INSECTS AND RAPESEED PLANTS

By

SUSAN K BARNABE

B.Sc., The University of British Columbia, 1971

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Plant Science)

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

December 1984

© SUSAN K BARNABE, 1984

22

Department of ___Plant Science_____

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date ___11 December 1984_____

ABSTRACT

Rapeseed is grown from two closely related species of <u>Brassica</u> in many varieties. The behaviour of seven insects was studied to determine their responses to low erucic acid rapeseed, represented by a typical and a Canola variety of each species. The Canola varieties have a lower gluco-sinolate concentration in the seed coat than typical varieties. The insects were chosen because they were oligophagous or polyphagous. The actions of adults of two species of moths, <u>Mamestra configurata</u> Walker and <u>Plutella maculipennis</u> (Curtis), were studied by using an olfactometer; four species of aphids, <u>Myzus persicae</u> Sulzer, <u>Macrosiphum euphorbiae</u> (Ashmead), <u>Brevicoryne brassicae</u> (Linnaeus), and <u>Acrythosiphon pisum</u> (Harris), were studied when the adults were placed at the base of each type of plant.

The insects responded in accordance with their normal associations with cruciferous plants as hosts. Their responses were not materially affected by genetic differences among the four varieties, even though these included distinct morphological and biochemical differences. Behavioural differences towards plant species were observed in the polyphagous aphids, which affected their distribution on the plants. These differences were not associated with varieties or glucosinolate contents.

These results indicated that the differences between the two rapeseed species and typical and Canola varieties would neither materially affect the responses of attacking insects nor the resistance of the plants to insect attack in the field.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

INTRODUCTION

Insects are diverse. Scientific classifications describe gross differences between their anatomies while their physiological capabilities in metabolic, reproductive and other processes result in further, more subtle differences. Their mouth parts accommodate a range of feeding mechanisms that include lapping, piercing and sucking, biting and chewing. Their glands and organs differ and result in varied abilities to produce sounds, light, and secretions and especially, to sense stimuli. Insects' life cycles vary, they molt as they mature and their metamorphosis may be slight, incomplete or profound. As adults they may even have different morphs or forms within a species. All these biological differences are associated with behavioural differences which may be further linked to the insect's external environment.

Most known insects depend on plants in their environment for food, shelter, or reproductive requirements. Several theories describe possible mechanisms in host plant selection (Kennedy 1965) and try to account for the variability among insects in the range and number of their host plant associations (Gilbert 1979). The importance of environmental factors in any insect-plant interaction is stressed in the literature. The complexity and dynamics of this interaction are illustrated by the selection of a plant for oviposition by an adult, whose action then predetermines the food and environment available to the immature insect, often many months in the future (Beck 1974, Chapman 1974).

"Two characteristics (physical and chemical properties) of
plants determine the degree to which a plant is consumed by
an insect ... "   Bailey (1976)

Mechanical or morphological factors which are important in insect-
plant interactions include the plant's colour, the character of its
covering such as thickness and toughness, hairiness, waxiness, the presence
of protective cell structures or mechanisms, and its growth habit and
vigour (Painter 1951).   The insect reacts to these remotely through
perception of shape and colour and closely through contact.   It responds
by feeding or ovipositing if the plant site is suitable.

"There is no question that patterns of chemicals in plants
may have profound effects on the life histories of insects"
Feeny (1976)

Plants comprise a storehouse of inorganic and organic constituents.
Carbohydrate, lipid and protein processes produce fundamental or primary
products which are nutritive, and secondary products which are not nutri-
tive but may affect the metabolic and physiological processes of an insect
(Reese 1977 and 1978, Reese and Beck 1976).

The secondary biochemicals are invariably more diverse than the
primary products.   Generally, they result from terpenoid, phenolic and
nitrogen pathways (Harborne 1977).   A given compound may be found in
different plant families in numerous species, or may be botanically
isolated (Levin 1976).   Compounds may vary with the plant part and age, be
associated with living or non-living cells, be in spaces between cells, or
in ducts and glandular hairs.   They may be released as volatiles or root
exudates and may be leached from plant material (Whittaker and Feeny 1971).
The physiological functions of secondary products in plants are rarely

known. Chew and Rodman (1979) have summarized suggested functions for various members of this group, such as:

regulators of plant growth or biosynthetic activities,

storage forms of plant growth regulators,

energy reserves,

transport facilitators,

waste products,

detoxification products of environmental poisons,

shields against excessive radiation, and as

effectors of allelochemical interactions between plants and their plant competitors and between plants and heteroptrophic organisms.

As early as 1888, Stahl suggested that secondary biochemicals provided plants with a chemical defense against insects (Jones 1972). In 1906, Cook attributed this function to gossypol in the oil glands of cotton (Stipanovic et al. 1977) and the idea was later confirmed by Dongre and Rahalkar (1980). Secondary chemicals that function to protect a plant are called allomones.

However, secondary biochemicals do not always provide protection, but may be used by the insects as kairomones, to provide cues and behavioural triggers for insect-plant interactions. This function was first described in 1910 by Verschaeffelt, who found that the selection of plants by the cabbage butterfly, Pieris rapae, was affected by glucosinolates, which had to be present if the adults were to select plants as oviposition sites and if the larvae were to select plants as food (Kennedy 1965). Non-nutritive secondary plant chemicals may act as kairomones by insects not directly

associated with the plants. A braconid wasp parasite, <u>Diaeretiella</u> <u>rapae</u>, responds positively to cruciferous volatiles using them to locate its host, the cabbage aphid (Whittaker and Feeny 1971).

Thus plant biochemicals may regulate or control insect behaviour. Insects have chemoreceptors for nutritive and non-nutritive plant biochemicals and can receive and recognize plant cues. Chemoreceptors of nutrients allow the insect to determine nutrient quality and quantity in the plant site. Chemoreceptors of non-nutrients are usually associated with insects that have restricted host ranges.

The cues may be direct, as when the biochemicals interact with gustatory organs on external or internal surfaces of the insect that touch the plant material, or they may be indirect so that the insect uses its olfactory organs to sense the plant volatiles. Insects are sensitive to volatiles and can monitor small numbers of molecules in the air (Osborne 1972) so that volatile reception is more specific and sensitive than gustatory reception.

The implications of chemoreception to insect survival and population growth are apparent. In this unidirectional communication, chemicals and the plants associated with them are specifically avoided or selected by the insect, an adaptation that increases insect survival by helping to locate suitable host plants. Staedler (1976) suggested that chemoreception is probably the dominant sense in insect-plant interactions. Verschaeffelt's 1910 observations (in Kennnedy 1965) influenced the development of many theories to explain and describe host plant selection, insect-plant interactions and especially adaptation and co-evolution. They were the starting point for many studies in chemical ecology, including this one.

RAPESEED PLANTS

Introduction

The first objective of this research was to study insect-plant interactions which involved a secondary product known to act as an allomone and a kairomone (Appendix A).

Eleven families of dicotyledons, including all Cruciferae, and some Capparidaceae, Resedaceae, Moringaceae, Tovariaceae, and Tropaeolaceae contain glucosinolates (Erdtman 1969). Glucosinolates, or mustard oil glucosides, or thioglucosides, are organic anions with a uniform structure:

$$R - C - S - glucose$$
$$\parallel$$
$$N - OSO_3-$$
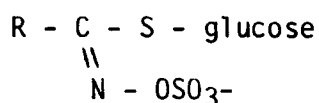
There are 70 known side chains (R), of which 60 are found in the crucifers (Kjaer 1976).

Myrosinase, or thioglucosidase, or thioglucoside glucohydrolase is present throughout plants which contain glucosinolates and may be enclosed in idioblasts or located in membranes or cytoplasm (Appelqvist 1972). Autolysis or the crushing of plant material results in the enzymatic hydrolysis of the glucosinolates. The general reactions (Fig. 1) result in the hydrolytic cleavage of the β - glucosidic bond which releases glucose, and a spontaneous re-arrangement which liberates sulphur as SO_4- and produces a nitrile or an isothiocyanate (Appelqvist 1972, Tsuruo and Hata 1968) which can cyclize to an oxazolidinethione (Tallent 1972). The isothicyanates are

Figure 1. Diagram of Glucosinolate – Myrosinase hydrolytic reaction, taken from Appelqvist (1972).
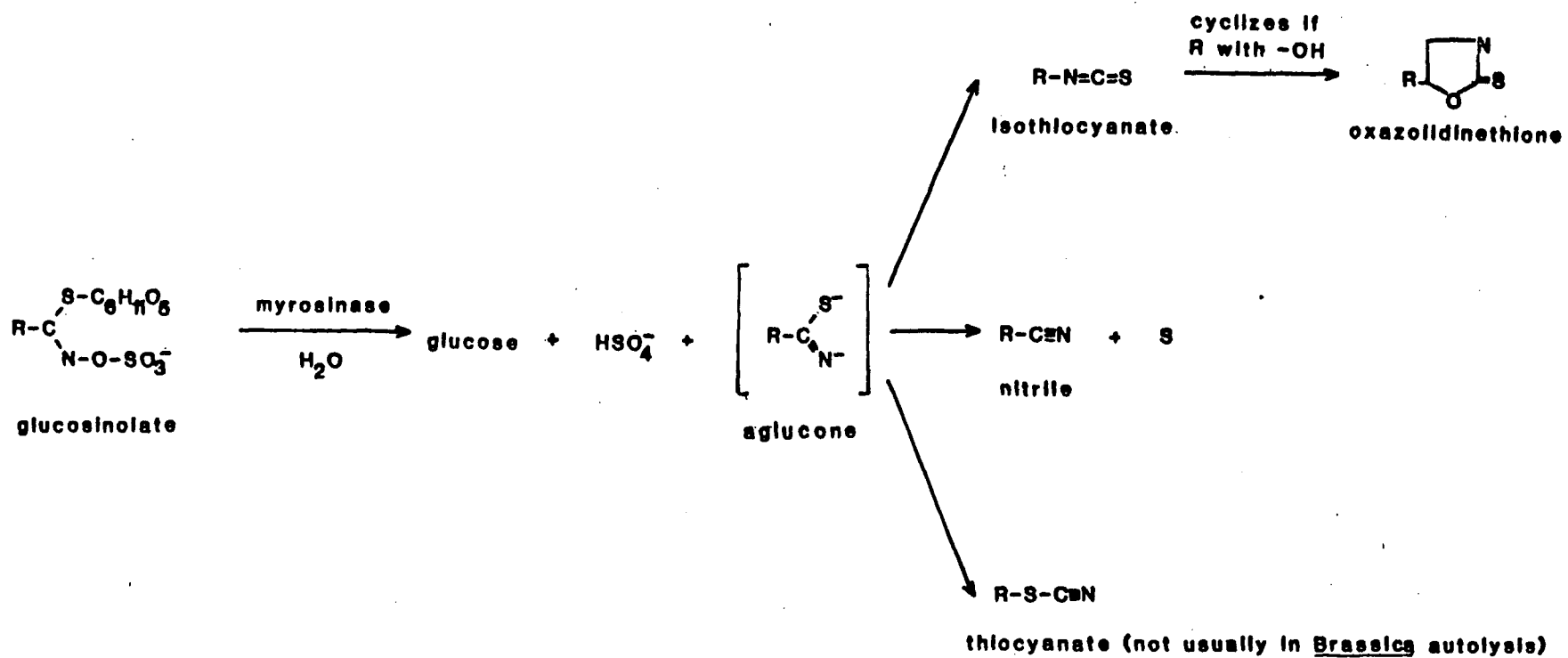
volatile and may be released into the environment.

A cruciferous plant was considered ideal for this investigation because glucosinolates are present in all members of the family and are otherwise limited botanically and because volatile and non-volatile secondary products are associated with the plants.

There are 2,500 species of plants in 350 genera in the Cruciferae (Kjaer 1976). Rapeseed includes two species, Brassica campestris, called Polish or turnip rape, and Brassicae napus, called Argentine rape or, simply, rape. Both species have summer and winter forms which are grown for seed and fodder respectively.

B. campestris is a diploid (n = 10) and it must cross-pollinate. B. napus is a hybrid (n = 19) resulting from the cross between B. oleracea (n = 9) and B. campestris and it can self-pollinate (Fig. 2). The morphologies of the species differ and the following descriptions are based on Bengtsson et al. (1972), Craig (1970), Agriculture Canada (1980) and personal observations.

The appearance of B. campestris is mustard-like and the surface has many hairs. Its yellow-green leaves have short petioles that clasp the stem. The foliage is closely spaced at the bottom and is less dense towards the top of the plant. The plants grow from 60-100 cm tall and have small, reddish-brown to black seeds that mature in 88 to 98 days. It yields about 25% less than B. napus but is somewhat resistant to shattering of the pods and to early spring frosts.

B. napus is cabbage-like and the plant surface is wax-coated and has few hairs. Its blue-green leaves are widely spaced with long petioles. The foliage at the top of the plant partly clasps the stem. The plants

Figure 2. Relationships of rapeseed to other <u>Brassica</u>, taken from Bengtsson et al. (1972) with n chromosome number.
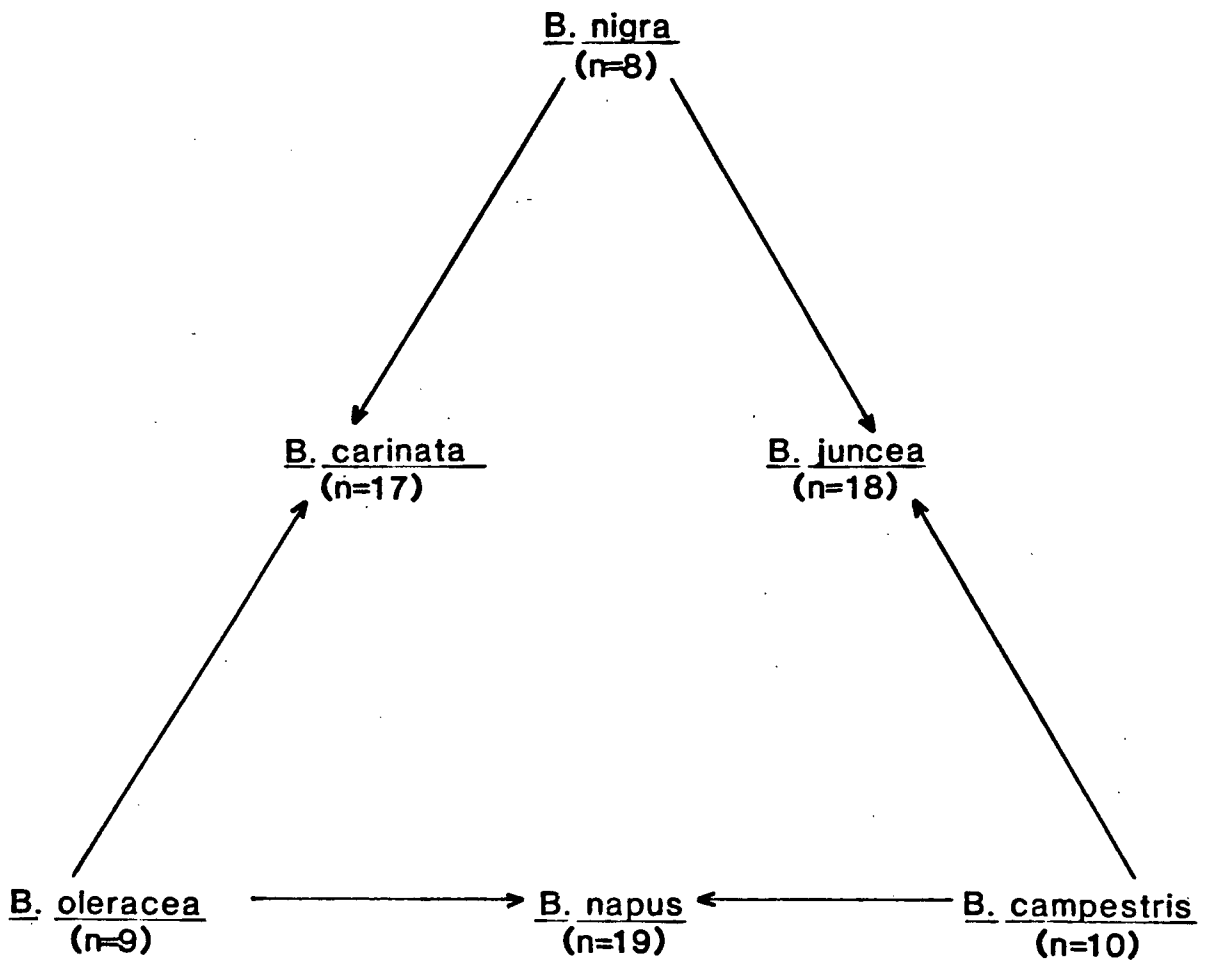
range from 75-120 cm tall and have large, dark brown to black seeds which mature in 102 to 104 days. The pods of B. napus shatter easily and the plant is susceptible to frost and drought.

Rapeseed has been grown in Canada since 1942 when it was a "war emergency crop" (Weinberg 1970) to supply oil for use as a lubricant in steam engines (Craig et al. 1973). The use of the seed shifted away from being a source of industrial oil only, when the fats were used for human consumption and the proteinaceous residues were used as animal feed and soil fertilizer (Sallans 1964). The presence of glucosinolates and erucic acid plus their products, in oil and meal used for nutrition, was undesirable and resulted in increased production costs and decreased quality (Loof and Appelqvist 1972). A ban on food use by the Canadian Department of National Health and Welfare was imposed in July and lifted in October 1956. There was every incentive to remove the undesirable biochemicals through breeding. Agriculture Canada at Saskatoon, through Dr. R.K. Downey and his colleagues, accepted the challenge to produce varieties of rapeseed with suitable edible oil-seed products. An extensive breeding programme resulted in varieties having reduced levels of glucosinolates in the oil and meal by the 1970's. The licensing and naming of Canadian-bred varieties as Canola, rather than rapeseed, acknowledged the presence of the desirable qualities and enabled Canada to become the world's first and largest producer of Canola rapeseed (Stefansson 1981). The objectives of plant breeding in rape are listed in Table I.

Table I. Objectives of plant breeding in rapeseed, taken from Loof and
         Appelqvist (1972).

.

Agronomic properties

1. Increased yield of seed.

2. Greater tolerance to low temperatures, water-logging, salinity,
    heat, and drought.

3. Increased resistance to insects and fungus pests and herbicides
    (Beversdorf 1981).

4. Adapted maturity, increased stalk strength, increased resistance
    to shedding.

Quality properties (of the seed)

1. Increased seed size.

2. Lower percentage of fibre and less pigmentation in seed coat.

3. Higher content of fat, protein and other valuable substances.

4. Lower content of fibre, glucosinolates and other toxic or less
    valuable substances.

5. Suitable fatty acid composition.

Materials and Methods

Appleqvist (1976) made this statement with its quote when describing rapeseed:

"For the precautious investigator of cruciferous lipids, the
statement of Carolus Linnaeus about the advantages of rape-
seed cropping can be applied metaphorically: '... those who
become interested in this crop have no reason to regret their
toil when they in this manner can derive rich remuneration
from a well cultivated soil (Linnaeus 1751)'"

The use of rapeseed as the cruciferous plant in my research seemed ideal: it is economically important, two plant species could be studied, and the plant breeding programme had developed varieties with reduced glucosinolates in the seed. Two varieties were selected from each rapeseed species. Table II summarizes their contributions to Canada's rapeseed acreage from 1977 to 1980. All yield low erucic acid rapeseed (LEAR) but Torch and Midas are no longer recommended for cropping because their gluco- sinolate content is too high (Agriculture Canada 1980) whereas Candle and Regent are Canola varieties. The second objective of this research was to determine if the Canola varieties had different susceptibility to insect attack, than the high glucosinolate varieties. The seed lots used here were not analyzed, but approximate contents were provided by Klassen, (personal communication 1980). The glucosinolate contents are listed by the varietal name:

Table II. Per cent of total rapeseed acreage seeded in the Prairie provinces for the selected varieties from 1977 to 1983 compiled from the Prairie Grain Variety Surveys.

	Year						
LEAR Rapeseed	1983	1982	1981	1980	1979	1978	1977
B. campestris							
Candle (Canola)	16.3	33.5	29.8	26.3	25.3	11.6	0.9
Torch	3.3	7.0	9.2	15.2	24.7	36.1	43.7
B. napus							
Regent (Canola)	18.8	28.3	27.0	25.2	20.3	1.1	Trace
Midas	<0.7	1.1	1.6	3.0	6.2	16.3	20.5

B. campestris (about 1% erucic acid):

Candle   about 1 mg/g

Torch   7.8 mg/g

B. napus (less than 1% erucic acid):

Regent   about 1.5 mg/g

Midas   12-13 mg/g

The rapeseed was supplied by Dr. A.J. Klassen, Research Scientist, Oilseeds, at the Research Station, Agriculture Canada, Saskatoon, Saskatchewan. The 100 g samples of each variety were the sources for all plants.

Greenhouse facilities at the Research Station, Agriculture Canada, Vancouver were used for starting the plants. These were seeded in a mixture of soil and peat in small pots and placed in a greenhouse with maximum temperatures of 16°C in the day and 14°C at night with a 14-10 h light-dark cycle. One week after planting the seedlings were thinned to one plant per pot.

Two- to three-week-old seedlings were moved to the UBC greenhouse facilities. They were transplanted to 16 cm pots and kept in a greenhouse with minimum temperatures of 18°C and a 14-10 h light-dark cycle. The plants were inspected and hand-cleaned to ensure that insect contamination was minimal, since no pesticides could be applied.

The two rapeseed species normally have slightly different developmental rates, so that B. campestris flowers and matures before B. napus. But the uniform environment in the greenhouses affected the growth patterns of

the two rapeseed species by reducing the normal developmental differences around the summer solstice. The plants used were selected to be typical, healthy, and in similar physiological states. The cultivars of each species were observed to have similar morphologies, although the hairs on Candle were more irritating to human skin than those on Torch.

FEMALE MOTHS AND RAPESEED PLANTS

Introduction

The two moth species selected were known to have different host plant ranges but to be regularly associated with rapeseed plants.

Mamestra configurata Walker, the Bertha armyworm is often a pest of crucifers and especially of rapeseed with some attacks attaining economic importance (Manitoba Department of Agriculture 1980). The female moth oviposits plaques containing up to 400 eggs. The first-instar larvae are motile and they disperse, airborne on silken threads and by crawling. The caterpillar is polyphagous and can feed and develop on numerous crop and ornamental plants in many families, most of which do not contain glucosinolates. Therefore, even though the female has a strong role in host selection, the biology of the caterpillar can compensate for the choice of an oviposition site which may be less than ideal as larval food.

Plutella maculipennis (Curtis) (= *xylostella* [L.]), the diamondback moth, is looked upon as a pest of rapeseed although not one of economic importance (Agriculture Canada 1980). Females oviposit single eggs. Early-instar larvae are leaf miners and are oligophagous on cruciferous plants. Larvae respond positively to glucosinolates (Nayar and Thorsteinson 1963, Thorsteinson 1953). Thus, the role of the female in host selection is important to the species. Indeed, electro-antennograms have demonstrated direct responses to glucosinolate volatiles (Underhill, personal communication 1981).

"A close relationship often exists between attraction to the host plant and egg laying behaviour of the insect. Females are attracted to suitable host plants which provide food for the larvae" Cole (1976)

The interactions of female moths with plants are more direct and important to a species than those of the males. Female moths must locate and select plant material suitable for oviposition. Numerous cues are important in these responses and the success of the resulting offspring is certainly affected by the choices of the female.

An objective of this study was to determine how rapeseed volatiles affect the plant attraction and oviposition responses in females of both moth species. Since oviposition in the field begins at bloom this plant stage was selected (Agriculture Canada 1980). The rapeseed volatiles, therefore, included isothiocyanates, bloom volatiles and, probably, additional components. An olfactometer was used to maximize these olfactory cues and minimize others, especially visual cues.

Synchrony is often a vital component of insect and plant interactions. For this reason both young and old female moths were studied in each of the species to determine the effect of this factor on their response to the plants. Young moths were newly emerged and presumably preparing to mate. One reason for the use of females only was to eliminate the possibility that a sex pheromone in either species might be involved as a stimulus. These females were held for several days and placed with males before being used again. The old moths were then likely to be mated and gravid and expected to be more responsive to plants than young moths since they would be searching for suitable oviposition sites rather than mates.

Within the host plant range of an insect certain plants may be more suitable than others for development of the species or be preferred by the insect for some reason, such as their nutritional quality or physical characteristics. The rapeseed varieties selected by the female moths were examined to determine any relative attractiveness in the plants which might indicate susceptibility to attack in the field.

Materials and Methods

Olfactometer

An olfactometer (Osgood and Kempster 1971) to test the reponses of the moths to rapeseed volatiles, was experimentally determined to be feasible in a preliminary trial on 9 October 1980. This olfactometer was not suitable for the present study because it had two, small chambers; thus Dr. R.H. Elliott designed and funded the construction of a plexiglass olfactometer (Figs. 3,4, and 5), which was built by P. Garnett and B. McMillan, technicians with the Department of Plant Science, Faculty of Agricultural Sciences, U.B.C.

The front wall of the four, large chambers was a single moveable panel which was braced with boards and elastic bands. Air from outside the olfactometer was drawn into the base of each chamber through an opening having a filter containing 85 g of activated charcoal and 0.5 g of glass wool (Fig. 4). The air containing the volatiles associated with the contents of the chamber, then flowed upward through each chamber and into

Figure 3. Olfactometer — photograph from position 4.

Figure 4. Olfactometer - side view diagram from position 1. The holding and mixing reservoirs were open across the width, whereas the channels and their connected chambers were discrete units at each position.

entry port with lid

mesh barriers

six light tubes located 143cm above chamber floor

one of two tubes on netted opening connected by Y-tube to the suction pump

channel 1

front wall panel

chamber 1

mixing reservoir

holding reservoir

pot containing plant which was folded

air flow

SCALE 0.5cm = 5cm

one of four filters on netted opening of chamber

19
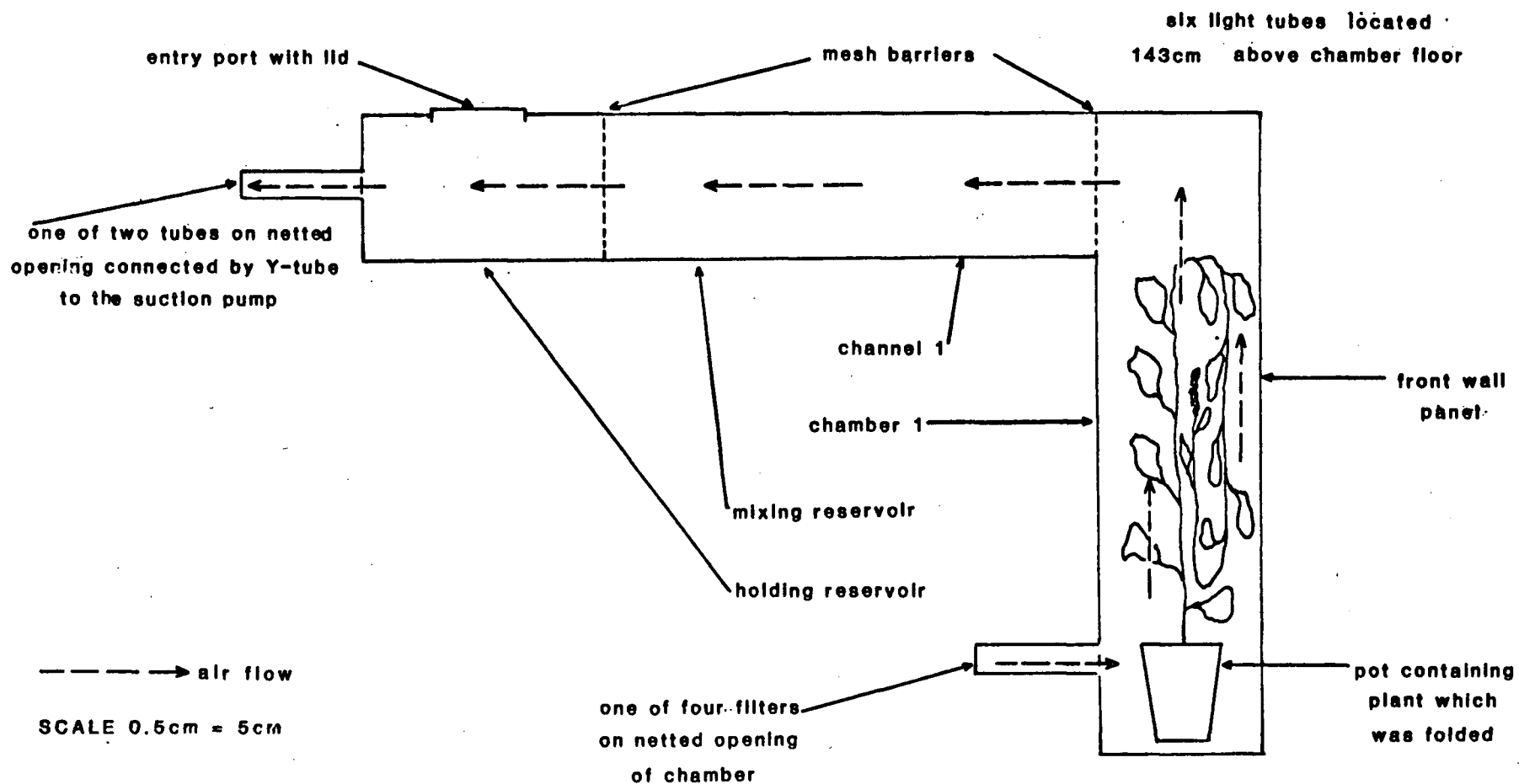
Figure 5.   Olfactometer – plan view diagram.

SCALE 0.5cm = 5cm
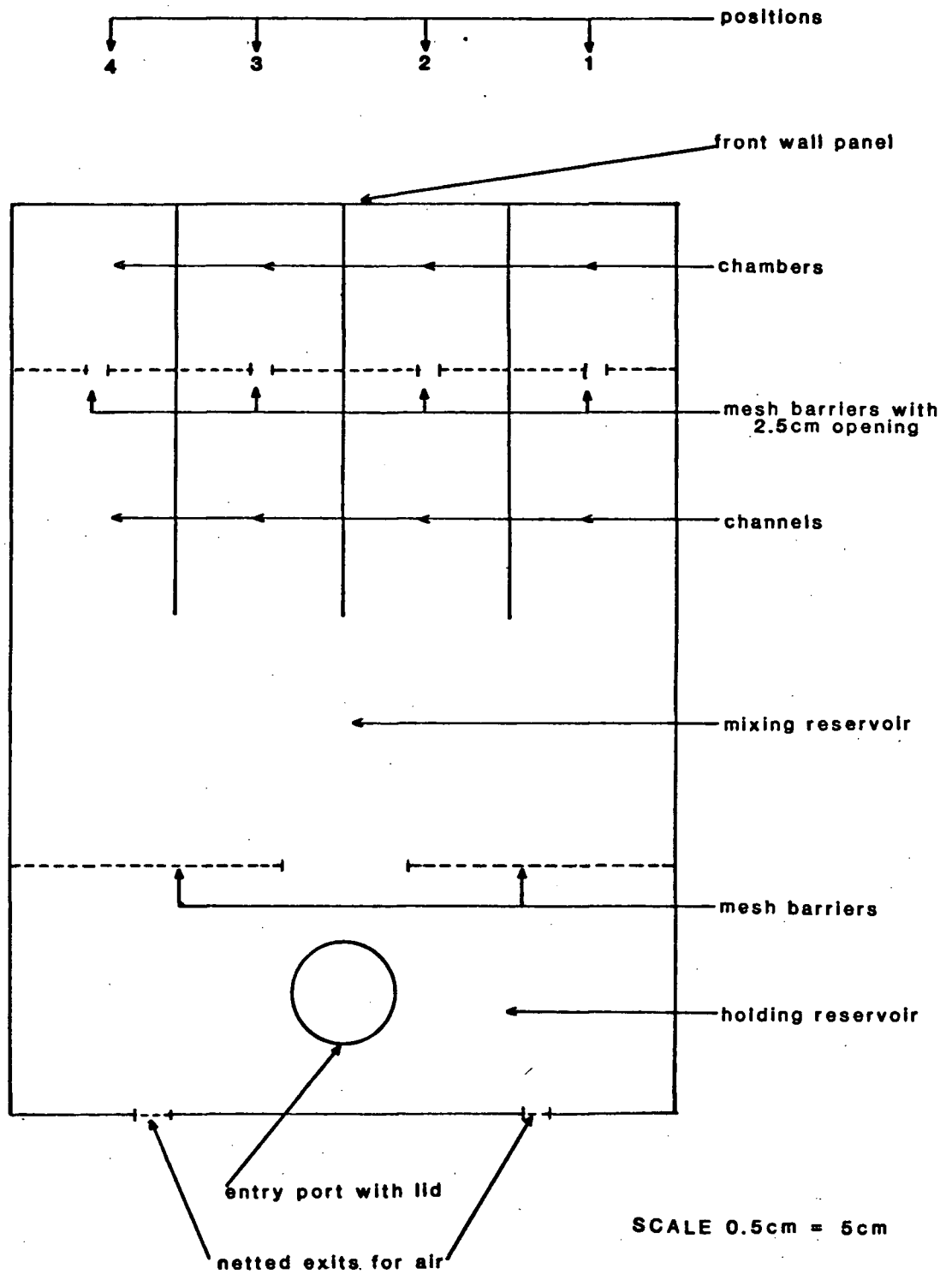
its channel. A 17 cm x 17 cm piece of plastic mesh with a hole of 2.5 cm diam. separated each chamber and channel. Anemometer readings without plants in the chambers showed that the air movement was not equal in each of the chamber-channel units. The flows were as follows: unit 1 was 0.045 to 0.075 m/s, unit 2 was 0.025 to 0.030 m/s, unit 3 was 0.025 m/s and unit 4 was 0.005 to 0.010 m/s. It was not possible to equalize the air flows. The four air flows from the units then combined in the mixing and holding reservoirs. Two plastic mesh partitions separated the reservoirs with a central opening which was 14 cm x 17 cm. Air was removed from the olfactometer and returned to the room using a suction pump (Dayton model 4K850, Revcor, Inc., Carpentersville, Illinois) operated by an autotransformer (type 3PN1010, Staco, Inc., Dayton, Ohio) which was attached by a 4 cm diameter Y-tube to the two outlets in the holding reservoir.

The olfactometer was set in a 61 cm x 131 cm x 170 cm steel frame on a 71 cm x 92 cm sheet of wood covered with brown paper. The frame contained a bank of six fluorescent light tubes (Westinghouse F48T12/WW/HOO) which ran parallel to the length of the olfactometer. The lights were 143 cm above the chamber floor. A 16-8 h light-dark cycle was used.

Experimental Design

The use of the olfactometer dictated the experimental design. A 4 x 4 Latin square with four trials was necessary to eliminate positional effects associated with the placement of the plants in the olfactometer, and to test the effects of the four varieties of rapeseed plants. A complete

experiment used two Latin squares and tested the effect of the ages of the moths. Repeating an experiment tested additional factors.

There were three armyworm moth experiments and one diamondback moth experiment. A programme written for an Apple computer by Dr. G.W. Eaton, Department of Plant Science, Faculty of Agricultural Sciences, U.B.C. was used to generate the arrangement of the plants for each of the 8 Latin squares in the study (Appendix B).

The variables in this study included the number of moths and the number of egg plaques for armyworm moths, or eggs for diamondback moths. Average fecundity was calculated with the number of egg plaques or eggs divided by the number of moths. Care in the interpretation of this value was important because it was possible for a moth to leave the channel after ovipositing and this result would then be lost despite the presence of egg plaques or eggs.

To be included in the results a moth had to leave its holding bottle in the holding reservoir and move through the mixing reservoir into a channel, where it could remain or move (Fig. 5). To move into the associated chamber the moth had to enter through an opening in the mesh barrier. Old moths were expected to deposit egg plaques or eggs. Moths and egg plaques or eggs in the channels were considered to be an effect of the olfactometer. Moths and egg plaques or eggs in the chambers were considered to be an effect of the rapeseed plants. The results were then analyzed by channels, by chambers and by the chambers + channels.

Bertha Armyworm Moth

The armyworm was reared with modifications to the technique and arti-
ficial diet of Bucher and Bracken (1976). The agar-based diet was prepared
somewhat differently. The ascorbic acid and vitamin solution was substi-
tuted with 50 g of Vanderzant Modification Vitamin Mixture for Insects (ICN
Pharmaceuticals, Inc., Cleveland, Ohio) plus 2.5 g choline chloride
(Nutritional Biochemicals Corp., Cleveland, Ohio). This vitamin solution
was mixed to 100 ml of which 96 ml were used in the preparation. The
content of this amount of solution was comparable to the one used by Bucher
and Bracken (1976) with excess amounts of ascorbic acid (3.9 g/100 ml) and
vitamin B12 (0.0999 g/100 ml). Alpha-tocopherol (0.4 g/100 ml) and inosi-
tol (1 g/100 ml) were included in the Vanderzant Mixture (Appendix C).

The agar (Bactoagar, Difco Lab., Detroit, Michigan) was not autoclaved
because the diet preparation was not aseptic at any other stage of prepara-
tion or use.

Caps were not used on the cups containing diet in order to facilitate
handling. Any cups of diet frozen for storage were inverted on trays lined
with wax paper and were used within one week. Paper towel discs were
adequate replacements for caps when using the diet for armyworm larvae.

When the armyworms had completed their larval growth, the pupae were
stored in closed petri plates with filter paper which was dampened with
distilled water every 3 or 4 days. Just before emergence the petri plates
were opened and placed in cages of wood frame and plastic mesh, with
dimensions of 51.5 cm x 25.5 cm x 53.5 cm. The emerged moths remained in
these cages to mate and ovipost.

Lambsquarter plants, Chenopodium album L., obtained from the green-houses of the Vancouver Research Station, were placed intact in the moth cages for egg collection.

Five growth cabinets were used at appropriate levels of temperature and light to rear the various stages of the insect. The RH of the chambers was not monitored but the quality of the diet showed that the RH was at an acceptable level, since the agar did not dry out, nor was there condensation.

Some observations on the behaviour of the moths warrant mention. The moths were not quiescent in light and were observed mating and ovipositing. Egg plaques were found not only on plants but also on plastic mesh, wood, glass, and paper towels.

Pupae of the armyworm, collected from the field in Manitoba during the summer of 1980, were received on 2 September, 1980 from Dr. W.J. Turnock, Head, Integrated Pest Control Section, Research Station, Agriculture Canada, Winnipeg, Manitoba. The adults from these emerged from 2 September to 5 October, 1980. The history of the lab-reared moths used in the experiments follows:

Generation Number	Date in 1980-81 for start of:			Experimental Dates
	Egg collection	Pupation	Emergence	
1	9 Sept	8 Oct	4 Nov	not used
2	8 Nov	3 Jan	14 Jan	19-27 Jan
3	18 Jan	15 Feb	24 Mar	31 Mar-9 Apr
3	18 Jan	15 Feb	15 Apr	17-26 Apr

The pupae of the 3rd generation were held at 0°C to delay adult emergence so that moths could be used in the final two experiments.

Young females were from 2 to 24 h old. They had been sexed as pupae and placed in a cage for emergence. The same females were used when they were 98 to 120 h old and had been in the presence of male moths for 24 h. This timing was chosen because gravid females deposit egg plaques within 24 h of fertilization (Bucher and Bracken 1976). Although mating was observed, it was not possible to ensure that each female had mated and was gravid.

Diamondback Moth

Diamondback moths were reared as suggested by Dr. A.P. Arthur, Research Scientist, Agriculture Canada, Saskatoon, Saskatchewan (personal communication 1980). They were maintained in cages 38 cm x 38 cm x 40 cm made with fine bolting cloth, in chambers at 27°C with a photoperiod of 16-8 h light-dark.

Kale plants, Brassica oleracea var. Maris Kestrel, were obtained from the greenhouses of the Vancouver Research Station. These were exposed 'to moths for oviposition through a period of 24 h, then removed and caged for larval development. The plants were replaced as required for larval feeding. Using this rearing technique one generation developed in a month. The moths were seen to oviposit on bolting cloth and glass, particularly if they were plant-starved. First instar larvae were observed spinning silk threads and moving away from oviposition sites, particularly when they were on unsuitable material, such as glass. They were more motile and hardy

than I had expected before they tunnelled into a leaf.

Larvae and pupae of the diamondback moth, field-collected from broccoli in the summer of 1980, were received on 9 September, 1980 from Dr. D.G. Finlayson, Research Scientist, Agriculture Canada, Vancouver. The following table describes their history:

Generation Number	Generation dates, first eggs to termination	
1	24 Sept 1980	5 Oct
2	9 Oct	12 Nov
3	16 Nov	21 Dec
4	25 Dec	29 Jan 1981

Egg collection for the fifth generation began on 27 February, 1981. The moths used in the trial emerged from 19 to 22 March, 1981.

The cocoons, containing pupae, had been placed individually in small capped vials and the moths were sexed on emergence. Young females, used in experiments were from 2 to 24 h old. The same moths which were from 98 to 120 h old when used again had been with male moths in the holding cage for 24 hours. These old females were collected in vials, and if they oviposited, then they were used.

Experimental Procedure

Rapeseed plants for the moth experiments were used from the early flower to the early seed stage, ranging from 4.2 to 5.2 in the growth stage

key for rapeseed (Harper and Berkenkamp 1975) (Fig. 6). The B. campestris plants were 11 weeks old; the B. napus plants were 13.

The plants were closely inspected, cleaned by hand, watered well, and arranged in the chambers. The flowering heads with their bright yellow blooms were folded within the chamber so that no visual stimulus would be provided from the plants. The front wall panel was replaced and the suction pump and lights were started. The moths were collected in glass bottles to reduce handling. These were then put into the holding reservoir of the olfactometer with a supply of adult food as used in rearing (Bucher and Bracken 1976).

Temperatures inside the olfactometer were a few degrees warmer than the room, which ranged from 20°C to 23°C. Humidity inside the olfactometer was not recorded but no condensation appeared on internal surfaces. Plastic garbage bags were used to enclose the system and to exclude external light sources and other stimuli. The apparatus was situated in a photographic dark room, of which the curtains, heat vents and access doors were closed.

The moths remained within the olfactometer from 4 p.m. until 4 p.m. the following day; the 24 h trial meant that every individual had ample opportunity to move. This period was chosen, also, as a standard to accommodate the biology of the two species since armyworm moths are most active at night, whereas diamondback moths are active only during the day.

The results were recorded. The olfactometer was emptied and cleaned. The moths were held in cages or returned to the stock colony. The plants were destroyed. This procedure was followed for each trial and 8 trials were required to complete each experiment.

Figure 6. Key to the growth stages in rapeseed (B. campestris and B. napus), taken from Harper and Berkenkamp(1975).

Descriptions are based on the MAIN STEM

Stage

0 - Preemergence

1 - Seedling

2 - Rosette

   2.1 First true leaf expanded
   2.2 Second true leaf expanded
        (add 0.1 for each additional leaf)

3 - Bud

   3.1 Inflorescence visible at centre of rosette
   3.2 Inflorescence raised above level of rosette
   3.3 Lower buds yellowing

4 - Flower

   4.1 First flower open
   4.2 Many flowers opened, lower pods elongating
   4.3 Lower pods starting to fill
   4.4 Flowering complete, seeds enlarging in lower pods

5 - Ripening

   5.1 Seeds in lower pods full size, translucent
   5.2 Seeds in lower pods green
   5.3 Seeds in lower pods green-brown mottled
   5.4 Seeds in lower pods brown
   5.5 Seeds in all pods brown, plant senescent

Results and Discussion

Analyses of variances were made using the UBC MFAV programme written by Le (1980) with assistance from Dr. M. Greig (personal communication 1981 and 1982). ANOVA tables are included in Appendix D.

The analysis of variance model for the armyworm was:

$$Y = \mu + E + A + T + P + V + EA + ET + EP + EV$$
$$+ AT + AP + AV + EAT + EAP + EAV + error.$$

that for the diamondback was:

$$Y = \mu + A + T + P + V + AT + AP + AV + error.$$

where:

μ = population mean.

E = experiment number; 1 through 3 for armyworm; not applicable for diamondback with E = 1.

A = moth age; 1 = young, 2 = old.

T = trial; 1 though 4.

P = olfactometer position; 1 though 4 from left to right facing front wall panel.

V = rapeseed varieties; B. campestris: 1 = Candle, 4 = Torch; B. napus: 2 = Midas, 3 = Regent.

grouped letters = describe interaction terms.

error = experimental error.

Bertha Armyworm Moth

There were differences in the stock colony used for the experiments. Experiment 1 used a second generation population which was larger than the third generation populations available for experiments 2 and 3. The number of moths placed in the holding reservoir for the trials of each experiment varied. The ranges were: experiment 1 with 15 to 20 moths, experiment 2 with 7 to 11 moths and experiment 3 with 8 to 12 moths. The numbers of moths which moved to the channels and chambers were affected and all results showed that the mean values for experiment 1 were larger than those of experiments 2 and 3, as expected (Table III).

Moths were affected by the horizontal positions in the olfactometer. For the chambers + channels analysis there were more moths in the outer units 1 and 4 than in the centre units 2 and 3 (Table IV). The design of the olfactometer was assumed to be responsible for this. Moths entered the mixing reservoir between two screens and received a direct air flow. Rather than moving directly upwind they were seen to turn left or right on entry and walk along in the angle made by the mesh screen and the plexiglass floor, as far as the outer wall (see Fig. 5). The air flows, discussed earlier, were not equal among the four units and may also have influenced the moths. This supported the assumption that positions, a consequence of the olfactometer design, did affect the experiments and, therefore, justified the analysis of results by locations in the chambers + channels, the channels and the chambers. Analysis of the results from the channels confirmed that the moths preferred the outer channels (Table IV). This supported the assumption that the number of moths in the channels was associated with an effect of the olfactometer itself.

Table III. Armyworm experiment effect significant at the 1% level for
number of moths, with the means and Duncan's multiple range
test groups designated by letters compared horizontally;
vertical comparison is not valid.

Analysis for location by	Number of moths by experiment		
	1	2	3
Channels	2.219 a	0.938 b	0.906 b
Chambers	1.781 a	0.875 b	0.625 b
Chambers + channels	4.000 a	1.813 b	1.531 b

Table IV. Armyworm experiment effect significant at the 1% level for
number of moths, with the means and Duncan's multiple range test
groups designated by letters compared horizontally; vertical
comparison is not valid.

Analysis for location by	Number of moths by position			
	1	2	3	4
Channels	2.042a	0.833 b	0.750 b	1.792 a
Chambers	not significantly different			
Chambers + channels	3.417 a	1.292 b	1.875 b	3.208 a

An age effect was important in the channels analysis (Table V); more young moths than old were present in the channels. Young moths were gregarious and gathered and remained in tight clusters in the corners and seams of the outer channels. An age effect was also important in the chambers analysis (Table V); thus more old moths than young were present in the chambers. The old moths moved more randomly and there was no preference for the outer chambers. Both age effects supported the hypothesis that old moths would behave differently from young ones. The behaviour of the old moths may have been the result of their previous experience in the olfactometer; or of their expected mated and gravid condition; or of dispersion activity. Further investigation would be necessary to ascertain which factor was important. However, if the insects were gravid and searching for plants then this would indicate that the presence of a plant of any variety increased the attractiveness of the chamber.

The old moths oviposited significantly more plaques than the young moths (Table VI). Since it was not possible to ensure that individual females had mated this confirmation showed that many of them were in fact gravid. The number of egg plaques and the fecundity average were not affected by the experiments, the varieties of rapeseed, the positions in the olfactometer or the trials in Latin square. Oviposition by a female was random and some females even deposited egg plaques inside their holding bottles. Thus the relative unimportance of the armyworm female in the selection of an oviposition site is associated with the motility and polyphagous ability of their emerged larvae during their initial period of establishment on a host.

Table V. Armyworm experiment effect significant at the 5% level for
number of moths, with the means and Duncan's multiple range test
groups designated by letters compared horizontally; vertical
comparison is not valid.

	Number of moths by age	
Analysis for location by	young	old
Channels	1.646 a	1.062 b
Chambers	0.771 b	1.417 a
Chambers + channels	not significantly different	

Table VI. Armyworm age effect significant at the 1% level for number of
egg plaques and average fecundity, with the means for the old
moths listed. No comparison is valid except with the means for
young moths which equalled 0.0.

Analysis for location by	Analyses for old moths	
	egg plaques	average fecundity
Channels	0.438	not significantly different
Chambers	1.417	0.527
Chambers + channels	1.854	0.412

As a final observation, most movement in the olfactometer by moths was by walking rather than flying. I considered this unnatural, but it was not unexpected; Bucher had suggested that it was a probability (personal communication 1980).

Diamondback Moth

The analysis of the chambers results confirmed the importance of moth age (Table VII). More old moths were present in the chambers than young moths. The number of young moths placed in the holding reservoir for the trials ranged from 15 to 43 while that for the old moth groups was 15. This factor did not influence the results except to strengthen the importance of the effect of moth age. With one alteration, the discussion for this age effect is the same as that for the armyworm moths. The diamondback moths were gravid and known (Fraenkel 1969) to depend on chemoreception for locating suitable plants.

All the old moths had already laid some eggs within their holding vials before being used in the olfactometer. The analyses for egg number and fecundity average reflected this (Table VIII) but they were not otherwise affected. It was this assurance which caused the variation in the starting number described in the preceding paragraph. The analyses for the fecundity averages in the chambers and the channels showed that the moths moved freely. Even in the chambers the females moved after having oviposited. The analysis for egg numbers in chambers showed that it was difficult to locate the single deposited eggs on the rapeseed plants because they were camouflaged by the texture, colour and mass of plant

Table VII. Diamondback age effect significant at the 5% level for number
of moths, with the means and Duncan's multiple range test
groups designated by letters compared horizontally; vertical
comparison is not valid.

Analysis for location by	Number of moths by age	
	young	old
Channels	not significantly different	
Chambers	0.188 b	1.250 a
Chambers and channels	not significantly different	

Table VIII. Diamondback age effect significant at the 5% level for number
of eggs and average fecundity, with the means for the old
moths listed. No comparison is valid except with the means
for young moths which equalled 0.0

	Analyses for old moths	
Analysis for location by	eggs	average fecundity
Channels	6.500	not significantly different
Chambers	not significantly different	not significantly different
Chambers + channels	8.750	2.734

material.

The oviposition behaviour of the diamondback moths appeared to be random. The presence of eggs on the plexiglass surface throughout the olfactometer was perplexing. The importance of the diamondback female in the selection of an oviposition site was less than expected. The successful establishment of the oligophagous, leaf-mining first instar larvae would appear to depend on other survival tactics than the female's placement of the eggs.

Summary

The selection of the numbers of moths, numbers of egg plaques or single eggs, and the average fecundities as the variables for the moth studies, was reasonable and representative of the behaviour of the adults during their 24 h within the olfactometer. Non-stop observation or a tracking procedure would have been useful for description and clarification of the dynamics involved.

The decision to record and analyze the results as the chambers + channels, the channels, and the chambers, was also reasonable and proved to be valuable. This technique clarified the effects of position which were regarded as confounded with the other effects despite the choice of an experimental design to adjust to these constraints. The design allowed for an examination of the effects of the stimuli selected. Finally, the techniques helped to qualify the types of responses from the moths. Statistical analyses between the armyworm moth and diamondback moth were

not possible. Nevertheless, comparisons and inferences were possible.

The hypothesis that young female moths would act differently from old ones was confirmed for both species. The old moths of both species tended to move into the chambers of the olfactometer. The diamondback moth was known to have a closer association with cruciferous plants than the armyworm moth, nevertheless, they behaved similarly. Further investigations would be needed to determine if the whole rapeseed plants were the attractive factor or if any volatile biochemicals were acting as kairomones within the small volume of the chambers.

Both moth species responded to the rapeseed plants with no preference for or selection of a species or variety. Since both armyworm and diamondback moths are known to oviposit and their larvae to survive on rapeseed it was concluded that no volatile biochemicals were functioning as allomones with immediate defensive functions, and that the four varieties were equally attractive to the moths as oviposition sites. Further investigation of the feeding response, growth and development of the larvae might determine how the attraction and oviposition responses of the female moths interact and how the choices of the adult affect the success of the larvae.

The olfactometer responses of the females of the polyphagous armyworm, and the oligophagous diamondback, were similar. The presence of rapeseed volatiles did not appear to be responsible for any apparent behavioural differences between the two moth species. The importance of glucosinolates and their volatile byproducts in the association of these moths with their cruciferous plant hosts remains to be determined.

APHIDS AND RAPESEED PLANTS

Introduction

Each aphid species has a host plant range that may be very wide or
sometimes so narrow that the aphid's common name reflects the summer host
plant species, e.g. the cabbage aphid. Some aphid species alternate
between a winter woody host and a summer herbaceous one; others do not.
The maintenance of such different associations requires very different
cues. Chemical cues, including secondary biochemicals, are so important in
host plant selection that van Emden (1972) called aphids "phytochemists".

The four aphid species in this study, all members of the sub-family
Aphidinae, were selected for their host plant ranges and biologies. Two
polyphagous and two oligophagous species having different associations with
cruciferous plants were chosen to examine and compare their responses to
the rapeseed varieties. The following short descriptions of the species
are based on Blackman (1974).

The green peach aphid, Myzus persicae Sulzer, overwinters on peach or
other Prunus trees and migrates to very many herbaceous plants in the
spring, including most plants from the Cruciferae. In mild climates it
overwinters on herbaceous hosts. It is typically found on senescing leaves
which are a good source of nitrogen. The colonies are seldom dense because
reproducing females move often. A study by van Emden and Bashford (1969)
showed that the aphid preferred old leaves on the Brussel's sprout plant
that were associated with lower concentrations of the mustard oil,
allylisothiocyanate, or sinigrin, than new leaves. Nault and Styer (1972)

observed that sinigrin seemed to be a stimulant. This aphid was chosen because it has a very wide range of host plants.

The potato aphid, Macrosiphum euphorbiae (Ashmead), overwinters on rose and flies in the spring not only to potato but also to other plants of many different families, including some of the Cruciferae. In mild climates it also can overwinter on herbaceous hosts. Although polyphagous, it does not have so broad a host plant range as the green peach aphid. There are two biotypes, respectively coloured pink and green. The colour of each biotype remains true in offspring from asexual or sexual reproduction and each biotype also has a similar range of host plants, although there are minor differences in suitability and acceptance. The green biotype prefers the lower parts of older plants, whereas the pink biotype is not so resricted a feeder (Kogan 1976). The biotypes were chosen to compare the responses to host plants between the two groups within the same polyphagous species.

The cabbage aphid, Brevicoryne brassicae (Linnaeus), normally lives only on plants of the family Cruciferae. It is an oligophagous species, laying fertilized eggs in the late fall on old cruciferous plants instead of on a woody host. The aphid is typically found in dense clusters near the growing points of plants, which are the sites of nitrogen accumulation. It responds positively to glucosinolates (van Emden 1972). MacGibbon and Allison (1968) described a specific enzyme system present in the cabbage aphid which functions to detoxify glucosinolates. Tapper and Reay (1973) confirmed that this enzyme was a thioglucosidase which metabolized isothiocyanates. This aphid was chosen because it responds to glucosinolates as kairomones.

The pea aphid, Acyrthosiphon pisum (Harris), another oligophagous species, lives only on plants in the family Leguminosae. When disturbed, it drops readily from its plant. Nault and Styer (1972) found that sinigrin had a powerful repellent effect. This aphid was chosen because it responds to glucosinolates as allomones.·

The biologies of various aphid species incorporate some remarkable strategies. The different forms, or morphs that exist within each species perform various functions. Sexual morphs which produce eggs in the fall are found only in holocyclic species, such as the four chosen for this study. Asexual morphs produce live nymphs parthenogenetically in the spring and summer and are found not only in holocyclic aphids but also in anholocyclic species which depend exclusively on this type of reproduction. Winged morphs, or alates, and wingless morphs, or apterae, are found in all species. Alates are more heavily sclerotised than apterae, have thoracic muscles for flight, are less prolific, and have more sensoria on the antennae.

Host plant responses of aphids, that lead to settling, feeding and reproducing, are necessary for the survival of an individual and the establishment of a colony. Flight responses are necessary both for dispersion to new hosts when the old plants deteriorate and for the spring and fall migrations of those aphids which alternate between hosts. These two responses are incompatible and even antagonistic (Blackman 1974).

The most common form, the asexual, wingless morph was chosen to examine the responses of these aphid species to rapeseed plants and determine the relative suitability of the plants as hosts.

<u>Materials and Methods</u>

<u>Experimental Design</u>

This study included five experiments, performed in the order of availability of the adult aphids, <u>i.e.</u> the cabbage aphid, the pea aphid, the green peach aphid, the green potato aphid and the pink potato aphid.

Each experiment used a design with two blocks dictated by the use of two growth chambers each with space for ten plants. Because the same growth chambers were used for each experiment, the chamber effect was nested in the experiment effect in the model.

Five host varieties from three species were tested for their effect. These included the rapeseed plants: <u>B. campestris</u>, vars. Candle and Torch; <u>B. napus</u>, vars. Regent and Midas; plus a standard. The standard plants representing a normal host for the aphids were:

Aphid Species	Standard Plant
Cabbage and Green Peach	kale, <u>Brassica oleracea</u> var. Maris Kestrel
Potato - Pink and Green	potato, <u>Solanum tuberosum</u> var. Kennebec
Pea	broad bean, <u>Vicia faba</u> var. Windsor Longpod

Each chamber contained two host plants of each variety. This replicate effect was nested in the experiment, chamber, and plant effects in the model. The ten plants in each chamber were arranged in a completely randomized design because the ten positions within each chamber were similar. A programme written for an Apple computer by Dr. G.W. Eaton was

used to generate the arrangement of the plants for each of the ten blocks used in the study (Appendix E). Finally, the effects of two plant sites, lower and upper, were tested.

The actual number of a possible ten adult aphids and the number of nymphs they produced at the upper and lower·sites on each plant were recorded every 24 h for 5 days. Two variables were calculated. The five daily totals for adults at each site were summed and the average fecundity per adult day at each site was found by dividing the total number of nymphs on day 5 by the appropriate sum.

The sums of adults represented the settling and feeding responses, and the movements of the original ten aphids on the plant during the 5-day experiment. The average fecundity represented the reproductive response of the original ten aphids on the plant during an experiment. The adult aphids used in the experiments had not developed on rapeseed. Thus, it was not possible to examine the effect of the rapeseed plants on the development of these individuals. The effect on the progeny could, however, be examined by using the number of nymphs on day 5, so the effect of the rapeseed plants on the development of a colony could be assessed.

Aphids

The Vancouver Research Station provided aphids of each species from their stock colonies, standard plants, and space and facilities in their insect rearing room. The room was maintained at 23°C with 50% RH, ventilation, and 16-8 h light-dark photoperiod.

Before each experiment, mature apterous aphids were removed from the stock colony and placed, uncrowded, on the appropriate standard plants. Apterae were selected since they were more likely to settle and larviposit than alatae. The uncrowded condition was important since crowding can be a factor in the production of migratory, winged forms instead of the wingless forms required here. The plants were then placed in cages of 38 cm x 38 cm x 40 cm, which were covered with bolting cloth.

At the end of 24 h the mature aphids were removed. If they were not placed on other plants for further nymph collection they were returned to the stock colony. The newborn nymphs were left on the plants where they remained until they were mature. When they began to reproduce they were ready for use in the experiment.

It was important during rearing to ensure that the environmental and plant conditions were good since 200 standardized, apterae of uniform age had to be attained from each aphid species. Reproductive capacity and developmental rates differed with each aphid species. A summary follows of the dates which were pertinent to the aphids of each species used in the experiments:

Aphids	Dates in August, 1981 for start of:		
	birthdate(s)	reproduction	chambers

Polyphagous species

Green Peach	4-5	12-13	14
	6-7	14-15	15
Potato-Pink	19	27	28
	20	28	29
Potato-Green	12	23	21
	13	22	21

Oligophagous species

Cabbage	22 July	31 July	1
	23 July	1	2
Pea	1	9	10
	2	10	11

In each aphid experiment the 100 nymphs born first were used in chamber 1; those second in chamber 2. Each chamber in the green peach aphid experiment contained aphids born during two days: the 50 nymphs born first were replicate 1 and those born second were replicate 2.

Experimental Procedures

None of the aphid species is looked upon as a major pest of rapeseed because they "seldom if ever cause losses" (Agriculture Canada 1980). Thus, no plant stage was closely associated·with aphid attack in the field. For this reason a stage was selected to simplify their handling: this was the late leaf to late bud stage, or 2.6 to 3.3 in the key (Harper and Berkenkamp 1975) (Fig. 6) and the plants were of about the same age at the beginning of each experiment. The standard plants for the experiments were similar in size to the rapeseed plants.

The plants were watered well, examined for insects, and the old or damaged leaves were removed. A collar, made of plastic treated with Fluon Ad-1 (supplied by Canadian Industries Ltd., North York, Ontario) was placed inside the rim of the pot. The purpose of the collar was to prevent aphids from leaving or entering the plant by walking across the soil, although aphids would leave plants by dropping from foliage that extended beyond the collar.

The mature wingless aphids used in each experiment were removed individually with a camel's hair brush from the standard plant on which they had been reared. Ten aphids were placed in a petri plate and then covered while the 90 remaining aphids were collected in the same way. The aphids in the plate which had been filled first were then placed individually on the soil near the base of the plant which occupied position 1 within a chamber. The placement of the aphids near the plant's base was to simulate the approach of a wingless, walking aphid from its host to a different plant with potential host status. The procedure was followed

until all ten plants were arranged in the chamber. This handling method resulted in a single dead aphid during the study. Particular care was taken to standardize the two growth chambers since aphids are acutely sensitive to all environmental conditions. The conditions were the same as those used in rearing the aphids.

Every 24 hr each plant was removed from the chamber and examined. Some of the aphids, especially the nymphs, were in dense clusters or hidden within plant structures and could not be disturbed at the risk of disruption or injury. Counting these was difficult. After the results for each leaf were recorded the plant was returned to the chamber. All the plants were then watered from the base of the pot. On day 5 the experiment terminated and the plants and aphids were destroyed. Because the plants were dissected then, the nymphal counts were most accurate on that date.

On the first day the leaves of each plant were numbered as 1 from the soil level upwards to a maximum of 12. The potato and broadbean had compound leaves; however, these were numbered and treated the same as the simple leaves found with the kale and the rapeseed varieties. The numbers of leaves on the plants on day 1 with the four rapeseed varieties pooled were:

Plant	Range of leaf numbers
kale	6-10
potato (compound leaves)	7-11
broadbean (compound leaves)	6-7
rapeseed	7-12

Although the plants continued to grow and produce leaves and flowers, these were not numbered, so that the topmost part of the plant was included as part of the highest numbered leaf.

The leaf numbers were not associated with the height or actual leaf position from the ground because of differing plant morphology, growth, and leaf removal. The first three leaves from the soil level were defined as the lower site, and the remaining leaves as the upper site.

Results and Discussion

The U.B.C. MFAV programme written by Le (1980) was used for the analyses of variances with assistance from Dr. M. Greig (personal communication 1981 and 1982). ANOVA tables are included in Appendix F.

The analysis of variance model for the aphid study was:

$$Y = \mu + A + C(A) + P + R(ACP) + S + AP + CP + AS$$
$$+ CS + PS + APS + CPS + error$$

where:

μ = population mean.

A = aphid; 2 = green peach, 3 = pink potato, 4 = green potato, 1 = cabbage, 5 = pea.

C = chamber; 1 or 2.

P = plant; B campestris: 1 = Candle, 4 = Torch, B. napus: 2 = Midas, 3 = Regent, 5 = Standard.

R = plant replicate; 1 or 2.

S = plant site; 1 = lower, 2 = upper.

grouped letters = describe interaction terms and nesting of terms.

error = experimental error.

Aphid Species

There was an aphid experiment effect that was associated with the aphid species and its known interactions with cruciferous plants (Table IX). The mean values for the adult sums were placed in four groups. The cabbage and green peach aphids had the largest mean values demonstrating that the conditions of the study were suitable for them. The conditions were less suitable for the potato aphid and the mean value for the pink biotype was larger than that for the green. This demonstrated differences within and between the responses of the polyphagous species. The conditions were least suitable for the pea aphid. The range between the mean values of the oligophagous species demonstrated the extreme difference between their responses. The average fecundities and nymphal counts on day 5 were not compared because of the insects' different reproductive abilities.

The green peach aphid adults found the rapeseed varieties more suitable as host plants than the standard plant, kale. They typically selected the lower sites on the B. napus varieties, on Torch, and on kale but were more evenly distributed on Candle (Table X). The average fecundity on kale was about 1 nymph/adult day and those on the rapeseed plants were similarly low. The stock colony had been reared on a number of plants including crucifers but not kale and, from observation, the transfer to and development on kale affected the aphids. The rapeseed plants were equally and more suitable than the standard for the development of the nymphs and the distribution of the nymphs at the lower site on B. napus reflected that of the adults.

Table IX. Aphid experiment effect significant at the 1% level for the sum
of surviving adults with the means and Duncan's multiple range
test groups designated by letters, compared vertically.

Aphid species	Sum of surviving adults
Polyphagous	
green peach	20.77 a
potato - pink	16.85 b
potato - green	13.02 c
Oligophagous	
cabbage	22.87 a
pea	5.25 d

Table X. Green peach aphid: plant effect significant at the 1% level, for the sum of the adults, the average fecundity and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5.

| Plant species | Sum of the adults | Plant site | | Average fecundity by plant | Number of nymphs on day 5 | Plant site | |
	plant	lower	upper		plant	lower	upper
Standard	14.00b	24.50cde	3.50m-r	0.850i	14.13f	25.50h-m	2.75lm
B. campestris							
Candle	22.63a	22.75d-h	22.50d-h	2.273fg	50.75de	56.50f-i	45.00g-k
Torch	21.75a	28.50bcd	15.00e-m	2.010gh	45.50de	65.25e-h	25.75h-m
B. napus							
Regent	22.25a	44.50a	0.0r	0.987hi	43.75e	87.50c-f	0.0m
Midas	23.25a	44.75a	1.75o-r	1.086hi	45.25de	89.00c-f	1.50lm

The pink potato aphid adults found the standard, potato, more suitable as a host plant and selected its upper site (Table XI). This was not as described by Kogan (1976) who found them to be general feeders. Although the rapeseed varieties were rated as suitable, the adults did not remain on plants. Most adults were on the upper sites of the Torch plants. The average fecundity was about 6 nymphs/adult day on the potato and the mean values on rapeseed, although not so large, were not far from this value. The day 5 nymph counts indicated that the standard was most suitable with nymphs at the upper site. The rapeseed was less suitable for the nymphs, which were located on B. campestris varieties at the upper site and on Regent at the lower site. Midas variety was not acceptable for nymphal development.

For the green potato aphid adults the standard, potato, was the most suitable as host and they were located at both sites (Table XII). Kogan (1976) described a preference for lower sites on plants. The green biotype responded differently to the rapeseed species. Most adults settled on the B. napus plants, which were more suitable than B. campestris plants. They selected the lower site on the B. napus varieties. Neither rapeseed species was acceptable; adults did not remain on the plants. The average fecundity on potato was about 2 nymphs/adult day. This was significantly higher than those on rapeseed varieties. Adults in both chambers had not begun to reproduce by day 1. The stock colony of green potato aphids was reared on Netted Gem potato and, from observation, the transfer to and development on Kennebec affected the adult aphids. The day 5 nymph counts reflected the low average fecundities.

Table XI. Pink potato aphid: plant effect significant at the 1% level, for the sum of the adults, the average fecundity and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5.

| Plant species | Sum of the adults | | | Average fecundity by plant | Number of nymphs on day 5 | | |
| | plant | Plant site | | | plant | Plant site | |
		lower	upper			lower	upper
Standard	24.00a	7.00l-r	41.00a	5.810ab	142.10b	38.25g-m	246.00a
B. campestris							
Candle	15.25b	9.50i-r	21.00d-i	5.005bc	75.00c	51.00f-j	99.00cde
Torch	16.75b	9.50i-r	24.00c-g	5.202bc	84.25c	53.75f-i	114.80bcd
B. napus							
Regent	15.38b	17.75de	13.00e-o	4.735c	75.00c	107.30bcd	42.75g-1
Midas	12.88b	13.25e-o	12.50g-p	4.462cd	58.63d	78.25d-g	39.00g-m

Table XII. Green potato aphid: plant effect significant at the 1% level, for the sum of the adults, the average fecundity and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5.

Plant species	Sum of the adults	Plant site		Average fecundity by plant	Number of nymphs on day 5	Plant site	
	plant	lower	upper		plant	lower	upper
Standard	22.13a	20.00d-j	24.25c-f	1.98gh	46.00de	30.25h-m	61.75e-h
B. campestris							
Candle	6.38c	4.50m-r	8.25k-r	0.31i	2.75f	4.75k-m	0.75m
Torch	8.63c	3.00n-r	14.25e-n	0.13i	1.13f	0.50 m	1.75lm
B. napus							
Regent	15.38b	24.50cde	6.25l-r	0.59i	10.00f	18.50i-m	1.50lm
Midas	12.63b	19.50d-k	5.75m-r	0.23i	4.25f	8.25k-m	0.25m

The cabbage aphid adults found all rapeseed varieties as suitable for host plants as the standard plant, kale, and they always selected, typically, the upper site of the plants (Table XIII). They were gregarious, clustered on leaves and, especially, on growing tips. The average fecundity on kale was about 4 nymphs/adult day and the averages on the rapeseed were similar. The day 5 nymph counts reflected those of the adults.

For the pea aphid adults the standard, broad bean, was the only suitable plant (Table XIV). Adults were located at the lower site on these plants but began to move upwards as the population of nymphs grew and further space was needed. The average fecundity on broad bean was about 6 nymphs/adult day. The rapeseed varieties were unacceptable. Adults would not settle and moved off these plants within the first 24 h. The day 5 nymph populations reflected those of the adults.

Chambers

There was a chamber effect in three experiments (Table XV). There were more pink potato aphid adults in chamber 2 than in 1. An equipment malfunction resulted in 8 of 12 lights being off for nearly 24 h in chamber 1 on 30 August, 1981 when day 2 was in progress. Apparently the adults dropped from the plants in response to this change of intensity. Thus the nymph population was larger in chamber 2 than 1.

There were more green potato aphid adults in chamber 1 than in 2. As a result of experimental constraints, the aphids in chamber 2 were one day younger and proved to be immature; moreover, some developed into alates.

Table XIII. Cabbage aphid: plant effect significant at the 1% level, for the sum of the adults, the average fecundity and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5.

| Plant species | Sum of the adults | | | Average fecundity by plant | Number of nymphs on day 5 | | |
| | plant | Plant site | | | plant | Plant site | |
		Tower	upper			Tower	upper
Standard	21.38a	14.00e-n	28.75bcd	3.57de	82.13c	49.75f-j	114.5bcd
B. campestris							
Candle	22.25a	3.50m-r	41.00a	3.17ef	78.63c	11.50j-m	145.80b
Torch	22.25a	5.00m-r	39.50ab	3.61de	79.25c	18.00i-m	140.50b
B. napus							
Regent	23.63a	12.75f-p	34.50abc	2.91efg	77.75c	35.50h-m	120.00bc
Midas	24.88a	12.00h-q	37.75ab	2.87efg	73.63c	34.50h-m	112.80bcd

Table XIV. Pea aphid: plant effect significant at the 1% level, for the sum of the adults, the average fecundity and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5.

Plant species	Sum of the adults			Average fecundity by plant	Number of nymphs on day 5		
		Plant site				Plant site	
	plant	lower	upper		plant	lower	upper
Standard	24.25a	39.50ab	9.00j-r	6.44a	162.40a	270.30a	54.50f-i
B. campestris							
Candle	0.63d	0.0r	1.25pqr	0.0i	0.0f	0.0m	0.0m
Torch	0.50d	0.25r	0.75qr	0.0i	0.0f	0.0m	0.0m
B. napus							
Regent	0.0d	0.0r	0.0r	0.0i	0.0f	0.0m	0.0m
Midas	0.88d	1.25pqr	0.50qr	0.0i	0.0f	0.0m	0.0m

Table XV. Aphid chamber effect significant at the 1% level, for the sum of the adults and the 5% level, for the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid for the chamber analysis within the sum of the adults of the number of nymphs on day 5.

Aphid species	Sum of adults in chamber		Number of nymphs on day 5 in chamber	
	1	2	1	2
Polyphagous				
Green peach	20.45b	21.10b	38.50d	41.25d
Potato-pink	15.55d	18.15c	80.90bc	93.10a
Potato-green	14.20d	11.85e	10.90e	14.75e
Oligophagous				
Cabbage	23.45a	22.30ab	84.85ab	71.70c
Pea	5.15f	5.35f	33.25d	31.70d

Apparently the aphids in chamber 2 were not ready to settle, and so left the plants more quickly than those in chamber 1.

There were more cabbage aphid nymphs in chamber 1 than in 2. Apparently temperature variation between chambers led to more favourable conditions for either survival of nymphs or adult reproduction.

Plants

If possible the standard for all the aphid species would have been the same host plant. This ideal could not, nor was it expected to be reached. Most host plant associations were very well-defined, as with the oligophagous pea and cabbage aphids, and were somewhat restricted, even with the polyphagous green peach and potato aphids. Thus, the laboratory-reared stocks of these species were affected by their transfer to other plants, even their host standard. The broad bean standard was the only host suitable for the oligophagous pea aphid.

The potato standard was of especial interest since it was used for two biotypes within the polyphagous potato aphid species (Table XVI). The adult response to these plants was similar, although their distributions differed. The average fecundities of the biotypes on potato were very different. The size of the day 5 nymph populations reflected this difference, with distributions similar to those of the adults. These results indicated that the physiology of the pink biotype was more suited than that of the green to the conditions on the potato.

Table XVI. Standard plant: plant effect significant at the 1% level, for the sum of the adults, the average fecundity, and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5. This table summarizes results from Tables X to XIV.

Plant and aphid species	Sum of the adults			Average fecundity by plant	Number of nymphs on day 5		
		Plant site				Plant site	
	plant	lower	upper		plant	lower	upper
Broad bean standard							
Pea	24.25a	39.50ab	9.00j-r	6.44a	162.40a	270.30a	54.50f-i
Potato standard							
Potato-pink	24.00a	7.00l-r	41.00a	5.81ab	142.10b	38.25g-m	246.00a
Potato-green	22.13a	20.00d-j	24.25c-f	1.98gh	46.00de	30.25h-m	61.75e-h
Kale standard							
Green peach	14.00b	24.50cde	3.50m-r	0.85i	14.13f	25.50h-m	2.75l-m
Cabbage	21.38a	14.00e-h	28.75bcd	3.57de	82.13c	49.75f-j	114.50bcd

The kale standard was used for the two species known to have associations with cruciferous plants (Table XVI). The oligophagous cabbage aphid found the kale more suitable than the polyphagous green peach aphid. The upper site was selected by the cabbage aphid and the lower site by the green peach aphid. This variation suggested that the physiologies of the species differed.

Kale is closely related to rapeseed since all are members of the same genus and kale is one parent, with B. campestris, of B. napus (Fig. 2). Not surprisingly, the two aphid species which were transferred from this standard found rapeseed plants to be as suitable as or better than kale.

In the analysis of variance all aphid species were grouped as a single population to examine the effect of the plants, to provide some generalized results, and to describe the response of the composite population toward each host plant (Table XVII). These results showed that the rapeseed varieties were less suitable than the standard plants for host plant responses and for development of the 5-day-old nymphs. The distribution pattern of the composite population varied with the rapeseed species: the aphids favoured the lower sites of B. napus plants and the upper sites of B. campestris plants. This was of interest since morphological and biochemical characteristics, both nutritive and nonnutritive (Appendix G), differ between the species and sites of rapeseed plants. Biochemical assays were outside the scope of this study since the techniques were complex and not fully adapted for vegetative material (MacGregor and Underhill, personal communications 1981). The following inferences were made based on the literature and the responses of the insects. Since the plants within a species were treated similarly by the composite population

Table XVII. Composite population of all aphid species: plant effect significant at the 1% level, for the sum of the adults, the average fecundity and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5.

| Plant species | Sum of the adults | | | Average fecundity by plant | Number of nymphs on day 5 | | |
| | plant | Plant site | | | plant | Plant site | |
		lower	upper			lower	upper
Standard	21.15a	21.00a	21.30a	3.73a	89.35a	82.80a	95.90a
B. campestris							
Candle	13.42c	8.05b	18.80a	2.15b	41.42b	24.75c	58.10b
Torch	13.97bc	9.25b	18.70a	2.19b	42.02b	27.50c	56.55b
B. napus							
Regent	15.32b	19.90a	10.75b	1.84b	41.30b	49.75b	32.85c
Midas	14.90bc	18.15a	11.65b	1.73b	36.35b	42.00bc	30.70c

the differences between varieties and individuals were, in this instance,
be considered minimal. The responses of the aphid species therefore were
examined to develop further inferences about the general trends for site
preferences in relation to the plant species.

B. napus plants were treated as suitable hosts by the cabbage and
green peach aphids (Tables XVIII and XIX), whose distributions were the
same as they had been on their kale standard. The cabbage aphids were at
the upper site and the green peach aphids at the lower. Apparently the B.
napus and the kale plants had similar morphologies and biochemistries for
these aphids. B. napus was a less suitable host for the potato aphid than
for the green peach aphid, indicating that even these polyphagous species
differed in their responses to the plant's chemistry. Furthermore, the
distributions of the potato biotypes were somewhat different statistically,
since the green biotype selected the lower sites whereas the pink selected
both lower and upper sites. The cabbage aphid's location at the upper site
was associated with its specialist behaviour. The pink potato aphid's
physiology apparently allowed it to be on the upper part of the plant when
neither the green biotype nor the peach aphid could be there.

B. campestris plants were suitable hosts for the cabbage and green
peach aphids (Tables XX and XXI). The cabbage aphid was, again, located at
the upper site; the green peach aphid, however, changed its pattern of
distribution. Although it still statistically selected the lower site of
Torch, it was located at both sites on Candle. This movement upward showed
that the green peach aphid was physiologically better adapted to this
species of rapeseed, thus indicating that B. campestris had more suitable

Table XVIII. B. napus, Regent: plant effect significant at the 1% level, for the sum of the adults, the average fecundity, and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5. This table summarizes results from Tables X to XIV.

Aphid species	Sum of the adults			Average fecundity by plant	Number of nymphs on day 5		
		Plant site				Plant site	
	plant	lower	upper		plant	lower	upper
Polyphagous							
Green peach	22.25a	44.50a	0.0r	0.99hi	43.75e	87.50c-f	0.0m
Potato-pink	15.38b	17.75de	13.00e-o	4.74c	75.00c	107.30bcd	42.75g-1
Potato-green	15.38b	24.50cde	6.251-r	0.59i	10.00f	18.50i-m	1.501m
Oligophagous							
Cabbage	23.63a	12.75f-p	34.50abc	2.91efg	77.75c	35.50h-m	120.00bc
Pea	0.0d	0.0r	0.0r	0.0i	0.0f	0.0m	0.0m

67

Table XIX. B. napus, Midas: plant effect significant at the 1% level, for the sum of the adults, the average fecundity, and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5. This table summarizes results from Tables X to XIV.

| Aphid species | Sum of the adults | | | Average fecundity by plant | Number of nymphs on day 5 | | |
| | plant | Plant site | | | plant | Plant site | |
		lower	upper			lower	upper
Polyphagous							
Green peach	23.25a	44.75a	1.75o-r	1.09hi	45.25de	89.00c-f	1.50lm
Potato-pink	12.88b	13.25e-o	12.50g-p	4.46cd	58.63d	78.25d-g	39.00g-m
Potato-green	12.63b	19.50d-k	5.75m-r	0.23i	4.25f	8.25k-m	0.25m
Oligophagous							
Cabbage	24.88a	12.00h-q	37.75ab	2.87efg	73.63c	34.50h-m	112.80bcd
Pea	0.88d	1.25pqr	0.50qr	0.0i	0.0f	0.0m	0.0m

Table XX. B. campestris, Candle: plant effect significant at the 1% level, for the sum of the adults, the average fecundity, and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5. This table summarizes results from Tables X to XIV.

| | Sum of the adults | | | Average fecundity by plant | Number of nymphs on day 5 | | |
| | | Plant site | | | | Plant site | |
Aphid species	plant	lower	upper		plant	lower	upper
Polyphagous							
Green peach	22.63a	22.75d-h	22.50d-h	2.27fg	50.75de	56.50f-i	45.00g-k
Potato-pink	15.25b	9.50i-r	21.00d-i	5.01bc	75.00c	51.00f-j	99.00cde
Potato-green	6.38c	4.50m-r	8.25k-r	0.31i	2.75f	4.75k-m	0.75m
Oligophagous							
Cabbage	22.25a	3.50m-r	41.00a	3.17ef	78.63c	11.50j-m	145.80b
Pea	0.63d	0.0r	1.25pqr	0.0i	0.0f	0.0m	0.0m

69

Table XXI. B. campestris, Torch: plant effect significant at the 1% level, for the sum of the adults, the average fecundity, and the number of nymphs on day 5, with the means and Duncan's multiple range test groups designated by letter, compared vertically. Horizontal comparison is valid only for the plant site analysis within the sum of the adults or the number of nymphs on day 5. This table summarizes results from Tables X to XIV.

| Aphid species | Sum of the adults | | | Average fecundity by plant | Number of nymphs on day 5 | | |
| | plant | Plant site | | | plant | Plant site | |
		lower	upper			lower	upper
Polyphagous							
Green peach	21.75a	28.50bcd	15.00e-m	2.01gh	45.50de	65.25e-h	25.75h-m
Potato-pink	16.75b	9.50i-r	24.00c-g	5.20bc	84.25c	53.75f-i	114.80bcd
Potato-green	8.63c	3.00n-r	14.25e-n	0.13i	1.13f	0.50m	1.75lm
Oligophagous							
Cabbage	22.25a	5.00m-r	39.50ab	3.61de	79.25c	18.00i-m	140.50b
Pea	0.50d	0.25r	0.75qr	0.0i	0.0f	0.0m	0.0m

morphology and biochemistry for nonspecialist aphids than $\underline{B}$. $\underline{napus}$. $\underline{B}$. $\underline{campestris}$ was less suitable as a host for potato aphids, than for green peach aphids, further demonstrating the differences between these polyphagous species. There was also a difference between the potato aphid biotypes since the pink biotype found this plant species more suitable than the green. Both biotypes had distributions which tended, if not always statistically, to have adults at the upper sites. Direct observations showed that the morphology of $\underline{B}$. $\underline{campestris}$, particularly its hairiness, was an unsettling factor for the green biotype at the beginning of the experiment.

Summary

The aphid species were chosen to represent a range of biologies. The parthenogenetic apterae were comparable and representative of their species despite the limitations of the morph. They were free from sexual and flight responses.

This study examined the responses of the aphids. Each aphid demonstrated its choice by moving to a site, then settling, changing sites, or leaving the plant. If enough aphids in a species behaved similarly their selection or preference was registered statistically. Examination of the values among the plants demonstrated if they were hosts and how acceptable. The terms, "suitable", "acceptable", "selection", and "preference", are relative and awkward, but the need for them reveals a common problem, expressed by Nielsen (1978) and Tjallingii (1976) and neatly stated by Chew (1980): "preferences among crucifers are usually statistical rather than absolute". In this study, suitability and selection occasionally were both statistical and absolute, as shown by the invariable departure of the pea aphid from the rapeseed plants and the preference of the cabbage aphid for the upper sites. Mostly, however, suitability and selection were neither statistical nor absolute as shown by the responses of the other aphid species to the plants. Suitability and selection were linked to the specificity and tolerance of the aphid species to cruciferous plants as summarized:

"the more specialized the association with its source of food the greater is the insect's physiological dependence upon the plant" Osborne (1972)

The aphid species demonstrated their ability to select sites which were suited to their physiological abilities, given the morphological and biochemical characteristics of the host.

Time was a factor in the aphid's responses to the host plant. Both of the oligophagous species had determined their interactions with the rapeseed plants well within 24 h. The glucosinolates affected the behavior of both, functioning as a plant defense, and, therefore, an allomone for the pea aphid and as a host cue, and, therefore, a kairomone for the cabbage aphid.

The two polyphagous species were shown to differ with time in their tolerance of the rapeseed plants. The adults of both species settled, fed and reproduced, but with time both biotypes of the potato aphid left the plants. Blackman (1974) noted that such behaviour is to be expected when the plant is unsuitable for food. The green peach aphid could tolerate the rapeseed plants as hosts and established host plant associations for the 5-day study.

The glucosinolates were again involved and functioning as an allomone for the potato aphid although this species' reaction was not so immediate as that of the pea aphid. The biochemical action of the defence thus varied with the species, acting as a poison with the potato aphid and as a repellent with the pea aphid.

The aphid species in this study and any other insects which associate with cruciferous plants, must have physiological mechanisms which enable them to tolerate the presence of glucosinolates. The mechanisms were not examined here but they were shown to differ and also helped to account for the host plant ranges of the four aphid species. Thus, the green peach

aphid, with an apparently broad tolerance has a wide host range, whereas the cabbage aphid, with a specialized mechanism has a narrow one.

DISCUSSION AND CONCLUSIONS

My original intent was to use the recently developed Canola varieties of rapeseed to answer the related questions implicit in the following quotations from three researchers:

> "the more specialized the association with its source of
> food the greater is the insect's physiological dependence
> upon the plant" Osborne (1972)

> "Little is known about the functions of glucosinolates in
> plants which produce them and of the ultimate effects their
> elimination through plant breeding will have."
> Underhill (1980)

> "such alteration in the plants' chemistry may alter the host
> selection patterns of cruciferous and non-cruciferous feed-
> ing insects." Mitchell (1978)

Put more directly, if the chemical makeup of a major crop is significantly altered through plant breeding, what might be the effects on:

> specialised insects or obligate feeders, which depend on the crop?

> those more adaptable, opportunistic forms which merely exploit the crop? and

> insects which use the reduced or eliminated chemicals as allomones or kairomones, or as attractants or repellents?

It became apparent as the work went on that even though the breeding programme had reduced the glucosinolates in seed by several percentage points in the new varieties, the growing plants were not treated differently by cruciferous or non-cruciferous insects. Other investigators have reported comparable results, e.g.: Bailey (1976) and Kapatsa (1979) with armyworm larvae, Gupta and Thorsteinson (1960) with diamondback moths, Nayar and Thorsteinson (1963) with diamondback larvae, Obadofin (1979) and

Gerber and Obadofin (1981) with larvae of the crucifer-feeding red turnip beetle.

One of the goals in the rapeseed breeding programme is to increase plant resistance to pests. Breeding resistant strains of plants has been more successful against fungi and bacteria than against insects (Kondra 1981, Ross and Brain 1977). Genetic resistance to disease is the most desirable method of control but it is a difficult task if the organism is non-specific in its host preference, as with Sclerotinia stem rot (Dueck 1981).

Progress in breeding resistance to insects has been made by changing the morphology of the plants. Thus aphid-resistant rape in India and Pakistan is very waxy. The cabbage flea beetle in Canada is affected by plant hairiness and by the size of the cotyledons (Downey, personal communication 1981). Russell (1978) described two similar examples of resistance: the cabbage butterfly did not select red cabbages or the turnip aphid hairy cabbages.

In some plant species resistance to insect attack has been associated with the presence or absence of specific chemicals (Waiss et al. 1977).

"There is less information available on substances responsible for different odors between plant varieties differing in attractiveness to insects. However, because of the behaviour of the insects these are presumed to exist. Plant breeders have produced cabbages and marigolds without their distinctive odor, thus indicating the possibilities of the production of plant varieties lacking odors that attract insects." Painter (1951)

Chapman (1974) suggested that breeding resistant plants by altering chemical traits would probably be most successful if the feeding behaviour of pests could be affected enough to change their selection. Flea beetles, in particular, have been observed to avoid volunteer rapeseed plants of high glucosinolate content (Thomas, personal communication 1981). The blister beetle, _Lytta nuttalli_, feeds on low, rather than on high glucosinolate varieties (Burgess 1983). Mitchell (Dolinski, personal communication 1981) is trying to breed resistance to rape, based on chemical feeding rather than attraction stimulants.

Havens in 1792 was the first to breed a resistant plant (Russell 1978). An observed change in morphology made wheat crops resistant to Hessian fly, but now biotypes of the fly are capable of infesting resistant wheat; two were found in a wild population in the field, one of which had been selected in the laboratory (Sosa 1981). A report by Palmer (1960) describing an aphid resistant rape was followed by one from Lammerink (1968) describing a new biotype of cabbage aphid capable of attacking the plant. It is apparent that the production of new strains of plants creates selection pressure which results in new insect biotypes. In effect the plant breeders and the adapatable insect pests move forward together, even though the present study showed that the tested Canola rapeseeds were not treated as appreciably different from the older varieties.

PERSONAL COMMUNICATIONS

Arthur, A.P. 1980. Research Scientist, Entomologist. Agriculture Canada. Saskatoon, Saskatchewan.

Bucher, G.E. 1980. Research Scientist, Insect Pathologist. Agriculture Canada. Winnipeg, Manitoba.

Dolinski, M.G. 1981. Supervisor, Entomology. Alberta Agriculture. Edmonton, Alberta.

Downey, Dr. R.K. 1981. Head, Oilseed Crops. Agriculture Canada. Saskatoon, Saskatchewan.

Greig, Dr. M. 1981 and 1982. Computer Science, U.B.C. Vancouver, British Columbia.

Klassen, Dr. A.J. 1980. Research Scientist, Oilseed Crops. Agriculture Canada. Saskatoon, Saskatchewan.

MacGregor, Dr. D.I. 1981. Research Scientist, Oilseed Crops. Agriculture Canada. Saskatoon, Saskatchewan.

Thomas, P.M. 1981. Oilseed Crops. Alberta Agriculture. Lacombe, Alberta.

Turnock, W.J. 1980. Head, Integrated Pest Control Section. Agriculture Canada. Winnipeg, Manitoba.

Underhill, T. 1981. Research Scientist. Prairie Regional Laboratory of the National Research Council. Saskatoon, Saskatchewan.

LITERATURE CITED

Agriculture Canada. 1980. Publication No. 56. prepared by D. Adolphe. Canola: Canada's Rapeseed Crop. Shaw Printing (1974) Ltd., Winnipeg. 39 pp.

Aplin, R.T., R. d'Arcy Ward, and M. Rothschild. 1975. Examination of large white and small white butterflies (Pieris spp.) for the presence of mustard oils and mustard oil glycosides. J. Entomol. Ser. A, 50:73-78.

Appelqvist, L.A. 1972. Chemical constituents of rapeseed. pages 123-173 in L.A. Appelqvist and R. Ohlson, eds. Rapeseed: Cultivation, Composition, Processing and Utilization. Elsevier, Amsterdam.

Appelqvist, L.A. 1976. Lipids in the Cruciferae. pages 221-277 in J.G. Vaughan and A.J. MacLeod, eds. The biology and Chemistry of the Cruciferae. Academic Press, London, New York, San Francisco.

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

Beck, S.D. 1965. Resistance of plants to insects. Ann. Rev. Ent. 10:207-232.

Beck, S.D. 1974. Theoretical aspects of host plant specificity in insects. pages 290-311 in F.G. Maxwell and F.A. Harris, eds. Proceedings of the Summer Institute on Biological Control of Plants, Insects and Diseases. University Press of Mississippi, Jackson.

Beck, S.D. and J.C. Reese. 1976. Insect-plant interactions: nutrition and metabolism. Recent Adv. in Phytochem. 10:41-75.

Bengtsson. L., A. von Holsten, and B. Loof. 1972. Botany of rapeseed. pages 36-48 in L.A. Appelqvist and R. Ohlson, eds. Rapeseed: Cultivation, Composition, Processing and Utilization. Elsevier, Amsterdam.

Beversdorf, W.D. 1981. Breeding triazine resistant Canola varieties for improved weed control. pages 65-66 in Proceedings of 14th Annual Convention, Canola Council of Canada, Vancouver, Canada, March 1981.

Blackman, R. 1974. Aphids. Ginn and Co. Ltd., London and Aylesbury. 175 pp.

Bonnemaison, L. 1965. Insect pests of crucifers and their control. Ann. Rev. Ent. 10:233-256.

Bracken, G.K. and G.E. Bucher. 1977. An estimate of the relation between density of the Bertha armyworm and yield loss on rapeseed based on artificial infestations. J. Econ. Ent. 70(6):701-705.

Bucher, G.E. and G.K. Bracken. 1976. The Bertha armyworm, *Mamestra configurata* (Lepidoptera, Noctuidae). Artificial diet and rearing technique. Can. Ent. 108(12):1327-1338.

Burgess, L. 1983. Damage to rapeseed plants by two species of blister beetles (Coleoptera: Meloidae). Can. Ent. 115:875-876.

Carroll, F.J.F., N.D. Morgan, and J.D. Weber. 1980. Bioassay of three isothiocyanate fumigants against larvae of a Caribbean fruit fly and the apple maggot. J. Econ. Ent. 73:321-323.

Chapman, R.F. 1974. The chemical inhibition of feeding by phytophagous insects: A review. Bull. Ent. Res. 64:339-363.

Chew, F.S. 1980. Foodplant preferences of *Pieris* caterpillars (Lepidoptera). Oecologia (Berl.) 46:347-353.

Chew, F.S. and J.E. Rodman. 1979. Plant resources for chemical defenses. pages 271-307 in G.A. Rosenthal and D.H. Janzen, eds. Herbivores: Their Interaction with Secondary Plant Metabolites. Academic Press, London, New York, San Francisco.

Cole, R.A. 1976. Isothiocyanates, nitriles and thiocyanates as products of autolysis of glucosinolates in *Cruciferae*. Phytochemistry 15:759-762.

Craig, B.M. 1970. Comparative characteristics of Canadian rapeseed oils. pages 158-170 in Proceedings of the International Conference on the Science, Technology and Marketing of Rapeseed and Rapeseed Products, Ste. Adele, Quebec, 1970. Rapeseed Association of Canada in cooperation with the Department of Industry, Trade and Commerce, Ottawa.

Craig, B.M., T.M. Mallard, R.E. Wight, G.N. Irvine, and J.R. Reynolds. 1973. Influence of genetics, environment, and admixtures on low erucic acid rapeseed in Canada. J. Am. Oil. Chem. Soc. 50:395-403.

Dongre, T.K. and G.W. Rahalkar. 1980. Growth and development of spotted bollworm, *Earias vittella* on glanded and glandless cotton and on diet containing gossypol. Ent. Exp. Appl. 27(1):6-10.

Dueck, J. 1981 Disease problems of cruciferous oilseed crops and the potential for their control. pages 67-69 in Proceedings of 14th Annual Convention, Canola Council of Canada, Vancouver, Canada, March 1981.

Duffey, S.S. 1980. Sequesteration of plant natural products by insects. Ann. Rev. Ent. 25:447-477.

Ediz, S.H. and G.R.F. Davis. 1980. Repellency of rapeseed extracts to adults of *Tribolium castaneum* and *Tribolium confusum* (Coleoptera: Tenebrionidae). Can. Ent. 112(9):971-974.

Erdtman, H. 1969. Recent developments in molecular taxonomy. pages 107-119 in J.B. Harborne and T. Swain, eds. Perspectives in Phytochemistry. Academic Press, London, New York.

Erickson, J.M. and P. Feeny. 1974. Sinigrin: a chemical barrier to the black swallowtail butterfly, Papilio polyxenes. Ecology 55:103-111.

Feeny, P. 1976. Plant apparency and chemical defense. pages 1-36 in J.W. Wallace and R.L. Mansell, eds. Recent Advances in Phytochemistry - Volume 10. Plenum Press, New York and London.

Feeny, P., K.L. Paauwe, and N.J. De Mong. 1970. Flea beetles and mustard oils: Host plant specificity of Phyllotreta cruciferae and Phyllotreta striolata adults (Coleoptera: Chrysomelidae). Ann. Ent. Soc. Am. 63(1):832-841.

Finch, S. 1978. Volatile plant chemicals and their effect on host plant finding by the cabbage root fly (Delia brassicae). Ent. Exp. Appl. 24:150-159.

Fraenkel, G. 1959. The raison d'être of secondary plant substances. Science 129:1466-1470.

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

Gerber, G.H. and A.A. Obadofin. 1981. Growth, development, and survival of the larvae of the red turnip beetle Entomoscelis americana (Coleoptera: Chrysomelidae), on Brassica campestris and Brassica napus (Cruciferae). Can. Ent. 113:395-406.

Gilbert, L.E. 1979. Development of theory in the analysis of insect-plant interactions. pages 117-154 in D.J. Horn, G.R. Stairs and R.D. Mitchell, eds. Analysis of Ecological Systems. Ohio State University Press, Columbus.

Gordon, H.T. 1961. Nutritional factors in insect resistance to chemicals. Ann. Rev. Ent. 6:27-54.

Gupta, D.D. and A.J. Thorsteinson. 1960. Food plant resistance of the diamond-back moth (Plutella maculipennis [Curt.]). I. Gustation and olfaction in relation to botanical specificity of the larvae. Ent. Exp. Appl. 3:241-250.

Harborne, J.B. 1977. Introduction to Ecological Biochemistry. Academic Press, London. 243 pp.

Harper, F.R. and B. Berkenkamp. 1975. Revised growth-stage key for Brassica campestris and Brassica napus. Can. J. Plnt. Sci. 55:657-658.

Hawkes, C. and T.H. Coaker. 1976. Behavioural responses to host-plant odours in adult cabbage root fly (Erioschia brassicae [Bouché]). Symp. Biol. Hung. 16:85-89.

Hedin, P.A., F.G. Maxwell, and J.N. Jenkins. 1974. Insect plant attactants, feeding stimulants, repellents, deterrents and other related factors affecting insect behaviour. pages 494-527 in F.G. Maxwell and F.A. Harris, eds. Proceedings of the Summer Institute on Biological Control of Plants, Insects and Diseases. University Press of Mississippi, Jackson, Mississippi.

Hovanitz, W. 1969. Inherited and/or conditioned changes in host-plant preference in Pieris. Ent. Exp. Appl. 12:729-735.

Jones, P.A. 1972. Cyanogenic glucosides and their function. pages 103-122 in J.A. Harborne, ed. Phytochemical Ecology. Academic Press, New York and London.

Josefsson, E. 1971. Studies of the biochemical background to differences in glucosinolate content in Brassica napus L. I. Glucosinolate content in relation to general chemical composition. Physiol. Plant. 24:150-159.

Josefsson, E. 1972. Nutritive value and use of rapeseed meal. pages 354-379 in L.A. appelqvist and R. Ohlson, eds. Rapeseed: Cultivation, Composition, Processing and Utilization. Elsevier, Amsterdam.

Josefsson, E. and R. Jonsson. 1969. Studies of variation in glucosinolate content of seed of Cruciferae plants, especially in material with a high erucic acid content. Z. Pflanzenzuecht. 62:272-283.

Kapatsa, G.M. 1979. Growth, development, and survival of Mamestra configurata Walker (Lepid.: Noctuidae) on various reported food plants. M.Sc. Thesis. University of Manitoba.

Kennedy, J.S. 1965. Mechanisms of host plant selection. Ann. App. Biol. 56:317-322.

Kjaer, A. 1976. Glucosinolates in the Cruciferae. pages 207-219 in J.G. Vaughan, A.J. MacLeod, and B.M.G. Jones, eds. The Biology and Chemistry of the Cruciferae. Academic Press, London.

Kogan, M. 1976. The role of chemical factors in insect/plant relationships. Int. Cong. Entomol. Proc. 15:211-227.

Kondra, Z.P. 1981. Rapeseed to Canola a story of progress. Farming with Uniroyal, Winter, Uniroyal Chemical, 5(1):2.

Kondra, Z.P. and R.K. Downey. 1969. Glucosinolate content of developing Brassica napus and Brassica campestris seed. Can. J. Plant Sci. 49:623-624.

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

Krutacek, M. and M. Kralova. 1972. Biosynthesis of the glucobrassicin aglycone from carbon-14 and nitrogen-15 labelled L-tryptophan precursors. Biol. Plnt. 14:279-285.

Lammerink, J. 1968. A new biotype of cabbage aphid (Brevicoryne brassicae [L.]) on aphid resistant rape (Brassica napus). N.Zl. Jl. Agr. Res. 11(2):341-343.

Le, C.D. 1980. UBC MFAV analysis of variance/covariance. Best-Printer Co. Ltd., Vancouver. 63 pp.

Levin, D.A. 1976. The chemical defenses of plants to pathogens and herbivores. Ann. Rev. Ecol. Syst. 7:121-159.

Loof, B. and L.A. Appelqvist. 1972. Plant breeding for improved yield and quality. pages 101-122 in L.A. Appelqvist and R. Ohlson, eds. Rapeseed: Cultivation, Composition, Processing and Utilization. Elsevier, Amsterdam.

MacGibbon, D.B. and R.M. Allison. 1968. A glucosinolase system in the aphid Brevicoryne brassicae. N.Zl. Jl. Sc. 11:440-446.

Manitoba Department of Agriculture. 1980. Field crop recommendations for Manitoba. Manitoba Agricultural Services Co-ordinating Committee, MG 2273. 71 pp.

Manitoba Department of Agriculture. no date. Rapeseed production in Manitoba. Agdex 149, MG 7081. 12 pp.

Martin, A.L.D. 1970. Rapeseed production in Canada, pages 31-34 in Proceedings of the International Conference on the Science, Technology and Marketing of Rapeseed and Rapeseed Products, Ste. Adele, Quebec, 1970. Rapeseed Association of Canada in cooperation with the Department of Industry, Trade and Commerce, Ottawa.

Miller, L.P. 1973. Glycosides. pages 297-375 in L.P. Miller, ed. Phytochemistry, vol. 1. Van Nostrand Reinhold Co., New York.

Mitchell, B.K. 1978. Some aspects of gustation in the larval red turnip beetle, Entomoscelis americana, related to feeding and host plant selection. Ent. Exp. Appl. 24:340-349.

Moericke, V. and T.E. Mittler. 1966. Oesophageal and stomach inclusions of aphids feeding on various Cruciferae. Ent. Exp. Appl. 9:287-297.

Munakata, K. 1977. Insect feeding deterrents in plants. pages 93-101 in H.H. Shorey and J.J. McKelvey, Jr., eds. Chemical Control of Insect Behaviours - Theory and Application. Wiley and Sons, New York, London, Sydney, Toronto.

Nault, L.R. and W.E. Styer. 1972. Effects of sinigrin on host selection by aphids. Ent. Exp. Appl. 15:423-437.

Nayar, J.K. and A.J. Thorsteinson. 1963. Further investigations into the chemical basis of insect-host plant relationships in an oligophagous insect, Plutella maculipennis (C.) (Lepidoptera: Plutellidae). Can. J. Zool. 41:923-929.

Nielsen, J.K 1978. Host plant discrimination within Cruciferae: Feeding responses of four leaf beetles (Coleoptera: Chrysomelidae) to glucosino-lates, cucurbitacins and cardenolides. Ent. Exp. Appl. 24:41-54.

Nielsen, J.K., L. Dalgaard, L.M. Larsen, and H. Sorenson. 1979. Host plant selection of the horseradish flea beetle Phyllotreta armoraciae (Coleoptera: Chrysomelidae): Feeding responses to glucosinolates from several crucifers. Ent. Exp. Appl. 25(3):227-240.

Obadofin, A.A. 1979. Growth, development, survival and food selection in larvae of the red turnip beetle, Entomoscelis americana Brown (Coleoptera: Chrysomelidae), on species of Cruciferae. Ph.D. thesis, University of Manitoba, Winnipeg. 163 pp.

Osborne, D. 1972. Mutual regulation of growth and development in plants and insects. pages 33-42 in Insect and Plant Relationships Symposium of the Royal Entomological Society of London No. 6. Blackwell Sc. Publ., Oxford, London, Edinburgh, Melbourne.

Osgood, C.E. and R.H. Kempster. 1971. An air-flow olfactometer for distinguishing between oviposition attractants and stimulants of mosquitoes. J. Econ. Ent. 64:1109-1110.

Painter, R.H. 1951. Insect Resistance in Crop Plants. McMillan, New York. 520 pp.

Palmer, T.P. 1960. Aphid resistant rape. N.Zl. Jour. Agric. 101:375-376.

Pettersson, J. 1976. Ethology of Daysenura brassicae Winn. (Dipt. Cecidomyidae) I. Lab studies of olfactory reactions to the host plant. Symp. Biol. Hung. 16:203-208.

Prairie Grain Variety Surveys. 1977-1983. Prepared by the Canadian Co-operative Wheat Producers. Looseleaf pub. n.p.

Reese, J.C. 1977. The effects of plant biochemicals on insect growth and nutritional physiology. pages 129-152. in P.A. Hedin, ed. Host Plant Resistance to Pests. ACS Symposium Series 62, Am. Chem. Soc., Washington, D.C., U.S.A.

Reese, J.C. 1978. Chronic effects of plant allelochemics on insect nutritional physiology. Ent. Exp. Appl. 24:425-431.

Reese, J.C. and S.D. Beck. 1976. Effects of certain allelochemics on the growth and development of the black cutworm. Symp. Biol. Hung.16:217-221.

Rodman, J.E. and F.S. Chew. 1980. Phytochemical correlates of herbivory in a community of native and naturalized Cruciferae. Bioc. Syst. Ecol. 8:43-50.

Ross, M.S.F. and K.R. Brain. 1977. Crop protection agents. pages 237-273 in M.S.F. Ross and K.R. Brain, eds. An Introduction to Phytopharmacy. Pitman Pub. Ltd., London.

Rothschild, M. 1972. Some observations on the relationship between plants, toxic insects, and birds. pages 1-10 in J.B. Harborne, ed. Phytochemical Ecology. Academic Press, London and New York.

Rothschild, M. 1973. Secondary plant substances and warning colouration in insects. R. Ent. Soc. (Lond.) Symp. 6:59-83.

Russell, G.E. 1978. Plant Breeding for Pest and Disease Resistance. Butterworths, London. 485 pp.

Sallans, H.R. 1964. Factors affecting the composition of Canadian oilseeds. J. Am. Oil Chem. Soc. 41:215-218.

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

Slama, K. 1969. Plants as a source of materials with insect hormone activity. Ent. Exp. Appl. 12:721-728.

Smith, J.N. 1955. Detoxification methods in insects. Bioc. Rev. Camb. Phil. Soc. 30:455-475.

Sosa, J.R. 1981. Biotypes J and L of the Hessian fly discovered in an Indiana wheat field. J. Econ. Ent. 74:180-182.

Staedler, E. 1976. Sensory aspects of insect-plant interactions. Int. Cong. Entomol. Proc. 15:228-248.

Steck, W., E.W. Underhill, M.D. Chisholm, C.C. Peters, H.G. Philip, and A.P. Arthur. 1979. Sex pheromone traps in population monitoring of adults of the Bertha armyworm, Mamestra configurata (Lepidoptera: Noctuidae). Can. Ent. 111:91-95.

Stefansson, B.R. 1981. Canola/rapeseed variety development. pages 47-50 in Proceedings of the 14th Annual Convention, Canola Council of Canada, Vancouver Canada, March 1981.

Stipanovic, R.D., A.A. Bell, and M.J. Lukefahr. 1977. Natural insecticides from cotton (Gossypium). pages 197-214 in P.A. Hedin, ed. Host Plant Resistance to Pests. ACS Symposium Series 62. Am. Chem. Soc., Washington, D.C., U.S.A.

Tallent, W.H. 1972. Improving high erucic acid oilseeds: chemically or genetically? J. Am. Oil Chem. Soc. 49:15-19.

Tallent, W.H. 1972. Improving high erucic acid oilseeds: chemically or genetically? J. Am. Oil Chem. Soc. 49:15-19.

Tapper, B.A. and P.F. Reay. 1973. Cyanogenic glycosides and glucosinolates (mustard oil glucosides). pages 447-476 in G.W. Butler and R.W. Bailey, eds. Chemistry and Biochemistry of Herbage - Vol. 1. Academic Press, London and New York.

Thorsteinson, A.J. 1953. The chemotactic responses that determine host specificity in an oligophagous insect (Plutella maculipennis [Curt.] Lepidoptera). Can. J. Zool. 31(1):52-72.

Thurston, R. and J.A. Webster. 1962. Toxicity of Nicotiana gossei Domin. to Myzus persicae (Sulzer). Ent. Exp. Appl. 5:233-238.

Tjallingii, W.F. 1976. A preliminary study of host selection and acceptance behaviour in the cabbage aphid, Brevicoryne brassicae L. Symp. Biol. Hung. 16:283-285.

Tookey, H.L., C.H. Van Etten, and M.E. Daxenbilcher. 1979. Glucosinolates. pages 103-142 in T.E. Liener, ed. Toxic Consitutents of Plant Foodstuffs. Academic Press, London, New York.

Tsuruo, I. and T. Hata. 1968. Studies on Myrosinase in mustard seed. V. On the β-glucosidic acitivity of Myrosinase and the interaction of Ascorbate with Myrosinase. Agric. Biol. Chem. 32(12):1425-1431.

Turnock, W.J. 1977. Adaptability and stability of insect pest populations in prairie agricultural ecosystems. Minn. Agric. Exp. Stn. Tech. Bull. 310:89-101.

Underhill, E.W. 1980. Glucosinolates. pages 493-511 in E.A. Bell and B.V. Charlwood, eds. Secondary Plant Products, Encyclopedia of Plant Physiology New Series, vol. 8. Springer-Verlag, Berlin, Heidelberg, New York.

van Emden, H.F. 1972. Aphids as phytochemists. pages 25-43 in J.B. Harborne, ed. Phytochemical Ecology. Acadmic Press, London.

van Emden, H.F. and M.A. Bashford. 1969. A comparison of the reproduction of Brevicoryne brassicae and Myzus persicae in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. Ent. Exp. Appl. 12:351-364.

van Etten, C.H. and M.E. Daxenbichler. 1971. Formation of organic nitriles from progoitrin in leaves of Crambe abyssinca and Brassica napus. J. Agric. Food Chem. 19(1):194-195.

Waiss, A.C., B.G. Chan, and C.A. Elliger. 1977. Host plant resistance to insects. pages 115-128 in Hedin, ed. Host Plant Resistance to Pests. ACS Symposium Series 62. Am. Chem. Soc., Washington, D.C., U.S.A.

Weinberg, B. 1970. Introduction. pages 1,2 in Proceedings of the
International Conference on the Science, Technology and Marketing of
Rapeseed and Rapeseed Products. Ste. Adele, Quebec, 1970. Rapeseed
Association of Canada in cooperation with the Department of Industry, Trade
and Commerce, Ottawa.

Whittaker, R.H. and P.P. Feeny. 1971. Allelochemics: Chemical
interactions between species. Science 171:757-770.

Yang, R.S.H. 1976. Enzymatic conjugation and insecticide metabolism.
pages 177-216 in C.F. Wilkinson, ed. Insecticide Biochemistry and
Physiology. Plenum Press, New York.

APPENDIX A. Glucosinolates as allomones and kairomones.

> "... evidence that sinigrin and other mustard oil glucosides
> serve a defensive function in Cruciferae family plants."
> Erickson and Feeny (1974)

Soil residues of glucosinolates and their byproducts from rapeseed left in the field have been shown to suppress the growth of wheat and oats (Martin 1970). This illustrates an allelochemic interaction with plant competitors, as well as to heterotrophic organisms. Glucosinolates and their toxic breakdown products have been demonstrated to have insecticidal or inhibiting effects on some caterpillars, aphids, grasshoppers, cockroaches, flea and flour beetles, mites, apple maggot, and fruit, house and vinegar flies (Carroll et al. 1980, Ediz and Davis 1980, Erickson and Feeny 1974, Levin 1976). Glucosinolates and their products may metabolize still futher within insects, and release other toxic substances. Erickson and Feeny (1974), using the glucosinolate, sinigrin, in a study with swallowtail butterfly larvae found that it was hydrolyzed in the insect's gut and then had toxic effects which interfered with digestion, assimilation, utilization and conversion processes and reduced respiration.

Isothiocyanates have been known for many years to act as fumigants against insects (Carroll et al. 1980) and as antibiotics against fungi and bacteria (Miller 1973). They irritate mammalian tissue (Erickson and Feeny 1974). Tapper and Reay (1973) suggested that the isothiocyanates and other hydrolysis products are more toxic than glucosinolates in their effects on animals. Harborne (1977) suggested that isothiocyanate is changed to thiocyanate in cattle and insects. Thiocyanate insecticides release cyanide ions which are general enzyme poisons and affect respiration (Ross and

Brain 1977).

Insects may feed at a plant site which does not contain allomones. The green peach aphid feeds in plant phloem and so avoids allomones contained in xylem, such as the alkaloid, nicotine, in tobacco (Beck 1965, Self et al. 1964) and the phenol, phlorizin, in green apple (Munakata 1977). Thurston and Webster (1962) described the toxic effects on this species from contact with leaf hairs that exude nicotine and are present on the aerial parts of some tobacco plants. Some insects establish successful associations with plants containing allomones and tolerate and may even use the biochemicals. Insects may ingest and excrete the allomone. Rothschild (1973) described this method of countermeasure by a homopteran of the Ricaniidae, which feeds on a toxic plant in southeast Australia. The repercussions of this illustration are interesting since humans have experienced severe symptoms of poisoning when they ingested honey produced from the excreted honeydew.

Insects may metabolize and detoxify allomones. Caterpillars' guts contain many microsomal mixed function oxidases which result in a range of abilities to deal with allomones depending on the effectiveness of the specific larval system (Krieger et al. 1971). Smith (1955) described the importance of oxidation with resulting products of reduced toxicity. Yang (1976) described an energy dependent process which attaches glucose, sulfate, glutathione, glycine or phosphate, especially in insects, to the compound or its metabolic products, forming a non-toxic conjugate. Insects may have specialized enzyme systems, e.g., rhodase which detoxifies sulphur and cyanide compounds (Rothschild 1972, Smith 1955).

Insects may sequester and store the allomones (Duffey 1980). The chemical, its concentration, metabolism or conversion, excretion, and storage vary with the species (Rothschild 1973). Insects may use these allomones or their products in their own physiological processes, e.g., terpenoids stimulate reproductive activities in the desert locust, Schisto-cerca gregaria (Beck and Reese 1976). Other plant terpenoids are used as hormonal compounds and reduce the metabolic demands on the insect (Slama 1969). Gordon (1961) found the green peach aphid able to tolerate nicotine three times more effectively when it had been feeding on turnip rather than lettuce. The presence of oesophageal and stomach inclusions in aphids feeding on various Cruciferae (Moericke and Mittler 1966) may explain this increased tolerance for other allomones. Insects may further use these compounds in interactions with individuals of their species or others. Plant-derived hexenal is used as a sex pheromone by three moth species (Fraenkel 1959, Slama 1969). The butterflies, Pieris rapae and P. brassicae, have accumulated levels of glucosinolates in their body tissue which provide chemical protection to the larvae, pupae and possibly adult stages from bird predators (Aplin et al. 1975, Erickson and Feeny 1974). The importance of cardenolides as a chemical defense and as a basis for an insect mimicry system is described extensively in the literature (Rothschild 1973).

> "glucosinolates are probably important in determining
> aspects of the behaviour of insects associated with
> cruciferous plants and although not fully established it is
> most likely that the volatile hydrolysis products are
> involved in the attraction to the host plant" Cole (1976)

The insects listed in Table XXII use glucosinolates and their byproducts as kairomones in their selection of plants for oviposition, feeding or both.

Table XXII. Insects which use glucosinolates or their byproducts as kairomones in their selection of plants for oviposition (O), feeding (F), or both (O,F).

Species	Common name	Use	Reference
Brevicoryne brassicae	cabbage aphid	F	Fraenkel 1969
Dasyneura brassicae (gravid)	cabbage midge	O	Pettersson 1976
Delia brassicae	cabbage root fly	O	Finch 1978
(=Erioischia brassicae)			Hawkes and Coaker 1976
(=Hylemya brassicae)			Hedin et al. 1974
Entomoscelis americana	red turnip beetle	F	Mitchell 1978
Eurydema ventralis	?	O,F	Bonnemaison 1965
Listroderes costirostris obliquus	vegetable weevil	O	Heden et al. 1974
Phaedon cochleariae	mustard beetle	F	Tapper and Reay 1973
Phyllotreta armoraciae	?	F	Nielson et al. 1979
Phyllotreta cruciferae	crucifer flea beetle	O	Feeny et al. 1970
Phyllotreta striolata	striped flea beetle	O	Feeny et al. 1970
Pieris brassicae	cabbage butterfly, large	O	Bonnemaison 1965
		F	Fraenkel 1969
Pieris napi	cabbage butterfly, small	O,F	Rodman and Chew 1980
Pieris rapae	cabbage butterfly, common	F	Bonnemaison 1965
	(=imported cabbageworm)	O	Hovanitz 1969
Plutella maculipennis	diamondback moth	O	Fraenkel 1969
		F	Hedin et al. 1974

APPENDIX B. Design for the experiments with female armyworm moths on rapeseed plants with the arrangement of the varieties designated by C= Candle, T= Torch, M = Midas, R = Regent and with trial 1 at the top, and chamber 1 at the left, in each Latin square. (See p. 22).

Moth age	Armyworm experiments			Diamondback experiment
	1	2	3	
Young	M R C T	M T C R	M T C R	T M R C
	C T R M	T M R C	T M R C	C R T M
	R M T C	C R M T	C R M T	R C M T
	T C M R	R C T M	R C T M	M T C R
Old	T C R M	T C M R	T C M R	T C M R
	R M C T	M T R C	M T R C	M T R C
	M R T C	R M C T	R M C T	R M C T
	C T M R	C R T M	C R T M	C R T M

APPENDIX C. Composition of Vanderzant modification mixture for insects. (ICN Pharmaceuticals, Inc., Cleveland, Ohio). (See p 23).

Chemical	Weight/kg mixture
Alpha Tocopherol	8 gm
Ascorbic Acid	270 gm
Biotin	20 mg
Calcium Pantothenate	1 gm
Choline Chloride	50 gm
Crystalline Folic Acid	250 mg
Inositol	20 gm
Niacinamide	1 gm
Pyridoxine HCl	250 mg
Riboflavin	500 mg
Thiamine HCl	250 mg
Vitamin B_{12} Trituration in Mannitol	2 gm

APPENDIX D. ANOVA tables for the experiments with female moths on rapeseed plants.

The analysis of variance model for the armyworm was:

$$Y = \mu + E + A + T + P + V + EA + ET + EP + EV$$

$$+ AT + AP + AV + EAT + EAP + EAV + error.$$

that for the diamondback was:

$$Y = \mu + A + T + P + V + AT + AP + AV + error.$$

where:

μ = population mean.

E = experiment number; 1 through 3 for armyworm; not applicable for diamondback with E = 1.

A = moth age; 1 = young, 2 = old.

T = trial; 1 though 4.

P = olfactometer position; 1 though 4 from left to right facing front wall panel.

V = rapeseed varieties; B. campestris: 1 = Candle, 4 = Torch; B. napus: 2 = Midas, 3 = Regent.

grouped letters = describe interaction terms.

error = experimental error.

Table XXIII. ANOVA of the armyworm moths for location by channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	0.70833	0.23611	0.16038	0.92228
P	3	31.208	10.403	7.0660	0.74522E-03
V	3	2.0417	0.68056	0.46226	0.71038
A	1	8.1667	8.1667	5.5472	0.24080E-01
AT	3	3.7500	1.2500	0.84906	0.47625
AP	3	10.583	3.5278	2.3962	0.84200E-01
AV	3	2.2500	0.75000	0.50943	0.67830
E	2	35.896	17.948	12.191	0.90594E-04
ET	6	16.354	2.7257	1.8514	0.11656
EP	6	4.1042	0.68403	0.46462	0.82978
EV	6	2.0208	0.33681	0.22877	0.96460
EA	2	1.3958	0.69792	0.47406	0.62630
EAT	6	7.6875	1.2813	0.87028	0.52610
EAP	6	9.1042	1.5174	1.0307	0.42162
EAV	6	3.6875	0.61458	0.41745	0.86251
Error	36	53.000	1.4722		
Total	95	191.96			

Grand mean   1.3542

Standard deviation   1.4215

Table XXIV. ANOVA of the armyworm moths for location by chambers.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	2.6979	0.89931	0.39183	0.75960
P	3	14.115	4.7049	2.0499	0.12419
V	3	7.0313	2.3438	1.0212	0.39468
A	1	10.010	10.010	4.3616	0.43892E-01
AT	3	5.5312	1.8437	0.80333	0.50026
AP	3	5.4479	1.8160	0.79123	0.50678
AV	3	14.365	4.7882	2.0862	0.11921
E	2	23.688	11.844	5.1604	0.10703E-01
ET	6	9.1458	1.5243	0.66415	0.67887
EP	6	17.229	2.8715	1.2511	0.30412
EV	6	4.0625	0.67708	0.29501	0.93533
EA	2	0.89583	0.44792	0.19516	0.82357
EAT	6	6.9375	1.1563	0.50378	0.80130
EAP	6	20.021	3.3368	1.4539	0.22177
EAV	6	16.354	2.7257	1.1876	0.33485
Error	36	82.625	2.2951		
Total	95	240.16			

Grand mean   1.0937

Standard deviation   1.5900

Table XXV. ANOVA of the armyworm moths for location by chambers + channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	5.1979	1.73631	0.50252	0.68295
P	3	76.365	25.455	7.3827	0.56070E-03
V	3	10.865	3.6215	1.0504	0.38218
A	1	0.9375E-01	0.93750E-01	0.27190E-01	0.86995
AT	3	1.3646	0.45486	0.13192	0.94045
AP	3	15.031	5.0104	1.4532	0.24358
AV	3	11.365	3.7882	1.0987	0.36227
E	2	116.90	58.448	16.952	0.64936E-05
ET	6	20.271	3.3785	0.97986	0.45304
EP	6	16.104	2.6840	0.77845	0.59222
EV	6	7.6042	1.2674	0.36757	0.89464
EA	2	0.18750	0.93750E-01	0.27190E-01	0.97320
EAT	6	3.9792	0.66319	0.19235	0.97699
EAP	6	23.813	3.9688	1.1511	0.35366
EAV	6	10.479	1.7465	0.50655	0.79926
Error	36	124.12	3.4479		
Total	95	443.74			

Grand mean   2.4479

Standard deviation   2.1612

Table XXVI. ANOVA of the egg plaques from armyworm moths for location by channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	2.1146	0.70486	1.5263	0.22429
P	3	1.1146	0.37153	0.80451	0.49962
V	3	1.7813	0.59375	1.2857	0.29404
A	1	4.5938	4.5938	9.9474	0.32446E-02
AT	3	2.1146	0.70486	1.5263	0.22429
AP	3	1.1146	0.37153	0.80451	0.49962
AV	3	1.7812	0.59375	1.2857	0.29404
E	2	1.7500	0.87500	1.2857	0.16505
ET	6	2.9167	0.48611	1.0526	0.40853
EP	6	3.9167	0.65278	1.4135	0.23636
EV	6	6.0000	1.0000	2.1654	0.69426E-01
EA	2	1.7500	0.87500	1.8947	0.16505
EAT	6	2.9167	0.48611	1.0526	0.40853
EAP	6	3.9167	0.65278	1.4135	0.23636
EAV	6	6.0000	1.0000	2.1654	0.69426E-01
Error	36	16.625	0.46181		
Total	95	60.406			

Grand mean   0.21875

Standard deviation 0.79741

Table XXVII. ANOVA of the egg plaques from armyworm moths for location by chambers.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	8.2500	2.7500	0.69110	0.56346
P	3	8.0833	2.6944	0.67714	0.57175
V	3	21.417	7.1389	1.7941	0.16575
A	1	48.167	48.167	12.105	0.13342E-02
AT	3	8.2500	2.7500	0.69110	0.56346
AP	3	8.0833	2.6944	0.67714	0.57175
AV	3	21.417	7.1389	1.7941	0.16575
E	2	1.5208	0.76042	1.19110	0.82688
ET	6	27.062	4.5104	1.1335	0.36299
EP	6	37.229	6.2049	1.5593	0.18742
EV	6	26.646	4.4410	1.1161	0.37247
EA	2	1.5208	0.76042	0.19110	0.82688
EAT	6	27.063	4.5104	1.1335	0.36299
EAP	6	37.229	6.2049	1.5593	0.18742
EAV	6	26.646	4.4410	1.1161	0.37247
Error	36	143.255	3.9792		
Total	95	451.83			

Grand mean   0.70833

Standard deviation   2.1809

Table XXVIII. ANOVA of the egg plaques from armyworm moths for location by chambers + channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	12.865	4.2882	0.84880	0.47638
P	3	7.7813	2.5938	0.51340	0.67564
V	3	23.031	7.6771	1.5196	0.22600
A	1	82.510	82.510	16.332	0.26721E-03
AT	3	12.865	4.2882	0.84880	0.47638
AP	3	7.7812	2.5937	0.51340	0.67564
AV	3	23.031	7.6771	1.5196	0.22600
E	2	0.89583	0.44792	0.88660E-01	0.91536
ET	6	39.354	6.5590	1.2983	0.28289
EP	6	59.187	9.8646	1.9526	0.98686E-01
EV	6	27.937	4.6562	0.92165	0.49099
EA	2	0.89583	0.44792	0.88660E-01	0.91536
EAT	6	39.354	6.5590	1.2983	0.28289
EAP	6	59.188	9.8646	1.9526	0.98686E-01
EAV	6	27.938	4.6563	0.92165	0.49099
Error	36	181.87	5.0521		
Total	95	606.49			

Grand mean   0.92708

Standard deviation   2.5267

Table XXIX. ANOVA of the average fecundities of armyworm moths for
location by channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	0.11480	0.38266E-01	0.64328	0.59223
P	3	0.19582	0.65273E-01	1.0973	0.36283
V	3	0.13100	0.43668E-01	0.73410	0.53852
A	1	0.21882	0.21882	3.6785	0.63076E-01
AT	3	0.11480	0.38266E-01	0.64328	0.59223
AP	3	0.19582	0.65273E-01	1.0973	0.36283
AV	3	0.13100	0.43668E-01	0.73410	0.53852
E	2	0.11473	0.57363E-01	0.96432	0.39087
ET	6	0.38586	0.64309E-01	1.0811	0.39203
EP	6	0.21455	0.35759E-01	0.60114	0.72748
EV	6	0.41827	0.69712E-01	1.1719	0.34282
EA	2	0.11473	0.57363E-01	0.96432	0.39087
EAT	6	0.38586	0.64309E-01	1.0811	0.39203
EAP	6	0.21455	0.35759E-01	0.60114	0.72748
EAV	6	0.41827	0.69712E-01	1.1719	0.34282
Error	36	2.1415	0.59485E-01		
Total	95	5.5103			

Grand mean   0.47743E-01

Standard deviation 0.24084

Table XXX. ANOVA of the average fecundities of armyworm moths for location by chambers.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	1.7743	0.59142	0.90956	0.44602
P	3	0.96580	0.32193	0.49511	0.68795
V	3	3.8577	1.2859	1.9776	0.13473
A	1	6.6600	6.6600	10.243	0.28641E-02
AT	3	1.7743	0.59142	0.90956	0.44602
AP	3	0.96580	0.32193	0.49511	0.68795
AV	3	3.8577	1.2859	1.9776	0.13473
E	2	0.75567	0.37784	0.58109	0.56445
ET	6	5.1329	0.85548	1.3157	0.27539
EP	6	3.1002	0.51671	0.79466	0.58027
EV	6	4.0568	0.67613	1.0398	0.41611
EA	2	0.75567	0.37784	0.58109	0.56445
EAT	6	5.1329	0.85548	1.3157	0.27539
EAP	6	3.1002	0.51671	0.79466	0.58027
EAV	6	4.0568	0.67613	1.0398	0.41611
Error	36	23.408	0.65022		
Total	95	69.355			

Grand mean   0.26399

Standard deviation 0.85443

Table XXXI. ANOVA of the average fecundities of armyworm moths for location by chambers + channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	0.20391	0.67969E-01	0.17610	0.91189
P	3	0.18858	0.62859E-01	0.16286	0.92066
V	3	1.8691	0.62304	1.6142	0.20310
A	1	4.0671	4.0671	10.537	0.25315E-02
AT	3	0.20391	0.67969E-01	0.17610	0.91189
AP	3	0.18858	0.62859E-01	0.16286	0.92066
AV	3	1.8691	0.62304	1.6142	0.20310
E	2	0.17671	0.88355E-01	0.22891	0.79655
ET	6	2.2350	0.37249	0.96508	0.46248
EP	6	1.7347	0.28912	0.74907	0.61413
EV	6	1.8001	0.30001	0.77728	0.59309
EA	2	0.17671	0.88355E-01	0.22891	0.79655
EAT	6	2.2350	0.37249	0.96508	0.46248
EAP	6	1.7347	0.28912	0.74907	0.61413
EAV	6	1.8001	0.30001	0.77728	0.59309
Error	36	13.895	0.38597		
Total	95	34.378			

Grand mean   0.20583

Standard deviation 0.60156

Table XXXII. ANOVA of the diamondback moths for location by channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	1.0938	0.36458	0.13725	0.93585
P	3	5.3438	1.7813	0.67059	0.58626
V	3	7.3438	2.4479	0.92157	0.45987
A	1	1.5313	1.5313	0.57647	0.46235
AT	3	0.84375	0.28125	0.10588	0.95504
AP	3	3.0937	1.0312	0.38824	0.76357
AV	3	1.5937	0.53125	0.20000	0.89438
Error	12	31.875	2.6562		
Total	31	52.719			

Grand mean   0.90625

Standard deviation 1.3041

Table XXXIII.   ANOVA of the diamondback moths for location by chambers.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	1.0938	0.36458	0.30435	0.82176
P	3	4.0938	1.3646	1.1391	0.37266
V	3	4.0938	1.3646	1.1391	0.37266
A	1	9.0313	9.0313	7.5391	0.17741E-01
AT	3	0.59375	0.19792	0.16522	0.91775
AP	3	5.5937	1.8646	1.5565	0.25102
AV	3	5.5937	1.8646	1.5565	0.25102
Error	12	14.375	1.1979		
Total	31	44.469			

Grand mean   0.71875

Standard deviation   1.1977

Table XXXIV. ANOVA of the diamondback moths for location by chambers + channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	1.2500	0.41667	0.92166E-01	0.96294
P	3	11.250	3.7500	0.82949	0.50283
V	3	4.2500	1.4167	0.31336	0.81545
A	1	3.1250	3.1250	0.69124	0.42198
AT	3	1.6250	0.54167	0.11982	0.94669
AP	3	5.6250	1.8750	0.41475	0.74554
AV	3	10.125	3.3750	0.74654	0.54487
Error	12	54.250	4.5208		
Total	31	91.500			

Grand mean   1.6250

Standard deviation 1.7180

Table XXXV. ANOVA of the eggs from diamondback moths for location by channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	38.250	12.750	0.19780	0.89587
P	3	153.25	51.083	0.79250	0.52118
V	3	165.75	55.250	0.85714	0.48952
A	1	338.00	338.00	5.2437	0.40938E-01
AT	3	38.250	12.750	0.19780	0.89587
AP	3	153.25	51.083	0.79250	0.52118
AV	3	165.75	55.250	0.85714	0.48952
Error	12	773.50	64.458		
Total	31	1826.0			

Grand mean   3.2500

Standard deviation 7.6748

Table XXXVI. ANOVA of the eggs from diamondback moths for location by chambers.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	49.500	16.500	1.6923	0.22146
P	3	60.750	20.250	2.0769	0.15683
V	3	15.750	5.2500	0.53846	0.66487
A	1	40.500	40.500	4.1538	0.64206E-01
AT	3	49.500	16.500	1.6923	0.22146
AP	3	60.750	20.250	2.0769	0.15683
AV	3	15.750	5.2500	0.53846	0.66487
Error	12	117.00	9.7500		
Total	31	409.50			

Grand mean   1.1250

Standard deviation 3.6345

Table XXXVII. ANOVA of the eggs from diamondback moths for location by chambers + channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	9.7500	3.2500	0.29828E-01	0.99269
P	3	193.75	64.583	0.59273	0.63157
V	3	116.25	38.750	0.35564	0.78601
A	1	612.50	612.50	5.6214	0.3540E-01
AT	3	9.7500	3.2500	0.29828E-01	0.99269
AP	3	193.75	64.583	0.59273	0.63157
AV	3	116.25	38.750	0.35564	0.78601
Error	12	1307.5	108.96		
Total	31	2559.5			

Grand mean 4.3750

Standard deviation 9.0865

Table XXXVIII. ANOVA of the average fecundities of diamondback moths for location by channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	40.281	13.427	0.22842	0.87482
P	3	101.16	33.719	0.57363	0.64314
V	3	125.34	42.781	0.71079	0.56401
A	1	185.28	185.28	3.1520	0.10118
AT	3	40.281	13.427	0.22842	0.87482
AP	3	101.16	33.719	0.57363	0.64314
AV	3	125.34	41.781	0.71079	0.56401
Error	12	705.37	58.781		
Total	31	1424.2			

Grand mean   2.4062

Standard deviation 6.7781

Table XXXIX. ANOVA of the average fecundities of diamondback moths for location by chambers.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	9.2109	3.0703	1.9552	0.17464
P	3	9.2109	3.0703	1.9552	0.17464
V	3	3.5859	1.1953	0.76119	0.53721
A	1	5.6953	5.6953	3.6269	0.81100E-01
AT	3	9.2109	3.0703	1.9552	0.17464
AP	3	9.2109	3.0703	1.9552	0.17464
AV	3	3.5859	1.1953	0.76119	0.53721
Error	12	18.844	1.5703		
Total	31	68.555			

Grand mean   0.42187

Standard deviation 1.4871

Table XL. ANOVA of the average fecundities of diamondback moths for location by chambers + channels.

Source	DF	Sum SQ	Mean SQ	F-value	Probability
T	3	4.9271	1.6424	0.16284	0.91932
P	3	18.702	6.2340	0.61811	0.61649
V	3	8.5584	2.8528	0.28285	0.83682
A	1	59.814	59.814	5.9306	0.31427E-01
AT	3	4.9271	1.6424	0.16284	0.91932
AP	3	18.702	6.2340	0.61811	0.61649
Av	3	8.5584	2.8528	0.28285	0.83682
Error	12	121.03	10.086		
Total	31	245.22			

Grand mean   1.3672

Standard deviation 2.8125

APPENDIX E. Design for the experiments with aphids on rapeseed plants with
the arrangement of the varieties designated by C = Candle, T =
Torch, M = Midas, R = Regent, S = Standard and the replicates
designated by number. The top row of plants was at the back
of the chamber. (See p. 45).

Aphid species	Chamber 1					Chamber 2				
Cabbage	M1	M2	R1	S1	T2	C1	M1	S2	T1	M2
	C1	T1	R2	C2	S2	C2	T2	R2	S1	R1
Pea	C1	R1	C2	S1	T1	T1	C1	R1	T2	R2
	S1	R2	M2	M1	T2	M2	S2	C2	S1	M1
Green Peach	R1	R2	M2	S2	T1	S2	C2	M2	T1	R1
	M1	C2	S1	C1	T2	T2	R2	S1	M1	C1
Potato - green	S2	R2	M1	T1	C1	M2	M1	C2	R2	S1
	S1	T1	C2	R1	M2	T1	C1	R1	T1	S2
Potato - pink	T1	R2	C2	M1	C1	M2	C2	T1	R2	T2
	T2	M2	S2	S1	R1	S2	M1	C1	S1	R1

APPENDIX F. ANOVA tables for the experiments with aphids on rapeseed

plants.

The analysis of variance model for the aphid study was:

$$Y = \mu + A + C(A) + P + R(ACP) + S + AP + CP + AS$$

$$+ CS + PS + APS + CPS + error$$

where:

μ = population mean.

A = aphid; 2 = green peach, 3 = pink potato, 4 = green potato,
1 = cabbage, 5 = pea.

C = chamber; 1 or 2.

P = plant; B campestris: 1 = Candle, 4 = Torch, B. napus:
2 = Midas, 3 = Regent, 5 = Standard.

R = plant replicate; 1 or 2.

S = plant site; 1 = lower, 2 = upper.

grouped letters = describe interaction terms and nesting of terms.

error = experimental error.

Table XLI. ANOVA for the sum of the adult aphids.

Source	DF	Sum SQ	Mean SQ	Error	F-value	Probability
A	4	7796.1	1949.0	C(A)	69.274	0.14453E-03
C(A)	5	140.67	28.135	R(ACP)	3.5016	0.86210E-02
P	4	1544.8	386.19	CP(A)	30.717	0.27746E-07
AP	16	4387.8	274.24	CP(A)	21.812	0.29890E-08
CP(A)	20	251.54	12.573	R(ACP)	1.5647	0.10107
R(ACP)	50	401.75	8.0350		0.11148	1.0000
S	1	47.045	47.045	CS(A)	1.0978	0.34274
AS	4	1474.1	3685.4	CS(A)	85.996	0.85116E-04
CS(A)	5	214.27	42.855		0.59459	0.70412
PS	4	3262.2	815.56	CPS(A)	18.147	0.19555E-05
APS	16	5024.9	314.06	CPS(A)	6.9880	0.44724E-04
CPS(A)	20	898.85	44.943		0.62355	0.87574
Error	50	3603.7	72.075			
Total	199	42315.				
Grand mean		15.755				
Standard deviation		14.582				

Table XLII. ANOVA for the average fecundities of adult aphids.

Source	DF	Sum SQ	Mean SQ	Error	F-value	Probability
A	4	514.46	128.62	C(A)	107.754	0.48883E-04
C(A)	5	5.9680	1.1936	R(ACP)	0.96049	0.45092
P	4	104.21	26.054	CP(A)	31.133	0.24754E-07
AP	16	205.56	12.847	CP(A)	15.352	0.69370E-07
CP(A)	20	16.737	0.83685	R(ACP)	0.67341	0.83238
R(ACP)	50	62.134	1.2427		1.3692	0.13497
S	1	9.1281	9.1281	CS(A)	10.899	0.21444E-01
AS	4	26.149	6.5373	CS(A)	7.8053	0.22336E-01
CS(A)	5	4.1877	0.83754		0.92281	0.47411
PS	4	7.2887	1.8222	CPS(A)	2.3175	0.92453E-01
APS	16	20.951	1.3094	CPS(A)	1.6653	0.13954
CPS(A)	20	15.726	0.78628		0.86633	0.62658
Error	50	45.380	0.90760			
Total	199	1037.9				
Grand mean		2.3282				
Standard deviation		2.2837				

Table XLIII. ANOVA for the number of nymphs on day 5.

Source	DF	Sum SQ	Mean SQ	Error	F-value	Probability
A	4	0.15840E+06	39601.	C(A)	57.135	0.23115E-03
C(A)	5	3465.5	693.10	R(ACP)	2.8359	0.242869E-01
P	4	77901.	19475.	CP(A)	120.83	0.10403E-12
AP	16	0.14248E+06	8904.8	CP(A)	55.249	0.47406E-12
CP(A)	20	3223.5	161.18	R(ACP)	0.65947	0.84510
R(ACP)	50	12220.	244.40		0.26933	1.0000
S	1	4474.6	4474.6	CS(A)	19.497	0.69206E-02
AS	4	0.15085E+06	37712.	CS(A)	164.32	0.17240E-04
CS(A)	5	1147.5	229.50		0.25291	0.93639
PS	4	20936.	5233.9	CPS(A)	9.1077	0.23316E-03
APS	16	0.16535E+06	10334.	CPS(A)	17.983	0.17086E-07
CPS(A)	20	11494.	574.68		0.63329	0.86774
Error	50	45372.	907.44			
Total	199	0.79731E+06				

Grand mean   50.090

Standard deviation 63.298

APPENDIX G. Glucosinolate biochemistry in rapeseed plants

> "... considered of interest to investigate the thioglucoside
> content in separated morphological parts of Brassica plants.
> The results might also increase our understanding of the
> biogenesis and metabolic pathways of these components."
> Josefsson (1969)

One result of the rapeseed breeding programmes is an increase in the literature describing the biochemistry of rapeseed. The analyses to determine content have focussed on the marketable seeds rather than on the plants themselves.

A list of glucosinolates present in rapeseed and previously compiled from the literature by Dr. D.I. MacGregor, Agriculture Canada, Saskatoon, Saskatchewan is shown in Table XLIV. Despite the literature, 4-hydroxybenzyl glucosinolate was not found in rapeseed by Dr. McGregor and was omitted from his list. Rapeseed does not contain sinigrin (Appelqvist 1972), which is probably the best known and studied secondary biochemical involved in insect interactions with plants.

Two routes are important in the biosynthesis of glucosinolate aglucones from amino acids, the "uncomplicated" and "complicated" paths of Krutacek and Kralova (1972). The "uncomplicated" path begins with tryptophan and ends with glucosinolates having side groups which are aliphatic or aromatic and heterocyclic (Kjaer 1976). Glucobrassicin, an indole glucosinolate found in rapeseed, is a member of this group and is found in both species in small but significant amounts (Underhill 1980). The content in vegetative parts of B. napus is comparable in the varieties and related to the sulphur content (Josefsson 1971). The roots contain more than shoots. Information on rapeseed indole glucosinolates is scarce because the assay systems do not detect them (Underhill 1980). Thus, rapeseed breeding has

Table XLIV. Glucosinolates present in rapeseed as adapted from a list

compiled from literature by Dr. D.I. MacGregor (personal

communication 1981) and from Tookey et al. (1979).

Semi-systematic name	Common name	Presence in rapeseed spp.	
		B. napus	B. campestris
3-butenyl-	gluconapin	+	+
4-pentenyl-	glucobrassicanapin	+	+
4-methylthiobutyl-	glucoerucin	-	+
5-methylthiopentyl-		-	+
4-methylsulfinylbutyl-	glucoraphanin	+	+
5-methylsulfinylpentyl-	glucoralyssin	+	+
2-hydroxy-3-butenyl-	progoitrin	+	+
2-hydroxy-4-pentenyl-		+	+
2-phenylethyl-	gluconasturtiin	+	+
3-indolylmethyl-	glucobrassicin	-	-
n-methoxy-3-indolylmethyl-	neoglucobrassicin	-	-

not altered the content of indole glucosinolates and further investigation is required and underway (Underhill 1980).

The "complicated" path begins with methionine, important in the production of rapeseed glucosinolates (Josefsson 1971), or with cysteine. Members of this path have side chains which are ω-alkenyl groups modified through homologization, or lengthening, or oxidation (Kjaer 1976). Homologization results in the formation of pentenylglucosinolate, glucobrassicanapin, and butenylglucosinolate, or gluconapin. Oxidation of the latter results in 2-hydroxy-butenylglucosinolate, or progoitrin. The differences in the seed content of these between species, varieties, and individual plants are quantitative rather than qualitative. B. napus seed generally contains more total glucosinolates than seed of B. campestris with the major glucosinolate in B. napus being progoitrin, and in B. campestris gluconapin (Appelqvist 1972; Kondra and Downey 1969). Both species contain pentenyl glucosinolate (Josefsson 1972).

Glucosinolate content varies in types and amounts depending on the species, variety, individual, environment, part and age of the plant (Underhill 1980). In the plants, the variability in content among individuals is sometimes greater than the variation between varieties of a species (Josefsson and Jonsson 1969). Studies with other crucifer plants have demonstrated that the content of total glucosinolates in the growing points and young leaves is greater than that in lower sites (van Emden and Bashford 1969). Josefsson (1971) confirmed this in studies on B. napus. The content of a single glucosinolate may vary in a plant, so that there is more progoitrin in seeds than in leaves and in young rather than mature leaves (van Etten and Daxenbichler 1971).

"The lower glucosinolate content of vegetative parts of
plants grown in the greenhouse compared with plants grown
outdoors makes the former location less suitable for
cultivation of selection material of fodder rape."
Josefsson (1971)

The activity of the enzyme, myrosinase, also differs with species and
varieties but probably does not affect the content of glucosinolates
(Josefsson 1971) although their accumulation would certainly be affected by
their hydrolysis and the associated release of volatile products. Cole
(1976) suggested that B. napus was expected to have lower amounts of
volatiles than B. campestris as a result of its low enzyme activity during
autolysis. Plant site is important in the production of volatiles. Roots
are capable of producing larger quantities of isothiocyanates than shoots
(Josefsson 1971). This may be associated with the enzyme which is in the
membranes of roots, whereas, in shoots it is in idioblasts which release
the enzyme only with a loss of integrity. Furthermore, the autolysis which
occurs in intact material would vary depending on plant growth and cause
the release of differing amounts of volatiles. Hydrolytic products are
said to increase rapidly from 16 to 28 days after pollination and then
slowly until maturity, in association with embryonic growth and development
of seeds (Kondra and Downey 1969). Enzyme activity so affects glucosino-
late content that damaged material would differ from intact material. Finch
(1978) analysed volatiles from 10-week-old B. napus, both intact and
macerated and the chromatograms were different qualitatively and quantita-
tively. Volatiles from intact plants would be expected to differ from
those in damaged plants.

APPENDIX H. Pest management in rapeseed.

This is an outline of a pest management programme for rapeseed. Its scope could be extended to include seed examination to protect against the introduction of pathogens, such as a Swedish strain of <u>Verticillium</u> <u>dahliae</u> which infects raspeseed, and soil examination to plot the spread of pathogens, such as clubroot (Dueck 1981). The programme could provide advice on the selection of seed, and could be extended to include cleaning and storage.

As a crop plant, rapeseed has requirements for long days and fairly cool, moist conditions which restrict the areas suitable for its growth. The selection of a variety for commercial growing should be based on its growth requirements, its length of season and other agronomic and quality characteristics as well as its levels of resistance to herbicides or diseases. A rotation scheme of at least four years, with careful selection of the other crops in the rotation, is essential to maximize productivity, quality and pest control in the rapeseed. Either fallow or cereal may precede rapeseed with profit, but rapeseed should not follow mustard, sunflower, beans or lentils, and should not be grown for two years following sugar beets, which foster a nematode pest. The soil preparation must ensure good drainage and yet be firmly packed. The assurance of a good stand makes the use of preventative chemical pest controls on the seed or soil worth considering.

The pests may be expected to increase with greater production of the oilseed, but the continuation and intensification of currently approved practices will reduce, inhibit, or control pests. This approach requires

an intensive, coordinated, mainly preventative management programme to protect the crops in the field. Knowledge of the area's history, its potential for pest problems, and the pests themselves is essential. For example, the armyworm is not a pest specific to rapeseed or other cruciferous plants but is an opportunistic species with pest potential under certain conditions (Turnock 1977). A management programme will ensure that the pest, the crop and environmental conditions are well-monitored, with thresholds established and depending upon the use of the crop for oilseed or for seed.

Growers should monitor the fungous pests of susceptible stages of the plants and, where possible, take a preventative approach by using seed of varieties known to carry genetic resistance. B. napus varieties have been shown to be more resistant than B. campestris to: stag head or white rust, Albugo candida, blackleg Leptosphaeria maculans, and brown girdling root rot, agent unknown (Dueck 1981). Rapeseed species are restricted geographically and can limit this approach.

Weed control is important, especially in the seedling stage to reduce competition. It is also important later in the season to reduce disease and pest populations which use the weeds as overwintering sites or additional hosts. For example, in some years the six-spotted leafhopper in Manitoba fields spreads aster yellows, a disease which has no practical control and can cause severe damage (Manitoba Department of Agriculture Agdex 149). It is likely that the insect lives on weed and other hosts of aster yellows and then moves to the rapeseed and transmits the disease. Weed control might reduce the problem.

Insect control would monitor for pests of the rapeseed plant stages. The seedling pests include flea beetles, red turnip beetle, and red backed cutworm. Those of the bloom and pod stage include Bertha armyworm, diamondback moth, beet webworm, loopers, clover cutworm, imported cabbageworm, aphids, and seed pod weevils. Monitoring has been shown to be important and the development of techniques is underway, e.g. a female sex pheromone trap to monitor male armyworm moths (Steck et al. 1979). Wet conditions have been shown to reduce the emergence and oviposition of armyworm moths and the survival of larvae (Turnock 1977). The damage by a first instar armyworm is minimal, but the large fifth and sixth instars move to the stems and pods where the damage can be devastating (Bracken and Bucher 1977). The natural enemies of a pest may be important in their control.

The crop must be monitored, too. Weather changes can affect the plant; e.g. when dry conditions make the seedlings susceptible to disease (Dueck 1981). The plants under good conditions are fairly resilient and if damaged respond with secondary growth of shoots. However, dry conditions at the pod stage may cause the leaves to drop off and thus increase the visibility of the pods and their susceptibility to pests (Bracken and Bucher 1977). Before chemical controls are used, alternatives should be considered, such as an earlier harvest. Sometimes, chemical control is not possible, as in a B. campestris field in bloom, because this species depends on bees for pollination and seed set.