EFFECTS OF FEEDING ON DIFFERENT VARIETIES OF *BRASSICA* SPP. ON THE GROWTH AND SURVIVAL OF BERTHA ARMYWORM, *MAMESTRA CONFIGURATA* WALKER, (LEPIDOPTERA : NOCTUIDAE)

A Thesis
Submitted to the Faculty
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Agab Atallah Al-Hitty

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TO MY

PARENTS

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ABSTRACT

Growth, development, and survival of the bertha armyworm, *Mamestra configurata* Walker, larvae were investigated on 13 host plants belonging to three *Brassica* spp. and on two synthetic diets. The host plants tested were: four cultivars of *Brassica campestris* L., a summer turnip, and three oilseed turnip rapes (Torch, Rapido III, and Candle); five cultivars of *Brassica napus* L., three oilseed rapes (Tower, Brink, and Regent), and two rutabagas (Laurentian purple top and Lift); three types of *Brassica oleracea* L., a broccoli, a cauliflower, and a cabbage); and the cultivar Gisilba of *Brassica hirta* Moench. Survival to the adult stage, developmental rate, pupal weight, sex ratio, malformed adults, and diapause pupae were the criteria used to judge the suitability of the host plants.

In the first experiment, each of 11 hosts (Candle and Regent were not tested in this experiment) was tested by incorporating freeze-dried leaves into a synthetic diet. The standard synthetic diet (alfalfa diet) and a cellulose diet were used as controls in this experiment. The highest survival (58-79%) and the most rapid larval developmental rate (25-30 days) occurred among insects reared on the cultivars of *B. campestris* and on *B. hirta* cv. Gisilba. Almost in the same category were the cultivars Tower (*B. napus*), broccoli (*B. oleracea*), and the artificial diet. Survival was slightly lower and the rate of development slightly longer on the other cultivars of *B. napus*. The lowest survival (18-31%) and the slowest larval developmental rate (31-32 days) were among larvae reared on cabbage and cauliflower (*B. oleracea*). On the cellulose diet, development was very slow (36 days) and only a few insects survived to the adult

stage (5%).

In the second experiment, only seven of the above host plants were tested by rearing the larvae on the living plants in a greenhouse. The cultivars tested were: summer turnip, Torch, and Candle (*B. campestris*), Brink and Regent (*B. napus*), and cauliflower and cabbage (*B. oleraceae*). Conditions in the greenhouse induced diapause in 22-45% of the pupae, so survival was calculated from the number of adults that emerged from non-diapause pupae plus the number of living pupae in diapause when emergence was complete. Survival was highest (74%) on summer turnip, lower (66-61%) on cauliflower, cabbage, and Brink and lowest (57%) on Torch. The larvae developed more slowly on cabbage and cauliflower than on the other plants and the average weight of pupae formed from larvae feeding on cabbage was less (0.28 g) than on the other plants (0.31-0.33 g). The cultivars Candle and Regent were tested separately, from different insect stock. Survival was very high on both (87-89%). The other criteria measured were not significantly affected by the diet. The two experiments indicated that all the *B. campestris* cultivars, *B. hirta* cultivar, Gisilba, some of *B. napus* (Tower and Regent), and of *B. oleracea* cultivar (broccoli) were good foods for *M. configurata* larvae. The other *B. napus* cultivars Laurentian purple top (rutabaga), Brink, and Lift and of the *B. oleracea* (cauliflower and cabbage) were inferior foods. For *B. campestris* cultivar, Torch, the results of the two experiments differed in that the early larval stages feeding on living leaves suffered higher mortality than those fed on freeze-dried leaves incorporated into a diet. The characteristics of the leaf surface (hairs, tough cuticle) may have inhibited larval feeding.

The difference in results of the two experiments for cabbage and cauliflower (high mortality on diets, low mortality on living leaves) could have been caused by the release of toxins from chemical compounds (e.g. degradation of the glucosinolates) during the incorporation of freeze-dried leaves into the diets. This could be the reason for the higher mortality (59%) on cabbage than on cellulose (39%) diets in the first 6 days. The cellulose diet which has no plant substances could be used as a basic diet for future nutritional studies by adding specific plant substances and investigating the effect. The high survival on the living plants gives this technique the priority as a best way to test the suitability of any host plant.

CHAPTER I

INTRODUCTION

1. Economic Importance, Distribution, and Life History of the Bertha Armyworm, Mamestra configurata Walker

(a) Economic Importance and Distribution

The bertha armyworm, Mamestra configurata, is a native insect of polyphagous habits. The larvae feed on many species of dictyledonous plants but favor plants in the families Chenopodiaceae and Cruciferae. The earliest records of this insect were on flax, alfalfa, and sweet clover. Cabbage, corn, peas, beans, and sugar beets also have been recorded as hosts. Weeds, particularly lambsquarters, were reported as hosts and favorable oviposition sites for this insect (King 1928).

In the mid 1940's when farmers on the Canadian Prairies began to plant larger acreage of rape, reports of the insect attacking rape began to appear with increasing frequency and rape became the main crop attacked (Canadian Insect Pest Review, Vol. 22-27, 31-35). In 1971, an outbreak of unprecedented severity occurred across an area roughly 50 miles wide, extending from Edmonton in Alberta to Swan River and Dauphin in Manitoba (Turnock and Philip 1977). In 1971, growers spent about $3.3 million for insecticides and spray application (Putnam 1975). In 1972, the government of Saskatchewan spent almost the same amount on insecticides and farmers bought insecticides through private channels.

In Canada, Saskatchewan, Alberta, and British Columbia are the provinces that have been affected by this insect. In general, the distribution of this insect is from Mexico (Mexico City), north along the Cordillera to British Columbia and east through the prairie provinces of Canada to North Dakota (Kapatsa 1979).

(b) Life History

Adult collection dates suggest that Mamestra configurata is bivoltine in California and Washington (Wylie and Bucher 1977). In the prairie provinces of Canada, bertha armyworm is univoltine; it completes one generation each year and only the diapausing pupal stage can survive the winter. The moths from the overwintering pupae begin to appear early in June and reach their maximum abundance in early July. Eggs are laid on leaves of rape or other suitable host plants. Normally, females deposit their eggs on the lower sides of the leaves in a tightly-arranged honeycomb pattern, one egg thick. A female may lay 100-400 eggs per plaque (Bucher and Bracken 1976). Larvae hatch about a week later and feed at first on the leaves and later also on the terminal shoots, flowers, pod petioles, and pods. There are six larval instars. The last larval instar consumes about 75-80% of the total food consumption (Bailey 1976; Bailey and Singh 1977; Kapatsa 1979). In general, green is the color of early stages which develop paired brown or black markings on each segment and yellowish and velvety black is the color of last or mature stages. Color may be affected by type and intensity of the light (G.K. Bracken, personal communication). Larvae may hide under debris on the soil surface during the day and feed at night. During late August and early September, fully fed larvae enter the ground to a depth of 5-15 cm and form an earthern cell in which they transform into pupae and pass the winter in a diapause state. Hegdekar (1977) reported that exposures of the last larval stages to short photoperiods accompanied by low temperatures is responsible for diapause induction in the pupal stage. In the prairies, only a small proportion of the larvae are exposed to the photoperiod and temperatures which do not induce diapause in the pupal stage. Occasionally, a few moths emerge in autumn but these do not produce progeny early enough to reach the overwintering stage.

2. The Problem

While it has been well established that different host plants vary in their impact on the growth, development, and survival of any phytophagous insect, the effect of different host plants on bertha armyworm is not well known. The availability of a favorable host plant is believed to be an important factor for insect population build-up and outbreaks (Van Emden 1972). The effect of different host plants on bertha armyworm has been studied by Bailey (1976) and Kapatsa (1979). Bailey (1976) reported that survival was good on two rape cultivars, *B. napus* cv. Zephyr and *B. campestris* cv. Span, and one weed *Chenopodium album* L., but poor on potato, *Solanum tuberosum* L. Kapatsa (1979) tested 13 host plants belonging to four families. He found that these host plants varied from good to very bad for development and survival of bertha armyworm. Some hosts gave high survival to the adult stage; others gave high survival to the late larval or pupal stages, but low adult emergence, while others caused high mortality to the early larval stages. He concluded that the hosts giving low survival are utilized only when the availability of suitable hosts in the field is low and that such hosts have a potential to decrease the insect population.

The objective of this study was to determine if potential resistance to bertha armyworm exists in some *Brassica* sp. The presence of resistance was evaluated by determining the effect of larval feeding on each plant type on the survival and development of the insect.

CHAPTER II

LITERATURE REVIEW

1. Insect/Plant Relationship

(a) Insect Specificity

Insect/plant relationship is a complex interaction between two living organisms. Some biologists relate this complexity to the long and continuous co-evolution of insects and plants (Dethier 1970; Singer 1971; Southwood 1973). Understanding this relationship is of vital importance so that we can manipulate our crops to reduce losses from their insect pest. Lipke and Fraenkel (1956) once described insect/plant relationship as "the very heart of agricultural entomology". It has become essential to understand how the insects and the plants are integrated within the agriculture ecosystem, in order to put a plan for insect control without disturbing the ecosystem (Kennedy 1965). Dethier (1970) described insect/plant relationship as a relation between two dynamic biological systems; each one subject to temporal changes in physical and physiological properties. Thus, there may be a "proper fit", "partial fit", and "no fit" between the plants and the insect.

Phytophagous insects differ in the plant species or even in the parts of the plant that they utilize for food. Insects may feed on only one species or on a few closely related plant species (Monophagy), on larger group usually confined within a certain plant family (Oligophagy), or on a wider group of plants (Polyphagy), but they never feed on all plants

(Fraenkel 1959; Thorpe 1947; Thorsteinson 1960). The question of whether host selection in phytophagous insects is governed by the nutritional superiority of the particular plant or part of the plant that serves as a food, or by the presence or absence of attractants and repellents in plants which are otherwise of more or less uniform food value has not been answered.

Fraenkel (1959) suggested that secondary plant chemicals are solely responsible for host plant selection. He based his theory on the assumption that the basic food nutrients of phytophagous insects are identical and can be provided by any living plant tissue. Only variation in the quantity and quality of secondary chemicals among plants causes the diversity between plant species which leads to the specificity in plant-eating insects. Secondary plant substances are largely thought to possess no primary function (as a nutrient or energy sources) in the plant or in the insect (Hedin et al. 1977). These substances occur in plants as a defence mechanism as a result of the co-evolution of insects and plants (Southwood 1973; Waiss et al. 1977) and also serve as token stimuli which are repellents to insects in general and attractants to those few species which feed on these plant species (Fraenkel 1959).

On the other hand, Thorsteinson (1960) supported the traditional view in which the primary nutrient composition of the plant plays a major role in insect host selection. The idea that differences in food habits reflected differences in nutritional requirements was an attractive theory to most early workers (Beck 1974). Thorsteinson (1960) reported that insects do, by and large, select food plants which are nutritious. Otherwise, the species would not survive. However, it is not necessary that the insect should sense the taste or smell of every essential nutrient. Some of the nutrients in plants act as gustatory indicators of a suitable food substrate, and many insects respond and discriminate between different concentrations of these essential nutrients such as sugar, amino acids (Dethier 1937).

Kennedy and Booth (1951) proposed the "dual discrimination" theory to explain the phenomenon of host alternation in aphids. Later, Kennedy (1965) generalized his theory for all phytophagous insects. In this theory, insects select their host by responding to two types of stimuli. One stimulus comes from the secondary chemicals (flavor stimulus) and the other from feeding stimulants and deterrents, which may or may not constitute primary nutrients (nutrient stimulus).

However, most entomologists reject the Thorsteinson theory (Thorsteinson 1960) which defines the host plant as the one which lacks rejectant substances. This theory describes the search for host plants as random, eliminating any kind of cue evoked from the plants and used by the insects to find their hosts. Experimentally, insects have been observed to respond to a wide range of phytochemicals, particularly volatile substances. Insects, in their response to these stimuli, display a sequence of behavior called host finding and selection behavior. Thus, host plant specificity is determined by both positive (acceptance-evoking) and negative (rejection-evoking) stimuli (Beck 1974). Both plant morphological characteristics (texture, shape, or color) (Gilbert 1971; Hedin _et_ _al_. 1977), as well as plant chemical composition (secondary and primary), could be involved. Chemical substances that evoke orientation, biting or piercing, and continuous-feeding are called attractants, incitants, and feeding stimuli, respectively. Chemicals that prevent these behavioral processes are called repellents, suppressants, or deterrents, respectively. (Dethier _et_ _al_. 1960; Beck 1965). Related plant species usually contain a similar array of attractants and stimulants. Host specificities of insects utilizing members of the plant group may then be determined by repellent and deterrent substances present in some of the plants (Beck 1974; Chapman 1974). Gravid females usually respond to plant stimuli in their selection of host plants for oviposition. Selection of the proper host is essential to the survival of the offspring. Chemicals that evoke this kind of stimuli are called "oviposition stimuli".

The observation that maxillectomized larvae may feed on some plants not normally accepted has led some workers to postulate that host plant specificity is principally determined by repellent and feeding deterrents. Insects would, therefore, feed on any plant that is not repellent or distasteful (Beck 1974). This supports the assumption of Fraenkel (1959) that any plant can satisfy insect requirements if the insect can be induced to eat enough of it. In contrast, Waldbauer (1962) showed that although maxillectomized larvae will eat some non-host leaves, they do not develop normally on them. Insects appear to get more information about the plant suitability than is given by one or more than one stimulants or inhibitors (Schoonhoven 1969). Therefore, although insects sometimes respond to a single dominant compound, probably no such domination exists in a much larger number of situations. Consequently, an adequate response more likely requires a complicated profile of compounds (Hedin *et al*. 1977).

(b) Impact of Plant on Insect Growth and Survival

Beck (1974) represented the insect/plant relationship by two axes; one for preference and non-preference and the other one for growth and survival. He pointed out that these two aspects are not completely independent aspects in determining host plant specificity. Painter (1951) referred to these two aspects as preference, non-preference, and antibiosis. However, host plants must meet the insect's requirements in respect to both behavior and general dietetics. But a distinction must be drawn between resistance to feeding and resistance that acts by interfering with physiological processes underlying growth and survival. Beck and Reese (1975) postulated that nutritional superiority of the plant does not determine host specificity but it does determine the degree that the insect can utilize the host.

It has been known for a great many years that plant species vary in their adequacy as hosts for even the most generalist polyphagous insects. Insects do not grow equally well on all plants or plant tissues, even when there are no apparent behavioral barriers to their feeding (Reese 1977). Painter (1951) described these effects as including: (a) increased mortality during specific feeding stages or later in the insect life, (b) abnormal length of life, particularly a lengthened growth period of the immature stages and a shortened adult life, (c) abnormal size or weight, (d) abnormal form such as deformation of the pupae or the adults, (e) decreased fecundity, (f) reduction in food reserves which can result in unsuccessful hibernation or other abnormal behavior. These deleterious effects can be caused by one or more of the following factors:

(1) Feeding inhibition: Many inhibiting factors interrupt the feeding process and lead to starvation (Mabry _et_ _al_. 1977; Painter 1969). The inhibitors could be physical characteristics (tough texture or hook-like hairs on the surface) (Beck 1974; Lamb 1980) or naturally occurring antifeedant and inhibitor chemicals (Munakata 1977).

(2) Poisoning: Some plants contain insecticides, e.g. nicotine, pyrethrins, rotenone, tannin, some terpenoids, gossypol. These toxic substances occur in agricultural and non-agricultural plants and have

deleterious effects at low concentration (Stipanovic et al. 1977; Waiss et al. 1977). Plants having such substances can be utilized only by insect species that have the ability to detoxify these chemicals (Schoonhoven 1969).

(3) Metabolic effects: Abnormal growth and survival can be caused by:

(a) Nutrient deficiency: Absence or deficiency in some of the essential nutrient requirements of the insect cause abnormal growth and decreased survival (Painter 1969; Fraenkel and Blewett 1945; Waiss et al. 1977).

(b) Unbalanced nutrition: The dietary proportion of the required nutrients may be of greater importance than their absolute quantities (Painter 1969; Kugelberge 1973; House 1971).

(c) Unavailability of nutrients: Plants containing the essential nutrients for insect growth and development may differ in the state in which these nutrients exist. Insects may not be able to utilize nutrients that exist in a complex state (Beck 1974).

However, most entomologists agree that insects are similar in the nutrients required for their metabolism and energy. The essential nutrients for growth and survival include sugar (Knapp et al. 1966; Hedin et al. 1977), amino acids (Van Emden and Bashford 1971; Benepall and Hall 1967), dietary fat or fatty acids (Grison 1958; Fraenkel and Blewett 1945), minerals such as N, P, K, Ca, Mg (Barker and Tauber 1954; Branson and Simpson 1966; Slansky and Feeny 1977; Scriber 1978; Hedin et al. 1977), and water (Mellanby and Fench 1958; Beenakkers et al. 1971; Waldbauer 1964). Although the secondary plant substances are largely believed to be unimportant for insects' metabolism and energy, their existence in the plant tissue has a great effect on insect growth and survival because they interact with essential nutrients. This interaction can result in (a) reduction in the availability of the nutrients, (b) complex compounds which can be toxic, (c) deactivation of some important enzymes such as digestive enzymes (Reese 1977; Rosenthal *et al.* 1976; Green and Ryan 1972; Waiss et al. 1977). Some plants contain juvenile hormone (JH)-mimicking compounds and some other insect growth hormones which have detrimental effects (Jacobson 1977).

(4) Chronic effects: The inhibition of growth may be due to an inhibition of ingestion, assimilation or efficiency of conversion of assimilated or ingested food. A feeding insect must ingest food that not only meets its nutritional requirements but also is capable of being assimilated and converted into the energy and structural substances required for normal activity and development (Reese 1977; Beck 1974). However, it is not easy to define the actual cause of all the effects on insects feeding on intact plants. A single compound, in the plant, could have different functions and effects depending on the whole nutritional composition of the plant.

2. The Family Cruciferae

(a) Genus *Brassica* Taxonomic Relationship

Brassica is the most important Genus in the family Cruciferae. It includes many economically important crops, including rapeseed and mustard. The common rapeseed cultivars belong to two species, *B. campestris* L. and *B. napus* L. Commercial mustard crops belong to two species, *B. hirta* Moench. and *B. juncea* (L.) Coss. The less important mustards belong to three other species, *B. nigra* Koch, *B. carinata* Braun., and *B. kaber* (DC) L.C. Wheeler. *B. oleracea* is closely related taxonomically to rapeseed and mustard and includes such important crops as cabbage and its related cultivars (Downey *et al*. 1975).

The first good analysis of the taxonomic relationship with the genus *Brassica*, based on cytological evidence (Figure 1) was done by the Japanese systematist-U (Bengtsson *et al*. 1972). Later, many chemotaxonomists have established that the amphidiploid species have arisen from interspecific crosses among the basic diploid species, i.e. *B. juncea* (n=18) from *B. nigra* (n=8) X *B. campestris* (n=10); *B. carinata* (n=17) from *B. nigra* (n=8) X *B. oleracea* (n=9); and *B. napus* (n=19) from *B. campestris* (n=10) X *B. oleracea* (n=9) (Vaughan and Waite 1967; Vaughan and Denford 1968; Dass and Nybom 1967). There is no clear taxonomic relationship between *B. hirta* and *B. kaber* and the other species in the triangle. Some taxonomists include them in *Sinapis* rather than in *Brassica* genus (Downey *et al*. 1975).

By natural selection during perhaps several thousand years and by recent breeding processes, different types and forms of most *Brassica* species and cultivars have been developed. Some of these types are not well differentiated from each other. Each species has different groups and varieties, some of which have been wrongly regarded as independent species (Nishi 1980).

(b) "Cruciferae as Host Plants for Phytophagous Insects"

The most common characteristic of Cruciferae, as insect host plants, is the occurrence of glucosinolates and thioglucosides (mustard oil glucosides). Glucosinolates are secondary compounds biosynthesized from amino acids. These compounds are found only in a few families of the dicotyledonous angiosperm plants, particularly in the order Capparales, which includes the families Capparaceae, Cruciferae, and Resedaceae.

Glucosinolates are sulfur compounds with a remarkably uniform structure, varying solely in the character of the side-chain (R) of the compound. Cruciferae contain more than 60 individual compounds (e.g. sinigrin, progoitrin, glucocheirolin, sinalbin, etc.), but usually each species varies in the number and concentration of these compounds from the other species (Kjaer 1976). When the plant tissue is damaged, glucosinolates are hydrolyzed by a group of enzymes (myrosinases) deposited in the plant tissue. Volatile isothiocyanates (mustard oil), thiocyanate, and nitriles are usually produced (Figure 2). Glucosinolates, as secondary phytochemical compounds, are believed to have been developed by the plants as defense mechanisms against pests (Feeny 1976). Kjaer (1976) reported that these compounds are partly responsible for the undesirable toxic manifestations occasionally observed when large amounts of crucifer material are used in animal or human diets.

Oligophagous insects associated with Cruciferae are believed to be related to the existence of glucosinolates or their hydrolysis products that have been found in all the Cruciferous species that have been tested. These compounds serve as long distance olfactory cues and as feeding stimulants for the specialist insect fauna of the Cruciferae (Finch 1978; Nielsen 1978; Nayar and Thorsteinson 1963). These insects will attack an unusual host plant if this plant has been cultured in any allylglucosinolate compounds such as sinigrin. They also attack some plant species in families related to Cruciferae (Capparidaceae, Tropaeolaceae, and Limnanthaceae) which contain glucosinolate compounds (Feeny _et_ _al_. 1970). Cruciferous plants containing a high concentration of glucosinolates (artificially concentrated) do not significantly affect the growth or survival of insects normally feeding on Cruciferae (Blau _et_ _al_. 1978). However, such plants are less attractive as food for these insects.

While glucosinolates serve as positive cues for cruciferous insects, they represent the primary chemical defense of Cruciferae plants to other insects (Whittaker and Feeny 1971). Glucosinolates usually occur of cruciferous plants in a quantity high enough to cause death or at least drastic reduction in fitness of insects outside the crucifer fauna. Insect species characteristic of the crucifer fauna have evolved means of avoiding or reducing the toxic effect of mustard oils as well as using them or their glucosides as behavioral attractants or feeding stimulants (Schoonhoven 1969).

Glucosinolates, therefore, serve as an evolutionary boundary between cruciferous specialists and other oligophagous insects. It needs at least two genetic mutations for other oligophaga (e.g. an Umbliferae specialist) to become a cruciferous specialist; the ability to detoxify the barrier toxic compounds, allylglucosinolates, and the behavioral mechanisms that make these substances attractive (James and Feeny 1974).

Since generalist insects are believed to be less adapted to any particular class of defensive compounds than are the relevant specialist, they may be more sensitive to the concentration of these compounds. High concentrations of allylglucosinolates usually inhibit feeding of the generalists (Blau et al. 1978).

However, not all cruciferous plants are equal as host plants to specialist species. Erikson and Feeny (1974) proposed that insects tend to narrow their host range rather than to widen it. Therefore, there is a possibility of more specialization among the cruciferous insects to special host plant species within the family. Thus, host restriction cannot be explained solely by a common chemical factor such as glucosinolates, but must include factors such as plant microhabitat, plant nutritional values, and other plant defenses, both physical and chemical (Dethier 1970). Some species of cruciferous plants cause abnormal growth and some species are completely rejected by specialist insects (Chew 1975; Feeny et al. 1970). Some cruciferous plants contain other inhibitory and toxic compounds such as cucurbitacins, cardenolides, and alkaloids. These compounds cannot be tolerated by some cruciferous specialists (Nielsen 1978).

While there are differences in quantity and quality of glucosinolate compounds among Cruciferous plants, insects also vary in their adaptation and response to these differences (Feeny 1976). In addition, the nutritional composition of the plant, the concentrationof proteins, carbohydrates, amino acids, or fatty acids could have an influence on the growth and survival of any insect, specialist, or generalist (House 1974).

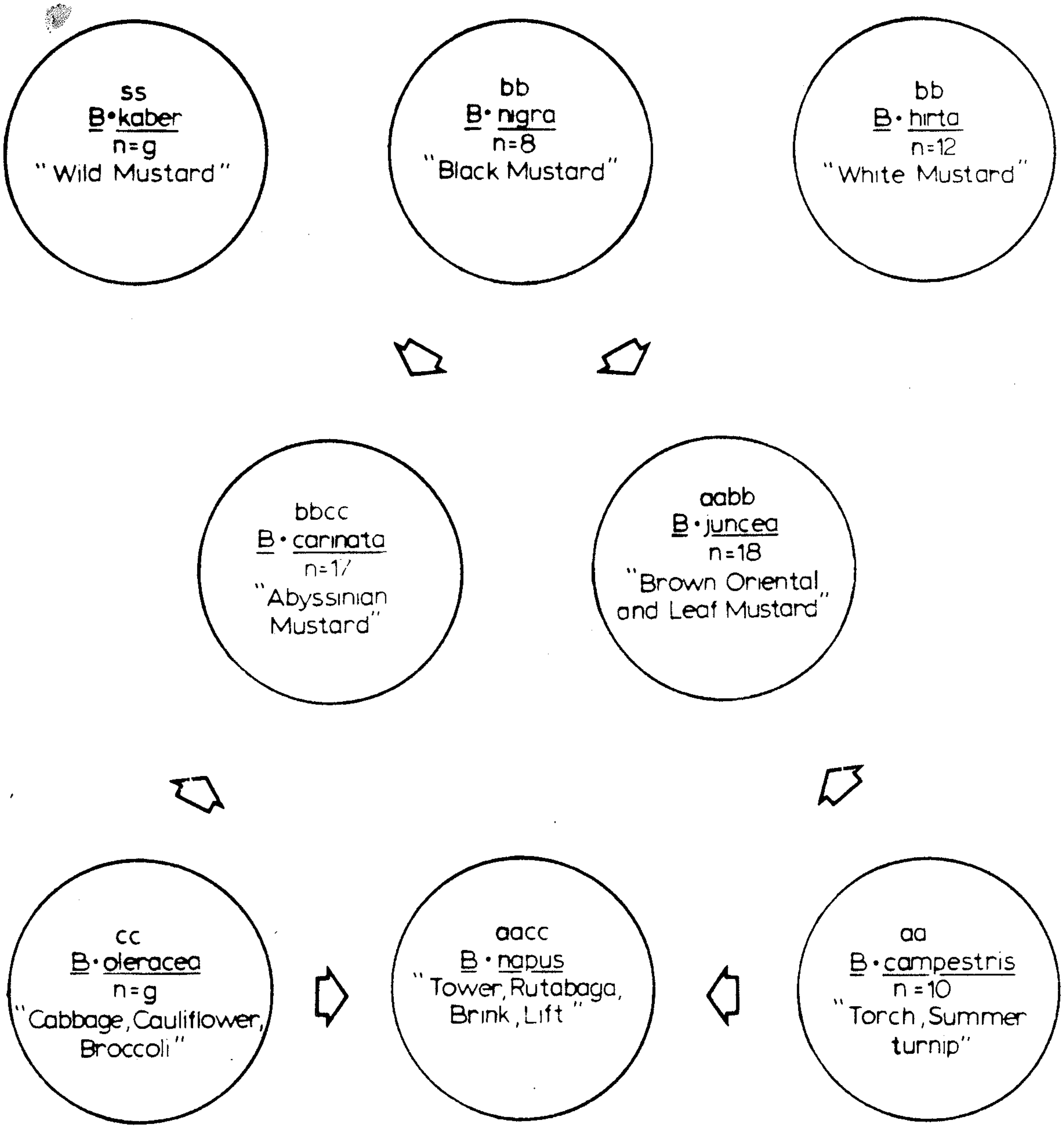

Fig.1 Genome and chromosome relationships of some economically important <u>Brassica</u> species. (From Downey <u>et</u> <u>al</u>. 1975).

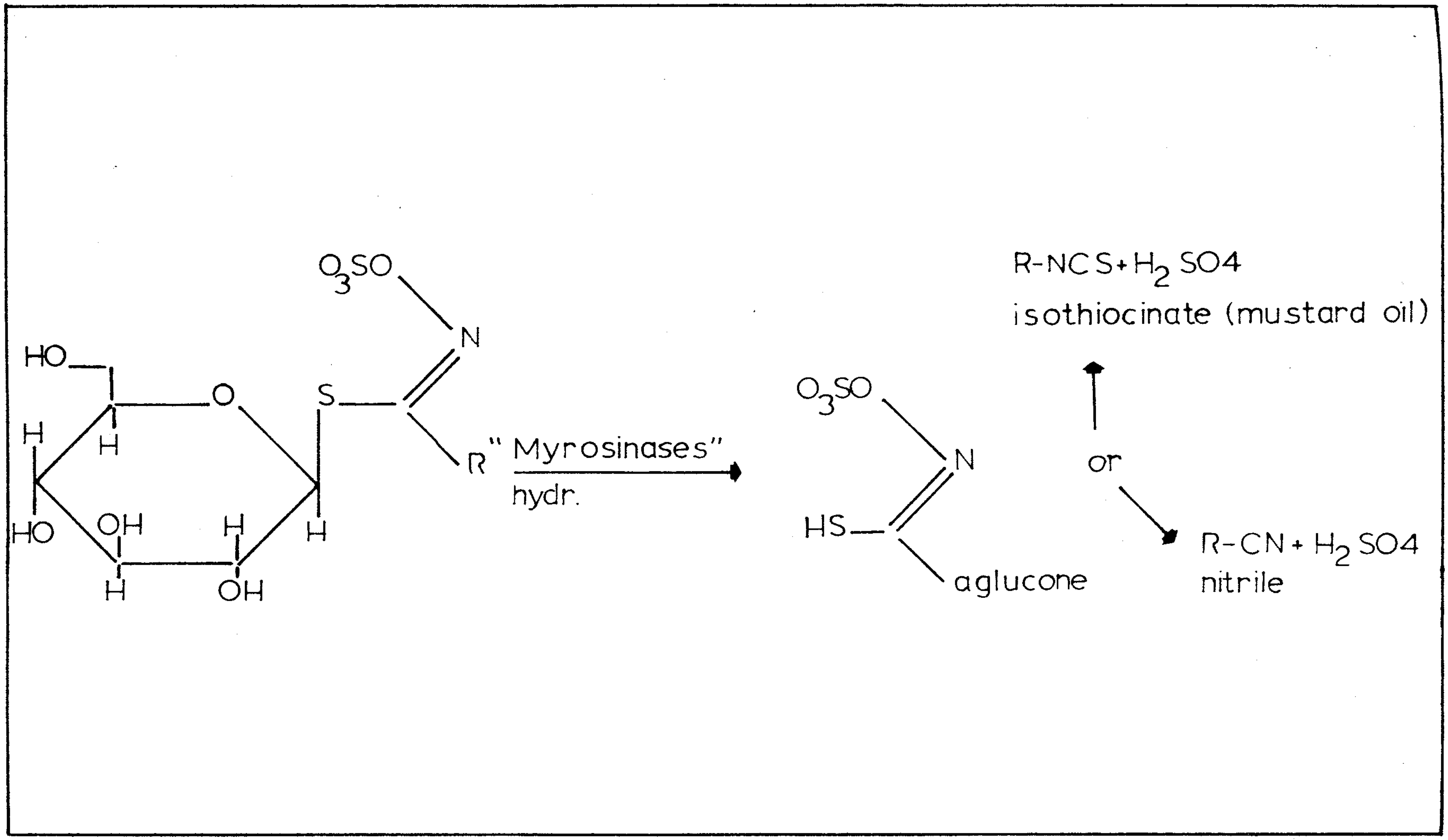

Fig.2 Hydrolization of glucosinolates to isothiocynate or nitrile, when plant tissue is damaged. (From Kjaer 1976)

CHAPTER III

MATERIALS AND METHODS

1. Insect Cultures

The eggs of *M. configurata* used in the experiments were obtained from the culture maintained at the Agriculture Canada Research Station, Winnipeg, on the synthetic diet developed by Bucher and Bracken (1976). Plaques of fertile eggs were collected daily and incubated at 25° C with 16:8 hr photoperiod and 70% R.H. One day before hatching, the eggs were placed in cups containing the diet. The larvae were allowed to complete the first instar on the diet. Newly-molted second instar larvae were used in all of the experiments because mortality of newly-hatched larvae is variable and apparently unrelated to the food provided (Bucher and Bracken 1976).

2. Host Plants

Eleven different cultivars within the genus *Brassica* were used in these experiments (Table 1). All seeds were obtained from commercial sources. The plants were grown in flats (38 X 10 X 40 cm) for the leaf diet experiment, or individually in cellulose pots (6 X 7 cm), for the living plants experiment. The plants were grown in a mixture of peat and sand (ratio 3:1) in a greenhouse at 25-27° C, 50% R.H., and 16:8 hr photoperiod. Fertilizer was added shortly after germination. Plants were used as food at age of 5-7 weeks, when four to six leaves were present.

3. Experimental Procedures

(a) Experiment 1

In this experiment, leaves of 11 cultivars of four *Brassica* spp. (Table 1) were tested as food for *M. configurata* by using each of them to replace dried alfalfa in the synthetic diet described by Bucher and Bracken (1976). Healthy leaves of each type of plant were collected, placed in a cloth bag at -20° C, and then freeze-dried and crushed to powder. To maximize the effect of the dried leaves in the diet, the weight of leaves used was twice the amount of alfalfa used in the standard diet. The standard diet, including dried alfalfa, was used as a control. In addition, a diet in which the alfalfa was replaced by an equal weight of cellulose was tested. This diet, since it contained the minimum amount of unknown or unquantified components, could be used as a basic diet to which extracts of leaves, or specific primary or secondary plant substances could be added to test their effects on the growth and survival of bertha armyworm. The diets were handled and poured into plastic cups in the same way. One hundred second-instar larvae were placed on each diet type, 25 larvae per cup. The number of larvae per cup was decreased at each growing stage to avoid crowding. The diet cups were replaced by fresh ones at least every 3 days. The cups containing the larvae were kept at 20 ± 1° C, 70% R.H. and 16:8 hr photoperiod. For each food type, records were kept of survival at intervals during the larval stage, at pupation, and at adult emergence; of the duration of the larval (L_2 to pupation) stage and of the pupal stage; the sex of each pupa; of any structural deformation in the adults.

(b) Experiment 2

For this experiment, whole plants were provided to the insects in cages. The host plants tested in this experiment were: Turnip 2520 and Torch cultivars of *Brassica campestris* L.; Brink cultivar of *Brassica napus* L.; and cauliflower and cabbage cultivars of *Brassica oleracea* L. Twelve pots, each containing a plant of the same cultivar, were placed in a flat (38 X 10 X 40 cm) which contained soil of 3 cm depth. A screen cage (38 X 70 X 40 cm) was placed over each flat. Each plant cultivar was represented by one cage. The plants inside the cages were watered from below. Individual plants were replaced every 10 days or when the leaves were consumed. Plants seeded at intervals were available, so that the same age of plant (5-7 weeks old) was available throughout the period of insect feeding.

A hundred second-instar larvae were placed into each cage. The cages were set in a greenhouse maintained at $20 \pm 5^{\circ}$ C, $70 \pm 5\%$ R.H., and 16:8 hr photoperiod. Twenty days after the larvae were placed in the cages, all plants and larvae were removed. The larvae were identified to instar and counted, then replaced in the cages with the plants. When pupation was complete in each cage, the pupae were removed, sexed, weighed, and counted. Some larvae remained in the prepupal stage long after the other larvae had pupated. The number of prepupae in each cage was, therefore, recorded. Dead pupae were recorded and removed, and the remainder were kept at 20° C, 70% R.H., and 16:8 hr photoperiod until adult emergence. Number of normal and malformed adults were recorded. The number of pupae that were in diapause was also recorded.

TABLE 1. Plant species, subspecies, cultivars, types and sources of the plants fed to larvae of *M. configurata*.

Species	Subspecies	Cultivars	Types and Sources	
Brassica campestris L.	--	turnip 2520	Summer turnip rape	(Canada)
	rapa	Torch	Summer oilseed rape	(Canada)
	rapa	Rapido III	Winter oilseed rape	(Europe)
Brassica napus L.	annua	Tower	Oilseed rape	(Canada)
	biennis	Brink	Winter rape	(Europe)
	Napobrassica	Laurentian purple top	Rutabaga	(Canada)
	--	Lift	Rutabaga	(Iraq)
Brassica oleracea L.	botrytis	Waltham (29)	Broccoli	(Canada)
	botrytis	--	Cauliflower	(Canada)
	capitata	Golden acre no. 84	Super snow ball cabbage	(Canada)
Brassica hirta Moench.	--	Gisilba	Yellow mustard	(Canada)

CHAPTER IV

RESULTS

1. Diets Incorporating Plant Leaves - Experiment No. 1

(a) Survival

The effect of food on the survival of bertha armyworm varied considerably among the types of food tested. The survival curves (Figure 3) from L_2 to adult emergence were of several types, depending on the diet. The highest survival was among larvae fed the Torch, Summer turnip, Rapido III, Tower, Broccoli, Gisilba, and alfalfa diets. Larval survival to the adult stage, on these diets, varied from 58-79% (Table 2). Survival was not quite as high among those fed the rutabaga, Brink, Lift, and Cauliflower diets where adult survival was 31-48%. Larvae fed the cabbage diet had the lowest survival (18%) among those fed diets containing plant leaves and only 5% of the larvae fed the cellulose diet reached the adult stage.

In general, most of the effect of diet on survival was expressed during the early larval instars, within 12 days of the beginning of the experiment (Figure 3). On unsuitable foods, such as cabbage, cellulose, and Cauliflower, mortality during the first 12 days was high while no mortality occurred among larvae fed Torch, Summer turnip, and Rapido III (Table 3). Mortality in the later larval stages and in the pupal stage. was similar for all diets except for high mortality in the 12-18 day period on Brink, in the 24-30 day period on Lift, and during the pupal

TABLE 2. Number of *Mamestra configurata* surviving at intervals (days) after 100 L_2 larvae were placed on cups containing 13 different diets. The number surviving to the pupal stage and to adult emergence.

Food	Days After Beginning of L_2								Pupal stage	Adult stage	
	6	12	18	24	30	36	42	45			
B. campestris											
Torch	100	100	98	94	86	82	81	81	81	79	a
Summer turnip	100	100	90	83	74	74	74	74	74	72	b
Rapido III	100	100	77	69	64	64	63	63	63	58	de
B. napus											
Tower	94	94	78	75	72	72	71	70	70	67	c
Rutabaga	94	89	81	73	67	63	59	58	58	48	e
Brink	88	83	55	52	46	43	43	43	43	41	f
Lift	91	79	62	57	47	45	42	42	42	38	f
B. oleracea											
Broccoli	98	94	80	71	69	68	66	66	66	63	cd
Cauliflower	77	53	40	40	39	34	34	33	33	31	g
Cabbage	41	32	25	25	23	20	20	19	19	18	h
B. hirta											
Gisilba	93	86	80	79	77	75	70	70	70	68	c
Synthetic diets											
Alfalfa	98	90	74	71	69	64	64	64	64	61	de
Cellulose	61	19	15	13	13	9	6	6	6	5	i

Different letters represent a significant difference in survival (P 0.05).

TABLE 3. Age-specific mortality (% of the number alive at the beginning of each period) from L_2 to pupation and during the pupal period of *M. configurata* that were fed on different diets.

	Days after Beginning of L_2									
Food	6	12	18	24	30	36	42	45	Pupal stage	Total
B. campestris L.										
Torch	0	0	2	4	9	5	1	0	2	21
Summer turnip	0	0	10	8	11	0	0	0	3	28
Rapido III	0	0	23	10	7	0	2	0	8	42
B. napus L.										
Tower	6	0	17	4	4	0	1	1	4	33
Rutabaga	6	5	9	10	8	6	6	1	17	52
Brink	12	5	33	5	11	6	0	0	4	59
Lift	9	13	21	8	17	4	0	0	9	62
B. oleracea L.										
Broccoli	2	4	15	11	2	1	3	0	4	37
Cauliflower	23	31	24	0	2	12	0	2	6	69
Cabbage	59	21	21	0	8	13	0	5	5	82
B. hirta Moench.										
Gisilba	7	7	7	1	2	2	6	0	2	32
Synthetic diets										
Alfalfa	2	8	18	4	3	7	0	0	5	39
Cellulose	39	68	21	13	0	30	33	0	16	95

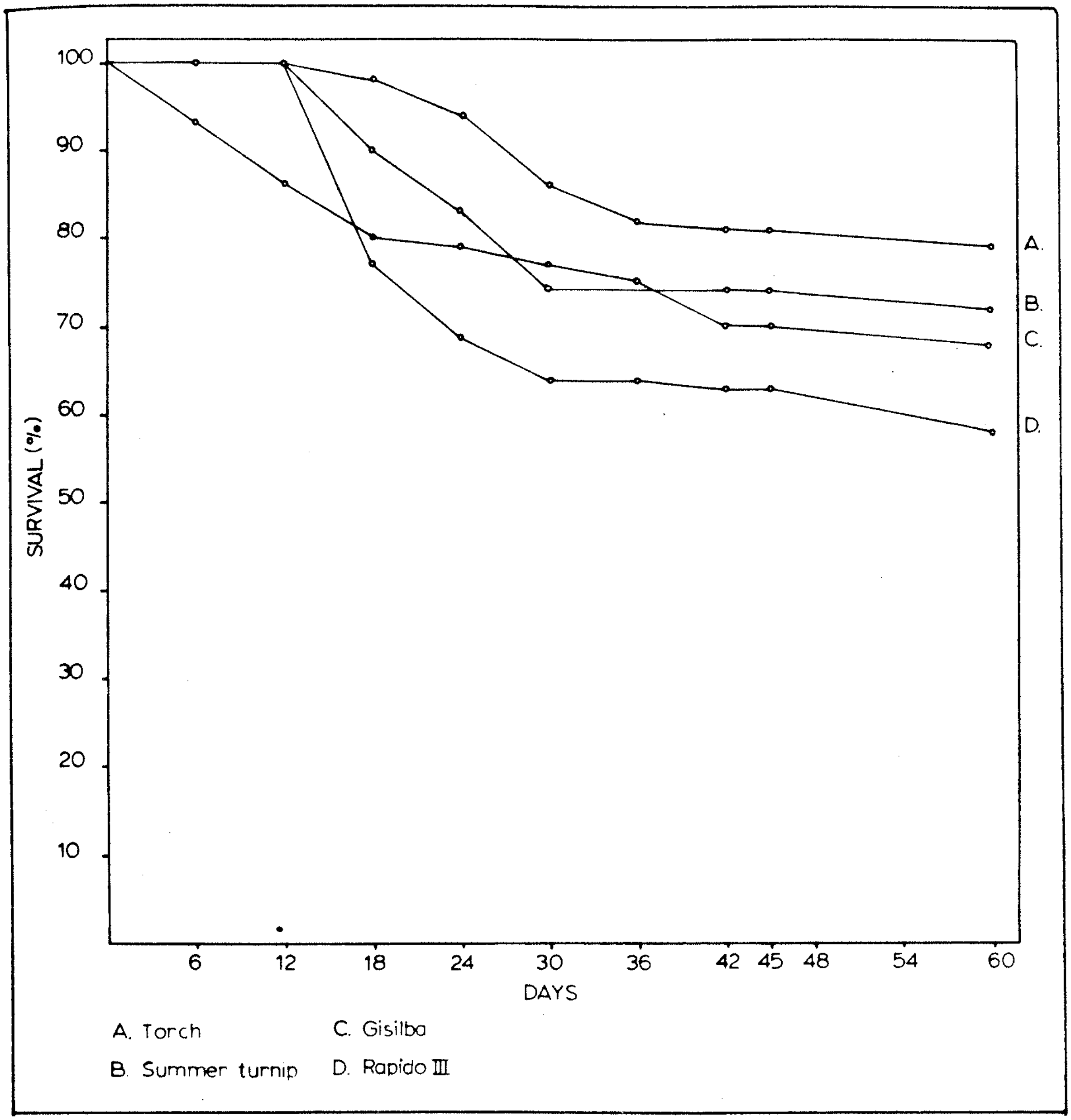

Fig.3a. Survivalship curve from the L_2 larval instar to adult emergence for M. configurata fed diet containing B. campestris cultivars Torch, Summer turnip, and Rapido III and B. hirta cultivar Gisilba.

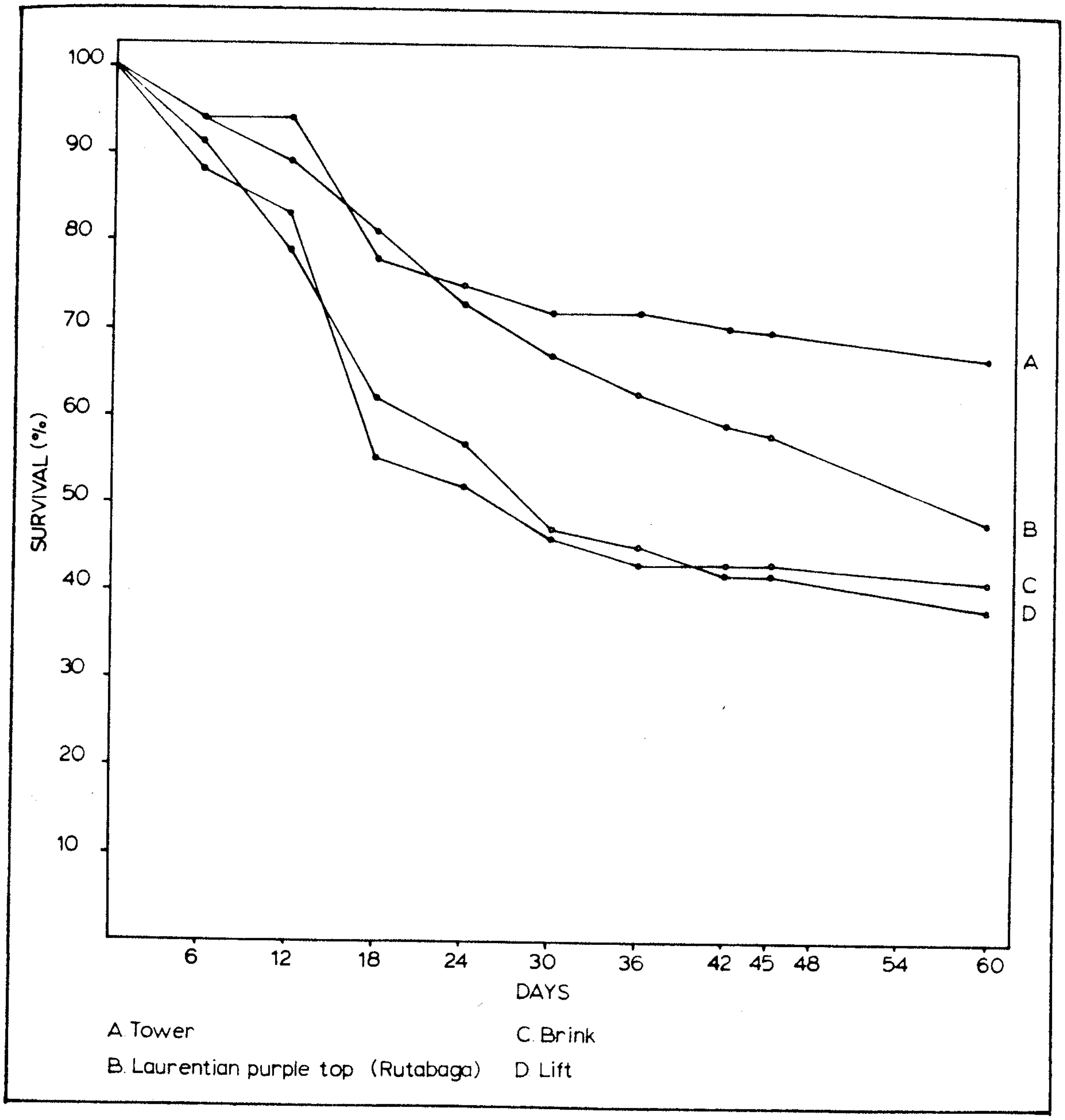

Fig.3b. Survivalship curve from the L_2 larval instar to adult emergence for M • configurata fed diet containing B • napus cultivars Tower, Rutabaga, Brink and Lift.

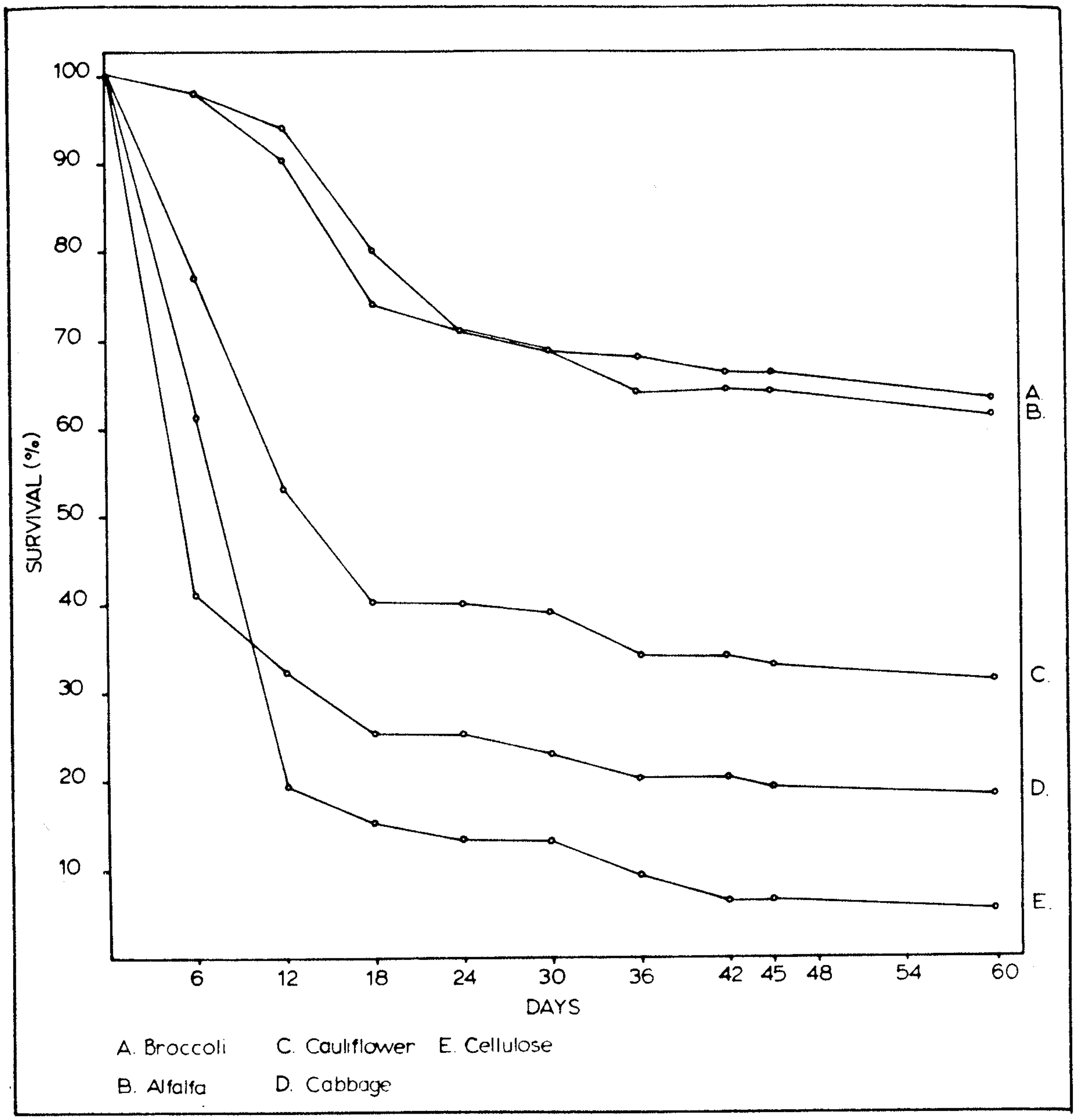

Fig.3c. Survivalship curve from the L_2 larval instar to adult emergence for M • configurata fed diet containing B • oleracea cultivars Broccoli, Cauliflower, and Cabbage and two synthetic diets Alfalfa and Cellulose.

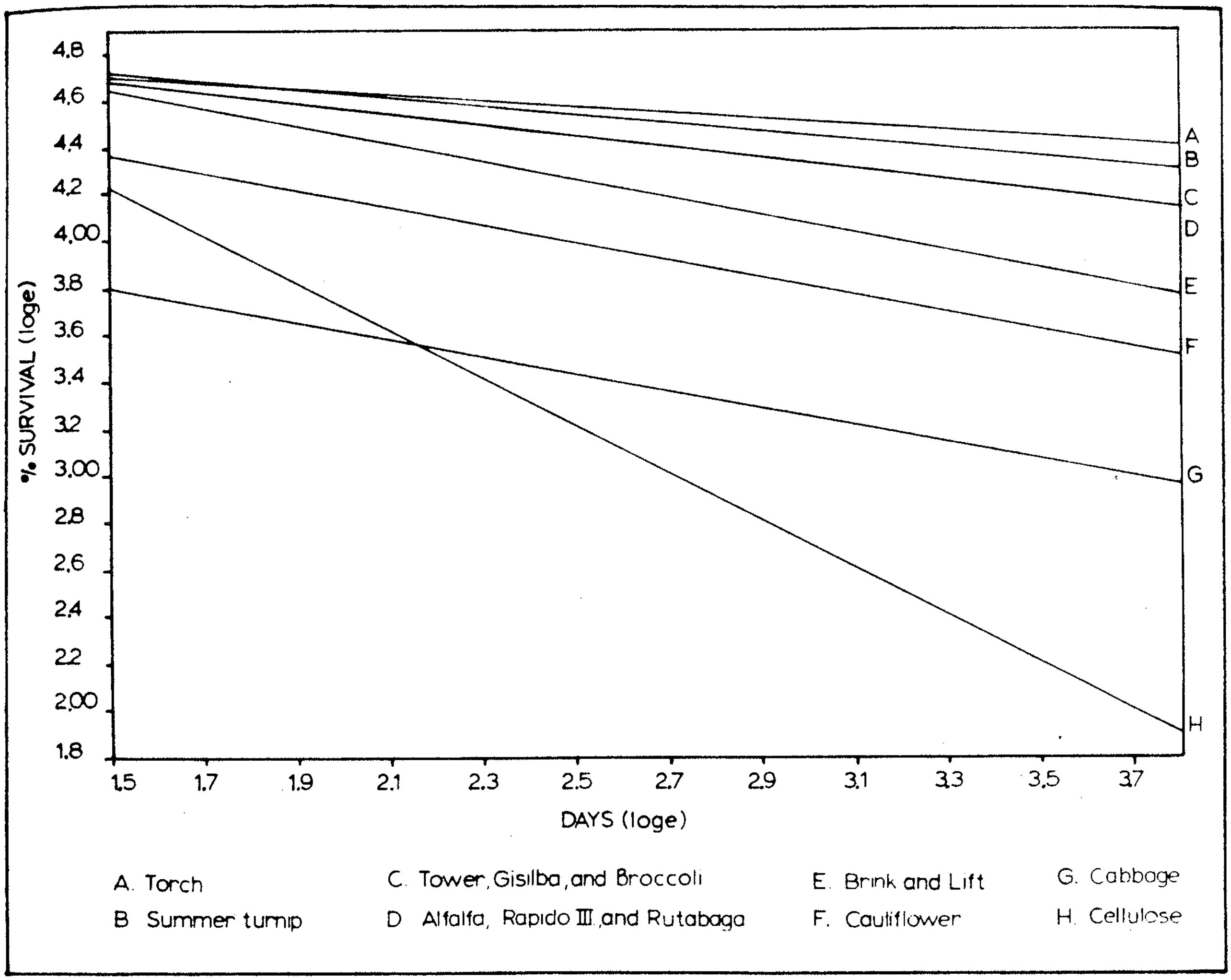

Fig.4 The relationships between survival (Log e) and age (Log e) of larvae of M • configurata fed diet containing B • campestris cultivars Torch, Summer turnip, and Rapido III, B • napus cultivars Tower, Rutabaga, Brink, and Lift, B • oleracea cultivars Broccoli, Cabbage, and Cauliflower, B • hirta cultivars Gisilba, and two synthetic diets Alfalfa, and cellulose.

FIGURE 4. The relationship between survival (Loge) and age (Loge) of larvae of *M. configurata* that were fed diets containing *B. campestris* cultivars Torch, Summer turnip, and Rapido III, *B. napus* cultivars Tower, rutabaga, Brink, and Lift, *B. oleracea* cultivars broccoli, cauliflower, and cabbage, *B. hirta* cultivar Gisilba, and two synthetic diets alfalfa and cellulose.

The equations of survivorship were:

Torch	$\underline{Y} = 4.89-0.12\ x$,	$R^2 = 0.84$
Summer turnip	$\underline{Y} = 4.96-0.17\ x$,	$R^2 = 0.89$
Rapido III	$\underline{Y} = 5.12-0.26\ x$,	$R^2 = 0.90$
Tower	$\underline{Y} = 4.86-0.16\ x$,	$R^2 = 0.91$
Rutabaga	$\underline{Y} = 5.15-0.29\ x$,	$R^2 = 0.91$
Brink	$\underline{Y} = 5.19-0.39\ x$,	$R^2 = 0.92$
Lift	$\underline{Y} = 5.30-0.41\ x$,	$R^2 = 0.97$
Broccoli	$\underline{Y} = 4.99-0.21\ x$,	$R^2 = 0.94$
Cauliflower	$\underline{Y} = 4.93-0.38\ x$,	$R^2 = 0.94$
Cabbage	$\underline{Y} = 4.35-0.36\ x$,	$R^2 = 0.98$
Gisilba	$\underline{Y} = 4.79-0.14\ x$,	$R^2 = 0.97$
Alfalfa	$\underline{Y} = 4.98-0.22\ x$,	$R^2 = 0.96$
Cellulose	$\underline{Y} = 5.77-1.02\ x$,	$R^2 = 0.95$

stage on rutabaga. There was little mortality after 24 days except among those fed Brink and rutabaga.

The relationship between survival (Log e %) and the time (Log e days) was found to be linear (Figure 4). The r^2 values varied from 0.84-0.98. Statistical analysis (Analysis of Variance of the regression lines) showed that the regression for Torch was significantly different ($P < 0.05$) from that of Summer turnip and both were different from the other diets. The intersect and/or the slope was slightly different between the regressions of Tower, Gisilba, and Broccoli, and of alfalfa, Rapido III, and rutabaga. These were significantly ($P < 0.05$) different from Brink and Lift which have almost the same regression lines. The regressions for Cauliflower and cabbage were significantly different (lower survival) than those for any other diet containing plant leaves. Cellulose was significantly the lowest ($P < 0.05$) in survival among the 13 diets tested. Different letters in Table 2 indicate significant difference in the regression lines.

(b) Developmental Rate

The developmental time for bertha armyworm was affected by the larval food (Table 4). The time spent in the larval stage (L_2 to pupation) ranged from 25 days on Summer turnip to 36 days on Cellulose. T-Test for Multiple Pairwise Comparison (Accomodates Unequal Variance) was used to analyze the variability in the developmental rate. Larvae reared on _B. campestris_ diets (Torch, Summer turnip, Rapido III) spent significantly fewer ($P < 0.05$) days before pupation than larvae on the other diets except for the _B. oleracea_ cultivar Broccoli. Larvae fed the Broccoli diet were 4-5 days faster than the larvae on the other _B. oleracea_ diets (Cauliflower, cabbage). The developmental rate of larvae on Cauliflower, cabbage, and rutabaga (_B. napus_) was the slowest (except for Cellulose

TABLE 4. Mean number of days ($\bar{x}$ ± S.D.) spent in the larval and pupal stages of *M. configurata* reared on different types of diet.

Food	Sex	Larvae			Pupae		Total Developmental Period		
		n	$\bar{x}$ ± S.D.	Range	$\bar{x}$ ± S.D.	Range	n	$\bar{x}$ ± S.D.	Range
B. campestris L.									
Torch	Female	37	28.2 ± 1.9	25-33					
	Male	44	27.6 ± 1.7	25-31					
	Both	81	27.9 ± 1.8 b	25-33	25.2 ± 1.4	22-29	79	52.9 ± 2.2	49-58
Summer turnip 2520	Female	34	26.1 ± 3.1	23-35					
	Male	40	24.7 ± 1.6	23-27					
	Both	74	25.3 ± 2.5 a	23-35	24.2 ± 1.1	21-28	72	49.0 ± 2.5	47-58
Rapido III	Female	21	27.5 ± 2.4	25-35					
	Male	42	26.7 ± 1.8	25-33					
	Both	63	26.9 ± 2.0 b	25-35	23.8 ± 1.8	21-28	58	50.7 ± 3.2	46-58
B. napus L.									
Tower	Female	36	28.7 ± 2.4	25-35					
	Male	34	29.1 ± 2.2	25-33					
	Both	70	28.9 ± 2.3 c	25-35	24.1 ± 1.9	21-28	67	52.9 ± 3.6	48-63
Rutabaga	Female	24	32.5 ± 4.8	27-39					
	Male	34	31.6 ± 4.8	25-41					
	Both	58	32.0 + 4.8 e	25-41	25.4 + 1.3	23-28	48	56.8 ± 4.2	51-67
Brink	Female	17	29.8 ± 3.0	27-35					
	Male	26	31.1 ± 3.7	25-41					
	Both	43	30.6 ± 3.5 de	25-41	25.9 ± 1.4	23-29	41	52.5 ± 3.9	50-68
Lift	Female	24	29.3 ± 4.3	25-39					
	Male	18	26.8 ± 1.5	25-29					
	Both	42	28.2 ± 3.6 bc	25-39	24.7 ± 1.8	21-29	38	53.3 ± 4.5	48-66
B. oleracea L.									
Broccoli	Female	30	27.5 ± 2.8	25-35					
	Male	36	27.5 ± 2.5	25-35					
	Both	66	27.5 ± 2.6 b	25-35	24.0 ± 1.7	21-29	63	51.4 ± 3.3	48-62
Cauliflower	Female	21	31.8 ± 3.3	27-37					
	Male	12	30.3 ± 2.6	27-37					
	Both	33	31.2 ± 3.1 de	27-37	25.6 ± 1.6	23-29	31	56.7 ± 3.7	51-64
Cabbage	Female	7	29.9 ± 3.0	27-35					
	Male	12	33.3 ± 4.1	29-41					
	Both	19	32.1 ± 4.0 e	27-41	25.4 ± 1.2	23-28	18	57.1 ± 3.5	52-68
B. hirta Moench.									
Gisilba	Female	32	30.3 ± 3.4	25-35					
	Male	38	29.3 ± 2.9	25-37					
	Both	70	29.7 ± 3.1 cd	25-37	25.7 ± 1.7	22-29	68	55.5 ± 3.8	49-66
Synthetic diets									
Alfalfa	Female	25	30.3 ± 2.9	27-39					
	Male	39	29.9 ± 3.5	25-45					
	Both	64	30.0 ± 3.3 d	25-45	25.4 ± 1.6	22-31	61	55.2 ± 2.8	52-68
Cellulose	Female	2	36.3 ± 2.3	35-39					
	Male	4	36.3 ± 1.2	35-37					
	Both	6	36.3 ± 1.6 f	35-39	23.4 ± 1.3	21-24	5	60.0 ± 2.6	56-63

diet) and was significantly (P 0.05) slower than on the alfalfa diet. Most of the larvae fed B. napus diets had almost the same developmental rate and this was similar to the alfalfa diet (30 days). In Table 4, any means with different letters are significantly different (P 0.05).

In general, females spent more days in the larval stage than males, except for those on Tower, Brink, and cabbage. However, the difference between sexes in developmental rate was small (1-3 days).

The developmental time for the pupal stage was almost the same on all the diets (23-25 days). Thus, the variation in the total developmental period was caused by differences during the larval stage. The total developmental period from L_2 to adult emergence ranged from 49 days on Summer turnip to 60 days in Cellulose. There was considerable variability in the length of the larval and pupal stages for individual insects but this variability was not related to diet rather than related to the natural differences between the individuals themselves.

(c) Sex Ratio, Diapause Pupae, and Adult Deformation

Although the number of males tended to be lower than of females (Table 5) the percentage females did not differ from 50% on any of the diets (chi-square analyses).

The conditions under which the larvae were reared (20 ± 2° C, 18:6 LD) normally produce non-diapause pupae (Hegdekar 1977). In this experiment, a few diapausing pupae (2%) were produced on some of the diets (Table 5) but their occurrence was not related to the effects of diet.

Most of the adults that emerged were normal in appearance. Among abnormal adults, some failed to completely shed the pupal integument but deformed wings or antennae were more common. Abnormalities occurred among adults from most of the diets but the number was small (8%) and the difference among diets was insignificant (P 0.05). The diets giving

TABLE 5. Percentage of females, diapause pupae, and deformed adults of *M. configurata* reared on different types of diet. The number of individuals is given in Table 2.

Food	Females (%)	Diapause pupae (%)	Deformed adults (%)
B. campestris L.			
Torch	46	1	8
Turnip 2520	47	1	6
Rapido III	33	0	1
B. napus L.			
Tower	51	2	3
Rutabaga	41	1	1
Brink	40	0	2
Lift	57	0	1
B. oleracea L.			
Broccoli	46	0	5
Cauliflower	64	1	0
Cabbage	37	0	0
B. hirta Moench.			
Gisilba	46	0	1
Synthetic diets			
Alfalfa	39	0	4
Cellulose	36	0	0

the lowest survival and longest feeding periods, such as Cellulose, Cauliflower, and cabbage, had no abnormal adults.

2. Rearing on Living Plants - Experiment No. 2

(a) Survival

Survival of bertha armyworm in this experiment was high on all the five host plants tested (Table 6). Because of the high percentage of diapause pupae which need a long time to emerge (months), survival was measured up to the pupal stage. Survival among larvae fed summer turnip (81%) was significantly higher ($P < 0.05$) than among those fed other plants. Percentage of insects reaching the pupal stage was almost the same (67-68%) on the other four cultivars.

Table 7 shows the mortality on different periods. During the first 14 days, survival was extremely high on all the cultivars (97-99%) except for Torch (87%). At the end of 14 days, most of the insects were in the fourth and fifth instars. Most of the mortality occurred after this period (L_5, L_6, and pupation). Mortality during L_5 and L_6 was higher among insects fed Brink, Cauliflower, and cabbage (29-32%) than among those fed Summer turnip and Torch (17-20%). Only 1% of the Cauliflower-fed insects died during the pupal stage while the others had 9-15% mortality. The number of insects surviving at the end of the experiment (emerged adults plus diapause pupae) was highest for those reared on Summer turnip (74%) and lower for those reared on Cauliflower (66%), cabbage (62%), Brink (61%), and Torch (57%).

(b) Pupal Weight

Table 8 shows the mean fresh-weights of pupae at the end of the experiment. The mean pupal weight varied according to the larval host

TABLE 6. Number of larvae surviving after 14 days of feeding, the number of unpupated larvae before the end of the experiment, and the number of pupae and emerged adults of *M. configurata* fed on various living plants in the greenhouse. The number of living pupae in diapause is also shown. N = 100 for each food plant.

Food	*B. campestris* L.		*B. napus* L.	*B. oleracea* L.	
	Torch	Turnip	Brink	Cauliflower	Cabbage
Survival up to 14 days	87	98	99	99	97
Unpupated larvae (few days before the end of the experiment)	2	5	7	21	11
Total pupae	67	81	68	67	68
Dead pupae	10	7	7	1	6
Living pupae	57	74	61	66	62
Diapause pupae	34	30	22	45	28
Emerged adults	23	44	39	21	34

TABLE 7. Mortality of larvae and pupae of *M. configurata* fed on various living plants in the greenhouse. N = 100 for each plant.

Food	Mortality (%)			
	Up to 14 days	Day 14 - pupation	Pupal stage	Total
B. campestris L.				
Torch	13	20	15	43
Turnip 2520	2	17	9	26
B. napus L.				
Brink	1	31	10	39
B. oleracea L.				
Cauliflower	1	32	1	34
Cabbage	3	29	9	38

plant. Those reared on cabbage ($\bar{x} = 0.28$ g) were significantly ($P < 0.01$) lighter than the others. The pupae from Cauliflower plants ($\bar{x} = 0.31$ g) were significantly lighter ($P < 0.01$) than those from Brink and Summer turnip.

Pupal weight also varied between the sexes. Male pupae were lighter than female pupae on all the host plants, but the difference was significant ($P < 0.05$) only for those reared on Summer turnip and Brink host plants. On Brink, the average female pupal weight was 40 mg heavier than for males. There was an individual variation in the pupal weight within host plants. The heaviest pupae, among those reared on Summer turnip, weighed 0.45 g, whereas the heaviest pupae among those on the other plants weighed 0.36-0.42 g. The lightest individual pupal weight (0.17 g) was among those fed Torch and cabbage plants.

(c) Sex Ratio, Diapause Pupae, and Developmental Rate

Pupae were sexed and the percentage of females was calculated (Table 9). None of the percentages differed significantly from 50%.

The percentage of pupae in diapause varied with the food plant: 60% on Torch, 68% on Cauliflower, 41% on Summer turnip, 36% on Brink, and 39% on cabbage. The temperature in the greenhouse ($20 \pm 5^\circ$ C) could be expected to induce diapause in some of the larvae (Hegdekar 1977), but the food plant also seems to have had an effect. There were more females in diapause than males on all the host plants, particularly on cabbage where 71% of the diapausing pupae were females.

The duration of the developmental period was not measured precisely because of the difficulty of observing the larvae in the cages and because pupation took place in the soil. However, a few days before the end of the experiment, the number of larvae that had not yet entered the soil

TABLE 8. Mean weight of pupae (gm ± S.D.) of *M. configurata* fed on various living plants in the greenhouse.

Food	Sex	n	$\bar{x}$ ± S.D.	Range
B. campestris				
	Female	31	0.32 ± 0.06	0.19-0.42
Torch	Male	26	0.32 ± 0.05	0.17-0.39
	Both	57	0.32 ± 0.05	0.17-0.42
	Female	37	0.34 ± 0.04	0.24-0.45
Summer turnip	Male	37	0.32 ± 0.03	0.25-0.40
	Both	74	0.33 ± 0.03	0.24-0.45
B. napus L.				
	Female	39	0.35 ± 0.03	0.24-0.39
Brink	Male	25	0.31 ± 0.03	0.27-0.38
	Both	64	0.33 ± 0.03	0.24-0.39
B. oleracea L.				
	Female	32	0.32 ± 0.04	0.22-0.39
Cauliflower	Male	33	0.31 ± 0.04	0.22-0.40
	Both	65	0.31 ± 0.04	0.22-0.40
	Female	31	0.28 ± 0.04	0.17-0.35
Cabbage	Male	31	0.27 ± 0.04	0.19-0.36
	Both	62	0.28 ± 0.04	0.17-0.36

TABLE 9. Pupae sex ratio and sex ratio of diapaused pupae of *M. configurata* fed on various living plants in the greenhouse.

Food	Pupal Sex Ratio			Diapause-Pupae Sex Ratio		
	Number of females	Number of males	% of females	Number of females	Number of males	% of females
B. campestris L.						
Torch	32	26	55	20	14	59
Turnip 2520	37	37	50	17	13	57
B. napus L.						
Brink	39	25	61	16	6	67
B. oleracea L.						
Cauliflower	32	33	50	24	21	53
Cabbage	31	31	50	20	8	71

was counted and used as an indicator of development. The number of unpupated larvae was: 2% on Torch, 5% on Summer turnip, 7% on Brink, 11% on cabbage, and 21% on Cauliflower (Table 6). The numbers were significantly higher ($P < 0.05$) on Cauliflower and cabbage which indicates that the developmental rate was slower on these two food plants.

3. Appendix to Experiment No. 2

Two other *Brassica* host plants have been tested, more recently, using the same methods described for the second experiment. The cultivars were Candle (*B. campestris*) and Regent (*B. napus*). Since each food was replicated thrice with 100 larvae/replicate, these results give an estimate of the variability in survival in experiments using living plants.

Survival and Pupal Weight

Survival to the pupal stage was high (86-89%) on both Candle and Regent (Table 10). The percentage of survival on Regent was slightly higher than on Candle, but the difference was not significant ($P < 0.05$). There was no significant difference ($P < 0.05$) in survival among the three replications of Candle, but among Regent replications, one was significantly lower ($P < 0.05$). The percentage of females that survived to the pupal stage was almost the same on both cultivars (48.1 vs. 50.1) and neither differed significantly from 50%.

The pupal weight on Regent was significantly heavier ($P < 0.05$) than on Candle. Also, the minimum and the maximum pupal weights (range) were heavier on Regent than on Candle. On both hosts, female pupae were significantly heavier than male pupae ($P < 0.05$). There were no significant differences ($P < 0.05$) in pupal weight related to the replications of Candle and Regent.

TABLE 10. Mean number of larvae survived to the pupal stage/percentage of female and pupal weight of *M. configurata* fed on the living plants of Candle, *B. campestris*, and Regent, *B. napus*, in the greenhouse. N = 100 X 3 for each food plant.

	Survival			Pupal Weight			
	n	Mean ± S.D.	Female (%)	Sex	n	$\bar{x}$ ± S.D.	Range
B. campestris							
Candle	300	86.7 ± 2.5	48.1	Female	126	0.36 ± 0.04	0.45-0.17
				Male	134	0.34 ± 0.03	0.41-0.22
				Both	260	0.35 ± 0.03	0.45-0.17
B. napus							
Regent	300	89.3 ± 9.8	50.1	Female	134	0.40 ± 0.03	0.50-0.29
				Male	133	0.36 ± 0.03	0.42-0.26
				Both	267	0.38 ± 0.04	0.50-0.26

CHAPTER V

DISCUSSION

1. Survival

The present study showed that the plants tested varied in their suitability as food for the larvae of M. configurata. The variation in survival was mainly among plants of different species (Figure 3a, b, and c). The difference may be related to the chemical composition of the plants. The differences in chemical composition among cultivars tend to be smaller than the differences between species. Different species of Cruciferae vary in their chemical composition which in turn may affect the survival of larvae feeding on them (Kjaer 1960; Cole 1976; Appelquist 1970; Maxwell 1972). In general, cultivars of B. campestris were the most suitable food for M. configurata and those of B. oleracea the least suitable. The intermediate situation of B. napus conforms to its genetic relationship to the previous two species, i.e. B. napus is a hybrid of B. campestris and B. oleracea (Downey et al. 1975; Hemingway 1976; McNaughton 1976). B. napus cultivars showed a wide range in their effect on survival of the larvae. Some of them such as Tower resembled B. campestris in their suitability while the others resembled cauliflower and cabbage, B. oleracea cultivars. The survival of early instars of M. configurata on B. campestris cultivars is in agreement with the results reported by Kapatsa (1979). He reported good survival of early instars of M. configurata larvae fed excised leaves of Summer turnip (B. campestris). He also tested two cultivars of B. napus (Zephyr and rutabaga) which were suitable food for the bertha armyworm larvae. Zephyr, which is an oilseed rape resembling Tower, was superior to rutabaga.

Cauliflower and cabbage (B. oleracea) were unsuitable food for M. configurata particularly for the early feeding stages. The mortality in the first 18 days was 60% on cauliflower and 75% on cabbage (Table 3). Kapatsa (1979) considered cabbage as an unsuitable food for bertha armyworm. The mortality on cabbage and cauliflower could not be caused by nutritional inferiority for two reasons. First, the mortality on cabbage in the first 6 days was higher than mortality on cellulose diet which lacked the plant substances. Second, feeding the larvae directly on cabbage plants, in the second experiment, gave a high survival. Thus, the mortality could have been caused by toxic substances produced when the leaves were crushed and incorporated in the synthetic diet. The cellulose diet, which contained no plant foliage, was less suitable as a food than any of the diets containing plant leaves. Only few larvae reached the adult stage. Thus, incorporating a plant substance in the diet is important for larval survival. There is a difference in the survival pattern between cellulose and cabbage and cauliflower, although all three were unsuitable food. The mortality on cellulose was consistent through all the instars while on cabbage and cauliflower it occurred mainly during the early larval stages. Most of larvae which survived the early deleterious effect of cabbage and cauliflower reached the adult stage. The surviving larvae apparently adapted to feeding on these unsuitable foods. Larval age in itself was not involved because 30 larvae transferred at the later stages from alfalfa diet to the cabbage and cellulose diets had high mortality (100-96%). Thus, the toxic effect for cabbage and the inadequacy of nutrition of cellulose, affects larvae of all ages. Most mortality in insect nutrition studies is in the early stages. Mortality at this stage can be caused by many factors such as toxic substances and nutritional inadequacy (Painter 1951; Van Emden and Way 1973), while mortality at the later stage (such as in cellulose diet) is usually related to poor nutrition (Obadofin 1979).

The second experiment showed that all of the cultivars tested (Torch, Summer turnip, Brink, cauliflower, and cabbage) were suitable as food for M. configurata. The survival was particularly high for the young larvae. Except on Torch, the mortality during the first 14 days was less than 4%. The higher mortality in the early stages on Torch could have been caused by the tough texture which is the characteristic of Torch leaves. Morphological characteristics such as cuticle thickness or hairy surfaces are important factors acting as a physical obstruction to feeding, particularly for young larvae (Bernays and Chapman 1973; Nielsen 1977). Hoxie et al. (1975) and Gallu et al. (1966) reported a reduction in survival and larval feeding as the density and length of the trichomes increased. Despite the early mortality on Torch, B. campestris cultivars (Torch and Summer turnip) were better food than the cultivars of B. napus (Brink) and B. oleracea (cauliflower and cabbage) (Table 6). This is in agreement with the results of the first experiment. However, survival on Brink, cauliflower, and cabbage was much higher than when leaves of these plants were incorporated into synthetic diets. The differences in results between the two experiments may be related to the both morphological characteristics of the leaves and to the chemical changes that could have occurred in preparing the diets (see General Discussion).

The later test of Candle, B. campestris, and Regent, B. napus (see Appendix to Experiment No. 2) confirms the result of high survival in the second experiment. The test was important because three replications were used, each one with 100 larvae. The survival was very high on both cultivars. The slightly higher survival on Regent, cultivar of *B. napus*, is not significant. The survival on Regent resembles the high survival on Tower in the first experiment. The two cultivars are a result of selection from the *B. napus* cultivars Turret, Liho, and Bronowski (Stefansson 1975). However, both *B. campestris* and *B. napus* are favored hosts of *M. configurata*. Bailey (1976) who used excised leaves to feed the larvae of *M. configurata*, reported only slight differences between the survival on Span (*B. campestris*) and Zephyr (*B. napus*).

The result of the replicated test showed no significant difference between the three replicates of Candle, whereas one of the Regent replicates had significantly lower survival than the others. The lower survival cannot be explained. Within *B. campestris*, the survival on Candle was significantly higher (P 0.05) than on Torch and Summer turnip. This could be related to the difference in insect stock used in the two tests or to the natural difference between the three cultivars as a suitable food. Comparison of Regent and Brink (*B. napus*) gave similar results.

2. Developmental Rate

Developmental rate is an important criterion in the evaluation of the effect of food on insects (Stewart and Baker 1970; Obadofin 1979). In the first experiment, the larval developmental rate on *B. campestris* (Torch, Summer turnip, and Rapido III) diets was faster than the developmental rate on diets containing *B. napus* or *B. oleracea*. The developmental rate on most of B. oleracea (cauliflower and cabbage) was slower. Waldbauer (1964) reported that a slow developmental rate could be the result of a low rate of feeding, nutritionally inadequacy of the food, or a combination of the two.

The histogram (Figure 5) shows that the larval developmental rate on the alfalfa diet is moderate. Larvae reared on some B. napus diets had a faster developmental rate than larvae reared on the alfalfa diet, but others were slower. The duration of the pupal stage was almost the same for larvae reared on all tested foods. This is in agreement with the results reported by Kapatsa (1979). Thus, the food affected the developmental rate only during the feeding stages.

The developmental rate on all the B. campestris cultivars was almost the same particularly in the range in days between the formation of the first and the last pupa (Table 4). The first pupae on these diets were 10 days earlier than on the other diets. There was a wide range between the first and the last pupae on all the diets tested, 7-19 days. Such differences between the individuals could be related to original differences between embryos. Bucher and Bracken (1976) ascribe the difference in mortality between the first instar larvae to the embryo difference between the eggs. On all diets, the mean number of days to adult emergence was less than the sum of the two means, the larval, and the pupal. This indicates that most of the individuals that died during the pupal stage were those which had a slower developmental rate during the larval stage. In contrast, Kapatsa (1979) reported that survival was higher among individuals with a slower developmental rate.

In the second experiment, although the developmental rate was not measured precisely, the difference in the number of larvae remaining on

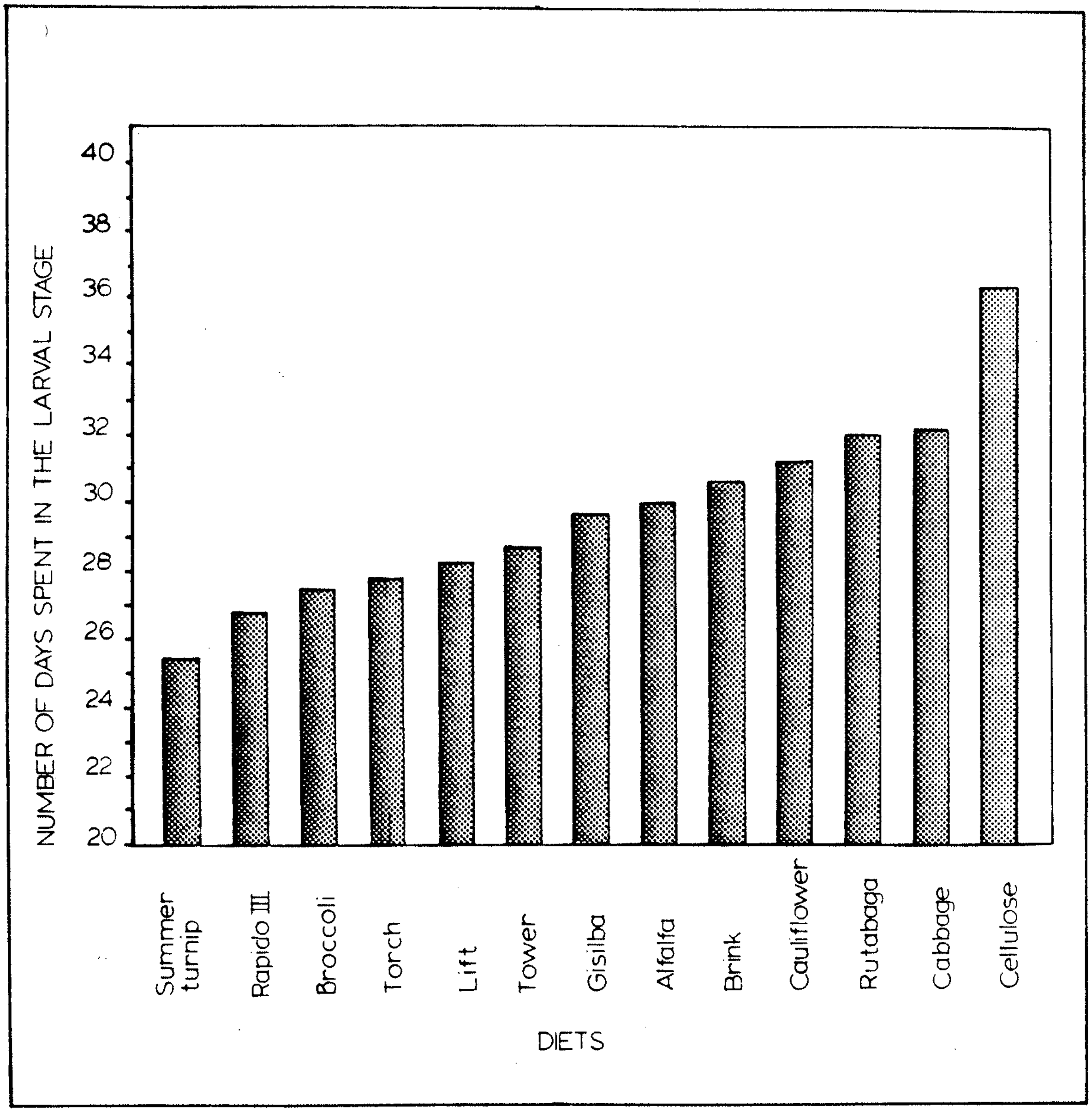

Fig. 5. Mean number of days spent in the larval stage of *M. configurata* reared on different types of diet.

the soil surface 5 days before the end of the experiment indicated that the larvae reared on cabbage and cauliflower developed more slowly than larvae on Torch, Summer turnip, and Brink. Thus, the second experiment is in agreement with the first experiment in which larvae reared on _B_. _oleracea_ had slower developmental rates.

3. Other Criteria and General Discussion

Many criteria were used to evaluate the effect of food on the bertha armyworm. Pupal weight was measured in the second experiment (Table 8). Larvae reared on cabbage plants had pupae significantly lighter ($P < 0.05$) than on other plants. The pupae on Summer turnip and Brink were the heaviest. Both of these plants were good food for _M_. _configurata_ in the first experiment. Heavy pupae is an indication of good food (Obadofin 1979). Thus, the _B_. _campestris_ cultivars in this experiment (Torch and Summer turnip) and the _B_. _napus_ cultivar (Brink) were better food than cabbage (_B_. _oleracea_). The pupal weight on both Candle and Regent was significantly heavier ($P < 0.05$) than any of the plants tested in the second experiment including Torch, Summer turnip, and Brink. Thus, the pupal weight is usually associated with the survival which was higher on Candle and Regent. The cause of heavy pupae on Candle and Regent could be the same cause of high survival which could be related to the difference in the insect stocks or to the suitability of these two cultivars. However, the pupal weight on Regent was significantly heavier ($P < 0.05$) than on Candle. Thus, Regent, _B_. _napus_, could be more suitable than Candle, _B_. _campestris_. In the first experiment, Tower, _B_. _napus_, was more suitable food than Rapido III, _B_. _campestris_. Male pupae were lighter than females. The difference was significantly ($P < 0.05$) higher, particularly among the later tested cultivars, Candle and Regent. Kapatsa (1979) reported similar results.

In the first experiment, malformed adults were counted. Higher percentage of adult malformation was recorded on the diets which gave a high survival. No malformed adults were found on diets that showed high mortality. This could be related to the low percentage of adult deformation, in general, and to the small number of adults which reached the adult stage on such unsuitable diets. However, there was no significant relationship between survival and malformed adults. Adult malformation was not recorded in the second experiment because a high percentage of the pupae entered diapause.

Only few pupae entered diapause in the first experiment while in the second experiment, about half of the pupae entered diapause. This is related to the temperature fluctuation in the greenhouse (Hegdekar, personal communication). Hegdekar (1977) reported that exposure of the larvae to 17° C induced diapause even under non-diapause photoperiod conditions. However, this does not explain the differences between food plants or between females and males.

The sex ratio was measured in the two experiments. In the first experiment, on most of the diets, there were fewer females than males. In the second experiment, there were more females than males. However, there was no correlation between sex ratio and survival. Probably the fluctuation of the sex ratio is related to chance. On plants where there was high survival, in general, the sex ratio tended to be 1:1. The ratio was almost 1:1 on both Candle and Regent cultivars (Table 10). Dingle (1966) found a higher mortality in females than in males in the fifth instar in crowded population of _Oncopeltus fasciatus_, but in a uncrowded population there was no such difference between the sexes.

Although many criteria can be used to evaluate the effect of food on phytophagous insects, survival, and developmental rate are the most important ones (Beck 1974; House 1963; Beck and Maxwell 1976). Survival and developmental rate in M. configurata were found to be associated and there was a negative correlation between the two criteria, particularly in the diets experiment (Figure 6). In the second experiment, the correlation was not clear because survival was generally high on all the plants and because the developmental rate was not measured precisely. High survival, in general, was associated with a fast developmental rate. Bailey (1976) reared M. configurata on the excised leaves of many host plants and reported that more days were needed to complete the larval stage on the plants which show less survival. Vickerman (1978) found that the duration of development of Oscinella frit (L.) was longer on barley which had low survival and shorter on wheat and oats which had high survival. Slower development on inferior food in association with higher mortality has been reported by many workers (e.g. Greenblatt et al. 1978; Atwal 1955).

In the first experiment, high mortality occurred on cabbage but when the larvae were reared on the plant (in the second experiment) the mortality was considerably less. David and Gardiner (1966) reported that some individuals of Pieris brassicae L. refused to feed on a cabbage diet, but fed when transferred to fresh cabbage. Even in the second experiment larvae reared on cabbage had a slow developmental rate and developed the lightest pupae. Thus, cabbage in both experiments was an inferior food. It has been reported that cabbage does not contain either of the two glucosides (glucocapparin and glucotropaeolin) which are known to be the most effective feeding stimulants (David and Gardiner 1966). Other substances could be involved in the inferiority of cabbage and cauliflower as a food.

Nielsen (1978) reported that glucosinolates were important in determining the suitability of cruciferous species as a host plant, but that some other compounds could have acted as inhibitors. Feeny (1976) reported that probably each insect adapted very well to a species "as an optimum host". Other varieties or species from the same taxon will differ chemically and be less suitable than the optimum host.

B. campestris cultivars were better food for the bertha armyworm than the B. oleracea cultivars that were tested. Daxenbichler et al. (1979) found that the glucosinolate composition of 14 varieties of Chinese cabbage (B. campestris spp. pekinensis) are different from those of common cabbage (B. oleracea var. capitata). Glucosinolates yielding five-carbon aglucons (excluding the sinolate carbon) predominate in the Chinese cabbage, whereas three- and four-carbon aglucons are the major ones from white and red cabbage varieties, respectively.

Turnip was reported to contain a substance **(2-phenylethylisothiocyanate)** having insecticidal properties (Lichtenstein et al. 1962). Since Summer turnip was a very good food for the bertha armyworm, this natural insecticide is ineffective or may even be used as feeding stimulant.

Cruciferous plants vary considerably in the rates of larval survival and growth they support (Obadofin 1979). Probably the effect is related to the effect of different glucosinolates between these different varieties. Nielsen (1978) reported that insects are obviously able to distinguish between different glucosinolate-containing plant species (Feeny et al. 1970; Hicks and Tahvanainen 1974; Nielsen 1977; Thorsteinson 1953). Obadofin (1979) suggested a possible effect of the quantity of glucosinolates in different cultivars of rape on their nutritional value to the red turnip beetle, Entomoscelis americana Brown. Feeny (1976) reported that the variation in glucosinolate content does not seem to affect greatly the growth rate of adapted insects such as larvae of the cabbage butterfly, Pieris rapae. Slansky (1979) suggested that glucosinolates had a toxic effect when the polyphagous yellow-striped armyworm, Spodoptera ornithogalli Guenee, was fed broccoli and other Cruciferous plants.

Lower survival in the diet experiment probably was related to toxic substances that could be released from hydrolysis of the glucosinolates in the leaves. The hydrolysis products of glucosinolates present in rapeseed and mustard meals can cause thyroid enlargement in non-ruminant animals (Joseffsson 1972). The growth and survival of an insect may be influenced by the type and amount of fat in the diet (Wigglesworth 1972; House 1974). In Cruciferae it is not known if there is a relationship between the fatty acids in seeds and insect survival on the plants (Obadofin 1979). However, many plant substances can play a major role in survival. It needs more investigation. One of the advantages of using cellulose diet, in this study, is that this diet can be used as a basic diet for future nutritional study. Specific plant substances could be added to the cellulose diet to identify the plant substances which affect feeding and insect survival.

Three techniques have been used to investigate M. configurata growth and survival. Two of them, diets with plant leaves incorporated and rearing the larvae on the living plants, have been tested in this study. In addition, Bailey (1976) and Kapatsa (1979) used excised leaves. Rearing the larvae on the living plants in the greenhouse gave the highest survival and this technique should give more accurate results for studies if the study of the interaction between the insect and the plant in the field. The problem with this method is the difficulty of determining larval survival by instar and their developmental rate. The diet technique has an advantage in that the chemical components of the plant can be tested. Using excised leaves could be less accurate because of the changes that can occur in the moisture and in the enzyme hydrolyzation of compounds in the excised leaves.

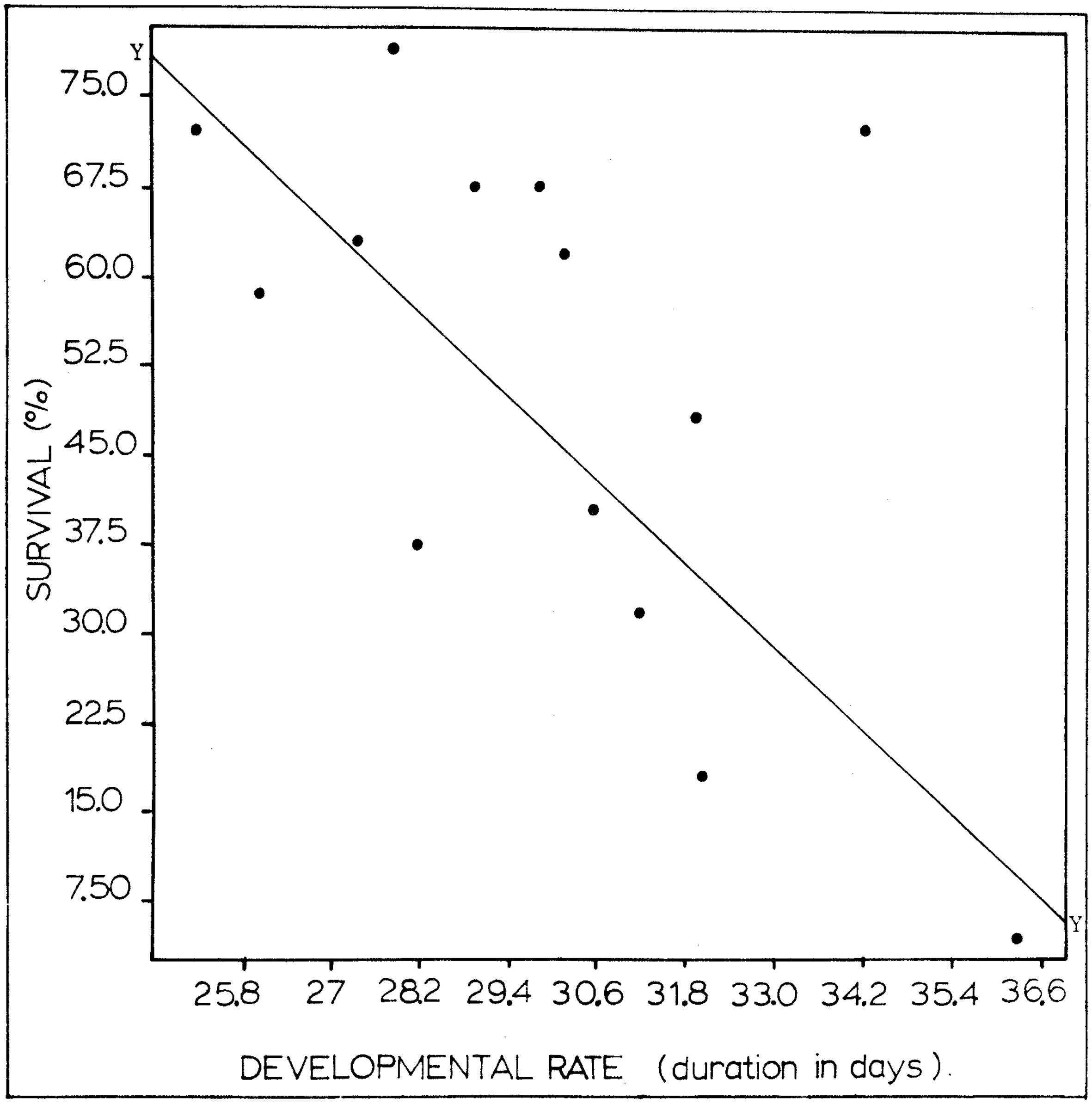

Fig. 6. The relationship between larval survival and developmental rate of M. configurata reared on different types of diets in the laboratory. The equation of the correlation was: Y=227.92-5.99x, R=0.62

CHAPTER VI

SUMMARY AND CONCLUSIONS

The host plants tested varied in their suitability as a food for the larvae of _M_. _configurata_. The impact of food clearly affected survival, developmental rate, and pupal weight. The two techniques used for this evaluation affected the results. Experiments in which plant leaves were incorporated into synthetic diet indicated that the species of _Brassica_ had large effect on survival and development. _B_. _campestris_ cultivars and _B_. _hirta_ cultivars were the best food while _B_. _oleracea_ cultivars were unsuitable as food. _B_. _napus_ cultivars were in an intermediate position; some of the cultivars resembled _B_. _campestris_ in their suitability while others approached the inferiority of _B_. _oleracea_ cultivars. This could be expected because _B_. _napus_ is a hybrid of _B_. _campestris_ and _B_. _oleracea_. The variation among cultivars of _B_. _campestris_ and _B_. _oleracea_ was generally small except for broccoli (_B_. _oleracea_) which was as good a food as the _B_. _campestris_ cultivars. This could be related to the selection of broccoli, resulting in a cultivar that approaches cultivars of _B_. _campestris_ in its nutritional and/or chemical composition.

The results of the second experiment indicated that living leaves provide better food than diets incorporating these leaves. The generally high survival, in this experiment, reduced the effect between plant species and cultivars. Nevertheless, there was a significant difference between _B_. _campestris_ as a good food and _B_. _oleracea_ particularly cabbage as a bad food. This was not only shown by survival and developmental rate but also by the weight of the pupae. In general, there was an association between the three criteria, i.e. high survival, fast developmental rate, and heavy pupal weight were a sign of suitable food. The general conclusions of this study could be summarized:

(1) Survival to the adult stage, larval developmental rate, and pupal weight are good criteria for identifying good and bad larval foods. Other criteria such as sex ratio, diapause pupae, and malformed adults were not significantly correlated with survival, development, or pupal weight. High survival, fast larval developmental rate, and heavy pupae were the indications of suitable food. Larval food had no effect on the pupal period.

(2) In general, _B_. _oleracea_ cultivars, particularly cabbage and cauliflower, were unsuitable food for _M_. _configurata_. _B_. _napus_ cultivars vary from bad to very good while all _B_. _campestris_ cultivars and _B_. _hirta_ cultivars were very good foods.

(3) Rearing the larvae on diets, containing the foliage of the host plants, gives different results from those obtained by rearing the larvae on living plants. In other words, a suitable host plant in the field can give a high mortality when its foliage is incorporated into a synthetic diet. Insects reared on the living plant are exposed to different micro-environment (plant texture, tissue moisture, light intensity, and environment moisture) as well as different chemical composition. The chemical composition of the leaves can be degraded to a different product, in the diet, which may be toxic to the larvae. Any volatile substances which could serve as stimuli had a great possibility to be missed in the diet or changed. These differences were considered the reason for the general high survival on the living plants, the high mortality on cabbage diet,

and the mortality of the young larvae on the living plants of Torch cultivar.

(4) Rearing larvae on living plants is the best way to compare their relative suitability as food but synthetic diets may be necessary to evaluate the cause of these differences. For example, the addition of specific chemical compounds to the basic cellulose diet could provide information on their effect on insect survival and development.

CHAPTER VII

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