THE UNIVERSITY OF MANITOBA

Growth, development and survival of *Mamestra configurata* Walker, (Lepidoptera:Noctuidae) on various reported food plants

A Thesis

Submitted to the Faculty

of

Graduate Studies

The University of Manitoba

by

Geoffrey Matongo Kapatsa

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

Department of Entomology

Winnipeg, Manitoba

October 1979

Growth, development and survival of *Mamestra configurata* Walker, (Lepidoptera:Noctuidae) on various reported food plants

BY

GEOFFREY MATONGO KAPATSA

A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

ABSTRACT

Growth, development and survival of the bertha armyworm, Mamestra configurata Walker, larvae were investigated in the laboratory on 13 plant species belonging to 6 plant families, and an artificial diet. The plants tested had all been reported as hosts of M. configurata. The plants tested for their suitability as hosts were: two cultivars of Brassica napus L. (Zephyr rape and American purple top rutabaga); B. campestris L. (Summer turnip); B. juncea L. (Lethbridge 22A mustard); B. oleracea L. (Pennstate ball head cabbage); Fagopyrum tataricum L. (Buckwheat); Beta vulgaris L. (Early wonder sugar beet); Amaranthus retroflexus L. (Red root pigweed); Phaseolus vulgaris L. (Pencil pod black wax beans); Melilotus officinalis L. (Sweet clover); Medicago sativa L. (Alfalfa); Linum usitatissimum L. (Flax); and Tagetis patula L. (Glitters marigold). The foliage was used when 5 to 10 weeks old. Four criteria were used in judging the suitability of the plants: the percent survival to adult emergence; the larval molting weights and pupal weights (growth); the length of the development period from larval eclosion to adult emergence; and the food utilization indices.

Highest survival, growth and development were obtained among insects reared on the artificial diet. Rape was the best foodplant for larval growth, development and survival and rutabaga was almost as good. The utilization

indices were relatively high on both food plants.

On cabbage, sugar beet and marigold, larval growth, development and survival were good up to the pupal stage but emergence was lower. Food utilization (from the regression coefficient) and ECI values were highest on marigold but this plant also produced much lighter pupae and smaller adults. The utilization and ECI values on cabbage were similar to those on rape but on sugar beet they were lower. On sweet clover, alfalfa, turnip and pigweed, larval growth and survival in the early instars were just as good but sixth instar mortality was higher and none reached the adult stage. The rate of development was variable, moderate on sweet clover and alfalfa, and slow on turnip and pigweed. The utilization and ECI values were much lower in the latter two food plants.

On buckwheat, beans, flax and mustard, larval growth, development and survival were poor from the first instar onwards. These plants appear to have been very unfavourable for larval establishment probably due to foliage physical characteristics or chemical factors (feeding deterrents or toxins).

The results suggest that only rape (Zephyr) and rutabaga (American purple top), both cultivars of B. napus, were suitable for growth, development and survival of M. configurata. The growth, development and survival on the other food plants tested are too low for M. configurata to increase its population level. These hosts are apparently

attacked by larvae when suitable host plants are absent or in low supply.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

This study was undertaken at the suggestion of my supervisor, Dr. W.J. Turnock, Head, Integrated Pest Control Section, Research Station, Agriculture Canada, Winnipeg, and Adjunct Professor of the Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada. I am deeply indebted to him for his guidance, counsel and encouragement during the course of my studies. I wish to thank members of my committee; Dr. R.A. Brust for his helpful suggestions and criticisms of the first draft and Dr. B.R. Stefansson for his helpful suggestions and criticisms of the final draft of this thesis.

My sincere gratitude is extended to Professor A.G. Robinson, Head, Department of Entomology, University of Manitoba, Winnipeg, for his invaluable assistance in all spheres of my academic struggle at this university.

I would like to express my appreciation to Messrs. B. Bilodeau and B. Wilson, both of the Agriculture Research Station, Winnipeg, for providing the bertha armyworm eggs used in this study. Acknowledgement is also given to Dr. G.K. Bracken, of Agriculture Canada, Research Station, Winnipeg, for permitting my use of the facilities available in his laboratory. Special thanks go to Dr. P.S. Barker, Agriculture Canada, Research Station, Winnipeg, for his advice on statistical analysis and providing the calculator for the purpose, and

Mr. D. Nelson also for providing a calculator.

Finally, I am grateful to the National Council for Scientific Research, Republic of Zambia for providing financial aid during the course of this study.

CHAPTER I

INTRODUCTION

1. Distribution, life history and the economic importance of the bertha armyworm, Mamestra configurata Walker .

(a) Distribution.

The bertha armyworm, Mamestra configurata has been recorded from Mexico (Mexico City), north along the Cordillera to British Columbia and east through the prairie provinces of Canada to North Dakota. The species has been taken within the grassland areas, the margin of the savanna and parklands.

(b) Life history of M. configurata.

Adults emerge from overwintering pupae from June through July. Egg deposition begins after a fairly short pre-oviposition period. The eggs are deposited in a tightly-arranged honeycomb pattern on the lower sides of leaves of food plants. A female may lay 100-400 eggs per plaque (Bucher and Bracken, 1976). Hatching occurs in a few days. There are six stadia and in the first few of these, larvae are mainly solitary in habit and feed on the underside of leaves. During this period, the caterpillars are green and inconspicuous. In the last two larval instars, the appearance and habits become more variable. Some larvae, while retaining the green colour, also develop paired brown or black markings on each segment. Others

develop a yellowish, velvety black or mottled appearance as they approach maturity. When feeding on rape, larvae in the last two instars may feed actively on the pods. Partial or complete consumption of pods may occur within a few days. The larvae may hide under loose soil, fallen foliage or debris during the day and feed at night.

When feeding is complete, larvae burrow into the soil to a depth of about 15 cm, form an earthen cell, and, after a short pre-pupal period, transform into pupae. Diapause occurs in this stage. A few pupae may develop without diapause and emerge as adults late in the fall. However, because of winter conditions in the prairie provinces, these moths die soon after emergence. They do not therefore constitute a second brood in any true sense. In the prairie provinces, therefore, the bertha armyworm is univoltine. Under laboratory conditions, the moth can be reared without diapause if kept at temperatures above 20°C with a 18:6 hr photoperiod (Bailey, 1976).

(c) Economic importance.

The first account of the economic importance of the bertha armyworm was written by King (1928). This was apparently initiated by reports of larval damage to sweet clover, alfalfa and flax during the period between 1922-1927.

The first confirmed record of bertha armyworm damage was on flax in the Moose Jaw district of Saskat-

chewan in 1922. There were sporadic reports of heavy infestations until 1927 when the outbreak affected Alberta and extended to the Fernie district of British Columbia. In Manitoba,Criddle reported considerable injury to sweet clover in 1925 and 1927 (see King, 1928). By the latter year, the outbreak had extended into the northwestern part of North Dakota where Munro (1930) reported damage to flax.

The reports of the bertha armyworm attacking rape (Brassica spp.) began about 1945 when prairie farmers began to increase the rape acreage. Reports in the Canadian Insect Pest Review (vols. 22-27, 31-35) indicate that numerous small outbreaks occurred in 1944-1949 and again in the mid 1950's. However, the main impact of bertha armyworm damage to the rape crop occurred during 1970-1973 when the bertha armyworm outbreak affected an estimated 1 million acres of the 5.5 million acres of rapeseed in the prairie provinces (McDonald, 1972, Philip, 1973, Taylor, 1973). During the same period, the bertha armyworm attacked and damaged truck crops in British Columbia (Banham and Arrand, 1970), and sugar beets in Washington (Tamaki et al., 1972). Ever since, however, the bertha armyworm populations have remained at or near zero in most areas (Dolinski, 1974, Gage and Taylor, 1976, Pankiw, 1976, Philip, 1973, Putnam, 1975, Turnock, 1974, 1977).

The bertha armyworm has also attacked a wide range of wild flowers, garden flowers, garden and several

truck crops, weeds and various wild mustards in addition to field crops. These reports clearly indicate that the bertha armyworm is polyphagous. However, the native hosts of the species are not known.

2. The problem.

While the bertha armyworm has been reported to attack many plant species, the effects of these plants on the growth, development and survival to the adult stage of the species are largely unknown. Host plant relationships may determine the survival, development and economic importance of the insect.

Quantitative studies of the effects of host plants on a number of species of Lepidoptera have been conducted (Beckwith, 1970, Hovanitzi and Chang, 1962, Mukerji and Guppy, 1970, New, 1971, Scriber, 1975, 1977, Soo Hoo and Fraenkel, 1966, Waldbauer and Fraenkel, 1961). However, for the bertha armyworm, only Bailey (1976) has described the effects of different host plants on the insect. He showed that Brassica napus var. Zephyr, B. campestris var. Span and Chenopodium album L. were good for the insect's survival and that Solanum tuberosum L. was bad.

The objective of this study was to determine the effects of several reported host plants on the growth, development and survival of M. configurata. These parameters were evaluated by determining the relative amounts of each food plant consumed and by establishing the relationships between food consumption, growth, development and survival. The role of these plants in

the development and maintenance of outbreaks of M. configurata was examined.

CHAPTER II

LITERATURE REVIEW

An attempt will be made to bring together the major references to Insect-plant relationships, particularly of the Lepidoptera. However, since only a few Lepidoptera have been fully investigated in respect to their host associations, the review will include several examples from other orders.

1. Insect growth and development on host plants.

In many phytophagous insects, feeding has been shown to be associated with specific chemical stimuli. A food-plant is characterized not only by the presence of specific chemical attractants or feeding stimulants (phagostimulants) but also by the absence of secondary plant substances which act as repellants (Dethier, 1954, Fraenkel, 1969). The basic behavioral and physiological processes mediated by these compounds are host finding by adult females for feeding and oviposition and host finding by immature stages for feeding, growth and development.

An acceptable host plant must provide the insect with a physical environment and a nutritional substrate that is adequate, non-toxic and utilizable from the standpoint of digestion, assimilation and conversion into insect tissues. Beck (1974) pointed out that even the best host plants may be suboptimal in some of these

characteristics and mortality among young larvae tends to be very high. The phenols, flavonoids, alkaloids and various glycosides contained in plants are basically deleterious and insects feeding on plants containing these substances must be able to degrade them metabolically. The ability to metabolize such plant components constitutes an important aspect of the adaptation of an insect species to a particular plant as a host (Self et al., 1964, Krieger et al., 1971). Since different plant species or populations may differ either qualitatively or quantitatively in respect to these substances, an insect that is metabolically adapted to one type of plant may not be able to meet the metabolic demands posed by another plant. Consequently, the insect will not be able to survive on it.

Basically, there are four factors which govern insect/plant relationships; physical characteristics, biochemical characteristics, digestibility and convertibility, and nutritional factors. These factors when working at the same time are not of equal importance but rather, a hierarchy is created where one becomes dominant (Legay, 1955). Since plants differ in these basic factors, most insects can only feed on a few selected food plants on which development and survival are optimal. The diet therefore plays an important role in influencing insect/host plant relationships. The factors essential to the adequacy of the diet are discussed below.

(a) Physical characteristics

The role of physical characteristics has been studied mainly in relation to host plant resistance. Characteristics such as pubescence, spacing of vascular bundles and tissue silica content have been investigated. Nothing is known of the effects of physical characteristics on the growth and survival of M. configurata.

For aphids, a sticky substance discharged from glandular hairs on the leaves of several Solanum spp. entraps the insects and prevents their establishment (Gibson, 1971). Gilbert (1971) also reported that small caterpillars are entrapped and effectively prevented from feeding by hook-like trichomes on the leaves of Passiflora adenopoda. Young larvae of Prodenia eridania (C.) are trapped and injured by fish-hook like spines on Dorsternia contrajerva (Soo Hoo and Fraenkel, 1966). Physical characteristics may therefore either injure the insect directly or prevent it from feeding.

(b) Biochemical characteristics

It is generally known that chemical sign stimuli play an important role in the feeding behavior of many phytophagous insects. Secondary plant substances guide the insect's choice of food and may be typical of the plant which is the insect's preferred or exclusive food. A non-food plant is characterized not only by the absence of specific chemical attractants or feeding stimulants

(phagostimulants) but also by the presence of other secondary plant substances which act as repellents (Dethier, 1954, Fraenkel, 1969). These compounds together with nutrients account for Insect/plant interactions.

Among the plant families tested in this study, Cruciferae are known to have an unusual method of sulfur metabolism. One of the characteristics of this process is the production of mustard oil glucosides (thioglucosides) (Kjaer, 1960). The enzyme myrosinase catalyses the hydrolysis of these glucosides; and usually accompanies the thioglucosides in plant tissue. When tissues are damaged, a number of compounds are formed, including glucose, sulfuric acid and corresponding mustard oils, most of which are isothiocyanates. Of more than 200 cruciferous species analysed, few have lacked a thioglucoside (Kjaer, 1960, 1976, Ettlinger and Kjaer, 1968). The glucosinolates sinigrin, glucocapparin and glucoiberin have been shown to be feeding stimulants for the imported cabbageworms, Pieris rapae L. and P. brassicae L. (David and Gardiner,1966). The compounds sinigrin, sinalbin and glucocheirolin are feeding stimulants for the diamond back moth Plutella maculipennis (Curtis) (Thorsteinson, 1953).

Within the Leguminosae, alfalfa has been shown to contain feeding stimulants for the alfalfa weevil, Hypera postica (Gryllenhull) (Yamamoto, 1963). Hsiao (1969) reported that these compounds are adenine salts and

nucleotides. The saponins in alfalfa have been indicated as possible resistance factors not only to white grubs (Horber, 1965) but also to stored product insects in legume seed (Applebaum et al., 1969). Tannic acid in alfalfa acts as a repellent for alfalfa weevil larvae (Bennet, 1965). Beans (Phaseolus spp.) have been shown to contain feeding stimulants, phaseolunatim and lautaustrin, for the mexican bean beetle, Epilachna varivestris (Mulsant) (Klingenburg and Bucker, 1960). Sweet clover, Melilotus officinalis L., and other clovers contain coumarin, which acts as a feeding attractant for the vegetable weevil, Listroderes costrirustris (Klug) at low concentrations but as a deterrent in higher concentrations (Matsumoto, 1962).

Plants of the family Solanaceae contain alkaloids. The host specificity of insects that feed on these plants appears to be determined largely by the insects' ability to metabolize the alkaloids of the host species (Hegnauer, 1973, Kogan and Goeden, 1970, Screiber, 1958, Self et al., 1964, Yamamoto and Fraenkel, 1960). Solanum spp. also contain steroidal compounds, some of which are highly toxic to insects. In addition, some Solanum spp. contain feeding repellents and deterrents to the Colorado potato beetle, Leptinotarsa decemlineata (Say) (Bongers, 1970). Mamestra configurata fed and developed on Solanum tuberosum although survival was lower than on other food plants (Bailey, 1976). This insect (M. configurata) must have some tolerance for some of these toxic steroids and

alkaloids.

Variability in concentrations of secondary substances may influence the feeding activity and developmental success of the insect. Colorado potato beetle larvae were observed to feed more readily and to grow better when fed young potato foliage than when given older tissues; senescent foliage of either potato or tomato tended to retard growth (Bongers, 1970, Cibula et al., 1967). These effects may be partly nutritional and partly the reflection of developmental differences in tissue concentrations of deleterious substances. In another case, Feeny (1968), showed that larvae of the winter moth Operophtera brumata consumed oak leaves early in the growing season, but not later, apparently because of a high concentration of tannins in older leaves. These results indicate that synchronization is an important factor in insect-plant relationships. Other researchers have emphasized the importance of proper synchronization between insect and host phenology for the development of most phytophagous insects (Embree, 1965, Eidt and Little, 1968).

(c) Food digestion and conversion

A feeding insect not only must ingest the tissues of its host but also must be able to digest, assimilate and convert these tissues into the energy and structural substances required for insect development. Protease inhibitors have been reported in legumes and grains (Borchers et al., 1947, Vogel, 1968) and in solanaceous plants,

tomato and potato (Green and Ryan, 1972). However, insects that normally feed on these plants appear to have evolved mechanisms to overcome this barrier (Applebaum and Konijin, 1967, Applebaum, 1964).

Plant tissues have been shown to differ in the degree to which they can be assimilated and converted into insect tissues after digestion. For instance, the digestibility and convertibility of various plant species were investigated for the southern armyworm, Prodenia eridania (Soo Hoo and Fraenkel, 1966). The insect was studied on 18 different plant species representing 13 plant families. The larvae utilized 10 of the plants quite effectively, but the others supported suboptimal larval growth. Poor utilization was caused by low feeding rates, poor digestibility or inefficient conversion. The digestibility (AD), ([g ingested - g feces]/ g ingested) X 100, ranged from 76% to 36% in the poorest host tested. The efficiency of conversion of digested food to body tissue (ECD), (g gained/[g ingested - g feces] X 100), ranged from 16 to 56% on Phaseolus vulgaris, Taraxacum officinale, Solanum tuberosum and Phytolaca americana, all of which are good food plants.

In general, the ECD is highest for the insects best food plants. On good food plants, for example, the ECD is 63% for Bombyx mori on Morus alba (Hiratsuka, 1920); 55%, 52% and 64% for Protoparce sexta on tomato, Taraxacum spp. and Solunum dulcamaca respectively (Waldbauer, 1964) and 56% for Celerio euphorbiae on Euphorbia cyparissias (New, 1971). In all these cases, the high ECD's are a result of highly

nutritious food. These researchers have also suggested, on the basis of consumption indexes, that several conditions can make food less nutritious. Some plants with high digestibility are eaten in comparatively small amounts and most of the digested material is used for maintenance and not for growth. When ingestion is high and the digestibility low, utilization for growth is low unless the food plant is exceptionally nutritious. For a comprehensive review of methods and data on the subject of digestion and conversion, see Waldbauer (1968).

(d) Nutritional requirements

By current usage, nutritional requirements are defined as being the set of chemicals obtained from the ingested diet that are indispensable to the metabolic and developmental processes of the organism. It is generally accepted that the nutrient level and nutrient balance of a food plant will determine its adequacy to an insect. House (1969) found that for Celerio euphorbiae L., the amount of food eaten was inversely proportional to its nutrient balance. Altering the nutrient balance resulted in lower food consumption and reduction in efficiency of conversion from 20% on a normal balance to 9.5% on an imbalanced diet.

Plants vary in their content of nutrients. These variations are dependent on the plant part, developmental stage, physiological condition and plant genotype, and have been shown to influence both the behavior and the development of plant feeding insects. Auclair et al., (1957), Maltais and Auclair

(1962) found resistance of varieties of peas to the pea aphid, Acyrthosiphon pisum (Harris) to be correlated with the relative concentrations of amino acids and glucose. Atwal (1955) observed that the diamond back moth, Plutella xylostella L. developed metabolic and morphological abnormalities when the nutrient proportions in the leaves were changed. Other researchers (Blais, 1952, de Wilde et al., 1969) have reported differences in nutrient content of plant structures of different ages and their apparent effects on insect growth, survival and reproduction. Some researchers have even suggested that dietary proportions of required nutrients may be of greater importance than their absolute quantities (House, 1969, 1970, 1971, Maltais and Auclair, 1962, McGinnis and Kasting, 1961).

The concentrations of some elements and minerals have been shown to have direct or indirect effects on the feeding behavior and survival of insects. Fukuda et al. (1962) showed that Bombyx mori ate more mulberry leaves with 3.14% than with 2.67% nitrogen. Allen and Selman (1957), working with Pieris brassicae, reported that deficiency of nitrogen and iron in a food plant caused a reduction in the relative growth rate of larvae and increased larval mortality. Deficiency of nitrogen, phosphorus and potassium throughout larval life caused a reduction in larval weight while a shortage of iron delayed pupation.

Water, although not usually classified as a nutrient, may be an important factor to plant-feeding insects. Lepidopterous larvae, for example, generally maintain a body water content of 85-92% (Cf. Bursell, 1970, Evans, 1939,

Rudolfs, 1926, Wigglesworth, 1965) and can easily be desiccated. The water content of leaves, particularly in trees, may be substantially lower than that of insect bodies (Likens and Borman, 1970, McHurgue and Roy, 1932). The possible effects of plant tissue water content were considered by Waldbauer (1964), who attributed some of the differences in the digestibility and conversion of host plants of Manduca sexta to differences in their moisture content. Mellanby and French (1958) observed that larvae of Diataraxia oleracea L. grew normally on turgid cabbage leaves (85% moisture) but became seriously dehydrated if fed wilted cabbage (75% moisture). Scriber (1977) found that low leaf water affects larval growth of Hyalophora cecropia by limiting the nitrogen assimilation efficiency and nitrogen accumulation.

2. Effects of host plants on M. configurata.

The nutritional requirements of the bertha armyworm are unknown. However, quantitative studies by Bailey (1976) indicate that plants vary in the degree to which they support the survival, growth and development of this insect. He showed that survival to the pupal stage was 82% on rape (Brassica napus var. Zephyr), 76% on rape (B. campestris var. Span), 69% on lambsquarters (Chenopodium album L.) and 34% on potato (Solanum tuberosum L.). Except on potato, the mortality occurred at pupation. On potato, 67% of the mortality occurred early in the sixth instar, the remainder occurring at the time of pupation. The larval developmental time was significantly shorter on both varieties of rape

than on either lambsquarters or potato. Significantly less potato and lambsquarters foliage were consumed than the rape varieties. However, utilization for growth was highest on potato. The efficiency of conversion of ingested food to body tissue (ECI), ([g gained/g ingested] X 100) was lowest on lambsquarters (19%) and highest on rape (Zephyr) (23%). The ECI is influenced by the digestibility of the food, its nutritional value and the level of nutrient intake (Waldbauer, 1964). The coefficient of digestibility (ECD) ranged from 40% on lambsquarters to 49% on rape (Zephyr). The highECI and ECD on rape indicate that rape is highly nutritious. Bailey noted, however, that the mean digestibility (AD), ECI and ECD were similar for all food plants. Potato, a poor host was digested and utilized for tissue growth at the same rate as better host plants although the consumption of potato was lower. Poor survival of the bertha armyworm on potato may have been due to lower ingestion or to a nutritional deficiency in the plant.

CHAPTER III

MATERIALS AND METHODS

1. Insects, plants and artificial diet.

(a) Insect cultures

Eggs of M. configurata were obtained from the laboratory culture of the bertha armyworm which is maintained at the Agriculture Canada Research Station, Winnipeg, on an artificial diet (Bucher and Bracken, 1976). When possible the larvae used in each experiment came from egg plaques containing more than 100 eggs of which at least 90% were embryonated. This reduced variability among test larvae, which could have occurred if larvae from different parents had been selected. Occasionally, egg masses from different parents belonging to the same parental generation had to be used.

Newly laid eggs were incubated in plastic cups at 25°C with 16:8 hr photoperiod and 70% R.H. They were assessed for fertility after 24 hours and the undesirable plaques were discarded. Infertile eggs fail to develop a pattern of brown spots around the micropile and near the equator after 24 hours (Bucher and Bracken, 1976).

(b) Plant cultures

The plants used in the food tests are given in TABLE 1. The plants were grown from seed in flats (38 x 10 x 40 cm) or individually in pots (20 x 12 cm) in a greenhouse maintained at 25-27°C with 50% R.H. and 16:8 hr photoperiod. Garden soil, a mixture of soil, sand and peat, was used in all cases. Soon after germination, the plants were given a

TABLE 1. Plant families, species, varieties and common names of the plants fed to larvae of *M. configurata*.

Family	Species	Variety	Common Name
Polygonaceae	*Fagopyrum tataricum* L.	-	Buckwheat
Chenopodiaceae	*Beta vulgaris* L.	Early wonder	Sugar beet
	Amaranthus retroflexus L.	-	Red root pigweed
Cruciferae	*Brassica napus* L.	Zephyr	Rape
	B. oleracea L.	Pennstate ball head	Cabbage
	B. campestris L.	-	Summer turnip
	B. napus L.	American purple top	Rutabaga
	B. juncea L.	Lethbridge 22A	Oriental mustard
Leguminosae	*Phaseolus vulgaris* L.	Pencil pod black wax	Beans
	Melilotus officinalis L.	-	Sweet clover
	Medicago sativa L.	-	Alfalfa
Linaceae	*Linum usitatissimum* L.	-	Flax
Compositae	*Tagetis patula* L.	Glitters	Marigold

fertilizer, mainly Nitrogen, Phosphoric acid and soluble Potash in the ratio 18:6:9. The fertilizer also contained macro-elements Sulphur (10%), Calcium (3%) and actual iron (0.1%). The plants were watered daily, usually in the evening.

In all cases, except one, the leaves of plants were used when the plants were between 5-9 weeks old. (See section 3(b)). Only leaves with the appearance of vigour were used.

(c) Artificial diet.

The semi-defined artificial diet developed by Bucher and Bracken (1976) was used as a control in some experiments. Bailey (1976) showed that the survival of the bertha armyworm was higher on the diet than on rape leaves.

2. Preparation of food plants.

The plants were collected from the greenhouse each morning the insects had to be fed. Individual leaves were plucked from the middle third of plants with simple leaves, carefully avoiding senescent and immature leaves. Whole plants of species with compound leaves (sweet clover, alfalfa, flax and marigold) were cut off at soil level. The leaves and plants were put in plastic bags immediately after being cut. These were then refrigerated at 2-5°C to avoid wilting. The plants were refrigerated for a short period until they were used to feed the insect larvae.

Material for feeding larvae and for determination of the dry weight of leaves was prepared as follows. Leaf

sections, about 2.5 x 2.5 cm, were cut from either side of the midrib for species with simple leaves. Each sample consisted of only one section. For species with compound leaves, each sample consisted of the 4 basal leaflets. Only leaves in the middle third of the stems were selected. The wet weight of each sample was obtained immediately.

Each determination of percentage dry weight was based on 50 samples of leaf sections or groups of leaflets. The samples were oven dried at 70°C to a constant weight (after 24 h). Dry weights were then determined and expressed as a fraction of the wet weight. The mean dry weight for each plant species is given in Table 2.

In feeding experiments, the size of leaf sections or number of leaflets were increased as larval food consumption increased in the successive stages. In the last 2 stages of the 6 stadia, whole (simple) leaves, excluding midribs, were fed to larvae. For plants with compound leaves, the number of leaflets provided was increased from 4 leaflets in the first instar to 10-14 leaflets in the last 2 larval instars.

3. Rearing Techniques

(a) Methods and measurements

A single batch of eggs did not provide enough larvae for most experiments, so eggs from 2-3 different females belonging to the same generation were used. The possible effects of using eggs from different parents were minimized

TABLE 2. Proportion dry matter ($\bar{X}$ ± SD) of leaves of plant species tested as food for M. configurata. The mean proportion dry matter is based on 50 samples of leaf tissue.*

Plant	Dry matter
Sugar beet	0.0840 ± 0.0116
Mustard	0.0944 ± 0.0112
Rape (Exp. 1)	0.1027 ± 0.0093
Rape (Exp. 2)	0.1137 ± 0.0125
Rutabaga	0.1247 ± 0.0156
Cabbage	0.1289 ± 0.0723
Buckwheat	0.1489 ± 0.0093
Marigold	0.1632 ± 0.0198
Beans	0.1883 ± 0.0252
Sweet clover	0.1888 ± 0.0097
Flax	0.2196 ± 0.1229
Turnip	0.2244 ± 0.0578
Alfalfa	0.2463 ± 0.0165
Pigweed	0.2623 ± 0.0510

* The leaves of plants were taken 36 days after the cotyledonous stage except those from Rape (Exp. 2) and Turnip which were taken 43 days after that stage.

by mixing newly-hatched larvae from several egg batches in a single container, and then selecting larvae for the different treatments.

The cardboard caps of the plastic cups (4.0 x 3.5 cm) were untreated with wax or glaze and permitted water vapour and gas interchange with the atmosphere. Both the cups and caps are supplied commercially.

The initial weight of larvae was estimated by weighing groups of 10 newly hatched larvae. Using a sterilized paint brush (Number 0, 1 or 2), larvae were randomly picked from the "hatching" cup and placed into a pre-weighed plastic cup. Five groups of 10 larvae in each were weighed on a Sartorius electronic balance. The average weight was obtained by adding up the individual weights of each group and dividing by the total number of larvae for all the groups.

Thirty larvae were reared individually on each diet or food plant. The cups were labelled and put into a dessicator (9 l) or plastic container (5.4 l). Wilting of excised leaves was minimized by filling the containers with distilled water to a depth of about 3 cm. A perforated porcelain disc was placed about 10 cm above the water level in each container and plastic cups containing test larvae were placed upside down over the surface of the disc. Thin perforated plastic discs were placed beneath each layer of plastic cups.

The dessicators or plastic containers were placed in an incubator at 25 ± 0.1°C and 70 ± 5% RH with a 16:8 hr

photoperiod. The incubator has 4 vertical, 4 ft, 40W fluorescent lamps delivering about 200 ft c at the centre.

The artificial diet and plant foliage were changed daily. The fresh weight of the plant foliage provided to larvae and the fresh weight of larvae at the beginning of each feeding period were recorded. The artificial diet was not weighed. After each diet change, the leaf portions remaining from the previous feeding period were individually oven dried at 70°C for 24 hrs and then weighed.

The pre-pupae were placed in fresh cups containing vermiculite and transferred to an incubator maintained at 20°C with 70% RH and 16:8 hr photoperiod. This is a standard rearing procedure since pre-pupae and pupae exposed to 25°C produce adults with severely reduced levels of copulation and spermatophore transfer (Bucher and Bracken, 1976).

The pupae were sexed under low magnification. A daily record of emerging adults was kept for insects on each diet.

Developmental rate was measured by noting the number of days it took for each larva to complete each larval stage. The total developmental time included the period between hatching and emerging into adults.

Growth was measured by weight of the larvae immediately after molting, and survival by keeping daily mortality records. Mortality was also calculated on an instar basis.

Food consumption was estimated in dry weights. The dry weight equivalents of the leaf tissue provided at the beginning of each feeding period was calculated by multi-

plying the fresh weight of the tissue by the percentage dry matter for each species. The dry weight equivalent of food consumed was then obtained by subtracting the dry weight of the unconsumed food from the dry weight equivalent of the food at the beginning of the feeding period.

In addition to the experimental group, a small number of larvae were reared on the artificial diet. Although not weighed daily, the molting periods were recorded. Second instar larvae from these rearings were tested on flax and third instar larvae on buckwheat when insects on these food plants had all died.

(b) Individual experiments

Each experiment included only a few of the host plants investigated (Table 3). The control was the artificial diet in Experiments 1, 3 and 4 and rape (Brassica napus var. Zephyr) in Experiment 2.

The statistical analysis of data was done on the SR52 programmable (Texas Instruments) and the Hewlett Packard 100. The analyses included one way analysis of Variance (Anova) (Snedecor and Cochran, 1967), t. test, Duncan's multiple range test and regression coefficients.

TABLE 3. Food tested and methods used in the four experiments on the effects of various plants on the growth, development and survival of M. configurata.

Exp. No.	Food tested	Results
1	(i) Artificial diet (Control) (ii) Brassica napus var. Zephyr (iii) B. juncea var. Lethbridge 22A (iv) Linum usitatissimum L.	30 larvae on each food. 4 newly molted second instar larvae were transferred from the artificial diet to flax (iv) when all the larvae on this plant had died.
2	(i) B. napus var. Zephyr (Control) (ii) B. campestris L. (white turnip)	30 larvae on each food. Plants 6 to 10 weeks old.
3	(i) Artificial diet (Control) (ii) Fagopyrum tataricum L.	40 larvae on each food. 9 third instar larvae were transferred from the artificial diet to buckwheat (ii) when all the larvae had died on the foliage
4	(i) Artificial diet (Control) (ii) B. napus var. American purple top (iii) B. oleracea var. Pennstate ball head (iv) Ameranthus retroflexus L. (v) Beta vulgasis var. Early wonder (vi) Tagetis patula var. Glitters (vii) Medicago sativa L. (viii) Melilotus officinalis L. (ix) Phaseolus vulgaris var. Pencilpod black wax.	The 30 larvae tested on each food plant were initially reared in groups of 5 per cup. Larvae were separated as they molted so that by the third instar, all of the larvae were reared individually. Diets were changed daily up to the third instar and every 30 hours thereafter.

CHAPTER IV

RESULTS

Larval survival, food consumption, growth and the duration of development will be discussed individually for each experiment.

1. Experiment No. 1.

(a) Survival

Figure 1 is a graphical representation of percent larval survival against age in days. Mortality throughout larval development was lowest among larvae fed artificial diet (control). During the first four days, larvae on this diet incurred 17% mortality. Then, between days 6 and 22 (instars 2-6), mortality was only 5%. Larvae dying during the first 4 days either failed to feed or fed but failed to molt into the second instar.

TABLE 4 shows mortality on an instar basis. In the control group, the first instar incurred 23% mortality. The remaining mortality (5%) was observed in the fifth instar and in the pupal stage. Survival to the adult stage was 70% in the control group.

On the food plants, early instar mortality was highest among larvae fed flax and mustard foliage, reaching 100% and 83% respectively on the fourth day of feeding. On rape, mortality in the first 4 days was 28%, only slightly higher than in the control group.

On an instar basis (TABLE 4), mortality in the first

Figure 1. Percent survival of larvae of M. configurata with age in days on the artificial diet, Rape, Mustard and Flax. The survival curve of larvae on flax from day 4 is based on second-instar larvae transferred from the artificial diet to flax.

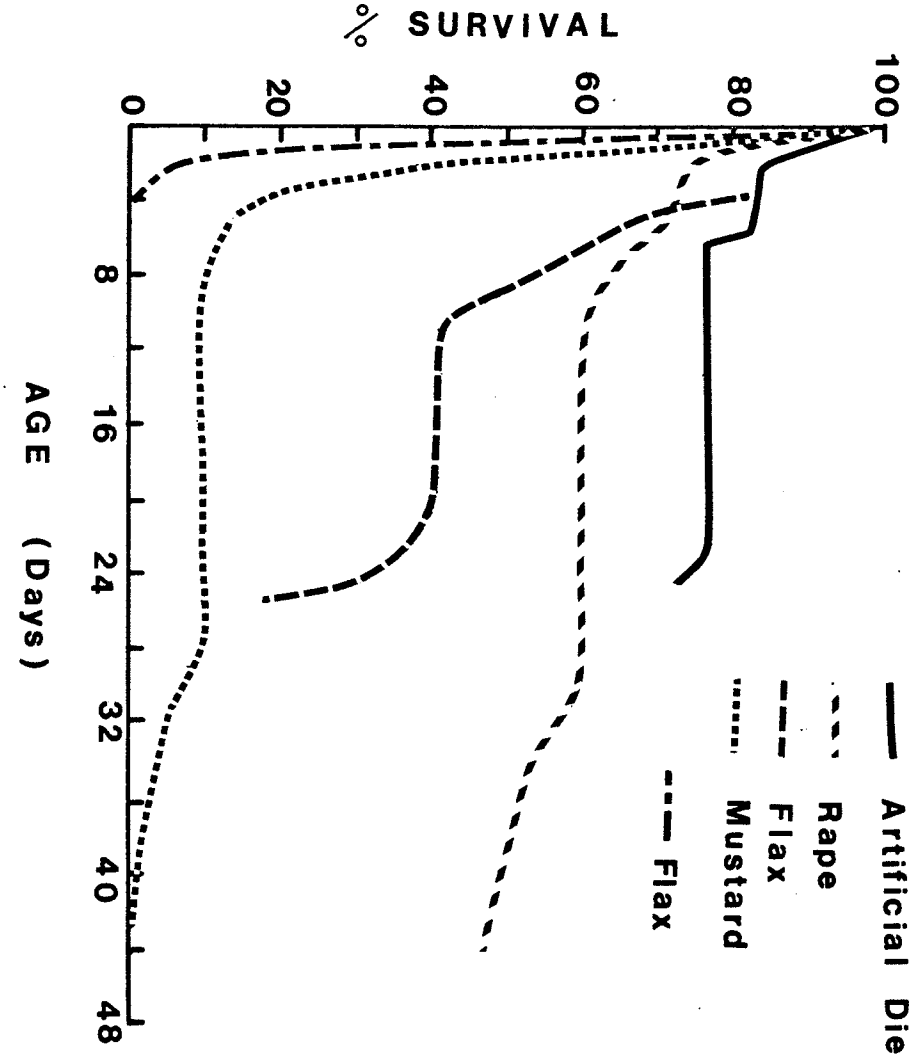

% SURVIVAL
0
20
40
60
80
100
8
16
24
32
40
48
AGE (Days)
Artificial Diet
Rape
Flax
Mustard
Flax

TABLE 4. Percent mortality of M. configurata based on the number of larvae surviving at the beginning of each stage on the various foods. The total mortality is based on the initial number of larvae (N) at the beginning of each test.

FOOD	N	STAGE							TOTAL
		I	II	III	IV	V	VI	PUPAE	
Exp. 1									
Artificial diet (control)	30	23.3	0	0	0	4.4	0	4.6	30
Rape	30	33.3	10.0	0	0	0	22.2	7.1	57
Mustard	30	86.7	0	0	25.0	66.7	100	-	100
Flax	30	94.1	100	-	-	-	-	-	100
Flax	4	-	75	0	0	0	0	100	100
Exp. 2.									
Rape (control)	30	23.3	13.0	5.0	0	0	36.8	0	60
Turnip	30	40.0	5.6	5.9	29.0	41.7	85.7	100	100
Exp. 3.									
Artificial diet	40	15.8	9.9	0	0	0	29.6	61.3	62
Buckwheat	40	97.5	100	-	-	-	-	-	100
Exp. 4.*									
Rutabaga	30	13.3	3.9	4.0	8.3	9.1	30.0	35.7	70
Cabbage	30	6.7	0	0	0	3.6	55.6	91.7	96.7
Marigold	30	6.7	0	0	3.6	7.4	64.0	44.4	83.3
Pigweed	30	3.3	0	3.5	7.1	0	65.4	100	100
Sugar beet	30	20.0	8.3	0	0	13.6	68.4	66.7	93.3
Alfalfa	30	3.3	0	0	13.8	32.0	100	-	100
Sweet clover	30	3.3	0	0	10.3	65.4	100	-	100
Beans	30	26.7	86.4	100	-	-	-	-	100

*Control not included

instar was 94% on flax, 86.7% on mustard and 33% on rape. Mortality between the second and fifth instars was low on rape and mustard. On flax no larvae survived past the second instar. Only one of the 4 larvae which were transferred from the artificial diet to flax in the second instar pupated and it died before emerging. In Figure 1, the graph of survival of larvae transferred to flax in the second instar is joined to that of larvae feeding on the artificial diet. The one pupa on flax represents 21% of the test larvae in this group when treated as a subsample of the siblings on the artificial diet. As an independent sample, it represents 25% pupation. Mortality in the fifth and sixth instar ranged from 22% on rape to 100% on mustard. The survival curves on rape and artificial diet are similar except that mortality of larvae on rape was higher on days 4 to 6 and after day 28.

Sixth instar mortality took three forms. In the first type, larvae failed to evacuate the gut contents. The feces became watery, the larvae eventually becoming soft and finally collapsing. Wylie and Bucher (1977) reported that this is caused by gut bacteria penetrating the body cavity. The second type consisted of larvae which had successfully evacuated their guts but failed to pupate. Such larvae either dried up or darkened without chitinization of the cuticle. This was common among larvae fed plant foliage. The third type consisted of failure to completely cast off the larval skin. This condition took a greater toll on foliage fed larvae than on artificial diet fed larvae.

Survival to the pupal stage ranged from zero on mustard

to 46% on rape. While survival to the pupal stage on food plants was better on rape than on flax or mustard, it was considerably lower than on the artificial diet (Fig. 1). Bailey (1976) also reported higher larval survival of the bertha armyworm on the artificial diet than on rape foliage.

Pupal mortality was mainly of two types, both previously described by Bucher and Bracken (1976). In the first type, called "syndrome", pupae showed a slight widening of the ventral surface of abdominal segment 4, often accompanied by abnormal thinness of the cuticle near the wing pads. When severe, the affected pupae shrivelled and dried within 7 days. Pupae with a mild form of syndrome formed normal adults. Syndrome was responsible for over 50% of the pupal mortality from artificial diet but only about 10% from plant foliage.

Morphological malformation, incomplete closure of the sutures between appendages, was the second cause of mortality among pupae. This was the largest single cause of mortality among the pupae from plant foliage.

In addition, a few pupae, although originally normal in appearance, shrank and died a few days following pupation. These pupae were generally smaller than others.

Overall survival to the adult stage was 70% on the artificial diet, 43% on rape and zero on mustard and flax.

(b) Larval food consumption

The amount of food (mean dry weight) consumed in each instar per larva varied considerably on the different foods

(TABLE 5). On rape, the amount of food consumed per larva ranged from 13 mg in the first instar to 3141 mg in the sixth instar. The latter instar accounted for 75% of the total food consumption (4190 mg) on this food plant. The final instar has been reported to consume more that 80% of the total food consumption (Bailey, 1976, Bailey and Singh, 1977). Females consumed more than males in most instars but the difference between sexes in mean total food consumption was not statistically significant ($P>0.2$)

Larvae feeding on flax and mustard consumed more foliage than did those on rape. In comparison to rape, first instar larvae consumed about 3x more mustard foliage. However, larvae fed mustard foliage showed greater variability in food consumption than those on rape. On flax, the first instar consumed about 17x more flax foliage than those fed rape foliage. On flax, the mean first-instar food consumption is based on the two larvae which successfully completed the first stage. None of these larvae developed beyond this stage. The remaining data on food consumption on flax are for the single larvae which pupated from the group transferred from the artificial diet.

In the second and third instars, mustard and flax were consumed in greater quantities than rape foliage and variability within instars remained higher on mustard. In the fourth and subsequent instars, mustard was consumed at a lower rate than either rape or flax while flax was consumed at significantly greater rates than the other two

TABLE 5. Mean dry weight (mg ± SD) of plant foliage consumed by M. configurata in each larval instar. Except where indicated, n = number of larvae which formed pupae [Exps. 1, 2, 4].

FOOD	n	SEX	AMOUNT OF FOOD CONSUMED I	II	III	IV	V	VI	TOTAL	
Exp. 1.										
	7	Males	13±5	57±19	71±26	261±155	577±231	2896±583	3869±622	
Rape	7	Females	14±8	55±28	141±35	347±267	588±177	3386±837	4510±786	
	14	Both	13±6	56±23	102±45	304±232	582±197	3141±738	4190±757	
Mustard *1	-	-	43±22 (4)	66±74 (4)	198±58 (4)	277±141 (3)	273 (1)	1999 (1)	2944	
Flax *2	1	Female	-	161	249	1075	2637	5383	9504	
Exp. 2.										
	5	Males	54±23	50±16	135±79	281±102	722±276	2216±500	3459±508	
Rape	7	Females	30±12	41±11	127±49	224±103	419±147	2898±879	3779±700	
	12	Both	40±21	45±13	130±50	247±102	545±253	2617±799	3646±623	
Turnip *3	7	Both	230±57	296±93	747±732	705±442	1296±236	3705±2085	6810±1851	
Exp. 4.										
Pigweed	9	Both	80±4	94±63	122±18	496±25	1571±451	4634±1645	6995±1514	a
Cabbage	12	Both	65±35	87±22	163±53	274±88	594±383	2715±644	4328±904	b
Sugar beet	6	Both	82±13	84±48	77±36	210±88	567±92	2807±591	3827±636	bc
Rutabaga	14	Both	49±21	40±18	70±26	230±264	580±187	2435±1029	3411±1153	c
Alfalfa *4	6	Both	67±12	61±62	179±10	391±74	938±414	1198±364	2855±737	cd
Marigold	8	Both	45±18	37±19	81±23	342±137	509±239	1387±634	2355±606	d
Sweet clover *4	4	Both	66±15	54±18	89±38	216±77	65±67	133±57	567±157	e

*1 n is indicated in parentheses. None pupated

*2 Started in second instar

*3 n is based on larvae which reached the pre-pupal stage

*4 100% mortality in sixth instar

NOTE: Any means with different letter in experiment 4 are significantly different ($P<0.05$).

food plants. The final instar (sixth) on mustard and flax accounted for 68% and 55% of the total food consumption (2944 mg and 9736 mg) respectively. In each case, only one larva survived to the sixth instar. On flax, the larva pupated but died before emergence. On mustard, the sixth instar larva successfully evacuated the gut but dried up without forming a pupa. There was no correlation between food consumption and survival.

(c) Larval and pupal weights

TABLE 6 shows the mean fresh weights of larvae after each molt and of day-old pupae. The mean fresh weight after hatching was estimated to be 0.8 mg for all samples.

In the early instars, differences in molting weight were not very great. On the artificial diet (control) and rape foliage, the molting weights were similar throughout most of the development period. However, individual variations within diets remained high. In the fifth instar, rape-fed larvae were 38 mg heavier than those on artificial diet. In the sixth instar, the artificial diet reared larvae were about 25 mg heavier at molting than those on rape. The mean molting weights of male larvae on the artificial diet were lower than that of females in all stages. On rape, females were lighter than males during the first 3 instars, but females were heavier than males in the later instars and in the pupal stage.

Pupae from the artificial diet reared insects were slightly heavier (3276 mg) than those from rape foliage

TABLE 6. Mean fresh weight (mg ± SD) of M. configurata larvae after each molt and of newly formed pupae on the various foods. Except where indicated, n = number of larvae which formed pupae [Exps. 1, 2].

FOOD	n	SEX	WEIGHT AT THE BEGINNING OF EACH STAGE I	II	III	IV	V	VI	PUPAE
Exp. 1.									
	11	Males	0.8	6.3±1.1	33.7±4.2	132.0±19.2	462.8±68.9	1785±295	3102±295
Artificial diet	11	Females	0.8	7.5±1.8	45.9±17.1	157.9±20.0	572.9±76.1	1935±210	3451±237
	22	Both	0.8	6.9±1.6	39.8±13.7	144.9±23.3	517.9±90.5	1859±182	3276±316
	7	Males	0.8	7.3±2.3	45.6±10.4	150.6±25.7	544.3±70.1	1808±94	2913±240
Rape	7	Females	0.8	7.1±1.7	36.1±6.2	155.9±22.2	567.1±25.5	1860±130	3218±317
	14	Both	0.8	7.2±1.9	40.9±9.6	153.2±23.2	555.7±52.0	1834±113	3065±314
Mustard *1	-	-	0.8	7.3±2.1 (4)	31.3±2.1 (4)	166.0 (1)	365.0 (1)	1267.0 (1)	-
Flax	1	Female	0.8	8.0	49.0	160.0	872.0	2640.0	2248.0
Exp. 2.									
	5	Males	0.8	6.4±1.7	43.8±10.9	142.6±36.2	791.8±144.8	1882±164	2110±496
Rape	7	Females	0.8	6.9±2.7	38.4±12.8	167.9±68.1	627.7±242.2	1896±128	2235±346
	12	Both	0.8	6.7±2.3	40.7±11.8	157.3±56.3	695.5±216.4	1890±137	2183±398
Turnip *2	(7)	Both	0.8	7.3±2.4	40.3±21.2	201.6±69.7	510.1±135.9	1371±228	1600(1)

*1 n is indicated in parentheses. None pupated.

*2 n is the number of larvae which entered the prepupal stage.

(3065 mg). The difference was not statistically significant ($P>0.1$). The mean weights of female pupae were significantly heavier than males on the artificial diet ($P<0.01$) and on rape ($P<0.05$).

On mustard and flax, the molting weights were different from those of insects reared on rape foliage and the artificial diet. The molting weights on mustard were lower and those on flax higher. However, those differences were low until the fifth instar when the weights ranged from 365 mg on mustard to 872 mg on flax. In the sixth instar, the weights ranged from 1267 mg for the larva fed mustard foliage to 2640 mg for the larva fed flax foliage. However, the ratio of lightest to heaviest larvae was about the same for all instars. The comparatively low molting weight in the final instar on mustard foliage may have been a result of low food intake during instars four to six (see TABLE 5). The greater molting weight of the larva fed flax foliage could have been a result of the prolonged development period leading to greater food consumption. However, the weight of the single pupa from flax fed larva, 2248 mg, was considerably lower than the mean pupal weights from both rape foliage and the artificial diet.

(d) Larval and pupal development

TABLE 8 shows the mean number of days spent in each of the larval instars and in the pupal stage. Larval development was fastest among larvae fed artificial diet. The first instars were of slightly longer duration than

TABLE 8. Mean number of days ($\bar{X}$ ± SD) in each larval instar and in the pupal stage of M. configurata on various foods. Except where indicated, n = number of larvae that emerged.

FOOD			Number of days in larval instar								
Exp. 1.	n	sex	I	II	III	IV	V	VI	TOTAL	Pupal	Total to Adult
Artificial diet	11	Males	3.4±0.5	3.2±0.8	2.6±0.7	2.9±0.7	2.7±0.7	10.6±1.0	25.4±1.6	25.5±2.0	50.8±2.3
	11	Females	3.8±0.8	2.7±0.7	2.3±0.5	2.7±0.8	2.5±0.5	10.6±1.0	24.6±1.2	25.1±1.5	49.7±1.5
	22	Mean	3.5±0.7	2.9±0.7	2.4±0.6	2.8±0.7	2.6±0.6	10.6±1.0	25.0±1.5	25.3±1.7	50.3±2.1
Rape	7	Males	4.3±0.5	3.3±0.8	3.6±0.5	2.9±0.7	2.7±0.8	9.4±1.3	26.1±1.4	24.9±2.4	51.0±3.4
	7	Females	4.2±0.8	3.6±1.0	3.3±0.8	2.6±0.5	2.7±0.8	10.6±1.1	27.4±1.7	25.3±1.6	52.8±2.3
	14	Mean	4.5±0.7	3.4±0.9	3.4±0.7	2.7±0.6	2.7±0.7	10.0±1.3	26.8±1.6	25.1±2.0	51.9±3.0
Mustard *1	-	-	7.0±2.7 (4)	8.3±4.0 (4)	5.3±1.6 (4)	5.0±2.8 (3)	6.0±(1)	14.0 (1)	40.0 (1)	-	
Flax	1	Female	10.0	6.0	5.0	5.0	3.0	13.0	42.0	-	
Exp. 2.											
Rape	5	Males	5.0±0.7	4.2±1.1	2.8±1.1	2.4±0.6	2.4±0.6	9.8±1.8	26.8±1.3	25.6±3.1	52.4±2.1
	7	Females	4.9±0.4	3.4±1.5	3.0±0.6	2.4±0.5	2.6±0.5	10.0±1.4	26.1±0.4	25.1±2.1	51.4±2.3
	12	Mean	4.9±0.5	3.8±1.4	2.9±0.8	2.4±0.5	2.5±0.5	9.9±1.5	26.4±0.9	25.3±2.5	51.8±2.2
Turnip *2	7		5.6±1.1	4.7±1.3	6.1±2.8	5.1±3.0	7.0±1.0	13.9±5.4	42.4±5.8	-	

*1 n is indicated in parentheses for each developmental stage. None pupated.

*2 Only one pupated and died before emerging.

the second to fifth instars. The sixth instar required about 43% of the total developmental period. The total larval developmental time, on the artificial diet, averaged 25 days. Pupal development also required 25 days, adding up to 50 days to emergence to the adult stage.

On rape, larval development was similar but slower than on the artificial diet. This difference in development time occurred during the first three instars. The mean larval development time on rape was 26 days, significantly longer than that on the artificial diet ($P<0.01$). Between the sexes, females developed slightly faster (26.6 days) than males (25.4 days) on the artificial diet whereas on rape males developed slightly faster (26.1 days) than females (27.4 days). These differences were not significant. The non significance may be due to the small sample size.

The mean pupal development time was 25 days for insects reared on both artificial diet and rape. Variability in development time was slightly greater for insects reared on rape. The mean total development time did not differ significantly between insects reared on rape and the artificial diet ($P>0.1$). The differences between sexes on either diet were not significant.

On mustard and flax, larval development was significantly slower than on rape or artificial diet. Throughout the successive stages, larvae on mustard and flax took longer to develop, with the lone survivor on each diet requiring

40 and 42 days to complete larval development. These periods are considerably longer than the 25 days on artificial diet or rape. On all diets, development was most rapid between the third and fifth instars.

2. Experiment No. 2.

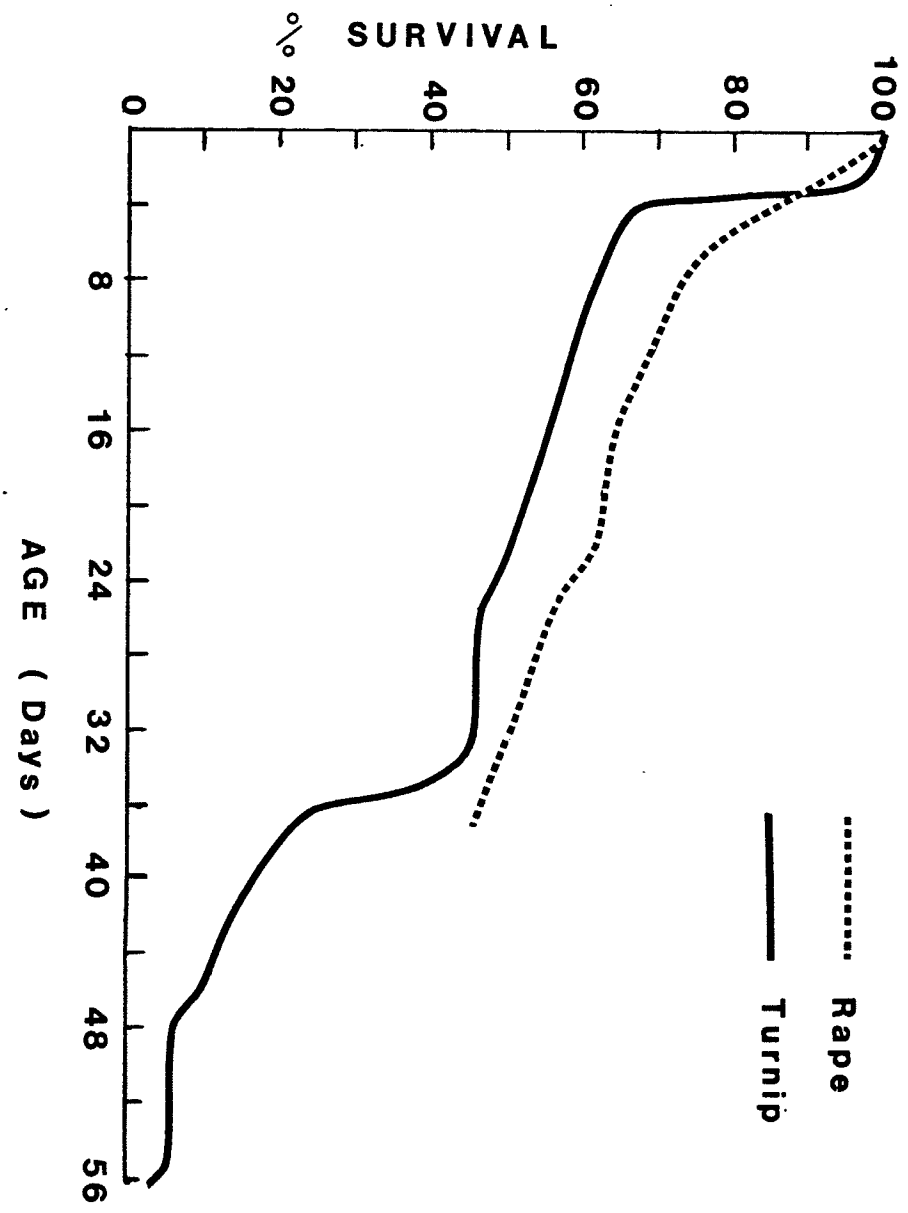
(a) Survival

Figure 2 shows percent larval survival with age in days. Larval survival was highest among larvae fed rape foliage (control). On this food plant, larvae incurred over 14% mortality during the first four days of feeding. This was considerably less than the 28% observed on the same food plant in the first experiment. Mortality occurred at a fairly constant rate throughout the larval development period. At the end of the feeding period, larval survival (45%) did not differ significantly from that in the first experiment (46%) where no mortality occurred between days 9 and 28.

The percent mortality of larvae during the first instar was lower on rape in the second experiment (23%) than on the same food plant in the first experiment (33%) (TABLE 4). However, the percent mortality in the second, third and sixth instars was greater in the second experiment than in the first. Of the larvae that reached the sixth instar, 36.8% died, representing about 40% of the total mortality on this food plant. Forty percent survived to both the pupal and adult stage. No pupal mortality was observed on rape in this experiment, the first experiment incurred 7% pupal mortality. Survival to the adult stage was slightly lower (40%) in this experiment than in the first (43%).

On turnip, 34% of the larvae had died by the fourth

Figure 2. Percent survival of larvae of M. configurata with age in days on Rape and Turnip.



day compared to only 14% on rape (Fig. 2). During the next 20 days, survival declined linearly, then remained at 46% between days 25-32. Survival then declined sharply to 23% on day 36 and more slowly to 3% on day 56. These larvae fed for a considerably longer period on turnip than did those on rape.

The percent mortality of larvae, based on numbers surviving at the beginning of each instar, was greater on turnip than on rape for all instars except the second (TABLE 4). In the first instar alone, larvae on turnip incurred 40% mortality compared to 23% on rape. As in the first experiment, most of the larvae that died in this stage did not feed. A smaller proportion fed little, remaining in the first instar long after their siblings had molted, but died before molting. Mortality was lower than on rape in the second instar but increased through instars 4-6. Eighty six percent of those that reached the final instar died without reaching the pre-pupal stage.

On turnip, only one larva (3%) successfully pupated. The pupa (female) was normal in appearance but died before emerging. On rape, all the larvae that survived the sixth instar successfully pupated and emerged.

(b) Larval Food Consumption

Food consumption (mg dry weight) per larva on rape ranged from 40 mg in the first instar to 2617 mg in the sixth instar (TABLE 5). The latter instar accounted for about 72% of the total (3646 mg) food consumption. First

instar larvae consumed about 3X more rape in this experiment than in the first. However, the total food consumption in this experiment was slightly but not significantly less ($P>0.1$). Males tended to consume more than females in all except the final instar, when females consumed considerably more (2898 mg) than males (2216 mg). However, individual variations in food consumption were high in both sexes so the slightly higher total food consumption of the females was not significantly different from that of the males ($P>0.5$).

The larvae on turnip consumed consistently more foliage in all stages than those on rape. The total consumption differed significantly ($P<0.001$). The final instar consumed 55% of the total food consumption. Variability in food consumption within instars was higher on turnip than on rape.

(c) Larval and pupal weights

On rape, the mean molting weights ranged from 6.7 mg to 1890 mg (TABLE 6). The molting weights were similar to those of larvae fed rape in the first experiment. During the larval instars, neither male nor female molting weights were constantly higher. Female pupae were slightly but not significantly heavier than males ($P>0.5$). The pupal weights in this experiment were significantly lower than those on rape in the first experiment ($P<0.001$).

On turnip, the molting weights of the first four instars were similar to those of larvae fed rape foliage

(TABLE 6). The last two instars on turnip were much lighter than those on rape. For instance, larval weight gain in the fifth instar was significantly greater on rape (1185 mg) than on turnip (861 mg) ($P<0.01$).

Only one larva pupated on turnip, with an initial weight of 1600 mg, which was very low compared to mean pupal weights for larvae fed rape foliage (2183 mg).

(d) Larval and pupal development

On rape (control) larval development was rapid. Slightly longer periods were needed to complete the first, second and sixth instars than the other instars (TABLE 8). The mean larval development time (26.4 days) was slightly longer than the mean pupal development time (25.3 days). The larval development time was very similar to that of larvae on rape in the first experiment. However, in contrast to the first experiment, females developed slightly faster than males. The total development time was 51.8 days; in the first experiment it was 51.9 days.

On turnip, larval development was significantly slower than on rape. For instance, the mean development time to the fifth instar* was significantly longer on turnip (28.6 ± 6.7 days) than on rape (16.5 ± 1.3 days) ($P<0.001$). On turnip there was not any significant difference between instars in the developmental time. The single pupa on

---

*The test could only be carried out for 5th instars owing to smaller numbers reaching the 6th instar on turnip.

turnip died without emerging into adult.

3. Experiment No. 3.

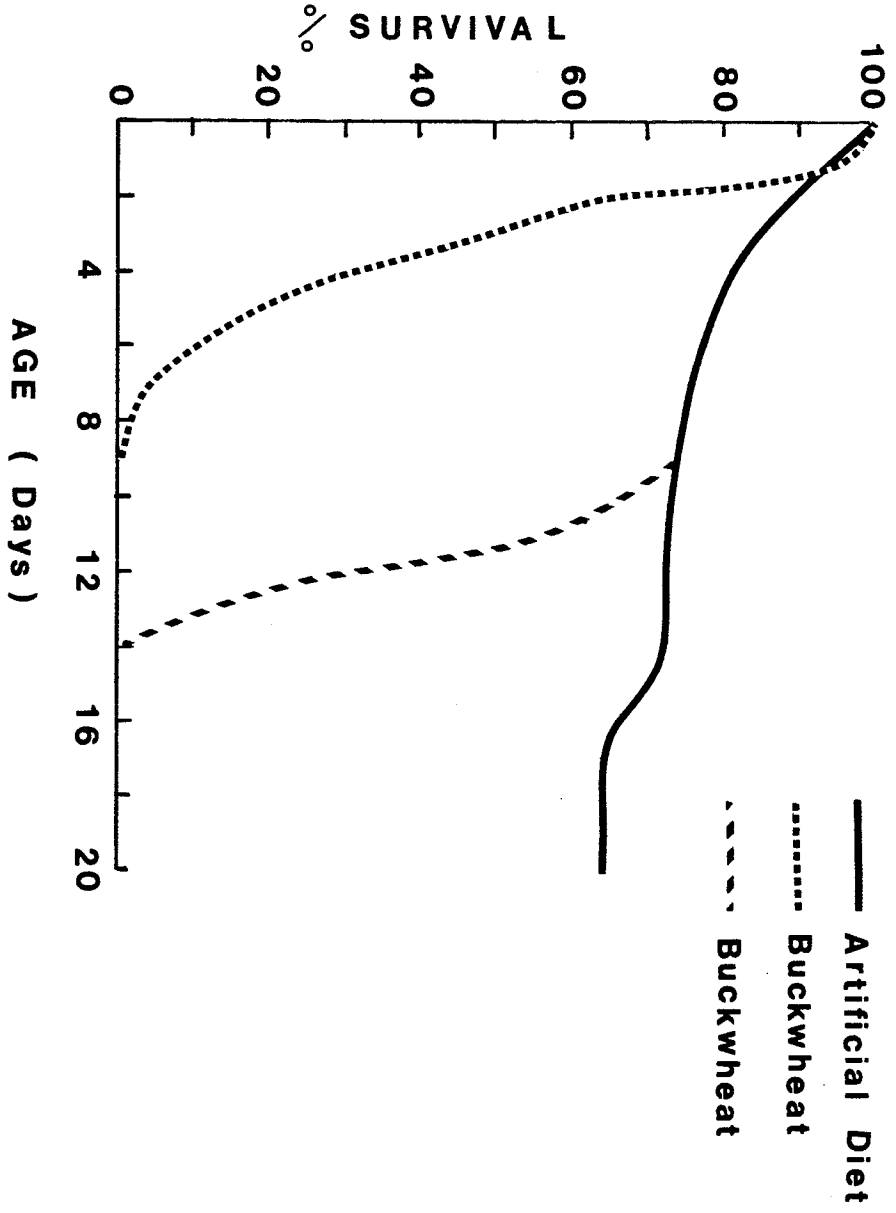
(a) Survival

Figure 3 shows percent survival of larvae with age in days on the artificial diet (control) and on buckwheat foliage. Survival throughout larval development was best among larvae fed artificial diet. On the artificial diet, the survival curve declined steadily to 72% on day 14. There was 7% mortality between days 14 and 16, then little mortality till pupation on day 20.

On an instar basis (TABLE 4), larvae in the first and second instars incurred 26% mortality. There was no mortality between the third and fifth instars, but 29.6% of the larvae which entered the sixth instar died before reaching the pupal stage. In all, 64% of the larvae entered the pupal stage. However, 61% of the pupae died, 21% of which had syndrome. Survival to emergence was 38.7%, which was slightly lower than that observed on rape in both the first (43%) and the second (40%) experiments.

The survival curves of larvae fed artificial diet in the first experiment and the present one appear to be different. In the first experiment, larval mortality was concentrated between days 1-2, 5-6 and 22-24 (Fig. 1). In the present experiment, larval mortality was more evenly spread out than in the former. However, on an instar basis, the difference was not great. Mortality during the first two instars differed by less than 3%. The real difference appears in the sixth instar and the pupal stage when

Figure 3. Percent survival of larvae of M. configurata with age in days on the artificial diet and Buckwheat. The survival curve of larvae of Buckwheat from day 9 is based on third-instar larvae transferred from the artificial diet to Buckwheat.


% SURVIVAL
0
20
40
60
80
100
4
8
12
16
20
AGE (Days)
Artificial Diet
Buckwheat
Buckwheat

mortality was higher in the present experiment than in the first. Survival to the adult stage was much lower in the present experiment (38%) than in the first (70%).

On buckwheat, larval survival was very poor compared to those in the control group. On the second day, larval survival had decreased to 62% on buckwheat compared to 89% on the artificial diet. Most of the larvae had fed briefly on the buckwheat foliage but only a few continued to feed. On the ninth day, mortality on buckwheat reached 100% compared to only 26% on the artificial diet. On buckwheat, 97% of the mortality occurred in the first instar (TABLE 4). The remainder died in the second instar.

Among larvae transferred in the third instar from the artificial diet to buckwheat, 67% died within 4 days. The remainder molted to the fourth stage but died soon after.

(b) Larval food consumption

The larvae which survived to the second instar on buckwheat consumed a mean dry weight of 95 mg in the first instar. The second group of larvae, transferred from the artificial diet at the beginning of the third instar, consumed a mean of 123 mg before molting to the fourth stage.

(c) Larval and pupal weights

On the artificial diet, the molting weights ranged from 6.6 mg in the first instar to 1895 mg. in the sixth instar. Individual variation within instars was great.

In the pupal stage, females weighed significantly more (3907 mg) than males (3227 mg) ($P<0.01$).

In the first experiment, insects reared on the artificial diet were slightly heavier at molting during the first three instars than those in the present experiment. For the remainder of the growing period, insects in the present experiment were heavier. The difference in pupal weights was statistically significant ($P<0.01$) On buckwheat, the few larvae that reached instar 2 had a mean molting weight of 7.5 mg. These fed little and died before reaching the third instar.

(d) Larval and pupal development

On the artificial diet, larvae required mean development times of 20.5 and 19.6 days to complete the larval and pupal stages respectively. Females developed slightly but not significantly faster than males. These mean development times are significantly shorter than those observed on the same diet in the first experiment ($P<0.001$). The reason is that in the present experiment, both the larval and pupal stages were reared at 25°C whereas in the first experiment, the pre-pupal and pupal stages were reared at 20°C (See Methods). The rate of development of M. configurata has been shown to increase with temperature (Bailey, 1976).

On buckwheat, first instar larvae took longer (7.7 days) to develop than their counterparts on the artificial diet (3.2 days). Furthermore, none developed beyond the second instar. The second group of larvae on buckwheat

required a mean of 4 days to complete the third instar. These larvae did not progress beyond the fourth instar.

4. Experiment No. 4.

The results of the control group, insects fed artificial diet, were not included in this experiment because the diet was too liquid and more than 80% of the larvae died in the first instar. Larval drowning occurs when there has been an error in the fabrication of the artificial diet (Bucher and Bracken, 1976). However, the low level of mortality in the first instar that was observed among larvae fed plant foliage (TABLE 4) indicates that these larvae were as vigorous as those used in previous experiments. Consequently, rutabaga was selected to serve as a model since survival to the adult stage was highest on this food plant.

(a) Survival

Figures 4 and 5 show the percent survival with age of larvae on various test plants. On rutabaga, survival was 90% on day 2 and then declined gradually until day 21 when it reached 76%. Larval mortality increased dramatically between days 21-23 when 13% of the larvae died. From then on until day 40, mortality was only about 10%. Survival declined sharply from this day until day 42 when it reached 46%. On an instar basis (TABLE 4), mortality was highest in the first and sixth instars. Thirty percent of the larvae which entered the latter instar died without pupating. Mortality was even higher in the pupal stage, where about 36% died. Survival to the adult stage was 30%.

On sweet clover, cabbage, marigold, alfalfa and pigweed, larval survival was higher than that on rutabaga for at least 18 days (Figs. 4, 5). On these food plants, larval

Figure 4. Percent survival of larvae of M. configurata with age in days on Rutabaga, Pigweed, Marigold, Cabbage and Sugar beet.

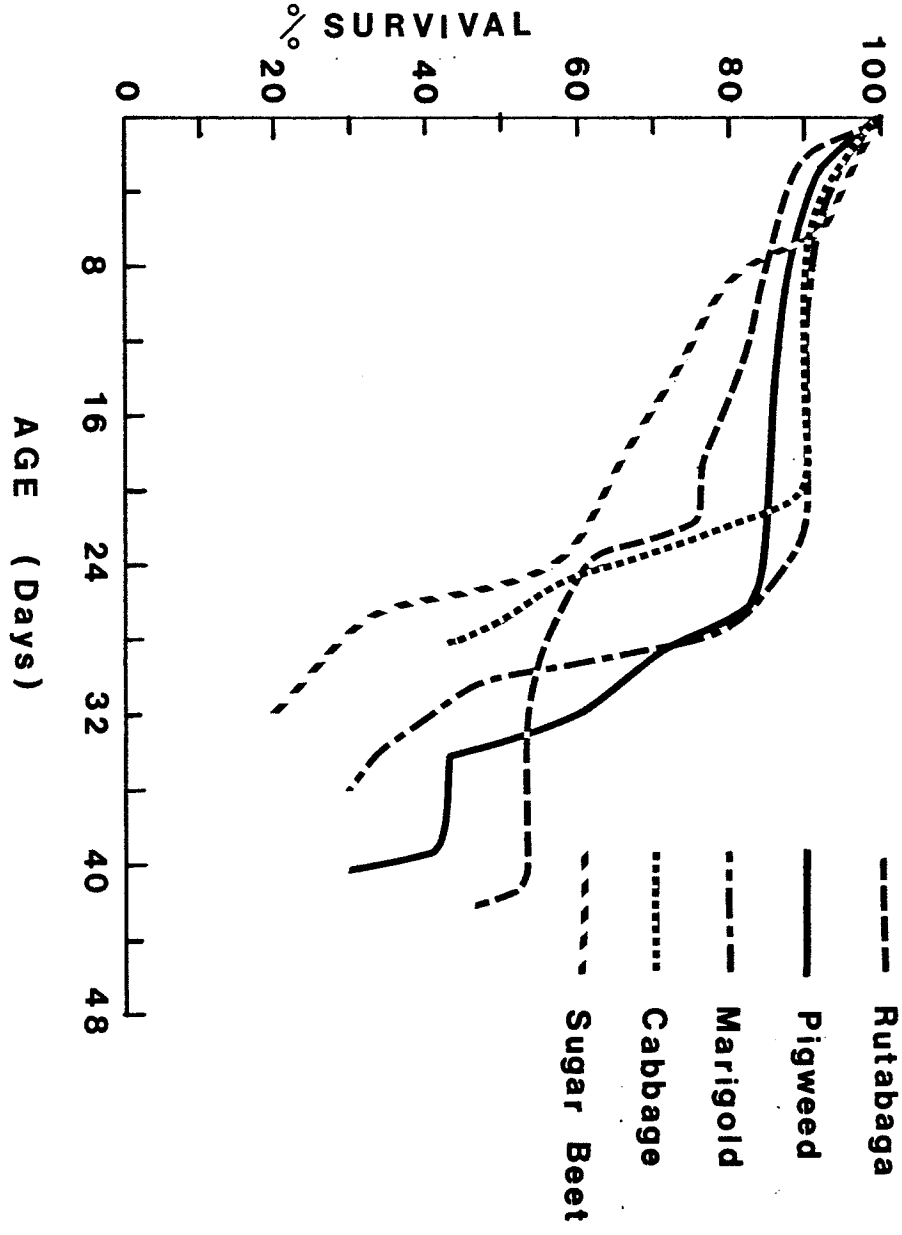
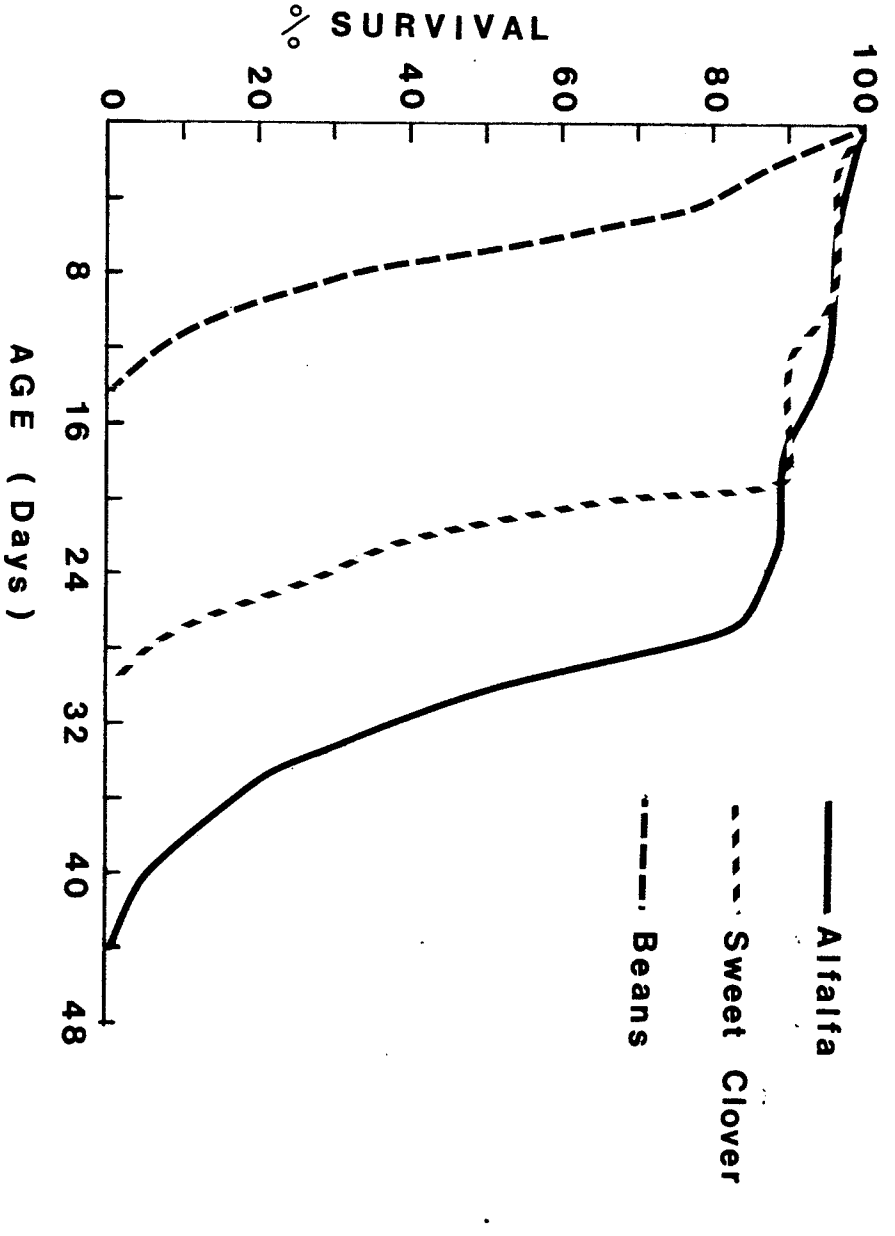

% SURVIVAL
0
20
40
60
80
100
8
16
24
32
40
48
AGE (Days)
Rutabaga
Pigweed
Marigold
Cabbage
Sugar Beet

Figure 5. Percent survival of larvae of M. configurata with age in days on Alfalfa, Sweet clover and Beans.


% SURVIVAL
0
20
40
60
80
100
8
16
24
32
40
48
AGE (Days)
Alfalfa
Sweet Clover
Beans

survival was 85-90% on day 18 compared to 76% on rutabaga. However, the pattern quickly reversed after day 18. On sweet clover, mortality increased sharply between days 19-22 when 46% of the larvae died. Survival reached zero on day 30. On cabbage, mortality increased sharply from day 20 onwards, exceeding that on rutabaga on day 24. On day 28, survival was significantly less than that on rutabaga. On marigold, survival declined rather sharply from 90% on day 22 to 46% on day 30 and then steadily to 30% on day 36. On alfalfa, survival declined sharply from 85% on day 26 to 4% on day 40 and then gradually to zero on day 44. On pigweed, larval survival remained higher than that on rutabaga until day 33. Only 30% of the larvae on pigweed survived to day 40.

On sugar beet, larval survival was initially higher than that on rutabaga. Mortality increased gradually from day 8 until day 24. Then survival declined sharply and reached 20% on day 32. On beans, larval mortality was severe from the onset of the feeding period and reached 100% on day 14.

On an instar basis (TABLE 4) mortality in the first instar ranged from 3% on alfalfa and sweet clover to 26% on bean foliage. On most food plants, mortality was either zero or very low between the second and fourth instar. However, on beans, 86% died in the second instar and the remainder in the third instar. On the other food plants, fourth instar larval mortality ranged from zero on cabbage and sugar beet to 13.8% on alfalfa. Larval mortality

increased through the fifth instar on most food plants, and in the sixth instar it reached 100% on alfalfa and sweet clover. The combined mortality in the fifth and sixth instar on alfalfa and sweet clover accounted for 83 and 87% of the total mortality respectively. On rutabaga, sixth instar mortality accounted for only 38% of the total larval mortality. On cabbage, pigweed and marigold, sixth instar mortality accounted for 83, 81 and 76% of the total mortality in the larval stage. On sugar beet, the final instar accounted for about 54% of the total larval mortality. Mortality in the final instar resulted mainly from failure to empty the gut or to cast off the larval skin, as described previously (p. 30).

Survival to the pupal stage was highest among larvae fed rutabaga foliage (46%). On cabbage, 40% survived to the pupal stage. On marigold and pigweed, 30% survived to the pupal stage. None pupated on beans, alfalfa and sweet clover. The main cause of pupal mortality was a morphological malformation of pupae. Some syndrome was observed. These conditions are described on p. 31. However, most of the pupae on cabbage, pigweed, marigold and sugar beet had no obvious malformations but failed to emerge.

Survival to the adult stage ranged from zero on beans, sweet clover, alfalfa and pigweed to 30% on rutabaga. There was 3.3, 6.7 and 16.7% survival on cabbage, sugar beet and marigold respectively. The adults from larvae fed marigold foliage were about two thirds the size of the emerging adults from other food plants.

(b) Larval food consumption

The amount of food consumed by the larvae varied among food plants and instars (TABLE 5). Individual variability within each instar was high. On rutabaga, larval food consumption ranged from 40 mg (mean dry weight) in the second instar to 2435 mg in the sixth instar. The latter consumed about 71% of the total food consumption.

On other food plants, the amounts of food consumed in the first three instars differed only slightly from that observed on rutabaga. Pigweed was consumed in greater quantities than the other food plants. The differences in food consumption increased through the fourth instar to the sixth instar when less of alfalfa and sweet clover were consumed. On sweet clover and alfalfa, the sixth instar consumed about 23 and 42% of the total food consumption respectively. These values are much lower than those reported on other food plants for the same instar. On other food plants, food consumption in the sixth instar ranged from 1387 mg on marigold to 4634 mg on pigweed. On rutabaga and sugar beet, the final instar consumed about 71 and 73% respectively, of the total food consumption. On marigold, cabbage and pigweed, the final instar consumed about 59, 63 and 66% of the total food comsumption respectively.

The total food consumption ranged from 567 mg on sweet clover to 6995 mg on pigweed. The differences in means were statistically significant ($P<0.05$). The amount consumed on pigweed was significantly greater than those on other

food plants. The amounts consumed on cabbage (4328 mg) and sugar beet (3827 mg) were not significantly different from each other but that on cabbage was significantly different from the others. The amounts consumed on sugar beet, rutabaga (3411 mg) and alfalfa (2855 mg) were not significantly different from each other but were significantly less than the amounts consumed on pigweed and cabbage; and significantly more than those on marigold (2355 mg) and sweet clover. The amounts consumed on alfalfa and marigold were not significantly different from each other. The amount consumed on sweet clover was significantly lower than those on other food plants. Among the food plants which supported larval development to the pupal stage, marigold was consumed in the smallest amount.

(c) Larval and pupal weights

The molting weights varied within and between instars on the various food plants (TABLE 7). On rutabaga, the molting weights increased from 7.4 mg in the second instar to 1699 mg in the sixth instar. On other food plants, second instar molting weights ranged from 6.8 mg on alfalfa to 13.3 mg on pigweed. Except on alfalfa, all the molting weights in this instar were greater than on rutabaga. In the third instar, the molting weights ranged from 23 mg on alfalfa to 76 mg on cabbage. Larvae on rutabaga had the second lowest molting weights after those on alfalfa. Fourth instar molting weights ranged from 121 mg on sweet

TABLE 7. Mean fresh weight (mg ± SD) of M. configurata larvae after each molt and of newly formed pupae on various food plants. Except where indicated, n = number of larvae which formed pupae. The significance test (ANOVA) is based on male pupal weights only (Exp. 4).

Food	Weight after each molt in instar						Sex	(n)	Initial pupal weight*	mean
	I	II	III	IV	V	VI				
Rutabaga	0.8	7.4±1.5	44.2±14.7	130.3±25	451.8±128	1699.3±189	Males	6	2182±321a	2298±361
							Females	8	2386±384	
Cabbage	0.8	11.4±3.4	76.5±19.7	273.9±67.2	728.3±113	1495.7±167	Males	8	1833±349a	1781±302
							Females	4	1679±177	
Pigweed	0.8	13.3±3.3	54.3±7.8	132.8±4.9	583.4±62	1779.3±252	Males	5	1770±337a	1729±305
							Females	4	1679±302	
Sugar beet	0.8	9.8±3.2	48.3±26.5	165.4±61.1	583.4±85	1768±242	Males	5	1670±262ab	1621±263
							Females	1	1376	
Marigold	0.8	12.4±8.6	51.9±22.6	156.4±34.1	655.4±187	1540.4±307	Males	5	1218±155b	1269±152
							Females	3	1354±125	
Alfalfa o	0.8	6.8±1.0	23.3±8.7	152.8±21.2	533±65	1347.3±364	-	(17)	-	-
Sweet clover o	0.8	9.3±3.5	45.0±15.6	120.7±119.5	478.0±42.1	470.2±48.7	-	(9)	-	-

* Means with different letters are significantly different ($P<0.01$)

o Non pupated.

clover to 274 mg on cabbage. Again, larvae fed rutabaga foliage had the second lowest molting weights. In the fifth instar, the molting weights ranged from 452 mg on rutabaga to 728 mg on cabbage. However, other than on cabbage, most of the molting weights were in the 500 mg region. In the sixth instar, larvae on sweet clover molted at 470 mg which was lower than the molting weight in the previous instar. Fifth instar food consumption on sweet clover was extremely low compared to that on other food plants (TABLE 5). On other food plants, sixth instar molting weights ranged from 1347 mg on alfalfa to 1779 mg on pigweed.

The mean pupal weights ranged from 1269 mg on marigold to 2298 mg on rutabaga. On all food plants except rutabaga and marigold, male pupae weighed slightly more than females. However, Bucher and Bracken (1976) reported that, on average, females weighed more than males. In the present study, the number of females on different foods was more variable than the number of males. Therefore, to test for significant differences between pupal weights on the different foods, only male pupal weights were used. The mean male pupal weights were significantly different ($P<0.01$) (TABLE 7). The mean male pupal weights for larvae reared on rutabaga, cabbage, pigweed and sugar beet were not significantly different from each other although the mean pupal weights on rutabaga were slightly higher. The mean pupal weights for insects reared on rutabaga were similar to those on rape in the second experiment (cf. TABLE 6). The mean male

pupal weights for larvae reared on sugar beet and marigold were not significantly different from each other but those on marigold were significantly lower than the mean male pupal weights on rutabaga, cabbage and pigweed.

(d) Larval and pupal development

On rutabaga, the mean larval and pupal development times were 24.6 and 25.3 days respectively (TABLE 9). These developmental times were very similar to those observed on the artificial diet in the first experiment and on rape in the first and second experiments (cf. TABLE 8). The mean larval development times on rutabaga, cabbage (21.8 days) and sugar beet (24.7 days) were not significantly different from each other but were significantly shorter than on pigweed (31.0 days) ($P<0.01$). The mean larval development time on cabbage was significantly different from those on marigold and pigweed. On marigold, the mean larval development time (25.4 days) was significantly shorter than on pigweed and significantly longer than on cabbage but not significantly different from sugar beet or rutabaga.

The mean pupal development times were not significantly different among larvae reared on various food plants (P 0.25) although development was slightly faster on marigold. Complete development time to emergence varied from 46.6 days on marigold to 50 days for the single adult on cabbage. While larval development was shortest on cabbage and increased through rutabaga, sugar beet and marigold, pupal development required shorter time in the reverse order.

TABLE 9. Mean number of days ($\bar{X}$ ± SD) in each larval instar and pupal stage and the total number of days taken to complete development of M. configurata on various food plants. The data for each developmental stage are based on the number of larvae in parentheses (Exp. 4).

	FOOD*	Pigweed	Marigold	Sugar beet	Rutabaga	Cabbage
1.	Total number of days in larval instars	31.0±1.9^{a} (9)	25.4±1.5^{b} (8)	24.7±2.3^{bc} (6)	24.6±3.4^{bc} (14)	21.8±2.1^{c} (12)
2.	Total number of days in pupal stage	-	21.8±0.8^{d} (5)	24.0±1.4^{d} (2)	25.3±4.6^{d} (9)	23.0^{d} (1)
3.	Total number of days to adult stage	-	46.6±1.1^{e} (5)	49.0±1.4^{e} (2)	49.6±6.9^{e} (9)	50.0^{e} (1)

*Food plants on which no pupation occurred were excluded from this table.

CHAPTER V

DISCUSSION

In this section, the results of the four experiments will be discussed under headings "Survival", and "Growth and Development". The first includes mortality in both the larval and pupal stages while the second includes food consumption and its relationships with larval growth and development.

(a) Survival

Mortality of first instar larvae was high on most test plants and the control foods, the artificial diet and rape foliage. The larvae which died either failed to feed or fed a little but did not molt. Mortality from these causes has been estimated to account for about 5 ± 5% of the total mortality or even higher depending on the vigour of the embryoes (Bucher and Bracken, 1976). The variations in first instar mortality between the control groups (16 to 23%) (TABLE 4) may be due to the genetic effects of inbreeding and/or small sample size. On rape foliage, the difference in leaf age between experiment 1 and 2 may have been an added factor.

On the control foods, artificial diet and rape leaves, larval mortality through the second instar ranged from 25-40% (Figs. 1-3). The mortality on turnip and sugar beet was similar to the controls (Figs. 2, 4). On rutabaga, cabbage, marigold, alfalfa, sweet clover and pigweed, larval mortal-

ity through the second instar was much lower than on the controls (Figs. 4, 5). On buckwheat, flax, mustard and bean foliage, mortality exceeded 85% by the second instar (Figs. 1, 3, 5). The high mortality on these food plants cannot be accounted for by any possible parental effect because larvae fed other foliage in the same experiments showed normal survival. This high mortality may be caused by toxic or repellent substances in the foliage or by its physical characteristics. Dethier et al. (1960) have suggested that some plants may contain substances which deter sustained feeding in addition to those having a toxic effect. Shaver (1974) suggested that high mortality can be caused also be metabolic inhibitors in plants or by insufficient quantities of specific nutrients required by the insect for growth. The importance of physical and chemical characteristics of plants in determining the degree to which a plant is consumed by an insect has been stressed by many researchers (Dethier, 1947, Friend, 1958, Lipke and Fraenkel, 1956, Painter, 1953).

On buckwheat, the undesirability of the foliage to larvae was confirmed by the high mortality among the third-instar larvae transferred from the artificial diet. The few which developed to the fourth instar died after a little feeding. On flax, the second instar larvae transferred from the artificial diet also incurred severe mortality. However, one of the larvae pupated. The comparatively high consumption rate on flax suggests that it is palatable. Some wild flaxes have been shown to contain toxic cyano-

genic glucosides. For instance, Linum mexicanus L. contains a poison "Linotoxin" which is fatal to mammals if large enough quantities are eaten (Eggleston et al., 1930). However, these poisons have not been demonstrated to occur in domestic flaxes.

The survival on bean foliage was much lower than on the other species tested in the same experiment (Figs. 4, 5). The low survival on beans appears to be related to the leaf characteristics, possibly the waxy, sticky substance which trapped and killed some larvae through starvation. However, the influence of chemical factors (toxins, repellents, etc.) on the larval food consumption and survival on bean foliage cannot be excluded. (see discussion on legumes below).

On mustard, the survival pattern was different from that on buckwheat, flax and beans only in one respect. Although mortality exceeded 80% in the first instar (TABLE 4), at least 10% survived to the fourth instar. However, survival from the latter instar was very poor and only one larva entered the sixth stage in which it died. This survival pattern appears to resemble that on turnip in two respects. On both food plants, the larvae may have increased the level of survival by reducing growth and prolonging development. Gordon (1959) and House (1965) suggested that reduced growth and prolonged development are means by which insects avoid wasteful and lethal biochemical imbalances until a more favourable food is available.

On sugar beet, the larval survival pattern, until the

fourth instar, was similar to that on turnip. However, there were two basic differences between the two food plants. The larval mortality was higher on turnip (97%) than on sugar beet (80%) (Figs. 2, 4) and development was slower on turnips (TABLES 8,9).

On sweet clover, alfalfa and pigweed, the mortality of immature stages was much lower than that observed on buckwheat, flax, mustard and turnip. On sweet clover and alfalfa, larval survival to the fourth instar was higher than on the control foods but mortality reached 100% before pupation (TABLE 4). On pigweed, survival to the fourth instar was almost as high as on sweet clover and alfalfa and the final instar took the greatest toll in mortality. Although 30% of the larvae on pigweed formed pupae, none survived to the adult stage.

The apparent differences in larval survival curves of pigweed, cabbage and marigold are related to the rates of larval development. Survival on an instar basis does not significantly differ between them (TABLE 4). For these foodplants, pupal mortality was high and survival to the adult stage was low (0-17%).

High mortality in the sixth instar was characteristic of many of the foodplants tested. This mortality usually occurred as a result of failure to empty gut contents, to cast off the larval skin or to chitinize all the body segments. The pupal mortality resulted mainly from the syndrome or morphological malformation. These malformations are a direct result of lack of specific nutrients in both the artificial diet and excised leaves. Although several

researchers have observed that the adverse effects of feeding insects on wilted foliage are associated with low moisture content (Beck, 1956, Kennedy and Mittler, 1953, Murthy, 1953, Snyder, 1954, Tuaber et al., 1945), the present findings are not consistent with this view (Fig. 6). Food plants with less than 83% moisture failed to support larval development to the adult stage but survival on plants with the highest moisture content (sugar beet, mustard) was also low. These findings suggest that moisture content was not a major factor in the survival of larvae on the test plants.

(b) Food consumption, larval growth and development.

When food consumption (mg fresh weight) was plotted against larval growth the relationship approximated a straight line (Figs. 7,8). The slopes of the lines represent the growth increment per milligram of food consumed (Turnbull, 1962). The slopes ranged from 0.23 on flax to 0.48 on marigold. The steepest slope, obtained for insects feeding on marigold, indicates higher utilization of ingested food on this plant than other plants. However, larval survival to the adult stage was low on marigold and the adults were smaller than those on other food plants. It appears, therefore, that marigold was a poor food because not enough of it was ingested (TABLE 5), or alternatively, because a nutritional deficiency in this plant adversely affected survival and growth. Among the insects fed rape foliage, the slope on rape in the second

Figure 6. Percent pupal formation and emergence of M. configurata with moisture content of food plants.

A = Pigweed; B = Alfalfa; C = Turnip; D = Flax; E = Sweet Clover; F = Beans; G = Marigold; H = Buckwheat; I = Cabbage; J = Rutabaga; K = Rape (Exp. 2); L = Rape (Exp. 1); M = Mustard; N = Sugar beet.

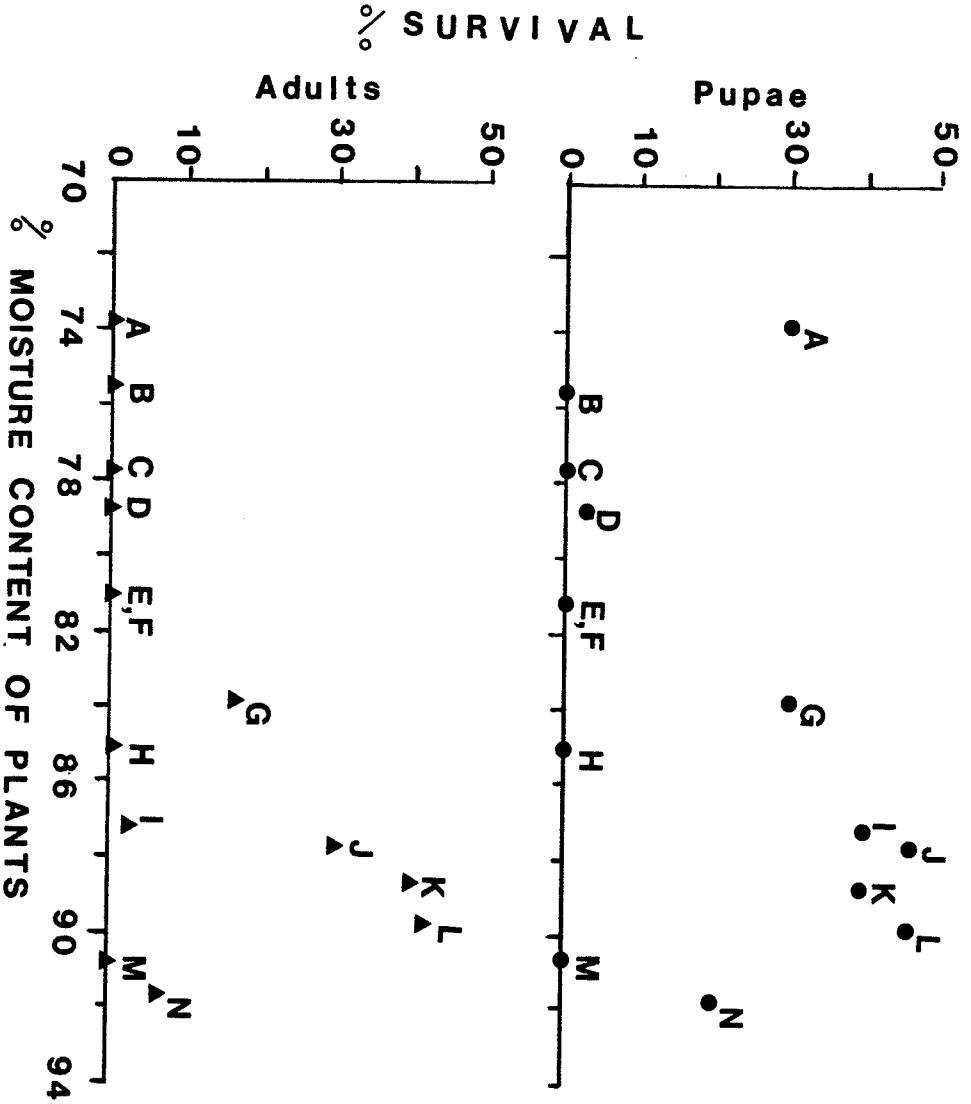

% SURVIVAL
Adults
Pupae
0
10
30
50
70
74
78
82
86
90
94
% MOISTURE CONTENT OF PLANTS
A
B
C
D
E,F
G
H
I
J
K
L
M
N

Figure 7. Relationship between mean food consumption and mean larval growth from the second to the sixth instar of M. configurata on various food plants.

The equations showing the relationships between food consumption and larval growth were:

(A) Rape (Exp. 1), $Y = -157.25 + 0.33x$, $R^2 = 0.96$

Rape (Exp. 2), $Y = -200.78 + 0.43x$, $R^2 = 0.99$

Rutabaga, $Y = -130.50 + 0.38x$, $R^2 = 0.99$

(B) Mustard, $Y = -209.23 + 0.32x$, $R^2 = 0.52$

Sugar beet, $Y = -195.50 + 0.29x$, $R^2 = 0.99$

Turnip, $Y = -384.90 + 0.28x$, $R^2 = 0.88$

Flax, $Y = -172.00 + 0.23x$. $R^2 = 1$

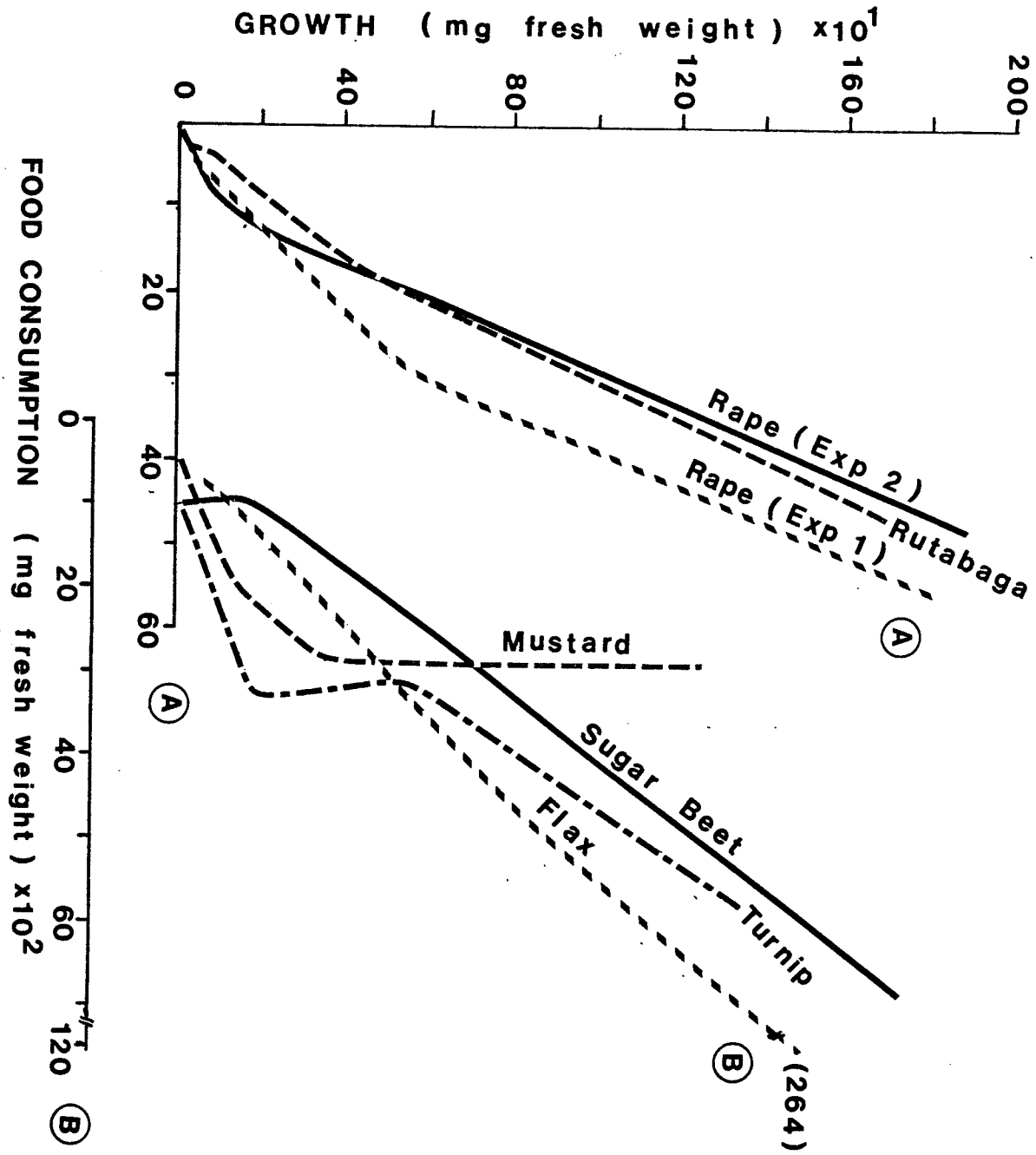

GROWTH (mg fresh weight) x10¹
0
40
80
120
160
200
20
40
60
Rape (Exp 2)
Rutabaga
Rape (Exp 1)
Mustard
Sugar Beet
Turnip
Flax
(264)
A
B
FOOD CONSUMPTION (mg fresh weight) x10²
0
20
40
60
120
A
B

Figure 8. Relationship between mean food consumption and mean larval growth from the second to the sixth instar.

The equations showing the relationships between food consumption and larval growth were:

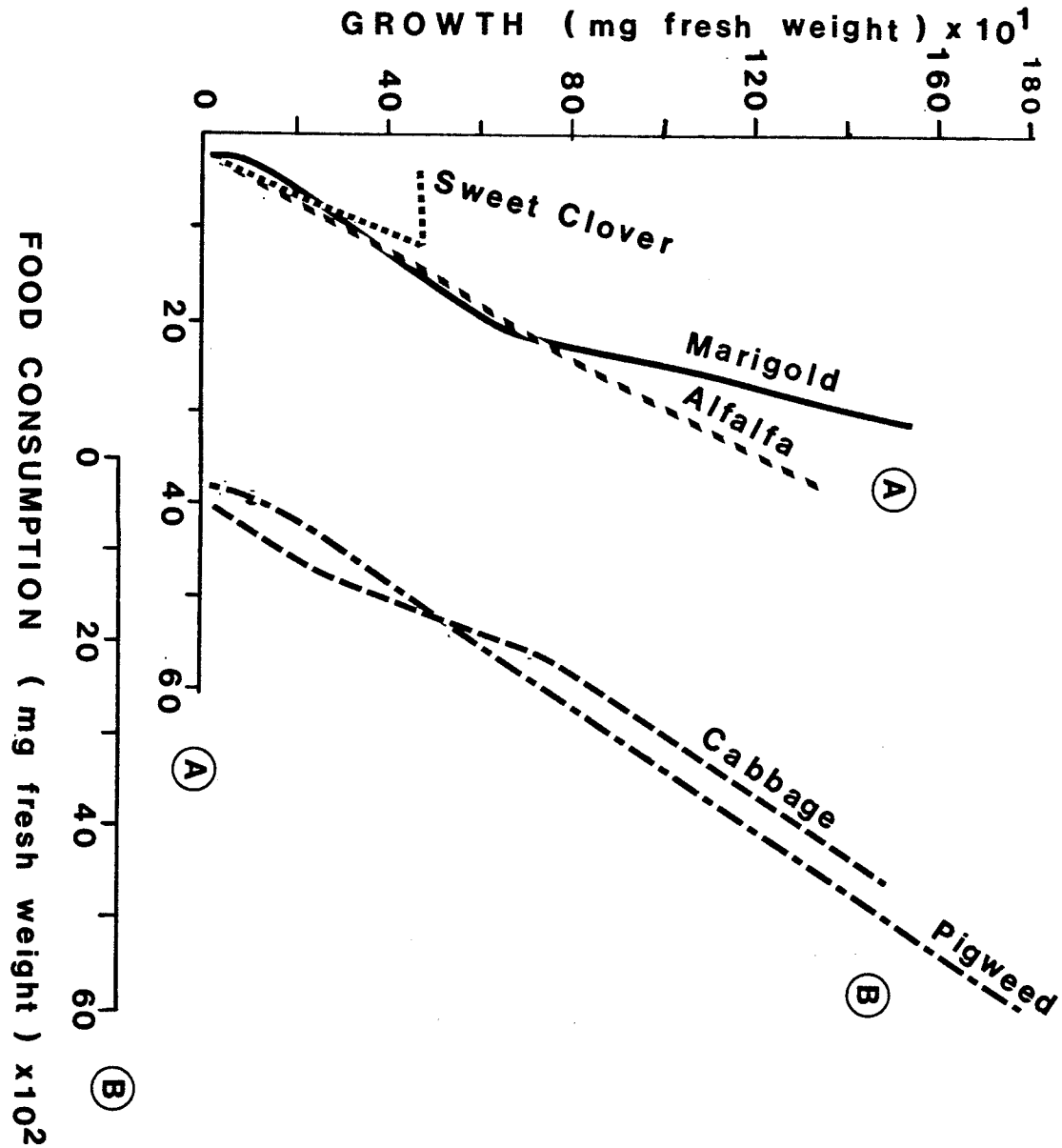
(A) Sweet clover, $Y = 20.83 + 0.39x$, $R^2 = 0.36$

Marigold, $Y = -116.07 + 0.48x$, $R^2 = 0.95$

Alfalfa, $Y = -90.21 + 0.38x$, $R^2 = 1$

(B) Cabbage, $Y = -153.31 + 0.37x$, $R^2 = 0.99$

Pigweed, $Y = -37.86 + 0.31x$, $R^2 = 1$


GROWTH (mg fresh weight) x 10¹
0
40
80
120
160
180
Sweet Clover
Marigold
Alfalfa
A
FOOD CONSUMPTION (mg fresh weight) x10²
0
20
40
60
A
0
20
40
60
B
Cabbage
Pigweed
B

experiment was steeper (0.43) than that in the first (0.33), suggesting higher utilization of older rape foliage. Although utilization was higher in the second experiment, larval survival was slightly lower than in the first experiment.

The slopes obtained for insects feeding on cabbage, rutabaga, alfalfa and sweet clover were similar to each other and intermediate to those on rape in the first and second experiments. However, on alfalfa and sweet clover, the larvae died in the sixth instar without reaching the pre-pupal stage. On cabbage, larval development was slightly faster and survival to the adult stage was much lower than that on rutabaga. On mustard and pigweed, the slopes (0.32 and 0.31) were similar to that of rape in the first experiment, but larval development was much slower. In addition, none of the larvae fed mustard or pigweed survived to the adult stage. On flax, turnip and sugar beet, the slopes (0.23, 0.28, 0.29) were shallower than on other food plants. Except on sugar beet, larval development on these food plants was slow and none developed to the adult stage.

The efficiency of conversion of ingested food to body tissues (ECI) (see Waldbauer, 1968) up to the sixth instar ranged from 21% on turnip to 74% on marigold (TABLE 10). The ECI values for larvae fed rape foliage in the first experiment (45%) was lower than that of larvae on rape in the second experiment (68%), where the larvae consumed foliage at a lower rate than in the first. These values on rape were much higher than the ECI of 25% reported by Bailey

TABLE 10. Efficiency of conversion of ingested food (ECI ± SD) into body tissue by M. configurata on different food plants. Except where indicated, n = number of larvae which formed pupae.

Food Plant	n	Mean ECI ± SD
Marigold	8	74.20 ± 26.70
Rape (Exp. 2)	12	68.41 ± 25.38
Mustard	1	63.3 *a
Rutabaga	14	57.14 ± 12.34
Sugar beet	6	47.06 ± 8.52
Rape (Exp. 1)	14	44.98 ± 8.50
Cabbage	12	39.14 ± 6.78
Flax	1	27.1
Pigweed	9	26.49 ± 6.02
Turnip	7	20.95 ± 5.05 *b
Sweet clover	9	87.93 ± 21.01 *c
Alfalfa	17	47.16 ± 12.84 *c

*a Larva died before pupating as pre-pupa

*b n = prepupa. Only one pupated

*c ECI calculated for fifth instar

(1976) for larvae fed the same rape species.

The ECI values for larvae on mustard and rutabaga were similar to that of larvae on rape in the second experiment. The ECI values for larvae on alfalfa, sugar beet and cabbage were similar to that on rape in the second experiment. The ECI values on flax, pigweed and turnip were much lower than those on other food plants. Food consumption was highest in the latter food plants. On sweet clover, the fifth instar ECI value was higher than on any other plant species. These larvae, like those fed alfalfa, died in the sixth instar before reaching the pre-pupal stage.

The results clearly indicate that the ECI values for larvae differ from one plant species to another. These differences have been shown to be influenced by the digestibility of the food, its nutritional value and the level of nutrient intake (Waldbauer, 1964) or proportions of nutrients (House, 1969). The comparatively high larval food consumption on pigweed, turnip and flax (TABLE 5) suggests that larvae may eat copiously in an attempt to compensate quantitatively for deficient nutrient levels of an otherwise satisfactory diet. Similar results have been reported for Celerio euphorbiae (House, 1965). The apparent differences in the nutritive quality of the rape plants used in the first two experiments is not surprising. The nutritive quality of plants has long been known to vary not only interspecifically but also intraspecifically with the variety, conditions for growth, age and other factors

that determine chemical composition (Morrison, 1941).

The role of chemical factors in influencing larval food consumption and survival cannot be overemphasized. However, on sweet clover and alfalfa, food consumption, growth, development and survival all appeared normal until later instars. Larvae suddenly reduced their food intake at the onset of the fourth instar on sweet clover and in the final instar on alfalfa. Severe mortality followed this reduction in food consumption on both plants. Whether the increased mortality was caused by undernourishment resulting from reduced food intake or by the accumulation of feeding deterrents or toxins is not known. However, legumes, including beans, alfalfa and sweet clover are known for their high content of tritepenoid saponins and coumestans. The alfalfa saponins have been shown to contribute to the occurrence of bloat in ruminants and to cause metabolic disorders in other domesticated mammals (Lindal et al., 1957). Some varieties of alfalfa have been reported to have some resistance to the spotted alfalfa aphid, Therioaphis maculata (Buck) (Howe and Smith, 1957, Harvey et al., 1960, Kishaba and Manglitz, 1963, Kindler and Staples, 1970). The true nature of this resistance is not known, but it is assumed that either the plants contain toxins or repellents or the plants do not meet the insects nutritional requirements. This resistance in alfalfa is not immutable, it can change with conditions (eg. temperature) (McMurtry and Stanford, 1960). In both cases, reduced ingestion occurred when the plants started blooming. Coumarin

production in sweet clover reaches a maximum at the blooming stage. This substance has been known to cause temporary rejection of foliage by mammals (see Range Plant Handbook, 1937, USDA). In Melilotus officinalis, coumarin has been shown to act as a feeding attractant for the vegetable weevil, Listroderes costrirustris oblignus (Klug.) when in low concentrations but highly deterrent in higher concentrations (Matsumoto, 1963). It is not known whether or to what extent these compounds influenced the survival of M. configurata on the test legumes.

The apparent lack of a direct relationship between total food consumption and growth was also evident among pupal weights. A plot of food consumption against pupal weights resulted in scatter diagrams whose regression coefficients ranged from zero on cabbage and pigweed to 0.31 on rutabaga. No significant correlation ocurred for larvae on any food plants.

CHAPTER VI

SUMMARY AND CONCLUSIONS

In the experiments described above, a small number of larvae was used in each test because of the work involved in feeding fresh foliage and weighing the larvae. The results, however, do have interesting ecological implications some of which will be pointed out below.

All the food plants fed to the experimental insects in this study were acceptable to some degree. However, not all the food plants had the nutritive qualities essential for adequate development, growth and survival of M. configurata. Larval growth, development and survival were best among insects reared on the artificial diet, indicating that it was nutritionally superior to all the plants tested in this study. Rape was the best food plant for larval growth, development and survival and rutabaga was almost as good.

On alfalfa, sweet clover and pigweed, larval growth, development and survival were good up to the sixth instar or pupal stage but no insects survived to the adult stage. On alfalfa and sweet clover, both the utilization and ECI's were high but development did not proceed beyond the sixth instar. The high mortality observed in the last two instars on these food plants may have been a result of the cumulative effects of the lack of certain essential nutrients or the presence of toxins. The possibility of the presence of feeding deterrents cannot be excluded. On pigweed, although food consumption was very high, the utilization and ECI values were low. Although immature larval survival was good,

development was comparatively slow and no adults emerged.

On marigold and cabbage, larval growth, development and survival were good up to the pupal stage. Between these test plants, food utilization and ECI values were higher on marigold but this plant also produced much lighter pupae and smaller adults. Marigold foliage apparently lacks some nutrients essential for the normal growth and survival of M. configurata. The utilization and ECI values on cabbage were similar to those on rape. However, the higher pupal mortality suggests lack of certain essential nutrients in the food plant.

The utilization of food on sugar beet and turnip was low compared to the other food plants. On both food plants larval survival was low and similar until the fifth instar. However, the ECI was higher and development faster on sugar beet than on turnip. Survival to the adult stage was zero on turnip and very low on sugar beet.

On buckwheat, flax, mustard and beans, larval survival in the first two instars was very low. Buckwheat appears to have been the worst food tested since larvae were unable to complete more than one molt, even if introduced to the foliage when in the third instar. On flax, introduction of first instar larvae resulted into 100% mortality, but 25% of the larvae introduced during second instar formed pupae. None emerged to the adult stage. On mustard, although the initial mortality was very high, a small percentage developed, though slowly, through the fifth instar. On bean foliage development did not proceed beyond the third instar. All

these food plants appear to have been highly unfavourable either because of foliage physical characteristics or chemical factors (deterrents or toxins).

The test plants may therefore be characterised into three major groups depending upon relative ability of larvae to grow, develop and survive on them.

(1) Plants which were highly unfavourable to larval establishment or if a few survived, development was slow and development beyond the pupal stage non existent.

(i) Buckwheat (Polygonaceae)
(ii) Beans (Leguminosae)
(iii) Flax (Linaceae)
(iv) Mustard (Cruciferae)

(2) The second group includes those plants on which survival of larvae in the early instars was moderate to high and can be divided into two subgroups:

(a) Plants on which sixth instar mortality was high and if pupation occurred, there was no emergence. Larval developmental rates were from very slow to normal.

(i) Sweet clover (Leguminosae)
(ii) Alfalfa (Leguminosae)
(iii) Turnip (Cruciferae)
(iv) Pigweed (Chenopidiaceae)

(b) Plants on which pupal mortality was high but some adult emergence occurred (3-17%).

(i) Cabbage (Cruciferae)

(ii) Sugar beet (Chenopodiaceae)

(iii) Marigold (Compositae)

(3) Plants on which larval growth, development and survival to the adult stage were relatively high (30-42%).

(i) Rape (Cruciferae)

(ii) Rutabaga (Cruciferae)

The present findings indicate that although M. configurata has been reported to feed on many food plants, very few of these can support its development to the adult stage. However, its potential as a pest of field and garden crops is great because of its ability to live at least temporarily on these crops although they may not provide its nutritional needs. It appears, therefore, that most reports of bertha armyworm damage to crops other than rape refer to populations that have built up on more favourable hosts and destroyed them before attacking the unfavourable hosts.

The native hosts of M. configurata have not been determined but populations may increase on the rape crop. In addition, the preference of females in laying eggs on Chenopodium spp. makes this group of plants a possible source of infestation to field crops. However, the food plants and environmental conditions which bring about the destructive phase of the armyworms are not known. From an ecological point of view, the present study seems to suggest that bertha armyworm populations attacking crops other than rape can be expected to decline rather sharply owing to greater mortality

among older larvae and pupae. Outbreaks can be expected to be relatively infrequent, increasing only under favourable conditions of weather and host plant availability.

VII. LITERATURE CITED

Allen, M.D. and I.W. Selman. 1957. The response of larvae of the large white butterfly (Pieris brassicae L.) to diets of mineral deficient leaves. Bull. Ent. Res. 48:229-242.

Applebaum, S.W. and A.M. Konijn. 1967. Factors affecting the development of Tribolium castaneum (Herbst) on wheat. J. Stored Prod. Res. 2:323-329.

Applebaum, S.W. 1964. Physiological aspects of host specificity in the Bruchidae. I. General considerations of developmental compatibility. J. Insect Physiol. 10:783-788.

Applebaum, S.W., J. Marco and Y. Birk. 1969. Saponins as possible factors of resistance of legume seeds to the attack of insects. J. Agr. Food Chem. 17:618-620.

Atwal, A.S. 1955. Influence of temperature, photoperiod and food on the speed of development, longevity, fecundity and other qualitities of the diamond back moth, Plutella maculipennis (Curtis) (Tineidae : Lepidoptera). Aust. J. Zool. 3: 185-221.

Auclair, J.L., J.B. Maltais and J.J. Cartier. 1957. Factors in resistance of peas to the pea aphid Acyrthosiphors pisium (Harr.) (Homoptera:Aphididae). II. Amino acids. Can. Entomol. 89:457-464.

Bailey, C.G. 1976. Temperature effects on non-diapause

development in Mamestra configurata (Lepidoptera:Noctuidae). Can. Ent. 108(12):1339-1344.

Bailey, C.G. 1976. A quantitative study of consumption and utilization of various diets in the Bertha armyworm, Mamestra configurata (Wlk) (Lepidoptera:Noctuidae). Can. Ent. 108:1319-1326.

Bailey, C.G. and N.B. Singh. 1977. An energy budget for Mamestra configurata (Lepidoptera:Noctuidae) Can. Ent. 109(5):687-693.

Banham, F.L. and J.C. Arrand. 1970. Recognition and life history of the major insect and allied pests of vegetation in British Columbia. British Columbia Dept. Agric. Ent. Br. 43pp.

Beck, S.D. 1956. The European corn borer Pyrausta nubilalis (Hbn), and its principal host plant. II. The influence of nutritional factors on larval establishment and development on the corn plant. Ann. Entomol. Soc. Amer. 49:399-405.

Beck, S.D. 1956. Nutrition of the European corn borer, Pyrausta nubilalis (Hbn) IV. Feeding reactions of first instar larvae. Ann. Entomol. Soc. Amer. 49:582-588.

Beck, S.D. 1974. Theoretical aspects of host plant specificity in insects. pp. 290-311. In: F.G. Maxwell and F.A. Harris eds. University Press. Mississippi. Proc. Summ. Inst. Biol. Contr. of Plant Insects and Diseases.

Beckwith, R.C. 1970. Influence of host on larval survival and adult fecundity of Choristoneura conflictana (Lepidoptera:Tortricidae). Can. Ent. 102:1474-1480.

Bennett, S.E. 1965. Tannic acid as a repellent and toxicant to alfalfa weevil larvae. J. Econ. Entomol. 58(2):372.

Bucher, G.E. and Bracken, G.K. 1977. The bertha armyworm Mamestra configurata (Lepidoptera:Noctuidae). Sterilization of adults by exposure of prepupal-pupal stages to 25 deg. C. Can. Ent. 109(4): 549-553.

Bucher, G.E. and G.K. Bracken. 1976. The bertha armyworm, Mamestra configurata (Walker) (Lepidoptera: Noctuidae). Artificial diet and rearing technique. Can. Ent. 108:1327-1338.

Burnell, E. 1970. An introduction to insect physiology. 276 pp. New York. Academic Press.

Blais, J.R. 1952. The relationship of spruce budworm (Choristoneura fumiferana Clem.) to the flowering condition of balsam fir (Abies balsamea L.M. II). Can. J. Zool. 30:1-29.

Bongers, H. 1970. Aspects of host-plant relationship of the Colorado potato beetle. Meded. Landbouwhog-eschool Vageningen. Nederland 70-10:1-77.

Borchers, R., C.W. Ackerson and L. Kimmet. 1947. Trysin inhibitor. IV. Occurrence in seeds of the Leguminosae and other seeds. Arch. Biochem.

13:291-293.

Cibula, A.B., R.H. Davidson, F.W. Fisk and J.B. Lapidus. 1967. Relationship of free amino acids of some Solanaceous plants to growth and development of Leptinotarsa decemlineata (Coleoptera: Chrysomelidae). Ann. Entomol. Soc. Amer. 60: 626-631.

David, W.A. and B.O. Gardiner. 1966. Mustard oil glucosides as feeding stimulants for Pieris brassicae larvae in a semi synthetic diet. Ent. Exp. and Appl. 9:247-255.

Dethier, V.G. 1954. Evolution of feeding preferences in phytophagous insects. Evol. 8:33-54.

Dethier, V.G., B. Browne and C.M. Smith. 1960. The designation of chemicals in terms of the responses they elicit from insects. J. Econ. Ent. 53: 134-136.

Dolinski, M.G. 1974. Various pests. In: J.S. Kelleher, compiler. Canadian agricultural pest review. 52: p. 26.

Eggleston, W.W., O.F. Black and J.W. Kelly. 1930. Linum neomexicanum (Yellow pine flax) and one of its poisonous constituents. Jour. Arg. Research. (U.S.) 41:715-718.

Eidt, D.D. and C.H.A. Little. 1968. Insect control by artificially prolonging plant dormancy--a new approach. Can. Ent. 100:1278-1279.

Embree, D.G. 1965. The population dynamics of the winter moth in Nova Scotia, 1954-1962. Mem. Ent.

Soc. Can. No. 46.

Ettlinger, M.G. and A. Kjaer. 1968. Sulfur compounds in plants. In: J.J. Mabry (editor), Recent Advances in Phytochemistry. Vol. 1:59-144.

Evans, A.C. 1939. The utilization of food by certain Lepidopterous larvae. Trans. R. Ent. Soc. Lond. 89:13-22.

Feeny, P.P. 1968. Effects of oak-leaf tannins on larval growth of the winter moth, Operophtera brumata. J. Insect Physiol. 14:805-817.

Fukuda, T., M. Sido and Kameyama, Kawasugi S. 1962. J. Arg. Chem. Soc. Japan. 36(829).

Fraenkel, G. 1969. Evaluation of our thoughts on secondary plant substances. Ent. Exp. and Appl. 12:473-486.

Friend, W.G. 1958. Nutritional requirements of Phytophagous insects. Ann. Rev. Ent. 3:57-74.

Gage, S.H. and Taylor. 1976. Pests of small grains. In: J.S. Kelleher, compiler. Canadian agricultural pest review. 54: p. 29.

Gibson, R.W. 1971. Glandular hairs providing resistance to aphids in certain wild potato species. Ann. App. Biol. 68:113-119.

Gilbert, L.E. 1971. Butterfly-plant coevolution: Has Passiflora adenopoda won the selection race with Heliconiine butterflies? Science 172:585-586.

Gordon, H.T. 1959. Minimal nutritional requirements of the German roach, Blattella germanica L. Ann. Ent. Soc. Am. 53:632-638.

Green, T.R. and C.A. Ryan. 1972. Wound-induced proteinase inhibitor in plant leaves: A possible defence mechanism against insects. Science 175:776-777.

Harvey, T.L., H. Hackerott, E.C. Sorensen, R.H. Painter, E.E. Ortman and D.D. Peters. 1960. The development and performance of Cody alfalfa, a spotted alfalfa aphid resistant variety. Kansas Agri. Exp. Sta. Tech. Bull. 144: 17 pp.

Hegnauer, R. 1973. Chemotaxonomie der Pflanzen. Band G, Dicothyledoneae:Rafflesiaceae, Zygophyllacea. Birkhauser Verlad, Basel. 882 p.

Hiratsuka, E. 1920. Researches on the nutrition of the silkworm. Bull. Seric. Exp. Sta. Japan 1: 257-315.

Horber, E. 1965. Isolation of components from the roots of alfalfa (Medicago sativa L.) toxic to white grubs Melolontha vulgaris F.) Int. Cong. Entomol. XII. Proc. pp. 540-541.

House, H.L. 1956. Effects of low levels of the nutrient content of a food and of nutrient imbalance on the feeding and nutrition of a phytophagous larva Celerio euphorbiae (L.) (Lepidoptera: Sphingidae). Can. Ent. 97:62-68.

House, H.L. 1969. Effects of different proportions of nutrients in insects. Ent. Exp. and Appl. 12:651-669.

House, H.L. 1970. Choice of food by larvae of the fly,

Agria affinis, related to dietary proportions of nutrients. J. Insect Physiol. 16:2041-2050.

House, H.L. 1971. Relations between dietary proportions of nutrients, growth rate, and choice of food in the fly larva, Agria affinis. J. Insect Physiol. 17:1225-1238.

Hovanitz, W. and V.C.S. Chang. 1962. The effects of various food plants on survival and growth rate of Pieris. J. Res. Lepidoptera. I:21-42.

Howe, W.L. and O.F. Smith. 1957. Resistance to the spotted alfalfa aphid in Lahontan alfalfa. J. Econ. Ent. 50:320-324.

Hsiao, T. 1969. Chemical basis of host selection and plant resistance in oligophagous insects. Ent. Exp. and Appl. 12:777-788.

Kennedy, J.S. and T.E. Mittler. 1953. A method of obtaining phloem sap via the mouth-parts of Aphids. Nature. 171:528.

Kindler, S.D. and R. Staples. 1970. Nutrients and the reaction of two alfalfa clones to the spotted alfalfa aphid. J. Econ. Ent. 63:938-940.

King, K.M. 1928. Barathra configurata (Wlk.), an armyworm with important potentialities on the Northern prairies. J. Econ. Ent. 21:279-293.

Kishaba, A.N. and G.R. Manglitz. 1963. Nonpreference as a mechanism of sweetclover and alfalfa resistance to the sweet clover aphid and the spotted alfalfa

Aphid. J. Econ. Ent. 58:566-569.

Kjaer, A. 1960. The distribution of sulfur compounds. p. 453. In: T. Swain, ed. Chemical Plant Taxonomy. Academic Press. London.

Kjaer, A. 1960. Naturally derived isothiocyanates (mustard oils) and their parent glucocides. pp. 122-176. In: W. Herz, H. Grisebach, and G.W. Kirby, eds. Progress in the chemistry of organic natural product. 18. Springer-Verlag, New York, N.Y.

Kjaer, A. 1976. Glucosinolates in the Cruciferae. pp. 207-219. In: J.G. Vaughan, A.J. Macleod and B.M.G. Jones (eds.), The biology and chemistry of the cruciferae. Academic Press, New York.

Klingenburg, M. and J. Bucher. 1960. Biological oxidations. Ann. Rev. Biochem. 29:669-708.

Kogan, M. 1976. The role of chemical factors in insect/plant relations. Proc. 15th Int. Cong. Ent. (Washington, D.C. 1976).

Kogan, M. and R.D. Goeden. 1970. The biology of Lema trilineata daturaphila (Coleoptera:Chrysomelidae) with notes on efficiency of food utilization by larvae. Ann. Ent. Soc. Am. 63:537-546.

Krieger, R.I., P.P. Feeny and C.F. Wilkinson. 1971. Detoxification enzymes in the guts of caterpillars: An evolutionary answer to plant defence? Science. 172:579-581.

Legay, J.M. 1955. Doctoral Thesis. Paris.

Lichtenstein, E.P., F.M. Strong and D.C. Morgan. 1962. Identification of 2-phenylethylisothiocyanate as an insecticide occuring naturally in the edible part of turnips. J. Agr. Food Chem. 10:30-33.

Likens, G.E. and F.H. Bormann. 1970. Chemical analysis of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Yale University School of Forestry. Bull. No. 79.

Lindahl, I.L., R.E. Davis, R.T. Tertell, G.E. Whitmore, W.T. Shalkop, G.R. Van Atta, R.W. Gougherty, C.R. Thompson, W.M. Bickoff, E.D. Walter, A.G. Livingston, J. Guggolz, R.H. Wilson, D.E. and M.B. Sideman, eds. 1957. Alfalfa Saponins. U.S.D.A. Tech. Bull. 1161. pp. 83.

Lipke, H. and G. Fraenkel. 1956. Insect nutrition. Ann. Rev. Entomol. 1:17-44.

Maltais, J.B. and J.L. Auclair. 1962. Free amino acid and amide composition on pea leaf juice, pear aphid haemolymph, and honeydew following the rearing of aphids on single pea leaves treated with amino acid compounds. J. Insect Physiol. 8:391-400.

Matsumoto, Y.A. 1962. A dual effect of coumarin, olfactory attraction and feeding inhibition on the vegetable weevil adult, in relation to the uneatability of sweet clover leaves. Japan J.

Appl. Entomol. Zool. 6:141-149.

McDonald, H. 1972. The Bertha armyworm crisis. Agric. Can. 17(1):10-12.

McHarque, J.S. and W.R. Roy. 1932. Mineral and nitrogen content of leaves of some forest trees at different times in the growing season. B.A. Gazette. 94:381-393.

McGinnis, A.J. and R. Kasting. 1961. Comparison of tissues from solid and hollow-stemmed spring wheats during growth. I. Dry matter and nitrogen contents of pith and wall and their relation to sawfly resistance. Can. J. Plant Sci. 41:469-478.

McMurtry, J.A. and E.H. Stanford. 1960. Observations of the feeding habits of the spotted alfalfa aphid on resistant and susceptible alfalfa plants. J. Econ. Entomol. 53:714-717.

McMurtry, J.A. 1962. Resistance of Alfalfa to the spotted alfalfa aphid in relation to environmental factors. Hilgardia 32:501-539.

Mellanby, K. and R.A. French. 1958. The importance of drinking water to larval insects. Ent. Exp. and Appl. 1:116-124.

Morrison, F.B. 1941. Feeds and feeding abridged. 7th Ed. Morrison, Ithica, N.Y.

Mukerji, M.K. and J.C. Guppy. 1970. A quantitative study of food consumption and growth in Pseudaletia unipuncta (Lepidoptera:Noctuidae) Can. Ent. 102: 1179-1188.

Munro, J.A. 1930. Bertha armyworm control. Bull. N. Dak. Agric. Exp. Stn. 233.

Murthy, M.R.V. 1953. Studies on the nutrition of the silkworm, Bombyx mori. L. Doctoral thesis, Univ. Bangalore, India.

New, T.R. 1971. The consumption of Euphorbia cyparissias (Euphorbiaceae) by larvae of Celerio euphorbiae (Lepidoptera:Sphingidae) Can. Ent. 103:59-66.

Painter, R.H. 1953. The role of nutritional factors in host-plant selection. Trans. 9th Int. Cong. Ent. 2:101-103.

Pankiw, P. 1976. Pests of small grains. In: J.S. Kelleher, compiler. Canadian agricultural pest review. 54: p. 43.

Philip, H. 1973. Various pests. In: J.S. Kelleher, compiler. Canadian Agricultural insect pest review. 51: p. 45.

Putnam, L.G. 1975. Pests of oil seed crops. In: J.S. Kelleher, compiler. Canadian Agricultural pest review. 53: p. 30.

Range Plant Handbook. 1937. Prepared by Forest Service. U.S. Dept. Agric. Washington, Govt. Printing Office.

Rudolfs, W. 1926. Studies on chemical changes during the life cycle of the tent caterpillar (Malacosoma americana Fabr.). Part I. Moisture and fat. J. New York Entomol. Soc. 34:249-256.

Schreiber, K. 1958. Uber einige Inhaltssloff der Solanaceen und ihre bedeutung fur die Karto-felkaferrestis-

tenz. Ent. Exp. and Appl. 1:28-37.

Scriber, J.M. 1975. Comparative nutritional ecology of herbivorous insects. Generalized and specialized feeding strategies in the Papilionidae and Saturniidae (Lepidoptera). Ph. D. Thesis. 289 pp. Ithaca N.Y., Cornell University.

Scriber, J.M. 1977. Limiting effects of low leaf water content on the nitrogen utilization, energy budget and larval growth of Hyalophora cecropia (Lepidoptera:Saturniidae). Oecologia (Berl.) 28:269-287.

Self, L.S., F.E. Guthrie and E. Hodgson. 1964. Metabolism of nicotine by tobacco feeding insects. Nature 204:300-301.

Self, L.S., F.E. Guthrie and G.E. Hodgson. 1964. Adaption of tobacco hornworm to the ingestion of nicotine. J. Insect Physiol. 10:907-914.

Shaver, G.N. 1974. Biochemical basis of resistance of plants to insects-antibiotic factors other than phytohormones. pp. 485-493. In: Maxwell, F.G. and F.A. Harris eds. Proc. Summ. Inst. Biol. Contl. of Plant Insects and Diseases. Univ. Press, Mississippi.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical Methods. Iowa State University Press, Ames, Iowa, U.S.A.

Snyder, K.D. 1954. The effect of temperature and food on the development of the variegated cutworm,

Peridroma margaritosa How. (Order Lepidoptera: Family: Noctuidae). Ann. Ent. Soc. Amer. 47: 603-613.

Soo Hoo, C.F. and G. Fraenkel. 1966. The consumption, digestion and utilisation of food plants by a polyphagous insect Prodenia eridania (Cramer). J. Insect Physiol. 12:711-730.

Tamaki, G, R.E. Weeks and B.J. Landis. 1972. Biology of the Zebra Caterpillar Ceramica picta. Pan. Pacific Ent. 48:208-214.

Taylor, M.E. 1973. Various pests. In: J.S. Kelleher, compiler. Canadian agricultural insect pest review. 51: p. 41.

Thorsteinson, A.J. 1953. The chemotactic responses that determine host specificity in an oligophagous insect Plutella maculipennis (Curt.) Canadian J. Zool. 31:52-72.

Tuaber, O.E., C.J. Drake and G.C. Decker. 1945. Effects of different food plants on egg production and adult survival of the grasshopper Melanoplus bivittatus(Say). Iowa St. Coll. J. Sci. 19: 343-359.

Turnbull, A.L. 1962. Quantitative studies of the food of Linyphia triangularis (Clerck) (Araneae: Linyphiidae). Can Ent. 94:1233-1249.

Turnock, W.J. 1974. Various Pests. In: J.S. Kelleher, compiler. Canadian agricultural insect pest review. 52: p. 21.

Turnock, W.J. 1977. In: J.S. Kelleher, compiler. Canadian agricultural pest review. 55: p. 36.

Vogel, R.J. 1968. Natural Proteinase Inhibitors. Academic Press. New York.

Waldbauer, G.P. 1964. The consumption, digestion and utilization of solanaceous and non-Solanaceous plants by larvae of the tobacco hornworm Protoparce sexta (Johan); Lepidoptera: Sphingidae. Ent. Exp. and Appl. 7:253-269.

Waldbauer, G.P. 1968. The consumption and utilization of food by insects. pp. 229-288. In: Advances in Insect Physiology. Vol. 5. Ed. by J.W.L. Beament, J.E. Treherne and V.B. Wigglesworth.

Waldbauer, G.P. and G. Fraenkel. 1961. Feeding on normally rejected plants by maxillectomized larvae of the tobacco hornworm, Protoparce sexta (Lepidoptera:Sphingidae). Ann. Ent. Soc. Am. 54:477-485.

Wigglesworth, V.B. 1975. The principles of insect physiology. 6th ed. 741 pp. London, Methuen.

Wilde, J. de, W. Bongers and H. Schoonveld. 1969. Effects of host plant age on phytophagous insects. Ent. Exp. and App. 12:714-720.

Wylie, H.G. and G.E. Bucher. 1977. The bertha armyworm, Mamestra configurata (Lepidoptera:Noctuidae). Mortality of immature stages on the rape crop 1972-1975. Can. Ent. 109(6):823-837.

Yamamoto, R.T. and G. Fraenkel. 1960. The specificity of

the tobacco hornworm Protoparce sexta (Johan) to Solanaceous plants. Ann. Ent. Soc. Am. 53: 503-507.

Yamamoto, R.T. 1963. Insect Plant Attractants. Feeding stimulants, repellents, deterrents and other related factors affecting insect behavior. Proc. Summ. Inst. Biol. Contr. for Pest Insects and Disease. pp. 494-527. Quoted from Hedin, P.A., F.G. Maxwell and J.N. Jenkins, 1974.