observed in non-host plant fields and this study shows that females lay eggs and larvae will survive on non-host plants tissue, field studies should be undertaken to establish the economic importance of this finding.

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APPENDIX I. Manuscripts and Presentations Based on this Thesis

Noronha, C. 1990. Oviposition competition between Seed Corn Maggot *D. platura* (Meig.) and Onion Maggot *Delia antiqua* (Meig.) (Diptera: Anthomyiidae), and its implications for effective control. Proc. Can. Pest Management Soc. p 138-140.

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Noronha, C., C. Vincent, G. Boivin and S.B. Hill. 1992. Effect of intraspecific competition on fecundity, rate of oviposition and mortality of *Delia radicum* (Bouché), *D. antiqua* (Meigen) and *D. platura* (Meigen) (Diptera: Anthomyiidae). (In preparation)

Noronha, C., S.B. Hill. G. Boivin and C. Vincent. 1992. Interspecific competition for oviposition sites between *Delia radicum* (Bouché) and *D. platura* (Meigen), and *D. antiqua* (Meigen) and *D. platura* (Diptera: Anthomyiidae). (In preparation)

Noronha, C., S.B. Hill. C. Vincent. and G. Boivin. 1992. Effects of pre-oviposition exposure to bean, onion, and cabbage plants on oviposition behaviour of *Delia platura* (Meigen) (Diptera: Anthomyiidae). (In preparation)

Noronha, C., G. Boivin, C. Vincent. and S.B. Hill. 1992. Effects of intraspecific competition on larval mortality, development rate and pupal weight of *Delia radicum* (Bouché). (In preparation)