BIOLOGY AND HOST PLANT RELATIONSHIPS OF *SCAPTOMYZA FLAVA* LEAF MINER

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In the Name of ALLAH the Most Merciful the Most Beneficent

I dedicate this disertation to Imam Khomeini and the blessed my deceased brother Ali Mohammad Seraj

ABSTRACT

Scaptomyza flava Fallén (Diptera: Drosophilidae) is a leaf miner of Cruciferous plants (Brassicaceae). It occurs throughout New Zealand and in many other parts of the world. *S. flava* attacks living plants but also lays eggs on dead leaves and larvae can develop in dead and decaying plant material. However, survival to the adult stage is greater when larvae develop on live leaves. Females are polygamous and mating begins soon after emergence. Female flies start puncturing leaves with their ovipositor ca. 4 h. after emergence and produce peak numbers of punctures within the first 12 h. of their adult lives. It is during this peak time of puncture production that egg laying begins. Oviposition starts on the day following emergence and lasts for about two weeks. After this oviposition rate declines slowly. Eggs are laid mainly between 06.00 and 10.00 h. and between 17.00 and 20.00 h. with a peak between 09.00-10.00 h. and 17.00-18.00 h. The mean number of eggs laid per female per day is dependent on the availability of host plants and ranges from 20.9 to 4.4 eggs per day. Maximum oviposition varies between different host plant species. The total fecundity of some females was as high as 320 eggs (on turnip and in contrast less than 12 eggs on cauliflower) over a lifespan of about 12 days. The larvae destroys the parenchyma of leaves. Although only a small portion of the lamina is damaged by a single larva - approximately 5 cm^2. Most plant injury is caused by feeding by the third-instar larva which lasts about one week. Sex ratios of adults were close to 1:1 with a slight bias in favour of males. Feeding punctures and fecundity of *S. flava* increase greatly when given honey solution. For both sexes, longevity is affected by adult food source. Caged adult female *S. flava* lived significantly longer when provided with honey solution and yeast than when confined on glass plates and starved or allowed access to yeast and water only. Virgin females lived only slightly longer than mated females and unmated males lived significantly longer than all other groups.

S. flava is an oligophagous insect with host plants restricted to the Brassicaceae. When *S. flava* adults were given a simultaneous choice of seven plant species for feeding and oviposition, there was a distinct hierarchical ordering in their ovipositional preference, with turnip, Chinese cabbage, and hedge mustard being preferred over all others. Percentage of punctures with eggs for turnip, Chinese cabbage and cauliflower (three main host plants of *S. flava*) in choice tests were 3.1, 3 and 6.4% and in non-choice tests 6, 5.4 and 28% respectively. In non-choice tests, females laid more eggs on Chinese cabbage and

turnip than other Brassicaceae. Egg production was also different between host plants. Females oviposited means of 255, 165 and 48 eggs during their lifespan when maintained on turnip, Chinese cabbage and cauliflower, respectively. Peak egg production period varied between host plants; on cauliflower, peak production occurred 3-7 days from adult emergence and on Chinese cabbage and turnip between days 7-11 from emergence. There were also significant differences in total developmental times of the insect between three Brassicaceous host plants (cauliflower 41d, Chinese cabbage 33.7d and turnip 31d). There were significant differences in duration of the 3rd larval instar among the host plant species with the longest duration on cauliflower (8d). Fecundity of *S. flava* was positively correlated with female body weight and greater female weights resulted when insects were raised on turnip and Chinese cabbage compared to cauliflower.

Although all leaf sizes and/or ages were accepted by the insects (with the exception of the smallest leaves) for egg laying, the number of feeding punctures and eggs per cm^2 leaf increased with increasing leaf size and/or age. Nitrogen content of leaves did not vary significantly with age. Previous larval feeding experience on turnip and Chinese cabbage appeared to modify adult host plant preference, but previous feeding experience as larvae on a poor host, cauliflower, did not increase egg laying on that host by adult females. Recently eclosed adult *S. flava* may show positive experience effects on turnip (and slightly on Chinese cabbage).

Over a two year period in the Manawatu adults and larvae of *S. flava* were present throughout the year with no evidence of diapause or aestivation. However, there were marked peaks during spring and early summer in numbers of adult flies caught, and again in autumn to early winter with troughs in early autumn and early spring. This pattern, obtained by sampling for adults, was paralleled by sampling for larvae. In a laboratory experiment simulated herbivore injury did not produce the same effect as feeding by *S. flava*. Total fresh-weight accumulation was reduced significantly with increasing levels of injury by *S. flava* feeding but this did not occur with artificial clipping. In another laboratory experiment, where individual plants were caged with 4 mated females for 24 h. reduced growth of Chinese cabbage and turnip occurred from ensuing larval damage.In two separate field experiments turnip tolerated low levels of leaf mining without reduction in weight of bulb but the net yield of Chinese cabbage was significantly reduced.

In the name of Allah the most compassionate the most merciful

By the *Pen* and by the record which men write

(The Holy Qur'ān 68:1)

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INTRODUCTION

Dipteran leaf miners are a large and widespread group of small flies, most with larvae attacking a wide range of plants. Most simply mine leaves but a few are gall makers (Hill, 1987). Some species are cosmopolitan, others solely temperate and some restricted to the tropics. The range of host specificity is great, from broad polyphagy to restricted monophagy on a single genus of host plant. About 150 species are regularly associated with cultivated plants, and these were the subject of a monograph by Spencer (1973); the total number of species recorded is about 1800 (Hill, 1987).

The leaf-mining larvae are characterized by making long winding tunnels (mines) in the leaf lamina; the tunnel appears whitish because of light reflection from the air trapped in the mine. Some species make blotch mines but this is generally more characteristic of other groups of leaf miners. Sometimes the mine starts in a linear manner and terminates in a large blotch. Pupation takes place usually in the mine but a few species pupate in the soil or in leaf litter.

Some crop plants are mined by different species of leaf miners in different parts of the world where they are allopatric in distribution, but some flies have overlapping distribution (*i.e.*, sympatric), and some are cosmopolitan. The end-result is that in any one locality some crops are attacked by several very similar leaf miners simultaneously.

Most leaf mining Diptera are from the family Agromyzidae but the larvae of some drosophilids have the leaf mining habit.

The identification of drosophilid leaf miners is extremely difficult and many species are only distinguishable by the male genitalia, but at generic level

there are some differences in acrostichal hairs on the thorax (Hackman, 1982). The crops most likely to suffer multiple leaf miner fly infestation (including Agromyzidae and Drosophilidae) are those belonging to the families Leguminosae, Gramineae, Solanaceae, Compositae, Chenopodiaceae, Cucurbitaceae, and Brassicaceae.

In New Zealand there are more than 30 species of native leaf mining insects, although only two, both flies, can be regarded as pests (Wise, DSIR files). The cabbage leaf miner, *Scaptomyza flava* (Fallèn) , is probably one of the most common leaf miners in New Zealand. These minute flies have been greatly neglected in this country. *Scaptomyza flava* commonly infests many cruciferous vegetables especially in the young plant or seedling stages. It occurs as a pest in temperate zones and at the margins of the subtropics. *S. flava* is widespread in Europe, Asia, North America, Australia, and throughout New Zealand.

The insect was not regarded as a major pest of *brassica* plant species in the North Island by Cumber and Eyles (1961a), but it has become increasingly important within the last few years as a pest of Brassicaceae plant species in the agricultural area of the Manawatu and other parts of New Zealand. Other *Scaptomyza* species are present in New Zealand, but little is known of their biology.

Damage by *S. flava* is caused by the mining of the larvae within the leaf tissue and also by the feeding and ovipositional habits of the adult female. Under favourable environmental conditions populations of it may reach high levels. The literature concerning *S. flava* is very limited, although Holloway (1990) reported some details of host plants.

Brassica leaf miners in New Zealand have previously been misidentified,

and attempted biological control failed probably due to mis-identification of the target (McGregor, 1989). The leaf miners were shown to be not Agromyzidae but two species of Drosophilidae: *Scaptomyza flava* (Fallèn) and *S. graminum* (Fallèn) (DSIR files). The initial assumption that the "brassica leaf miner" was *Chromatomyia syngenesiae* was wrong.

Two factors that have complicated research on *Scaptomyza flava* have thus been misidentification of species and also lack of basic biological knowledge. The information presented in this thesis should contribute to the overall understanding of host plant utilization by this insect and to the development of more comprehensive and soundly based pest management strategies.

Studies have been conducted on various aspects of the biology, ecology and host plant relationships of *Scaptomyza flava* to better understand its role as a pest of *Brassicaceae* plant species. The symptoms and extent of damage caused and the relationship of insects to their host plants are of fundamental importance to understanding pest biology and abundance and critical to the development of pest management systems. My research has been directed towards determining the basic biology and behaviour of *Scaptomyza* on selected hosts, the economically important brassica species (Chinese cabbage, turnip and cauliflower).

The main objectives of my research programme were to develop information that would enable a comprehensive picture to be built up of:

- seasonal life cycle, simple population dynamics, ecology and behaviour of *Scaptomyza flava*,
- pest status; this to involve determining the relationship between pest incidence and yield/quality of produce for two vegetable brassicas, and
- aspects of host plant relationships including preference for feeding and oviposition.

To achieve this I did the following:

1. Carried out a literature review of leaf mining insects with particular reference to Dipterous leaf miners of *Cruciferae* and to the Australia / New Zealand region to cover taxonomy (see Appendix 1), host-plant relationships, ecology and control,

2. to improve my taxonomic understanding of the *Drosophilidae*, I spent two periods with Diptera taxonomists in Auckland (DSIR), and Australia (CSIRO),

3. collected larval samples from a range of cultivated and wild Cruciferous plant species affected by leaf miners and reared out adults. A reference collection of authoritatively identified specimens was established,

4. determined the occurrence and seasonal life cycle of the leaf miner on two types of vegetable brassicas at Palmerston North,

5. assessed experimentally the effects of *Scaptomyza flava* on the growth and yield of two vegetable brassicas, and

6. investigated various aspects of the insect's host-plant relationships.

Chapter 1

LITERATURE REVIEW

INTRODUCTION[1]

The development of specialised feeding habits by insects is in some cases characteristic of the species concerned. Leaf-mining insects are one such specialised group and feed on tissues between or in the epidermal layers of leaves for all or part of their larval development. Possible advantages of this feeding habit include avoidance of digestibility reducing compounds in certain leaf tissues, protection from natural enemies, and amelioration of harsh external weather conditions, particularly protection from desiccation during dry periods.

Leaf mining Diptera are very common on seedlings, young plants and in some cases mature plants of most cultivated Cruciferae (cabbage, turnip, cauliflower, broccoli, radish, watercress, bittercress and fodder brassicas) in New Zealand, but very little is known about them as to their ecology, host plant range, natural enemies and pest status. In the past, confusion has existed as to species involved.

As pointed out by Hering (1951), two groups of plant feeding insects have for a long time attracted special attention from entomologists. These are the gall makers and leaf miners. In both cases the insect larva lives and feeds inside plant tissue *i.e.* is endophagous, and does not merely chew from the outside.

This particular interest derives from both the distinctive form of leaf mines and the often remarkable structure of galls. The uniformity of pattern is often very pronounced and characteristic for a particular species. In many cases this makes it

[1] Major publications concerned with leaf mining insects are "Biology of the leaf miners" (Hering, 1951) and "Bionomics of leaf-mining insects" (Hespenheide, 1991). Most of my knowledge concerning the leaf miner literature comes from studies of them (especially the comprehensive review of Hespenheide). These published reviews provide a good starting point for those interested in these kinds of insects (leaf miners).

easier to identify the genus or species of insect responsible from its feeding pattern rather than from examination of the insects themselves (Hering, 1951). Most insects that live in galls or mines are highly specialised and show a number of adaptations to their habitat (Houser, 1923 cited by Hering, 1951).

Cecidology, the study of galls, was studied systemically considerably earlier than its sister science, hyponomology or the study of mines, which only fully developed in the twentieth century. Leaf-miners were first mentioned by Beckmann in 1681 who discussed and illustrated the strange forms which had appeared in great numbers the previous year on cherry trees in the Frankfurt / Oder area in Germany (Basden, 1954). The popular conception at this time was that these mines represented little serpents which had descended from the skies or emanated from the foul air of the local swamps. However, Beckmann was able to show that the mines were caused by insects and illustrated the lepidopterous larvae responsible. Then in 1737, Reaumur discussed and illustrated Agromyzid leaf-miners on *Sonchus oleraceus* L., *Trifolium, Ranunculus* and *Lonicera.* These species were not given names but are readily identifiable from their host-plants (Hering, 1951).

DEFINITION, SHAPE AND DISTRIBUTION OF MINES AND MINERS

Mines may be defined as feeding channels formed by insect larvae inside the tissues of plants, in which the epidermis, or at least its outer wall, remains uninjuried (Hering, 1951). Thus miners are insects which feed in such channels for at least part of their larval lives (Claridge and Wilson, 1982).

Naturally, the mine cavity is extended inside the green parenchyma of a leaf, but in the same way, feeding channels, which can be designated as mines, may be established inside the parenchyma of fruits, stems or roots. The channels established in different types of pith tissue of the stem, roots and fruit and which lie below the green parenchyma layer of the organ in question obviously do not fall within the same category as leaf mines (Hering, 1951).

Potter (1989) has pointed out that some insects that specialize on young leaves, including certain leaf miners, appear to be resource limited in that natural or experimental induction of a secondary leaf flush results in increased feeding damage or rapid population increase.

The physiologically essential aspects of insect leaf-mining activity, *i.e.* feeding exclusively on parenchyma or epidermis cells and simultaneously being cut off from the outer world by a dividing barrier (Stiling and Strong, 1984), are also to be found in a whole series of other feeding patterns occurring not in leaves but in other plant organs. In such cases there is a clear relationship to leaf-mining from the point of view not only of plant anatomy but also of insect classification, even though they are usually less conspicuous and diverge widely in form from leaf-mines (Hering, 1936 cited by Hering, 1951). Essentially the same families and genera are concerned; in many instances even the same species, either through choice or compulsion during later stages of development, change their habits for example, from leaf-mining to stem-boring. If the leaf is very small and provides insufficient food for the larva, it may move on through the petiole into the stem (Hering, 1951).

Leaf miners show spatial patterns in distribution and are of particular interest because they are often abundant and can affect growth and reproduction of both native and cultivated species (Collinge and Louda, 1988).

Hespenheide (1991) mentioned that the distribution of leaf-miners has been discussed at several different spatial scales; between different habitats, among and within plants within a single habitat, and among and within leaves of a single plant. A leaf mining moth, *Stilbosis quadricustatella,* exhibited a clumped distribution of mines among leaves of the evergreen oak. Mines tended to be on large, peripheral, and undamaged leaves so that leaves were often multiply mined. Over successional gradients, major faunal components change between annuals, which are dominated by Agromyzids, and perennials which are dominated by Lepidopterans; a large number of species occur on perennials and earlier plant stages have a greater density of miners

(Godfray, 1984 cited by Hespenheide, 1991). Within habitats, miners are unequally distributed among trees (Bultman and Faeth, 1986 cited by Hespenheide, 1991), in some cases preferring younger trees over older ones (Martin, 1956 cited by Hespenheide, 1991). Densities often decrease from edges to the interior of a habitat, in one case because of parasite pressure (Stiling *et al.*, 1982 cited by Hespenheide, 1991). The distribution and abundance of leaf miners on some trees should not be viewed as the turnover of reproductive populations on individual trees, but rather as the immigration and failed colonization of species whose movements encompass several trees (Connor *et al.*, 1983). Connor *et al.* (1983) investigated the leaf miner guilds of several species of oak trees to determine to what extent species distributions are maintained by *in situ* reproductive recruitment and to what extent by continued immigration. Complementary caging experiments were performed to exclude immigration and to exclude *in situ* recruitment from overwintering populations. Collinge and Louda (1988) have reported that oviposition and leaf mining damage were concentrated on the lower central leaves of a stem in *Drosophila* leaf miners.

Within a plant (usually a tree), miners may prefer upper portions of the canopy (*e.g.*, the larvae of *Cameraria hamadryadella* and *C. cincinnatiella* form a solitary blotch mine in the upper portion of oak leaves) (Hinckley, 1972) or more usually, lower portions, for example, the mines of *Lithocolletis salicifoliella* are found on the underside of the leaves (Martin, 1956), or show no preference. One phenomenon suggesting that resource limitation was or is an important factor in the population dynamics of some insects is the presence of spacing or oviposition-deterring pheromones (Quiring and McNeil, 1984). Such preferences are usually presumed to be for sun or shade (Bultman and Faeth, 1988), but shaded plants may show more damage than preferred plants in the sun (Collinge and Louda, 1988), and miners may prefer leaves in the sun but survive better in the shade (Bultman and Faeth, 1986). They demonstrated that total insect herbivore load on bittercress is greater on plants in the shade and that there were increases in the water associated soluble (nitrate) nitrogen concentrations in leaves. Story *et al.* (1979) stated that feeding activities of adult leaf miner on turkey oak, *Brachys tessellatus* shifted to the more shaded middle and lower

crown levels during the warmer days of late May and June. The hypothesis that generally higher levels of herbivory on bittercress *Cardamine cordifolia* A. Gray (Cruciferae), especially by leaf miners, are related to the earlier phenological development of plants in the sun was tested in field studies in Colorado by Colling and Louda (1989). The dominant insect at the site was the Drosophilid leaf miner *Scaptomyza nigrita*. Adult flies were at least twice as frequent on bittercress plants in sun-exposed than in shaded areas, and were most active from mid-day to late afternoon. Female flies were on average 26% larger than male flies, but there were no differences in size of adults between the two habitats. Larval damage to bittercress was generally much greater on plants in sunny areas than on those in the shade, possibly due to the increased activity of ovipositing flies in these areas (Collinge and Louda, 1989).

LEAF-MINER TAXONOMY[1]

Leaf miners which feed only within the tissues of leaves are restricted to the orders Lepidoptera, Diptera, Coleoptera and Hymenoptera. Leaf mining insects therefore form a distinct feeding guild (in the sense of Root, 1973 cited by Claridge and Wilson, 1982) which is taxonomically very diverse. The greatest diversity of forms and number of species are in Lepidoptera (fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships), then in the fly family Agromyzidae and relatively fewer in the Coleoptera and Hymenoptera (Hespenheide, 1991). In Slovenia / Yugoslavia, Maček (1972) recorded 118 species of leaf miners from 51 weed species. Diptera predominated, with Coleoptera, Hymenoptera and Lepidoptera being only sparsely represented. In Germany Bächli *et al.* (1985 cited by Maček, 1972), described 11 hitherto unknown leaf-mines and allocated positions in Hering's classification. In two cases the insects responsible for the mines were known genera of Lepidoptera and in 6 cases, perhaps those of Coleoptera or Hymenoptera. Fifteen new types of leaf-mines caused by larvae of Diptera were described and classified by Zoerner (1971). Of these, nine were caused by Agromyzids, two by Chironomids, one by Cecidomyiids, one by a Drosophilid and two by unknown Diptera. For Britain and a fauna of nearly

[1] Taxonomy of *Scaptomyza flava* leaf miner has been elaborated in Appendix 1

700 species of leaf miners the proportions were 57% Diptera, 33% Lepidoptera, 8% Coleoptera, 3% Hymenoptera (Godfray, 1985). This overall pattern is probably maintained in most localities (Askew and Shaw, 1974), but varies from habitat to habitat (Askew, 1980; Godfray, 1985) and shows some change with geography, perhaps especially in the relative importance of the Coleoptera and Agromyzidae.

Leaf-mining flies are predominantly Agromyzidae, but leaf-miners also occur in the Anthomyiidae (Godfray, 1986), Drosophilidae (Collinge and Louda, 1988,1989) and Ephydridae (Stiling *et al.*, 1982, 1984), among others. Agromyzids have been extensively studied, perhaps because of their temperate distribution, but also because of their economic importance. Some important Dipterous leaf miner pests (Agromyzidae) and a full list of leaf miner species associated with British trees is given by Claridge and Wilson (1982). Major families in the Lepidoptera include the Cosmopterygidae, Gelechiidae, Gracillariidae, Heliozelidae, Incurvariidae, Lyonetidae and Nepticulidae (Simberloff and Stiling, 1987). Thus leaf-mining microlepidoptera form a large assemblage whose larvae mine the leaves of both angiosperms and gymnosperms. Beetle leaf-miners are concentrated in the three families: Buprestidae, Chrysomelidae, and Curculionidae. Hymenoptera that mine leaves are sawflies of the family Tenthredinidae (Toumi *et al.,* 1981 cited by Hespenheide, 1991).

In New Zealand two orders, Diptera and Lepidoptera are important as leaf miners. Diptera include Agromyzidae: Beet leaf miner *(Liriomyza chenopodi* Watt), hebe (koromiko) leaf miner (*Liriomyza* spp.), *Phytobia* spp., and kaka beak leaf miner *Phytomyza syngenesiae* Hardy); and Drosophilidae: *Scaptomyza flava, S. flavella, S. elmoi,* and *S. fuscitarsis.* A study during 1974-75 recorded 41 Agromyzid flies and, while no recent study of the moth miners has been made, there were 18 recorded species by 1923 (Scott, 1984). In Spencer (1976) 16 known species of Agromyzidae hitherto in New Zealand and subantarctic islands have been revised, and 19 new species are described: *Cerodontha sylvesterensis, Hexomyza coprosmae, Liriomyza oleariae, L. wahlenbergiae, L. craspediae, L. watti, L. plantaginella, L. hebae, L. vicina, L. penita, L. homeri, Melanagromyza senecionella, Phytoliriomyza cyateae, P.*

bicolorata, P. huttensis, P. convoluta, P. tearohensis, Phytomyza imporvisa, and *P. lylli.* Lepidoptera leaf-miners in New Zealand include the families Gracillariidae and Nepticulidae.

DURATION OF MINING

Hering (1951) has pointed out that a comparison of the time required by a mining larva for its development with the duration of the larval stage of free-living insects shows that in the majority of cases mining insects have a shorter larval development than external feeders. Although details of extremely short larval stages may be based on inaccurate observation, owing to the minute, hair-like early channel being frequently overlooked, it is nevertheless a fact that the larval stage, especially in the first larval generation, is often extraordinarily short. Webster and Parks (1913 cited by Hering, 1951) recorded that in an American species of *Liriomyza* the duration of the larva stage was four days and that the shortest time of development from oviposition until the emergence of the imago was 18 days. Similar short periods of development are found in many other miners, especially in the genus *Nepticula.*

Two principal reasons may be adduced to explain the shortening of the larval stage by comparison with free-feeding forms. The larva of mining insects which live inside the mine and feed exclusively on mesophyll, consumes qualitatively highly nutritious food but apparently quantitatively less than free-living larvae (Crawley, 1983). It is not forced to eat quantities of indigestible food of low nutritive value like the free-feeding larva, which in addition to the green leaf tissue with its high protein content is also compelled to eat the epidermal cells (Chapple, 1929) which are often thickened by a cuticle, as well as many strengthening elements in the leaf, such as are found in the vicinity of the vascular bundles. The mining larva can thus develop with a far smaller quantity of food; as the larval stage is essentially devoted to the consumption of food, it is naturally shortened by its abundant supply. That this is the decisive factor is shown by the fact that even in its living quarters inside the leaf the larva seeks to avoid as far as possible having to consume the more indigestible substances (Hering, 1951).

ADULT BIOLOGY

Male and female of leaf miners usually mate more than once (Story *et al.,* 1979). The norm of protracted copulation is nearly 1 hour (Parella, 1987). Pre-oviposition feeding by adults can be extensive and damaging to plants-both hosts and nearby plants. It has been estimated that alfalfa blotch leaf miner (*Agromyza frontella)* females make over 3700 feeding perforations (with their ovipositor), equivalent to 1.1 cm^2 per female in damage to alfalfa. Dehiscence of leaflets by adult feeding occurred when adult populations reached high levels (Hendrickson and Barth, 1978).

Egg-laying has been measured for relatively few species (Askew and Shaw, 1979; Condrashoff, 1964; Martin, 1956; Miller, 1973) and depends on food resources for the adults in those cases examined. Dimetry (1971) found that different food sources affected fecundity and the oviposition period of *Liriomyza congesta.* Females provided honey laid more eggs over a greater period of time than females provided other food sources. Labeyrie (1957) reported that some Lepidoptera with access to water laid twice as many eggs as those denied it (mean of 84), and that adults provided with honey in addition to water laid 3 times as many eggs as those not fed (absolute maximum 336). Charlton and Allen (1981) observed that the fecundity of *Liriomyza trifolii* increased greatly when given honey. They also suggested that aphid honeydew and floral nectars could increase leaf miner populations. Adult female *L. trifolii* (Burgess) lived significantly longer when confined on tomato leaves than when confined on glass plates and starved. Continuous exposure of adults to aphid honeydew on tomato leaflets resulted in increased fecundity of females relative to adults exposed to tomato foliage without honeydew (Zoebisch and Schuster, 1987).

Most leaf mining insects lay eggs singly *(e.g., Liriomyza trifolii* and *Scaptomyza flava),* but a few species lay eggs in a group from which the larvae will form a communal mine. For example *Pegomya nigritarsis* is a gregarious leaf-mining fly attacking *Rumex* and larvae from one clutch of eggs all inhabit the same mine (Godfray, 1986).

Total time required for development is dependent on temperature; for example for alfalfa blotch leaf-miner it is 52 days at 16.7°, 36 days at 20°, 31 days at 22.8 ° and 27 days at 25.6°C (Parella, 1987). William and Robert (1978) determined median developmental rates at constant temperatures between 10° and 25°C for all immature stages of the alfalfa blotch leaf-miner *Agromyza frontella*. The preoviposition period and adult male lifespan were also determined. Larval survival was maximum at 20°C and minimum at 15°C although the developmental rates differed little between these two temperatures. The developmental rate-temperature relationship for egg period ranged from 3.5 to 12.4 days. The relationship was sigmoid for each larval instar. The total larval period ranged from 5.9 to 16.4 days. The relationship was exponential for pupae. The pupal period ranged from 15.9 to 61.5 days. Developmental rates for pupae under constant temperatures yielded valid simulations of adult emergence patterns under fluctuating temperature regimes in the field.

Survival varies widely among different leaf miner species and depends much on feeding habits, life history and protection of young (Pedigo, 1989). Insects that feed on a wide variety of food sources and protect their young to a degree have greater survival potential (Pedigo, 1989). In the latter instance, viviparous birth types generally have less mortality of newborns than oviparous birth types (*S. flava* is oviparous birth type). This is because the offspring are in a protected environment, inside the females, much longer than are those of oviparous species.

It is now more than 40 years since Dethier (1954) remarked that "no one attractant alone performs the service of guiding an insect to its proper host-plant, food or mate, and that the desired end is achieved only by a complex array of stimuli, such as chemical, light, temperature and humidity, acting in harmony."

For many plant-feeding insects, the selection of an oviposition site is a critical stage in their choice of host. This is especially true when the newly hatched offspring are not capable of searching for additional hosts (*e.g.* leaf-miners, but see Miller and Strickler, 1984). Thus the choice of feeding site lies with the adult female.

Miller and Miller (1986) used the term "acceptability" to describe the likelihood that a plant will be accepted if it is encountered and "suitability" to encompass the various aspects of host quality that affect insect performance.

Studies of survivorship in leaf-mining insects usually means larval survivorship. Mortality of eggs is either infrequently estimated (Day and Watt, 1989; Pottinger and LeRoux, 1971; Turnbow and Franklin, 1981 cited by Hespenheide, 1991), or often underestimated in death-assemblage studies (Connor, 1988 cited by Hespenheide, 1991), and may result from parasitoids, predation (Pottinger and LeRoux, 1971 cited by Hespenheide, 1991), or unknown causes (Pullin, 1985). Turnbow and Franklin (1981) found that of a total of 346 eggs oviposited on 200 leaves of turkey oak (*Quercus laevis*) by leaf miner adults (*Brachys tessellatus*), only 13.3% hatched. The others were lost to parasitism (13%), predation (35.1%) and miscellaneous or undetermined causes (infertility, desiccation, thermal death, undetected parasitism, *etc.*) (38.5%). Unknown factors of leaf miner mortality might include bacterial, fungal, and viral diseases, host plant nutrition, and abiotic forces such as weather (Faeth and Simberloff, 1981). Some authors (*e.g.*, Newman and Clark, 1929 cited by Mazanec, 1987) speculated that bush fires would cause high mortality of leaf miner larvae aestivating in soil (Mazanec, 1978). Over-winter mortality is usually a combination of terrestrial predators and abiotic factors (Hespenheide, 1991). According to Bultman (1988), leaf-miner survival on oaks was less than expected for four of five species when co-occurring on leaves with conspecifics than when mining with heterospecifics or alone. The mortality factors of oak leaf miner in New Zealand are discussed in detail by Swan (1973).

Survival of leaf miners may be a negative function of clumping among and within leaves. Small-leaved branches and trees appear to be less susceptible to leaf miner attack because adult females deposit fewer eggs overall, and eggs are more frequently laid singly on leaves of inadequate size for development or are more frequently clumped on leaves with competing conspecifics (Faeth, 1991).

HOST SPECIFICITY AND SPECIES DIVERSITY

"Leaf-miners have generally narrow host preferences. Most are monophagous, a smaller proportion oligophagous, and only a few are polyphagous (Liriomyzidae)" (Hespenheide, 1991). Thus polyphagy is unusual among leaf-miners. In a survey of Agromyzids associated with British Umbelliferae, Lawton and Price (1979) found that a combination of geographic area, plant size, leaf form, and occurrence in aquatic habitats explained about 50% of the variation in size of the fauna when effect of each plant's local abundance and the number of occupied habitats within its geographic range were examined by Fowler and Lawton (1982), addition of the latter explained a total of 61% of variation.

Scaptomyza spp. adults have been collected from tomatoes (Berlinger *et al.*, 1988; Collins, 1956), banana (Bächli, 1973), some flowers, grass, radish (Torrent, 1955), cauliflower, turnip (Frey, 1951 cited by Stapel, 1961), cabbage (Szwejda, 1974), endive, lettuce, spinach (Osmelak, 1983), hedge mustard, onion, flax, cucurbits, swede (Hardy *et al.*, 1979), carrot, broccoli, garden pea, watercress, nasturtium (Holloway, 1990) and many other crops and wild plants (Singh and Bhatt, 1988). Although the cosmopolitan genus *Scaptomyza* contains about 400 species or slightly over one-quarter the number of known *Drosophila* species, only four occur in New Zealand. The highest populations of *Scaptomyza fuscitarsis* in New Zealand were taken from swedes (Cumber and Eyles, 1961b). Harrison (1959) recorded this species in association with rotting swedes, but it occurred on all types of crops studied with the exception of pampas. Its frequent occurrence in association with maize suggests that it may breed in moist materials held in leaf axils and sheaths (Scott, 1984). *Scaptomyza fuscitarsis* Hardy was taken on 52 occasions by Cumber and Eyles (1961a) and is present throughout the North Island of New Zealand.

In pastures leaf miner species composition is strongly related to plant species composition, but modified by plant structure under different grazing treatments. There is a strong successional trend in miner assemblies, even when the effects of changes in

plant composition have been taken into account. Conversely, local variation in miner species composition generally reflects food plant distribution alone. Grazed treatments have fewer mines than controls, but there are also species specializing in grazed areas, despite the abundance of their food plants elsewhere. There is a weak indication that miner species in grazed treatments are more likely to fluctuate in abundance than those in ungrazed controls (Stering *et al.*, 1992). Opler (1974) showed that the number of species of leaf-mining insects on California oaks was very closely related to the geographic area occupied by the oaks.

BIOGEOGRAPHIC PATTERNS OF DIVERSITY

"Most basic ecological studies of leaf-miners have been carried out in temperate zone localities (England, California) or at the margins of the subtropics (Florida, Arizona), although a few economically important tropical species have also been studied. Leaf-miners are common in the tropics and it is clear that these faunas differ from those in temperate zones" (Hespenheide, 1991). Within Australia, many lepidopteran leaf miner species are widely distributed both geographically and ecologically (occurring in a range of woodland and other ecosystems), with extension of their natural geographical range. Powell (1980) quotes Opler as having found leaf miners on half of 102 tree species in Costa Rica (Hespenheide, 1985). Although beetles are a minor component of temperate zone faunas, they are much more numerous in the tropics.

Scaptomyza spp. are found everywhere (endemic). These species occur on cabbage in Poland (Michalska, 1973; Szwejda, 1974; and Pol, 1974) and Islamic republic of Iran (personal observations), on turnip in England (Frey, 1954) and India (Gupta, 1970/75; Gupta and Singh, 1981; Kumar and Gupta, 1992), on field and forage crops in the following places: Tasmania (Bock and Parsons, 1977), Japan (Kaneko and Tokumits, 1969; Okada, 1973), Nepal, Taiwan, Portugal (Rochapite, 1979), Afghanistan (Hackman, 1969), Czechoslovakia (Máca, 1972), Mongolia (Okada, 1973), Italy, Algeria, Jamaica, France (Rossi and Rossi, 1979), Peru (Ramirez, 1988), Slovenia (Yugoslavia) (Maček, 1972), Egypt (Hafez and Ziady, 1970), Nearctic, Germany (Becker, 1908;

Sturtevant, 1918 cited by Bächli *et al.,* 1985) and Switzerland (Bächli, 1973,1974). They have been recorded from Canada (Torrent, 1955), Chile (Hedqvist, 1977), and collected from tomatoes in New Jersey, USA. *Scaptomyza caliginosa* is a species endemic to the island of Hawaii (Takada, 1970; Montague and Kaneshiro, 1982; Roger and Lewin, 1985). *Scaptomyza (Bunostoma) australis* Malloch is a common species widespread throughout Australia (Bock and Parsons, 1977; Rockwell and Grossfield, 1977) and most recently reported as well from Norfolk and Pitcairn Islands (South Pacific Islands) (Bock, 1986; Grimaldi, 1990). New species are described by McEvey (1990) from Madagascar and Mauritius; two are classified in *Scaptomyza* s.str. and one in the subgenus *Parascaptomyza*; the latter species closely resembles S.(P.) *pallida* Zetterstedt.

Harrison (1959) found the grey pasture fly, *Scaptomyza fuscitarsis* to be widespread but not abundant in the pastures of North Island of New Zealand. Its host is not known but *Scaptomyza* spp. (Drosophilidae) are regarded as leaf miners in grasses. *Scaptomyza graminum* was recorded in small numbers at three sites. This species has been also reared from brassicas.

Scaptomyza flava is also widespread in Europe, Asia and North America. In the latter area it appears to be an introduction which has spread in association with cultivated members of the cabbage group (Bock, 1977).

The leaf-miner *Liriomyza trifolii* has been reported to cause almost near collapse of cow pea, *Vigna unguiculata,* crops (Jackai and Daoust, 1986) in Tanzania (Price and Dunstan, 1983; Singh and Merrett, 1980). This same species is also known to attack cow peas in the USA and in central and South America (Chalfant, 1976; Daoust *et al.*, 1985). In Southeast Asia this species is capable of causing significant yield reductions (Singh *et al.*, 1978). A long-term survey (1965-1989) (Macek, 1990) showed that leaf-miners were not very widespread on cereal weeds in Slovenia and that their levels of infestation were seldom high enough to markedly injure the weeds. Leaf-mining Diptera are also recorded as damaging in Egypt (Hafez, Ziady and Dimetry, 1970).

Pest species of Agromyzidae are widely distributed throughout the world and infest many important crops. New Zealand has 41 described species of Agromyzidae in the genera *Cerodontha, Hexomyza, Liriomyza, Melanagromyza ,Phytoliriomyza,* and *Phytomyza* (Spencer, 1976). Some species present in New Zealand are serious pests overseas, but their pest status in New Zealand is uncertain. The cosmopolitan pest *Liriomyza brassicae* Riley is not recorded as a significant pest in New Zealand. **Appendix 2** shows some important Agromyzidae leaf miner pests.

Holloway (1990) has pointed out that in New Zealand, different species of *Scaptomyza* were bred from the following plants:

Scaptomyza flava: Adult flies were bred from leaves of cabbage, turnip, swede, radish, broccoli, garden pea, wild mustard, watercress, and nasturtium (*Tropaeolum majus).*

S. elmoi: Adult flies have been reared from leaves of radish and *Senecio glomeratus* (previously known as *Erechtites*).

S. fuscitarsis: Adult flies were bred from leaves of broccoli and watercress and were swept from grass, carrot and swede.

S. flavella: No breeding was recorded (it is represented in NZAC [New Zealand Arthropoda Collection] only by the type series from Mokohinau Is.).

COMPARISON OF PLANT SPECIES AS HOSTS FOR LEAF MINERS AND HOST PLANT DEFENCE

Host plant species is one factor that may influence insect behaviour and numbers of eggs laid. Host plant quality may affect amount of adult feeding, number of eggs laid and survivorship of juvenile stages through alterations in leaf nutrition or toxins. Soluble foliar nitrogen is considered a reliable estimate of the amount of protein available to the herbivore, and therefore indicative of plant nutritional quality (for reviews, see Feeny, 1970).

For a general treatment of host-seeking behaviour in phytophagous insects see

Ahmad and Allen (1983). Saxena (1969) pointed out that host-plant location may be essentially by random, or at least undirected, movement, so that contact with suitable plants is by chance, or by orientation in response to some perceived properties of the plant. From a distance the latter can only be by visual or chemical means (Fenemore, 1988).

Each phytophagous insect species is associated with a group of plants, large or small in number, which we designate as its food-plant range. The food-plant range of some insects is often correlated with natural taxonomic plant groupings (genera or families, *etc.*), but the food plants of many insects are distributed in an apparently random pattern among plants without special regard to botanical affinities. In host-plant selection insects make a number of decisions. An insect continuously evaluates the information from its surroundings, compares this impression with its own internal standards, and decides to continue or change its motor patterns (Visser, 1986). Host selection in phytophagous insects consists of a sequence of behavioral responses to an array of stimuli associated with host and nonhost plants. The oviposition step is particularly crucial in the leaf miner insects, because the hatching larvae are often relatively immobile and thus depend on the judicious choice of food plant by the adult female (Renwick and Chew, 1994).

Phytophagous insects vary greatly in the number of parasitoid species they support (Price *et al.*, 1980). Host plant characteristics may cause much of this variability by directly or indirectly affecting herbivore vulnerability to parasitoids (Price *et al.*, 1980). Direct effects occur when such plant characteristics as glandular leaf trichomes or gall structures (Cornell, 1990) impede parasitoid searching, or when plant odours or nectar attract parasitoids (Gross and Price, 1988). Leaf trichomes can interfere with access to the leaf surface (Ezcurra *et al.*, 1987). *Tildenia inconspicuella* (Lepidoptera: Gelechiidae) on horsenettle *(Solanum carobinense)* is apparently forced to be endophytic and suffers higher parasitism because of dense trichomes, whereas *Tildenia georgei* on ground cherry *(Physalis heterophylla* var *iambigue)* where trichomes are thin and flexible, is more vagile and can escape parasitoids (Gross and Price, 1988 cited by

Hespenheide, 1991).

Three main host plants of *Scaptomyza flava* differ in colour, cauliflower being dark green, turnip light green and Chinese cabbage yellowish, though these terms can only be vague descriptions of the colours of plants. To describe colours more precisely requires consideration of *hue, saturation,* and *intensity (brightness).* A specific colour can attract insects to plants for oviposition (Finch, 1986; Prokopy *et al.*, 1983b). Female *Delia radicum* flies use leaf colour to distinguish between turnip, radish and green cabbage prior to landing, preferring green cabbage (Prokopy *et al.,* 1983b). The pattern of multi-leaved plants plays a significant role in determining landings, suggesting that the total area and colour of foliage is important to plant-seeking flies (Nottingham, 1988).

Chemical properties play an important role in host plant selection. Plant chemistry is probably the most important source of information contributing to the final decision by a insect to oviposit or not (Renwick and Chew, 1994). One method of dealing with chemical defense might be to avoid tissues with defensive compounds and to mine cell layers without them (Feeny, 1970). However, only one of 18 species of leaf miners studied on oak in Florida restricted mining to cell layers low in tannin (Faeth *et al.,* 1981).

Cell growth in the vicinity of leaf miner eggs, encapsulation of endoparasitoids eggs, venation of leaves and abscission of mined leaves can be other host defense mechanisms (Hespenheide, 1991).

The role of competition in structuring phytophagous insect communities encompasses two distinct perspectives. Janzen (1973) proposed that insects that feed on plants "automatically compete with all other species" on the plant. Conversely, Lawton and Strong (1981) contended that " resource-based competition does not occur 'automatically' at low or even moderate levels of phytophagy", and concluded competition is relatively unimportant in structuring phytophagous insect communities.

Competition between leaf-miners and externally feeding larvae may (Faeth, 1985, 1986) or may not (Hawkins, 1988) be mediated by parasitoids. Plants of *Cardamine cordifolia* that were experimentally stressed had increased herbivory by the leaf-miner *Scaptomyza nigrita.* In two other situations, one experimental (Potter and Redmond, 1989) and one natural (Auerbach and Simberloff, 1984), stressed trees experienced leaf-miner outbreaks after defoliation (Hespenheide, 1991).

Distribution and damage of *Scaptomyza nigrita* Wheeler on its host bittercress, *Cardamine cordifolia* A. Gray (Cruciferae), a native perennial crucifer, were examined over two growing seasons in relation to leaf position by Collinge (1987). Concentrations of defensive compounds (glucosinolates) and of nutritive compounds (total nitrogen, free amino acids, soluble carbohydrates) were also examined. The fly-host plant relationship was studied in sun and shade habitat at two sites. Oviposition and leaf-mining damage were concentrated on the lower central leaves of the stem in both habitats. These mature leaves had lower glucosinolate concentrations than new leaves and total insect herbivore load on bittercress was greater on sun than on shade plants (Collinge, 1987). Collinge and Louda (1988) tested the hypothesis that light intensity was the direct, proximal mechanism causing significantly higher vulnerability of bittercress clones in the sun to herbivory by *S. nigrita* Wheeler. Leaf-mining damage was significantly higher on artificially-shaded plants, the opposite of expectation. Shading plants shifted their growth pattern toward that of naturally-shaded plants. No significant differences were detected in leaf water status or glucosinolate concentrations, eliminating water stress and variation in defensive posture for mediating the between habitat differences in levels of herbivory.

LEAF SELECTION

Leaf selection is an important aspect of plant/insect interactions because, for some phytophagous insects such as leaf miners, oviposition by the adult insect determines where the larva will feed (Faeth *et al.,* 1981). Most endophagous insects such as leaf miners cannot move to more suitable plants or leaves as many external-feeding insects can. Therefore, natural selection for oviposition should act to minimize risks

associated with host plant (and other phytophagous insects and natural enemies under field conditions). Host plant factors influencing plant quality include size and position of leaves, nutritional and defensive chemistry, physical barriers, and phenological changes *(e.g.,* qualitative seasonal changes in leaves or leaf abscission). Previous or concurrent feeding by other phytophages may alter physical and chemical aspects of the leaf or reduce leaf size so that insufficient area remains for development. Finally, attack by predators and parasitoids may render certain leaves less suitable for oviposition and development if search for hosts on different leaf types is nonrandom (Schultz, 1983).

Many folivorous insects prefer young leaves over mature ones when both resources are simultaneously available (Cates, 1980; Fowler and Lawton, 1982). Other phytophages completely restrict feeding to young leaves (Feeny, 1970; Rockwood, 1974; Auerbach and Strong, 1981). This pattern is related to the generally higher food quality of young leaves (Potter, 1989). This restriction can be imposed by synchrony between bud break and termination of diapause (Feeny, 1970), or chemosensory cues can lead to oviposition preference or avoidance of mature leaves (Auerbach and Strong, 1981; Faeth *et al.,* 1981a).

Chemical and physical differences between young and mature leaves presumably form much of the basis for leaf-age preferences among phytophagous insects. Young leaves generally have higher protein, amino acid and water concentrations and are less tough than mature leaves (Scriber and Slansky, 1981). Morphological differences between young and mature leaves also may impose selective pressures determining leaf-age preferences. Young rolled leaves of *Heliconia* protect Hispine beetle larvae from most parasitoids and predators (Auerbach, 1982). Larvae of four species of leaf-mining Lepidoptera commonly found on water oak, *Quercus nigra* (L), restrict feeding to young leaves. Two of the phenologically restricted leaf-mining species feed only on supple, first-flush leaves produced in March and April.

Peripheral leaves may be more heavily mined than interior ones (Simberloff and Stiling, 1987). The dispersion of mines among leaves is often aggregated rather than uniform, but this varies among species (McNeil and Quiring, 1983).

"Leaf size may not influence but usually does; smaller leaves are preferred by smaller species, or larger leaves are simply preferred (Bultman and Faeth, 1986 cited by Hespenheide, 1991). Large leaves may increase the probability of survival of single larvae, but may also increase the density of mines; communal mines have been suggested to be an adaptation for exploiting larger leaves " (Hespenheide, 1991). Tuomi *et al.* (1981) demonstrated that leaf miners on multiply-mined leaves occupy large leaves and that larval mass is a negative function of the number of mines per leaf. Leaf size selection by endophagous insects may only become important when densities are sufficiently high that insects are forced to occupy leaves with other insects or when an individual insect requires large portions of a leaf for development. *Stilbosis juvantis* did not select leaves different in size from those available for colonization on individual trees (Faeth, 1985). However, larval weights may vary considerably among individuals utilizing the same leaf (Petitt and Wietlisbach, 1992).

Zucker (1982) has shown an inverse relationship between leaf size and concentrations of phenolics in narrow leaf cottonwood. Choosing the correct leaf is particularly crucial when an insect is confined to a single leaf for a majority of its lifetime as are leaf miners (Hering, 1951). If large leaves are superior we would expect them to be preferentially selected for oviposition (Tuomi *et al.,* 1981).

Leaves chosen for oviposition by leaf miners are usually undamaged and may be either younger (4 of 18 species) or older (14 of 18 species) (Godfray, 1984). *Stilbosis juvantis* selected intact leaves over damaged leaves for oviposition (Faeth, 1985). Of 141 mines observed, the expected distribution, based on 55% leaves damaged and 45% undamaged for all trees (18 oak trees, *Quercus emoryi*), is 75.5 mines on damaged and 63.5 on intact leaves; the observed distribution was significantly different (Faeth *et al.*, 1981). Successful emergence was greater for *S. juvantis* on intact leaves (70.2%) than on damaged leaves (51.4%). *Stilbosis juvantis* on damaged leaves experienced significantly lower survivorship, owing to increased parasitism, than did miners on intact leaves (Faeth, 1985).

"Mines may be more frequent toward the base of the leaf or toward the apex or be randomly distributed (Gross and Price, 1988). When more than two mines occur on a leaf, they are often on opposite sides of the midvein (Auerbach and Simberloff, 1984). Mines may be superficial or full-depth, and the two sides of a leaf may serve as discrete habitats for superficial miners (Connor, 1984). Mines of different species may co-occur on leaves more frequently than expected by chance without apparent competition, perhaps because of preferences for different portions of the leaf" (Hespenheide, 1991).

Mining larvae in many cases retain throughout their life the same type of mine and in this way feed consistently only in upper surface or in lower surface mines. In other cases, however, larvae change the type of mine on one or more occasions (Nielsen, 1978). Such changes in feeding behaviour frequently occur after completing a moult and often run parallel to changes in the structure of the mouthparts, which are now adapted to a different type of food (Martens and Trumble, 1987).

There are many linear mining dipterous larvae which initially live on the under-side of the leaf in the spongy parenchyma, later continuing their channel in the palisade parenchyma on the upper-side, and then often transfer the last part of the channel back to the under-side, where they can pupate in a less exposed position (Parella, 1987). Such a double change of the side of the leaf can be frequently observed in the polyphagous *Phytomyza atriconis* Mg. The change from a linear mining to a blotch mining existence can also often be found to be related to moulting.

The depth of the mine in the leaf tissue is also subject to remarkable variations during the course of a larva's life. In general the type of depth with which feeding commences is retained throughout. What starts as a full depth mine does not later become upper surface or under surface, and vice versa. However, a few exceptions do exist. The initial channel of *Philophylla heraclei* L., for instance, is normally a full depth mine on the leaves of Umbelliferae, the subsequent blotch on the other hand is upper surface and greenish **(Fig. 1.12)** (Hering, 1951).

Sometimes mines have a distribution among leaves (Heads and Lawton, 1983). However, mine placement within leaves frequently is non-random because of either preference for certain leaf locations or avoidance of conspecific eggs.

Selective pressures should result in females ovipositing in leaves which promote increased larval development and survival (Mitchell, 1975; Larsson *et al.*, 1986 cited by Colling and Louda, 1988). Therefore, larval occurrence and damage should reflect qualitative and quantitative differences in leaf quality detectable by the ovipositing female (Chew, 1977; Rausher, 1979 cited by Colling and Louda, 1988). Adult females of some leaf-mining species appear to sample plant quality. For example, agromyzid females puncture holes in the leaf cells with their ovipositor and then "test" the sap (Hering, 1951); it is not clear whether they are merely sampling the leaf tissue or are actually feeding. However, mandibular chemoreceptors exist in many insect species, including dipteran crucivores that feed on plants, which are sensitive to characteristic host plant chemicals and primary nutrients (Chapman, 1982).

LEAF ABSCISSION

The importance of leaf abscission in the population dynamics of insects was first recognized by Clark (1962) for psyliids, and later by Owen (1978) and Faeth *et al.*, (1981) for leaf-mining and other sessile insects. They studied a number of species of dipteran, lepidopteran and coleopteran leaf miners whose development is restricted to a single leaf, and reasoned that for leaf-mining insects early leaf fall will most likely lead to mortality unless the larvae is near pupation, or has pupated (Connor, *et al.* 1994).

Recent studies by Preszler and Price (1993) showed that premature leaf abscission has a strong negative impact on some endophagous insects *(e.g.*, leaf miners) while others, which nearly complete feeding by the time of early leaf abscission, do not suffer increased mortality in abscised leaves. They investigated the causal relationship between leaf mining and leaf abscission by experimentally isolating the effect of leaf mining on leaf abscission. They concluded that: (i) Early abscission of mined leaves is

an important mortality factor for some leaf miners (*e.g., Phyllonorycter* species). *Phyllonorycter* survival was greatly reduced in these abscised leaves. (ii) Leaf-mining by *Phyllonorycter* was associated with increased early leaf abscission. An egg removal experiment demonstrated that leaf mining induced an increase in leaf abscission. (iii) The induction of early leaf abscission was dependent upon the timing of herbivory and simulated herbivory (mechanical damage). Early mechanical damage induced leaf abscission, late mechanical damage did not. Mines which expanded early were more likely to induce leaf abscission than mines which expanded more slowly.

Circumstantial evidence strongly suggests that Dipteran and Lepidopteran leaf miners can induce early leaf abscission on a variety of woody plants *(e.g.*, Faeth *et al.*, 1981; Maier, 1982; Owen, 1978).

Other reports show early abscission of mined leaves to be a major mortality factor for some leaf miners (Owen, 1978; Askew and Shaw, 1979; Faeth *et al.*, 1981; Potter, 1985 cited by Simberloff and Stiling, 1987), though Pritchard and James (1984a) found for two *Phyllonorycter* species that abscission causes <3% of larval death. Kahn and Cornell (1989) argued that leaf abscission may not increase mortality of leaf miners for two reasons. One reason for lack of a nagative effect was that leaves were not dropped until mines had pupated in the leaf. Second, some leaf miners form "green islands" of healthy tissue around themselves when the leaf falls. Engelbrecht *et al.* (1986 cited by Simberloff and Stiling, 1987) suggested such islands may be generated by high cytokinin levels. Faeth (1986) reported green islands for *Stilbosis juvantis* on emory oak, but Simberloff and Stiling (1987) have found none for *S. quadricustatella*. Kahn and Cornell (1989) also argued that, because some parasitoids do not search the ground, a miner might be better off there. Faeth *et al.* (1986) showed that mined leaves abscised significantly earlier in three oak species and constituted one third of the mortality of two species of miners. Most researchers believe that abscission is a general response to damage and not an attempt to adjust miner numbers (Pritchard and James, 1984). The clumping of mines by *Stilbosis* larvae seems to increase the likelihood of early abscission. This increase appears to be due to the clumping and not to the type of leaves

chosen. When the leaf abscises early, miners are likely to die; this is the greatest source of larval mortality.

Stiling *et al.* (1984) state that premature leaf fall is by far the largest source of larval mortality in *Hydrellia valida* (Diptera: Ephydridae). Auerbach and Simberloff (1989) noticed that dominant sources of larval mortality of a leaf-mining moth on aspen (*Quercus calliprinos*) leaves were premature leaf abscission and death from unknown causes.

Abscission timing determines the effect on herbivore demography. The amount of early abscission is affected by extent of injury, the timing of damage or both (Maier, 1989). When miners in an abscised leaf of oak were very near to pupation, abscission killed them (Simberloff and Stiling, 1987). Delayed (4 to 5 months) post-hatch development of larval *Phytomyza ilicis* synchronizes adult emergence with leaf flush and postpones early leaf abscission of infested leaves (James and Pritchard, 1988). Leaflets mined by a single larva of *Agromyza frontella* in third-cutting alfalfa abscised an average of 12.9 days after the larva emerged from the leaflet to pupate in the soil. Abscission of mined leaflets was detectable in first and second cutting alfalfa only if harvest was delayed at least 10 days (Hendrickson and Dysart, 1983). Fourth-instar larvae of *Coptodisca* on *Vaccinium* had 90% survival from abscised leaves (Maier, 1989), and for the univoltine leaf-mining moth, *Lithocolletis quercus* on *Quercus calliprinos* (Auerbach and Simberloff, 1988), leaves on vegetative shoots abscised significantly earlier if mined than if unmined.

Hendrickson and Barth (1978) reported that mined leaflets tended to abscise more rapidly than unmined leaflets on potted alfalfa maintained in rearing rooms. I observed the same phenomenon with Chinese cabbage, turnip and cauliflower in the field and under greenhouse conditions.

Faeth (1991) showed that leaf abscission rates are greater in unshaded leaves compared to shade leaves and this can explain some variation in larval distribution and

mortality. Others (Askew and Shaw, 1979; Faeth *et al.*, 1981; Potter, 1985; Stiling *et al.*, 1984; Auerbach and Simberloff, 1989) have shown that premature leaf abscission reduces survival of leaf miners. High rates of premature leaf abscission for unshaded leaves (Bultman and Faeth, 1986) may contribute partly to lower densities in this region if females also select leaves based on their propensity to abscise (leaves were censused for densities before most premature abscission associated with mining occurs so differential leaf abscission cannot account for differences in densities). However, unshaded leaves are typically smaller than shade leaves in Emory oak trees.

INTER - INTRASPECIFIC COMPETITION

Interspecific competition is unlikely without intraspecific competition (Strong *et al.*, 1984). Over the last several years ecologists have questioned the importance of competition, particularly in phytophagous insect communities (Rathke, 1976; Bultman and Faeth, 1985). Cases in which insects do compete often involve sedentary insects which feed on discrete patches of food for extended periods of time. For example, competition was documented for eight species of leafhopper on American sycamore (McClure and Price, 1975) and for two leafhopper species on stinging nettles (Stiling, 1980). Sedentary insects, such as leaf miners, may experience food or space limitation if putative competitors are in the same food patch. Most leaf-mining insects feed on single leaves for the entire larval stage. Hence, competition seems more likely between leaf miners than between more mobile insects, which can move within and between plants while foraging.

For phytophagous insects, experimental field studies demonstrating intraspecific competition at natural densities are few. By experimentally caging individual sycamore leaves, McClure and Price (1975) showed intraspecific competition in several species of the leaf hopper genus *Erythroneura*. For leaf miners, however, Faeth and Simberloff (1981) contend that natural enemies, particularly hymenopteran parasites, keep populations far below levels at which intraspecific competition occurs.

Two major forms of intraspecific competitive interactions have been described. Scramble (Nicholson, 1954 cited by Quiring and McNeil, 1983) or exploitation (Birch, 1957; Miller, 1967 cited by Quiring and McNeil, 1983) competition occurs when individuals do not interact aggressively but compete for the use of a limiting resource. Interference competition denotes interactions that limit access to a necessary resource or requirement. In its most extreme form this results in contest competition where there is a winner, which obtains as much of the governing requisites as it needs for survival and reproduction, and a loser which does not (Quiring and McNeil, 1983). "Intraspecific competition can either take the form of cannibalism, in which one larva kills a conspecific that occurs with it in a mine (interference competition), or of preempting the conspecific's use of the leaf by mining it first (exploitation [starvation] competition)" (Hespenheide, 1991). A form of larval interference competition, by the production of chemicals affecting conspecific, has been suggested for several *Drosophila* species, concurrent with exploitation competition for the available resources (Neilson, 1968; Quiring and McNeil, 1983). Competition among members of the same species is frequently observed in nature (Fox, 1975; Polis, 1981; Inove, 19834; Persson, 1983; Stiling *et al.*, 1984 cited by Dohse and McNeil, 1988). Intraspecific competition depends on the presence of at least two mines in a leaf and then on either large numbers of mines (Wallace, 1970) or large mines relative to the size of the leaf (Guppy, 1981). It may not occur at all when densities of mines are low, or be relatively minor as a source of mortality (Askew and Shaw, 1979).

Martin (1956) has pointed out that in larva-larva competition, attacks were provoked by the introduction of larvae into tenanted mines, and the results were observed. The first larva to sense the presence of the other immediately attacked and killed it by tearing a hole in the central portion of the abdomen and consuming the body fluids. The larva on the defensive did not, as a rule, put up much resistance. The size of the larva involved did not seem to have any bearing on the outcome of the struggle, the smallest individual often being the victor. In the first and second instars, the bodies of the dead larvae were usually moved to the frass pile, whereas in the third instar they were moved to the margin of the mine (Martin, 1956).

In the aspen blotch miners, larval competition occurs only in the first three instars (Martin, 1956). Competition between larvae of similar age of *Agromyza frontella*, second instar larvae are very aggressive, active cannibals while third instar larvae generally do not attack each other (Quiring and McNeil, 1984). When interactions between third instars occur, they only last a few seconds and do not result in death. Thus it appears that third instar larval behaviour changes depending on the size (or behaviour) of the opponent, while the first and second instar larvae attack any individual encountered.

Although interspecific competition of phytophagous arthropods may be rare, intraspecific competition could be important in maintaining individual populations at levels below which interspecific competition would occur (Faeth and Simberloff, 1981). Experimental field studies demonstrating intraspecific competition of phytophagous insects at densities usually found in nature are few. McClure and Price (1975) showed that populations of leaf hoppers can compete both intra- and interspecifically during certain times of the growing season, although not to the extent of excluding any species. Stiling (1980) demonstrated that field populations of leaf hoppers on stinging nettles could reach densities where intra- and interspecific competition occurred. In both examples intraspecific competition was deemed to be greater than interspecific competition.

Exploitation competition depends on multiple mines in a leaf as well as their size and distribution on the leaf. In the field confluent mines of *Labdia* occurred on 17% of multiply mined *Acacia phyllodes* and on less than 8% of all mined phyllodes (New, 1979). Although multiple mines are readily induced in the laboratory, most field samples have few mines per phyllode and the incidence of confluent mines is low. "Interference" between larvae is thus likely to be relatively rare, as is food shortage; the completed larval mine may comprise only a small proportion of available phyllode area, the incidence of "untenable" oviposition is thus low (New, 1979). As many as 210 mines of *Perditha* can occur on jarrah leaves; 64 insects matured in one leaf with 178 mines, but the usual maximum is 40-60 (Wallace, 1970). Some leaves were mined so intensely

that no larvae matured and the leaf was totally consumed. If the number of mines per leaf increases, either survival (Guppy, 1981) or pupal weight (Bultman and Faeth, 1986) or both decrease (Stiling *et al.*, 1984). Guppy (1981) noted that survival of the larvae of alfalfa blotch leaf miner was higher in leaflets with solitary mines than in those with multiple mines; only 25% of the leaflets with two mines gave rise to two mature larvae; three larvae seldom survived in a single leaflet.

Success in contest competition depends upon superior combative abilities while exploitation competition requires rapid accumulation of the limiting resource and (or) a lower minimal mass required for survival (Quiring and McNeil, 1983).

Field studies on lepidopterous leaf miners have found intraspecific competition to be of minor importance (Dye, 1982), but in some Diptera leaf miners (alfalfa blotch leaf miner) intraspecific competition is a major mortality factor, both in laboratory and field conditions (Quiring and McNeil, 1983). Interference (cannibalism) reportedly occurs in several species other than *Agromyza frontella* (Diptera: Agromyzidae), although it has been reported not to occur in some species (Simberloff and Stiling, 1987 cited by Hespenheide, 1991). Swan (1973) considered that cannibalism is an important mortality factor in high infestation of oak leaf miner *(Phyllonorycter messaniella)* in New Zealand. Overall mortality from cannibalism was 11% for *Phyllonorycter* on apple in Japan and increased with larval density to nearly 50% for approximately 25 larvae/leaf (Sekita and Yamada, 1979). Larval mortality owing to interference competition (cannibalism) among similarly aged larvae of the alfalfa blotch leaf miner, *Agromyza frontella* during the first two larval instars, and exploitation (starvation) competition during the third and final instar, increase in density-dependent manner. Larval competition caused 53% mortality of *Lithocolletis salicifoliella* on *Phyllonorycter tremuloides* (Martin, 1956). The effect of competition among same-aged larvae of the vegetable leaf-miner *Liriomyza sativae* Blanchard was investigated by Petitt and Wietlisbach (1992) in laboratory studies over a range of densities from 0.1 to 2.9 larvae per cm^2 of lima bean primary leaf area. Both exploitative and interference competition occurred among larvae. Cannibalism was observed primarily between first or second

instars, and was not density-dependent at < 1.0 first instars per cm^2. Exploitative competition occurred between third instars at higher densities.

Greater mortality of oak leaf miners in high-density treatments resulted from increased mortality of miners on singly mined leaves compared to those on singly mined leaves in low-density treatments (Bultman and Faeth, 1986). Larval mortality owing to interference (cannibalism) during the first two larval instars, increased in a density-dependent manner. Prepupal and pupal mortality increased and pupal weight decreased as larval density increased (Bultman and Faeth, 1986). Quiring and McNeil (1984) have pointed out that in some species, adults of *Agromyza frontella* (Diptera: Agromyzidae) will cannibalize younger individuals. When two larval mines of *Lithocolletis salicifoliella* (Lepidoptera: Gracillaridae) coalesced, one larva attacked and killed the other. In rare cases, the coalescence of mines resulted in the death of all larvae concerned (Marten and Trumble, 1987). There is little supporting evidence that competition increases larval susceptibility to parasitoids.

NATURAL ENEMIES OF LEAF-MINERS

Interspecific competition is comparatively uncommon because many populations are kept rare, relative to the availability of potentially limiting resources, by the impact of natural enemies-insect parasitoids, insect predators, birds, pathogens, *etc.* Hence the major processes acting in many conite work vertically through the food chain, not horizontally with other pecies in the same trophic level. (Strong *et al.,* 1984). The effects of natural enemies are much more important than intraspecific competition by a ratio of at least 2:1.

PARASITOIDS

The foraging behaviour of parasitoids is the subject of numerous studies because of the direct link between successful searching and parasitism (see Casas, 1989) Parasitoids of leaf-miners are much more easily studied because leaf-miners are

relatively immobile compared to external feeders and are more conspicuous than other endophytic forms such as gall-makers. Possible adaptations for the leaf mining habit include avoidance of digestibility-reducing compounds in certain leaf tissues (Feeny, 1970), protection from desiccation during dry periods (Hering, 1951), and reduction of predation and parasitism by concealment within the leaf (Faeth, 1980). There is, however, little experimental evidence demonstrating that the leaf-mining habit is indeed adaptive in any of these respects. To the contrary, there is evidence, at least in regard to reducing predation, that leaf mining is not particularly advantageous.

When leaf miner densities are high parasitoids may be an important source of mortality. Parasitoids may kill leaf-miners by oviposition and subsequent feeding by the parasitoid larva, as well as by feeding of the adult parasitoid on the larval host. The principal enemies of leaf miner insects are undoubtedly parasitic Hymenoptera, which penetrate the mines with their eggs placed in or on the bodies of the mining larvae. They also destroy many larvae merely by feeding on their body fluids. These Hymenoptera belong mostly to the Chalcidoidea, especially the family Eulophidae, with Ichneumonoidea being generally much less strongly represented (Askew and Shaw, 1974). Host feeding by adults is difficult to separate from plant antibiosis (Askew and Shaw, 1979 *cf* West, 1985), but has been observed or measured in the field or in laboratory studies and at times appears to be a more frequent cause of host death than oviposition (Simberloff and Stiling, 1987 cited by Hespenheide, 1991).

Egg parasitoids of leaf-miners have been little studied, although a number of parasitoid taxa are involved and host mortality rates can be high. Mymarids have been reared from eggs of the Buprestid genus *Taphrocerus,* and up to 70% of *Taphrocerus* eggs are parasitized toward the close of the season (Claridge and Wilson, 1982). Two species of Eulophidae were reared from *B. tessellatus* on oak and 13% of eggs were parasitized. Other egg parasitoids have been reared from *Pachyschelus psychotriae* and emergence holes have been seen in eggs of Hispine beetles.

Swan (1973) compared the levels of oak leaf miner infestation in Nelson (New

Zealand) and found that the number of mines per leaf on *Quercus robur* had declined from more than 40 mines per leaf prior to the release of parasitoids, to around 2.3 miner per leaf in 1969-1970. In an analysis of the parasitoids of leaf-miners of British deciduous trees, Askew and Shaw (1979) found that most belonged to three subfamilies of the Eulophidae, with a fourth Eulophidae subfamily parasitizing weevils and pteromalids parasiting agromyzids. There are fewer ichneumonid than braconid parasites of leaf-miners, perhaps because leaf-miners are too small to be exploited by the relatively larger Ichneumonids (Shaw and Askew, 1976). A broader perspective both in terms of geography and in host taxa would lengthen the list of parasitoid taxa (Marten and Trumble, 1987). Braconids are often important parasitoids (Mair, 1989; Goppy *et al.*, 1988), as are pteromalids and chalcidids on tropical Buprestidae and Hispines as well as tachinids on Hispinae (Hespenheide, 1991).

Twenty-one species of parasites were reared from natural populations of the chrysanthemum leaf-miner, *Chromatomyia syngenesiae* Hardy (Diptera: Agromyzidae), 15 endoparasites and 7 ectoparasites. The rank order of importance of the parasites on *Sonchus* spp. and *Senecio* spp. was significantly correlated (Cornelius and Godfray, 1984). There is little supporting evidence that competition increases larval susceptibility to parasitoids (Osmelak, 1983).

Foraging behaviour of parasitoids has received some attention. In the field, mines are detected in flight, apparently visually, although the mode of distinguishing suitable plant hosts is unknown. Laboratory experiments suggest plant hosts are located chemically, mines by vision, and feeding larvae by sound (Sugimoto and Ishii, 1979 and references therein). Parasitoids might mediate competition between miners and externally feeding herbivores by being attracted to damaged leaves (Faeth *et al.*, 1979, 1980), but experimental damage had no effect on parasitism (Hawkins, 1990). Oviposition in or feeding on the host is influenced by host density (Sugimoto and Ishii, 1979). Parasitoid longevity and rates of foraging, oviposition, and host feeding have been shown in the field (Bultman and Faeth, 1985) or experimentally to be temperature dependent (Sugimoto and Ishii, 1979).

Relatively little attention has been paid to the potential influence of mine morphology on susceptibility to parasitism. The observation that Eulophids parasitizing tentiform miners have longer ovipositors than those parasitizing other types of mines suggests tentiform mines may be a defense against parasitoids. Unusual larval refuges have been observed in several tropical Hispines that may reduce parasitism.

Notable examples of biological control of leaf-mining herbivores have been achieved for the Hispines *Promecotheca coeruleipennis* and *Promecotheca cumingi* on coconut *Cocos nucifera* in Fiji and Sri Lanka, respectively, as well as for *Agromyza frontella* in the United States (Drea and Hendrickson, 1986).

The braconid parasitoid *Opius dissitus* Muesebeck is reared and released at the Land, EPCOT Centre, Florida, to reduce damage caused by *Liriomyza sativae* (Petitt, 1988). CIBC (Commonwealth Institute of Biological Control) began a survey of parasitoids of *Scaptomyza* spp. in Pakistan in March 1971 but found none [DSIR (Department of Scientific and Industrial Research) files].

In some studies rates of parasitism are higher later in the season (Gross, 1988; Miller, 1973 and Wallace, 1970), while, in others, they have been higher on the first than on the second host generation (Askew and Shaw, 1979; Maier, 1982), although either overall mortality was greater in the second generation (Askew and Shaw, 1979) or parasitism was higher again in the third generation. Rates of parasitism have been shown to vary with leaf size (Connor, 1984). Also this rate in some cases was dependent on density and in other cases density independent (Heads and Lawton, 1983; Sekita and Yamada, 1979).

Rearing records are presented by Shaw and Askew (1976) for 14 species of Braconidae and 13 species of Ichneumonidae from leaf-miners of the orders Lepidoptera, Hymenoptera and Coleoptera in England. Braconids were more abundant and specialised than Ichneumonids in the parasite faunas of leaf-miners on both deciduous trees and low-growing plants. Although seldom comprising a major element in the parasite

complex on deciduous trees, braconids were sometimes numerically the dominant parasites on low-growing plants.

Moderate to heavy infestations of *Liriomyza munda* and *L. pictella* (Diptera: Agromyzidae) were sustained in alfalfa during the hot summer months, late July to early October, in the Sacramento and San Joaquin Valleys, California. *L. pictella* is more numerous during the early part of the growing season, *L. munda* during the hotter months. Parasites destroy most of the immature stages of the two species from April to June. Parasitization drops to less than 50% from July to September but increases slightly in autumn (Jensen and Koehler, 1970).

Some species of *Stigmatomyces* (Ascomycetes) are parasitic on some Dipterous leaf miner, for example: *S. scaptomyzae* on *Scaptomyza* spp. in the USA, Venezuela, France and Poland (Watt, 1923 cited by McGregor, 1989). *Dacnusa scaptomyza* (Hymenoptera: Ichneumonidae), parasitises the dipterous leaf-miner *Scaptomyza flaveola* (Valentine, 1967). *Scaptomyzella flava* is parasitised by *Dacnusa temula* and *Pleurotropis flavis* (Valentine, 1967). A number of Hymenoptera have also been reared from dipterous pupae. These include *Phaenocarpa (Asobara) persimilis* Papp (Braconidae: Alysiinae) and two Chalcids, *Hemiptrasenus semialbiclava* Girault (Eulophidae) and *Trigonogastrella sp.* (Pteromalidae) (Spencer, 1976). Many Chalcids and Ichneumonids are recorded parasitizing Agromyzidae, and under normal conditions population control is effected by these natural enemies, which are undoubtedly major factors in maintaining population equilibrium (Szwejda, 1974). Biological control of alfalfa blotch leaf-miner *Agromyza frontella,* was attained in 1981 in Delaware by using the exotic parasite species *Dacnusa dryas* (Hymenoptera: Braconidae), and *Chrysocharis punctifacies* (Hymenoptera: Eulophidae), which were released at two Newark fields in 1977 and became established in 1978. During the pre-establishment period, parasitism in the first cutting was 18% by native parasites; yearly maximum number of mines per stem in first cutting was 10 to 25. In 1981, imported and native parasites produced 71% parasitism and reduced host populations to an average maximum of two mines per stem (Hendrickson and Barth, 1978).

In New Zealand two species of Hymenoptera have been recorded as parasitizing *Chromatomyia syngenesiae* before introductions for biological control began. These were *Chrysocharis sp.* (Eulophidae) probably *C. pubicornis* [DSIR (Department of Scientific and Industrial Research) files] and *Dacnusa areolaris* Nees (Braconidae). Watt (1923 cited by McGregor, 1989) recorded 90% parasitism of *Chromatomyia syngenesiae* larvae but did not identify the species and Kelsey (1937) claimed that 40-65% parasitism of *C. syngenesiae* was normal. This parasitoid was presumably *D. aerolaris. Hemiptarsenus sp.* (Eulophidae) has also been recorded from *Cerodontha australis* (Valentine, 1967). This was probably *Hemiptarsenus semialbiclavus.* Cumber and Eyles (1961) recorded *Hemiptarsenus sp.* associated with various crops including brassicas. *Diglyphus isaea* Walker (Eulophidae) apparently established in New Zealand on *C. syngenesiae* before its introduction for leaf-miner control (McGregor, 1989).

Parasitoids already present in New Zealand may restrict populations of potentially damaging agromyzid leaf miners. McGregor (1989) concluded that further biological control attempts for Agromyzidae are not warranted. First priority for leaf-miners on brassicas in New Zealand must be identification of the insects and the extent of their damage (Pearson and Goldson, 1980).

PREDATORS

The effectiveness of natural enemies of arthropods can be directly influenced by morphological characteristics of the host plant or secondary plant compounds (Vinson, 1976). Plants may also affect natural enemies of arthropods through induced physiological modifications of the host or prey which render them either more or less suitable for predation (Moraes and McMurtry, 1987). The major vertebrate predators of leaf miners are probably birds (Hering, 1951), which are frequently observed on isolated trees (Faeth and Simberloff, 1981). Faeth (1980) considered predation on leaf miners to be energetically feasible for birds when at least 10% of the leaves were mined. For large predators, searching for and opening leaf mines when they are at low densities would seem energetically prohibitive because of the small size of leaf miners relative to those

of most external feeding insects.

Although it seems that leaf mining larvae might be a more suitable food item for invertebrate predators, there have been only a few accounts of invertebrates other than ants, hemipterans, lacewings and mites feeding upon leaf miners.

Some birds particularly titmice, are known to peck open leaf mines, and predacious Hemiptera sometimes feed upon the larvae through the leaf epidermis. It is likely, however, that leaf mining larvae suffer much less than exposed phytophagous larvae from predator attack (Askew and Shaw, 1974).

Observations of ants preying upon leaf miners in temperate zones are rare (Hering, 1951). But according to Faeth (1980b) certain ant species are important invertebrate predators of leaf miners and are commonly found in agricultural fields. All stages of the jarrah leaf miner are eaten by predators. A small number of eggs, usually at sites of high leaf miner population density, were eaten by an unidentified predator, probably a mite (Mazanec, 1987). Predation on leaf mining larvae by non-arthropods is recognised by torn, empty mines. the general pattern is illustrated by the numbers of larvae eaten by birds. In the study by Mazanec (1987) the numbers of larvae eaten amounted to 32.7% of total. Predation by birds depends on the leaf miner occurring at the canopy levels they exploit. Unlike the parasitoids, the avian predators tend to attack only the large larvae. They consumed the highest number of jarrah leaf miner larvae, but caused the lowest percentage of mortality (Mazanec, 1987). Spraying with dieldrin on sweet potato for weevil control had an adverse effect on parasitisation (Hinckley 1963), and he attributed the subsequent outbreaks of two species of lepidopteran leaf-miners to elimination of ant predation.

An inverse relationship between predation by *Parus* and density of *Phytomyza* might result from the difference in scale between the foraging of the larger bird and the dispersion of the smaller mines, rather than to numbers of prickles (Heads and Lawton, 1983). Itamies and Ojanen (1977 cited by Hespenheide, 1991), on the other hand, found

that leaves of *Alnus* with greater numbers of mines of *Lithocolletis* spp. had higher predation rates by *Parus* spp. They also suggested that the birds preferred full size mines and thus avoided parasitized larvae that were smaller, and consequently had a greater influence on the populations of the moths. *Parus* species also prey on *Rhynchaenus* larvae (Pullin, 1985). Larvae of *Perthida* were found in the stomachs of 9 species of birds. Mazanec (1985) has shown that large larvae of *Perthida glyphopa* were the most preyed upon (33%) by 9 species of birds at intermediate population densities. At high population density, 3 species of ants collected some 30% of the fallen mature larvae and a further 21% were eaten by earwigs, Carabid beetles and ants during summer aestivation. The importance of predators on *Phyllonorycter messaniella* (oak leaf miner) in New Zealand is unknown, but a number are known to attack *P. blancardella* in Canada (Thomas and Hill, 1989).

Although studies of leaf-miner mortality have concentrated on larvae, adults are also susceptible to predation and have evolved antipredator defense. Hispine chrysomelids are often involved in mimicry complexes, usually with beetles in the *Lycidae* or *Lampyridae* (Bale, 1981), that are probably Mullerian in character. Leaf-mining *Buprestidae* of the genera *Taphrocerus* and *Leiopleura* have been hypothesized to mimic flies (Hendrickson and Plummer, 1983).

ABIOTIC MORTALITY FACTORS

Weather conditions (temperature, precipitation, wind) have been postulated to be the most important overall cause of dramatic changes in pest abundance in ecosystems. Weather may directly influence the physiology (*e.g.,* developmental rate and water regulation) or behaviour (*e.g.,* locomotion, orientation and dispersal) of an insect, and/or indirectly affect the insect population through its effect upon the host plant and natural enemies (Nestel, *et al.,* 1994).

Indirect effects of temperature and/or precipitation upon the population of the leaf-miner are less clear. It has been argued that climatic events can induce insect

outbreaks by decoupling the relationship between parasitoids and hosts (Risch, 1987). Climatic stress may increase the availability of nitrogen in the host plant, making the tissue more palatable to the herbivore, and/or disrupt the plant chemical defence. In the case of meristematic feeders (leaf miner), this mechanism may be more important than the direct effect of weather in the regulation of the insect population (Nestel *et al.*, 1994).

Temperature is a key environmental factor determining the duration of survival and life stage of insects (Adler, 1987; McCreadie and Colbo, 1990). The time that an organism can survive at a temperature can be related to such factors as duration of exposure, external or internal *(e.g.*, leaf miners) activities, and acclimation or hardening (Baust, 1982). Abiotic mortality factors include the coincidence factors in which cool weather delays larval development as the leaf matures. Freezing injury can encourage leaf miner outbreaks by inducing an abundance of soft, protein rich young leaves late in the adult activity period, when availability of vulnerable leaves becomes limited. However, frost caused some overwintering pupae of apple leaf miner to die (Potter and Redmond, 1989). The action of wind or rain weakens and opens mines and could be a mortality factor (Pullin, 1985); this may especially be a problem in the wet tropics.

The coffee leaf miner *Leucoptera Coffeella* Guerin-Meneville (Lepidoptera: Lyonetiidae) population increased significantly during the period of intermediate temperature and low precipitation. Elevation also affected the population load of the insect: leaf miner populations were larger at low elevations (where temperatures are high and precipitation low) than at high elevations (Nestel *et al.,* 1994).

Duration of each stage of the alfalfa blotch leaf-miner, *Agromyza frontella* decreased with rise in temperature up to 25°C but none of the stages survived 30 °C (Goppy, 1981). Median developmental rates at constant temperatures were between 10 and 25 °C for all immature stages of the alfalfa blotch leaf-miner, *Agromyza frontella.* Larval survival was maximum at 20 and 25 °C although developmental rates differed little between these two temperatures. The role and importance of climate and weather

in the dynamics of insect populations has long been recognized by insect ecologists and agricultural entomologists (Nestel *et al.*, 1994).

POPULATION DYNAMICS

There are at least 10 400 known secondary plant substances, and an estimated 100 000 - 400 000 unknown ones, implying that plants have a considerable impact on dynamics of insect herbivores (Stiling, 1988).

Host plant influences on insect population dynamics can be subtle but profound. A host plant not only directly affects herbivore development, fecundity and mortality, but acts indirectly as well through interactions with herbivore natural enemies (Price *et al.*, 1980).

Hespenheide (1991) states that the number of generations per year, generation times and occurrence of diapause are interrelated. Most temperate species of leaf miners undergo a winter season diapause. However, Opler (1978, 1981 cited by Hespenheide, 1991) found that California leaf-miners feeding on evergreen oaks had fewer annual generations, longer larval periods, lower populations, greater host specificity, and were larger in size compared to those using deciduous oaks.

Finch (1986) observed the importance of soil type and compaction, and Rockwood (1974) suspected sandy soil to be more conducive than moist forest soils to successful insect population growth, but Mopper *et al.* (1984)'s results did not support these observations. They found no significant differences in miner overwintering success between soil types, or moisture regimes. However, soil predators, which they did not examine, may influence pupal survival (Mopper *et al.*, 1984).

Diapause can occur at any stage with species overwintering as eggs, larvae, pupae, or adults, but it commonly occurs in the egg or pupal stage (the latter being most common in leaf miners [Hering, 1951]) as these do not require food and can remain in

an inactive condition for long periods. According to Condrashoff (1964) pupae or prepupal larvae are the most common diapausing stage of leaf miners. Larvae of several species of leaf-miners feeding on evergreen trees exhibit protracted development and continue to mine through the winter, pupating and emerging when new leaves are flushed in the spring (Auerback and Simberloff, 1989; Potter, 1985; Potter and Kimmerer, 1986). Some leaf miners form "green islands" on abscised leaves and survive and mature long after the leaf has fallen in winter (Hering, 1951). Condrashoff (1964) states that the aspen leaf miner spends its hibernation as an adult.

Explanations of outbreaks or cycles in herbivore population density fall into two broad categories: extrinsic and intrinsic causes. The extrinsic explanations include parasitism and predation, pathogens (Myers, 1988 cited by Ruohomäki and Haukioja, 1992), variation in plant resistance (Benz, 1974 cited by Ruohomäki and Haukioja, 1992), climatic factors or some combination of these (Watt and Leather, 1988). Explanations based on intrinsic factors propose that some inherent mechanisms in individuals cause density fluctuations. For instance, the genotype of individuals may be different at different population densities, so that at low, but not at high densities, population growth is rapid. This may contribute to mass outbreaks taking place more or less regularly (Ruohomäki and Haukioja, 1992). When refoliation coincided with emergence of ovipositing leaf miner adults, *Acrocercops* sp. and *Neurobathra strigifinitella* densities increased dramatically, indicating that both species are at times limited by availability of young leaves (Auerbach and Simberloff, 1984).

An insect outbreak is a rapid increase in the abundance of a particular species that occurs over a short period of time. The concentration of nitrogenous compounds available in plant food, estimated by foliar nitrogen and amino acid concentrations, has been used to explain the occurrence of herbivore-insect outbreaks (White, 1978 cited by Silvanima and Strong, 1991). Host-plant qualities are determined in part by concentrations of nutrients, of noxious phytochemicals and morphology (cuticular toughness, type and number of trichomes, *etc.*). Total nitrogen content can influence insect generation time, efficiency of food use and abundance of natural enemies (Way,

1972 cited by Silvanima and Strong, 1991). All three of these factors can affect insect mortality rates. Insect abundance and distribution also may be directly affected by the availability of nitrogen (Silvanima and Strong, 1991). No clear population cycles were detected in a ten-year period study of *Rhynchaenus fagi* (a beech leaf mining weevil) in Ireland (there were years of sustained decline, but not enough evidence to suggest a cycle) (Day and Watt, 1989).

Adults and larvae of *Agromyza frontella* share the same food resource and the presence of nutrition holes indirectly modifies the population dynamics of *Agromyza frontella* in several ways. At high population densities, both exclusion (starvation competition) and interference intraspecific larval competition (cannibalism) are important mortality factors. The number of nutrition holes per leaflet is high under such conditions (Quiring and McNeil, 1984).

COLOUR AND DISCOLOURATION OF MINES

There is usually a distinct variation of colour between mines and surrounding leaf. Feeding channels in other parts of the plant, such as roots, pith of the stem and fruits, are less conspicuous and do not show the peculiarities which are characteristic of each species, as clearly as is the case with leaf-miners. It is not always the mine itself which stands out so distinctly as a result of its different colouration; in some cases the mine is less obvious but its surroundings are discoloured in a characteristic fashion due to the influence of the mine. Both the colour of the mine and the discolouration of the surrounding leaf are frequently of great value for determining the species of the mine-producer (Hering, 1951).

A. Colour of the Mine:

The colour of the mine, which often deviates strikingly from that of its surroundings and emphasises clearly every detail of its shape, is usually the result of the fact that parts have been eaten out of the plant tissue. Air normally penetrates the

resulting cavities and this produces a different colour from that of the rest of the leaf. The colour of the mine may also vary according to which parts of the leaf have been eaten away. It is often possible to deduce which tissue has been removed from the leaf, from the difference of colour of the mine without having to make a microscopic examination of the inside of the leaf. The colour also varies according to the type of light in which the mine is examined (Hering, 1951).

The various types of mine colouration range over:

- Light green in transmitted light, grey-green in direct light.
- Yellowish green in both direct and transmitted light.
- Darker green than that of the rest of the leaf (arises not from the production of a cavity but from the filling up of this cavity).
- Pure to yellowish white in direct and transmitted light.
- Silvery white in direct light.
- Silvery white with patches of rust-brown.
- Greenish-white mottling (particularly common and striking in mines of the genus *Lithocolletis*).
- A reddish-brown colouration of the mine may be based on two separate causes.
- Brown to deep black.
- Red to blue anthocyanine colouration.

B. Discolouration:

The mine may be as follows:

- Ringing of discolouration surrounding the mine.
- Necrobioses (necrotic areas).
- Red or blue caused by anthocyanines.
- "Green islands" in the autumnally discoloured leaf.

THE SUBSEQUENT FATE OF THE MINE

In most cases, mines have a one-to-one relationship with the larvae which make

them. The mines also persist for some time after a larva has ceased to feed, and are relatively conspicuous (Sterling *et al.*, 1992).

When the larva is mature it leaves the infested part of the plant in order to pupate. It is important for anyone wishing to identify a mine to know what changes occur in mines after the larva has completed its feeding. Two different possibilities must be taken into account:

- The larva pupates inside the mine, *i.g.*, some Lepidoptera leaf miners.

- The larva leaves the mine and pupates outside. This applies to the majority of mines. In this case mined parts are soon destroyed (with dampness, rain and *etc.*) making leaf mining identification difficult. Faeth (1985) recovered all available mines of oak on abscised leaves from leaf litter. Over 75% of the mines were recovered in the leaf litter. All miners recovered in the litter had either emerged or died; none was still feeding. For each leaf mine he recorded whether it occurred on a damaged (manually or herbivore-damaged) or an intact leaf, and its fate.

EFFECTS OF LEAF-MINERS ON CULTIVATED PLANTS AND ECONOMIC IMPORTANCE

Wit (1985) stated that whether quantitative damage occurs to cultivated plants or not depends on the type of crop, the growing stage, the amount of insect injury, and plant growth factors. He studied the relation between artificial simulation of insect injury to the leaves, and yield in spring cabbage to obtain information on the threshold values to be used for leaf-miners in this crop. The effects of four percentages of defoliation (0, 25, 50, 75%) applied at four or five treatment dates during the preheading stages of the crop, were investigated. Sensitivity to defoliation increased during the period from transplanting to head-formation reaching a maximum after plants had reached a total leaf area of approximately 2000 cm^2. In plants of this size the author deduced that a 5% reduction of the leaf area would cause a yield reduction of 3%.

Because the amount of leaf area mined affects photosynthesis, leaf-miners often prefer shaded or older leaves (Hileman and Lieto, 1981) that are less productive photosynthetically. For example with 15-50 mines of the pear leaf miner photosynthesis decreases 10-30% respectively (Fujiie, 1982). Shading invariably reduces net photosynthetic rate and levels of foliar sugar, starch and protein, reduces leaf thickness, increases leaf area, and apparently reduces levels of some noxious secondary compounds in leaves (Schultz, 1983). Changes in leaf chemistry with shading, if widespread, suggest phytophagous insects might prefer shade plants owing to the reduction of secondary compounds, or avoid them because of low levels of sugars and proteins compared to unshaded leaves. On the other hand, photosynthesis may be affected in disproportion to the area mined if the leaf is abscised prematurely (Hespenheide, 1991). Palisade mesophyll tissue removed from mature leaves of *Phaseolus lunatus* L. by *Liriomyza trifolii* (Burgess) was replaced with photosynthetically active cells, permitting virtually complete recovery from injury (Martens and Trumble, 1987). No significant differences in biomass production or levels of ribulose-1,5-biophosphate carboxylase were observed between damaged and control plants. Decreases in photosynthesis did not exceed 10% for leaves with approximately one-fourth of the leaf area mined. According to Livene and Daly (1966) the trifoliate leaves of rust-attacked primary bean leaves can increase their photosynthetic rate almost twice. Furthermore, the trifoliate leaves tend to be more resistant to continuous *L. trifolii* infestations, although secondary rust-infections impair their function. For potato, it has been postulated that a leaf-miner may be responsible for virus dissemination (Bethke and Parrella, 1985).

Leaf-miners typically cause a relatively small amount of damage to an individual tree because of low population densities and minor damage from single mines. Densities of individual species and cumulative density of all leaf-miners were less than 1% on *Betula pendula* (Godfray, 1985). Heavy attack by leaf-miners (up to 80% leaf destroyed by larvae), may result in complete defoliation of plants in outbreak situations (Notly, 1948, 1956 cited by Hespenheide, 1991).

Condrashoff (1964) reported that when 80-90% of leaf surfaces of aspen plant

contained mines, about one half the epidermis on a tree was destroyed, and growth reduced. When more than 90% of leaf surfaces were affected by aspen leaf miner, *Phyllocnistris populiella* Cham (Lepidoptera: Gracillariidae) the leaves dried and shrivelled and dehisced. Other than larvae, heavy feeding damage (>50% of the leaf area destroyed) was caused by adult of locust leaf miner on woody plants (Williams, 1989). However, outbreaks of locust leaf miner are often described as patchy in distribution and short in duration.

At high infestation levels, the wheat sheath miner, *Cerodontha australis* (Agromyzidae: Ephydridae) is capable of suppressing ryegrass growth in many parts of the world (Barker *et al.,* 1984). Alfalfa yield losses caused by alfalfa blotch leaf miner averaged 7.7% in some years in USA (Hendrickson and Day, 1986). The economic injury level for *Leucoptera* leaf miners (Lepidoptera) on coffee was calculated at 30 large mines per stem, which causes an 11% yield loss (Notley, 1956).

The economic impact of *Liriomyza* leaf-miners in the United States and throughout the world has been considerable; in California alone it was estimated that the chrysanthemum industry lost approximately 93 million US dollars ($ 93 000 000) to *Liriomyza trifolii* from 1981 through 1985. During the past 15 years there has been a dramatic increase in the economic importance of *Liriomyza* leaf-miners (Parella, 1987). The leaf-miner *Liriomyza trifolii* has been reported to cause almost near collapse of cow pea *Vigna unguiculata* L. crops in Tanzania. The cosmopolitan pest *Liriomyza brassicae* is not recorded as a significant pest in New Zealand.

Infestations of *Phyllonorycter crataegella* (Clemens), the apple blotch leaf miner, averaging more than two mines per leaf caused premature fruit drop from 'McIntosh' apple trees in eastern New York and reduced fruit set the following season (Reissig *et al.*, 1982). Infestations of alfalfa blotch leaf miner averaging more than four mines per leaf reduced the size of 'Red Delicious' apples. In western New York, varying populations of *P. blancardella* (F), the spotted tentiform leaf miner, had little effect on the growth or production of two apple cultivars during the initial year of infestation but

reduced fruit set and consequent production during the following season. Leaf-miners can produce other effects on plants. The locust leaf-miner *Odontota dorsalis* is destructive to its noneconomic host *Robinia pseudoacacia,* but has become of economic importance because of its use of such alternate larval hosts as soybean, *Glycine max* (Poos, 1940 cited by Hespenheide, 1991), and ornamental plants (Hespenheide, 1991). Reports on adult leaf miner feeding under field or laboratory conditions are scarce. A few investigations revealed that leaf miner adults can cause feeding damage on leaves of plants in addition to damage caused by their larvae (Bale and Luff, 1978). They and an anonymous writer (1960 cited by Bale and Luff, 1978) reported that the beech leaf mining weevil, *Rhynchaenus fagi,* made feeding holes in eighteen tree and shrub species other than beech and two of them were the most acceptable plants if beech was not available. The oil palm leaf miner beetle, *Coelaenomenodera elaeidis* (Chrysomelidae: Hispinae) has become a major pest throughout West Africa and cyclic outbreaks resulted in serious damage to foliage and reduced production of oil palm, *Elaeis guineensis,* (Bernon and Graves, 1979).

Plant damage relates directly to the extent of tissue destroyed by mining. Mines may be so extensive that a significant loss of effective photosynthetic tissue results and the plant becomes unthrifty. Also the mines may be so extensive that there is deterioration of commercial or aesthetic value of the plants (Aiello and Vogt, 1986; Hespenheide, 1973).

In New Zealand damage from leaf-miners is seldom serious, although leaf-miners are usually quite conspicuous and often common. However, sometimes economic injury is inflicted. Although the leaf-miner host range is very wide, some species such as kaka beak (*Clianthus puniceus*) leaf-miner (*Liriomyza clianthi*) restrict themselves to one or a few species of plant. Commonly leaf-miner species are capable of mining many members of one plant genus, *e.g., Hebe* (koromiko) miners and oak leaf-miner. The wheat sheath miner is the most common leaf mining insect in New Zealand pastures (Barker, 1984). Although, it is not an economic pest it contributes to the overall pest fauna in suppression of pasture growth (Barker, 1984).

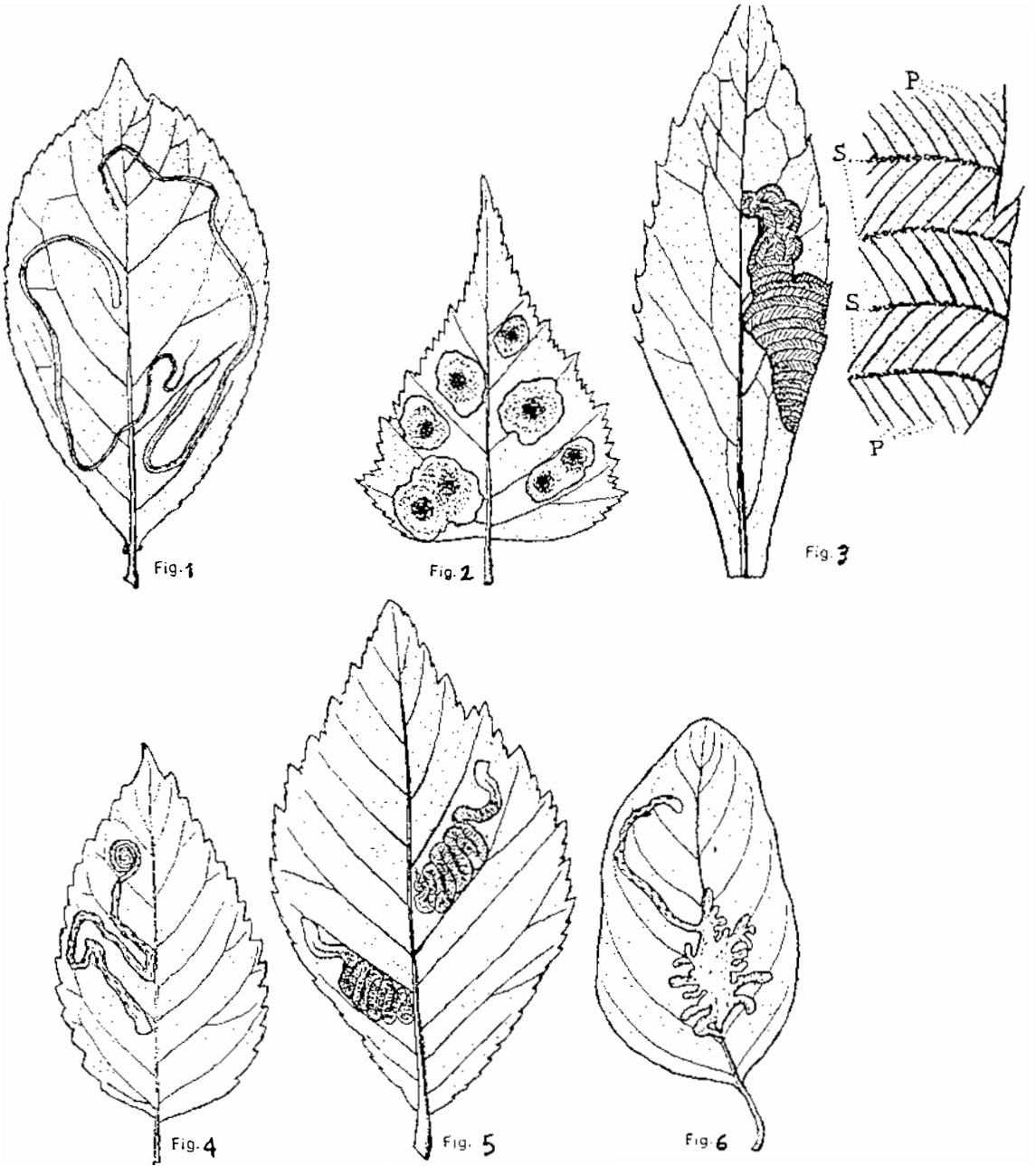
Chromatomyia syngenesiae Hardy has been regarded as not economically important in cultivated crops in New Zealand (Valentine in DSIR files). The economically damaging leaf-miners of Cruciferae in New Zealand are not Agromyzidae but two species of Drosophilidae: *Scaptomyza flava* Fállen and *Scaptomyza graminum* [known then as *Scaptomyza elmoi* (DSIR files)]. Leaf-mining Agromyzidae do not appear to be as economically important in New Zealand as they are overseas. This may be because the most serious pests such as *Liriomyza trifolii* are not present or because economic injury levels have not been assessed.

The spread and host range of oak leaf miner in New Zealand were recorded by Wise (1953a, 1953b, 1954, 1955, 1958 cited by Thomas and Hill, 1989). The high incidence of mines on exotic hosts together with attack on apple and the indigenous forest species *Nothofagus* spp. were seen as a major threat to the fruit-growing and forestry industries (Given, 1959 cited by Thomas and Hill, 1989). The role of *Scaptomyza* spp. as leaf-mining pests of brassicas in New Zealand is not understood as no pest assessment studies of *Scaptomyza* spp. have been carried out. There are no published records of damage attributed to *Scaptomyza* spp. in New Zealand, although Cumber and Eyles (1961b) associated *Scaptomyza fuscitarsis* with various crops. The New Zealand Arthropod Collection contains *Scaptomyza elmoi* reared from various brassicas, *Tropaeolum majus* L. and *Pisum sativum* L. (B. A. Holloway pers. comm.). The genus *Scaptomyza* contains known pests of brassicas in other parts of the world (Cumber and Eyles, 1961).

Conversely, leaf-miners have been considered for biocontrol of pest plants; of *Lantana camara* by *Octotoma* and *Uroplata* (Harley, 1969; Winder and Harley, 1982, 1984 cited by Hespenheide, 1991) and of *Echium plantagineum* by *Dialectia* (Wapshere and Kirk, 1977 cited by Hespenheide, 1991). The possible interactions of the snail *Bostryx conspersus* with a species of the Drosophilid genus *Scaptomyza* was discussed by Ramirez (1988). Larvae and eggs of *Scaptomyza* were found in 4.4% of individuals of *Bostryx conspersus* examined, and could be the biological cause of mortality of the snail in its first stages.

Very few Agromyzidae have been used extensively or even actively considered for possible control of weeds but one species, *Phytomyza orobanchia* Kaltenbach, has been conspicuously successful in controlling *Orobanche* (broomrape) which affects a variety of crops in the U.S.S.R.; another, *Ophiomyia lantanae* Froggatt has been introduced to many parts of the world where *Lantana* (Verbenaceae) has become a problem, but its effectiveness in controlling *Lantana* has been very limited. Three further species have been or are being investigated for possible use against *Convolvulus arrensis* L. (field bindweed), *Cuscuta* (dodder) and *Striga* (witchweed); these are *Melanagromyza convolvuli* Spencer, *Melanagromyza cuscutae* Hering and *Ophiomyia strigalis* Spencer. A long-term survey (1965-1989) showed that leaf miners were not very widespread on cereal weeds in Slovenia and that their levels of infestation were seldom high enough to markedly injure the weeds. Of the 118 species of miner recorded on 51 weed species, Diptera predominated, with Coleoptera, Hymenoptera and Lepidoptera being only sparsely represented (Maček, 1990).

In New Zealand, like the endemic *Melanagromza senecionella* Spencer, *Chromatomyia syngenesiae* also infests the weed ragwort (*Senecio jacobaea* L.) (Asteraceae) and has been considered to have limited potential as a biological control agent for this weed (Kelsey, 1937). Kelsey also suggested that *Phytomyza syngenesiae* Hardy might have some value in controlling ragwot in New Zealand.



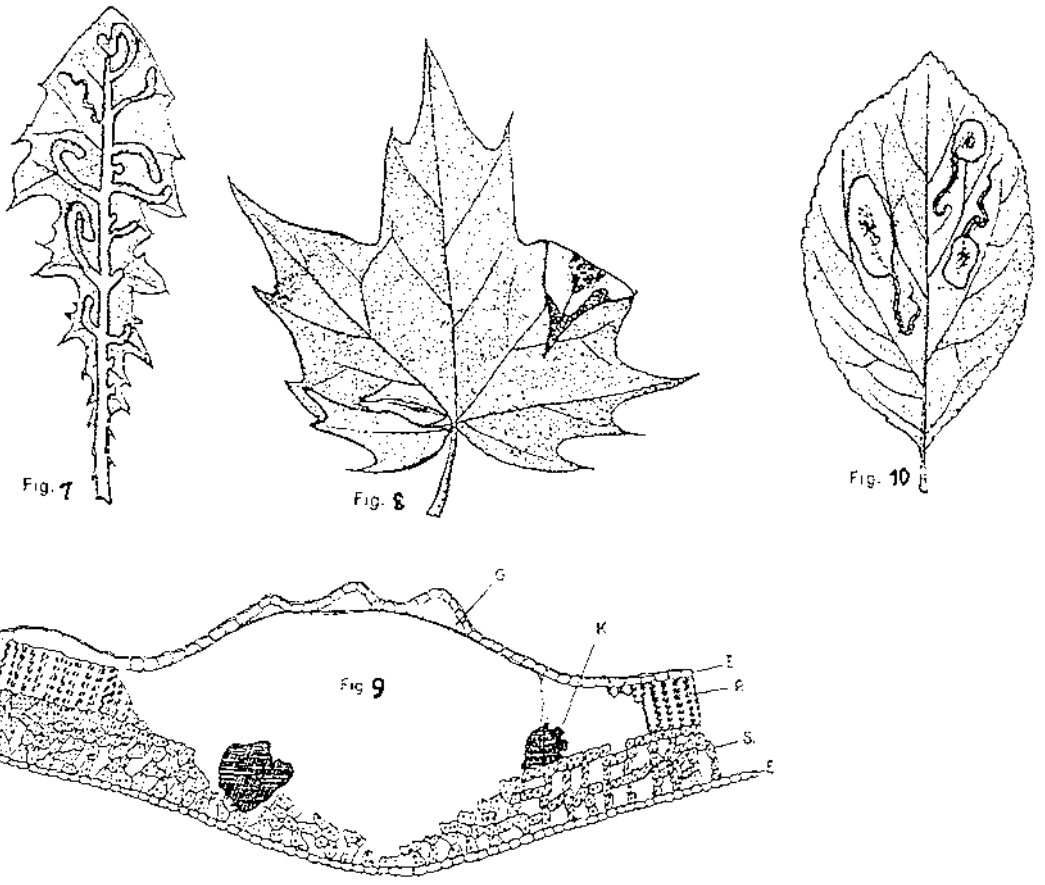
3. Solidago: ophiogenous stigmatonome of *Dizygomyza posticata* Mg., on the right a part with greater magnification shows the primary (P) and secondary (S) feeding lines, the "herring-bone" pattern.

4. Galeopsis: Heliconome of *Liriomyza eupatorii* Kaltenb.

5. Ulmus: Visceronome of *Nepticula viscerella* Stt.

6. Lonicera: Asteronome of *Phytomyza (Napomyza) xylostei* Kaltenb.

Fig. 1: Types of mines (From Hering, 1951).



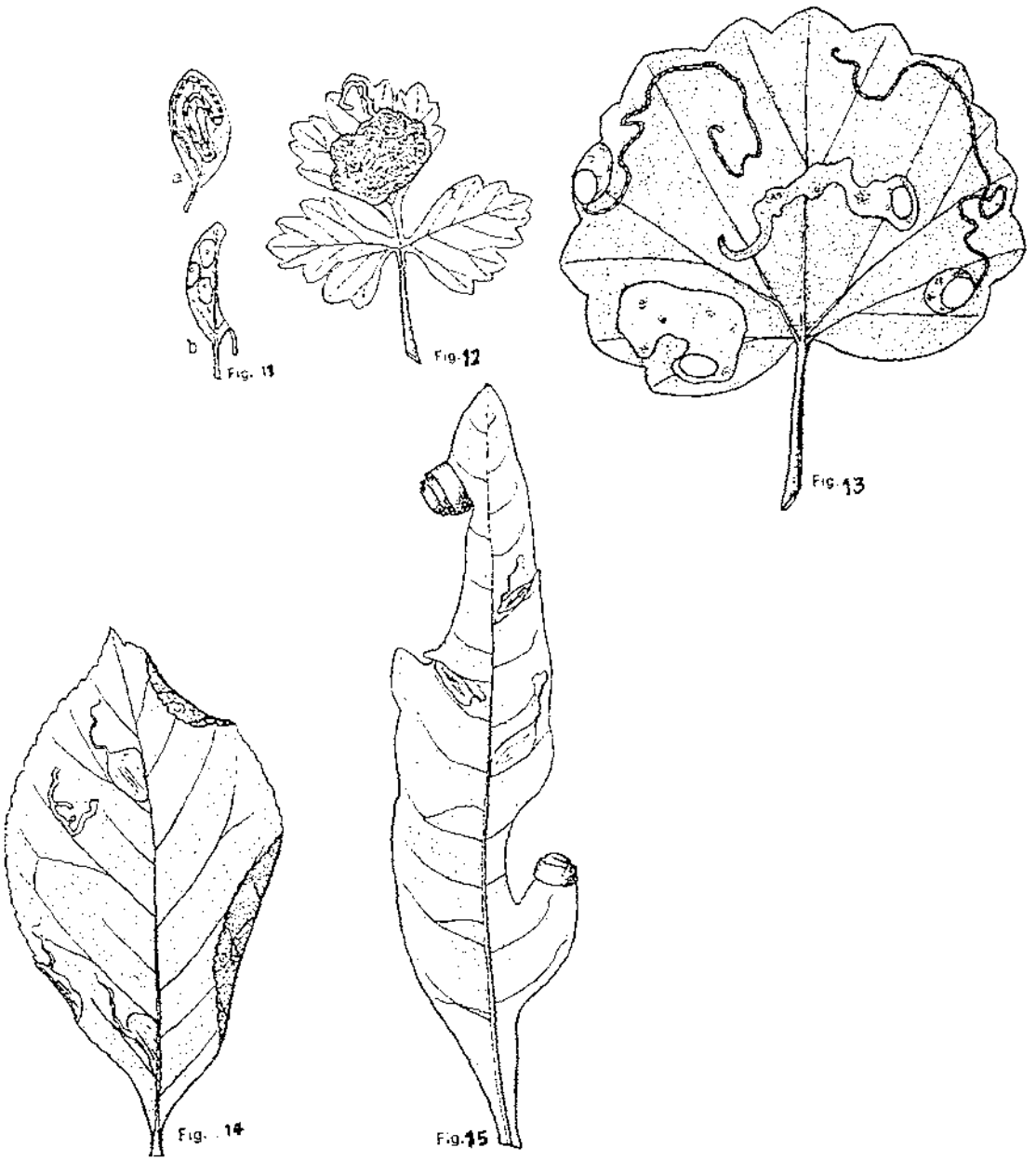
7. Taraxacum: Asteronome of *Liriomyza strigata* Mg. along the leaf veins.

8. Acer platanoides: ptychonomes of *Lithocolletis platanoidella* de Joan. Left, in the centre of the leaf; right, within a folded oven corner of the leaf.

9. Section of an upper surface mine of *Lithocolletis* (E_ epidermis, P_ palisade parenchyma, S_ spony parenchyma, K_ frass, G_silk). Top left, an early epidermal mine.

10. Prunus domestica: ophistigmatonome of *Nepticula plagicolella* Stt.

Fig. 1: Continued.



11. Arctostaphylos: *Coleophora arctostaphyli* Med. a) Initial mine b) Later mines and case cut-out.

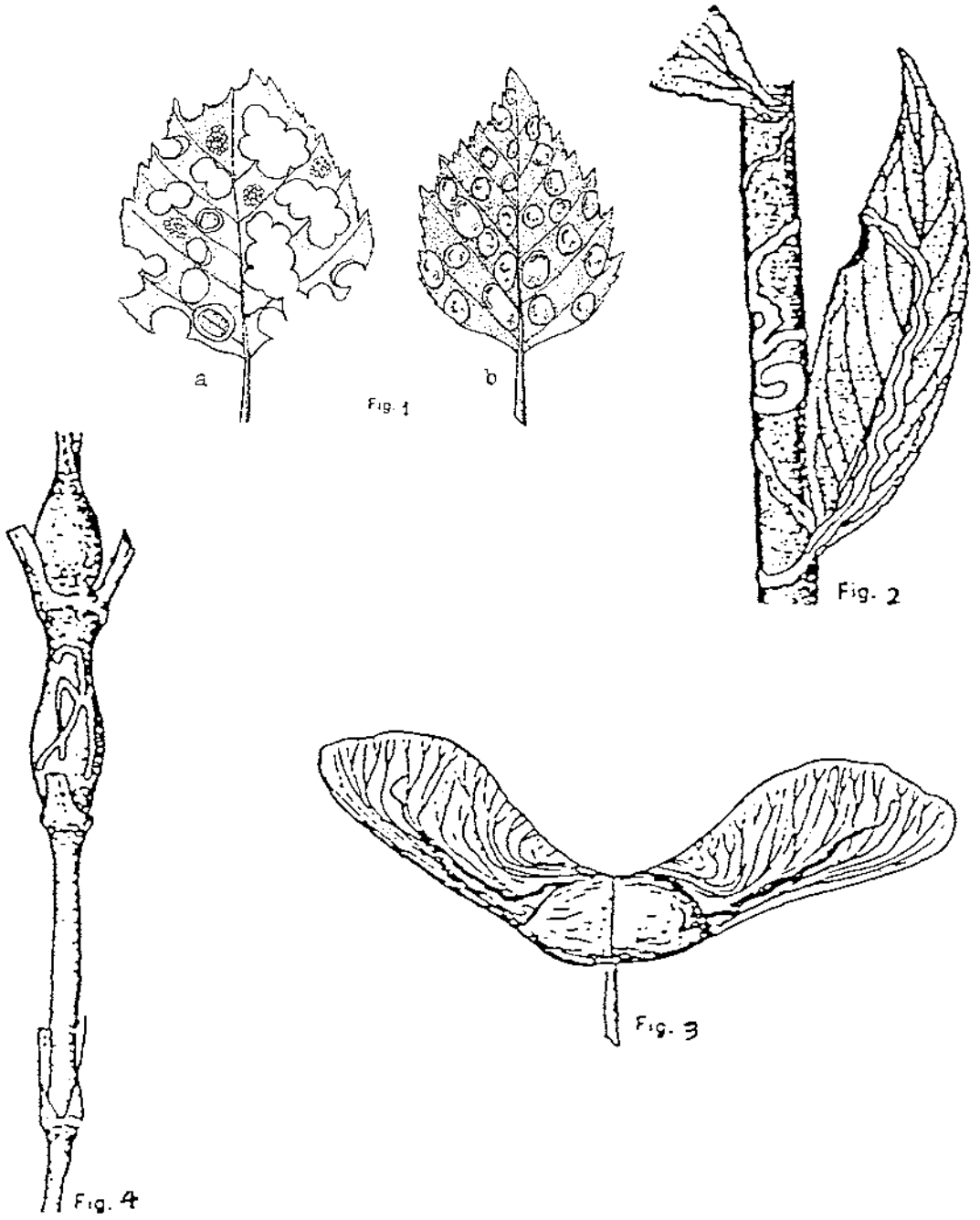
12. Apium: *Philophylla heraclei* L. (celery fly), initial channel full depth and transparent, later blotch upper-surface, greenish.

13. Saxifraga rotundifolia: Early linear mines, blotch mines, and areas cut out (*Incurvaria trimaculla* HS).

14. Malus: *Callisto denticulella* Thbg. First instar epidermal mines and folded over leaf-edges.

15. Polygonum: *Euspilapteryx phasianipennella* Hb. with initial mines and later leaf cones.

Fig. 1: Continued.



1. Betula: *Incurvaria pectinea* Hw. a) Leaf after construction of cases b) mined leaf.

2. Salix: Ophionome of *Phyllocnistis saligna* Z., leaf_stem cortex leaf. At the end, the edge of the leaf is curled over the pupal chamber.

3. Acer platanoides: carponome of *Nepticula sericopeza* Z.

4. Silene: linear mine of *Liriomyza strigata* Mg. on the gall of *Gnomoschema cauliginella* Schmid.

Fig. 2: After leaf mining (Hering, 1951).

Chapter 2

THE BIOLOGY OF *SCAPTOMYZA FLAVA* [1]

INTRODUCTION

An intriguing characteristic of the leaf miner *Scaptomyza flava* female is that she makes hundreds of punctures with her ovipositor in host plant leaves for feeding. This feeding probably greatly enhances her reproductive capacity (Minkenbreg, 1988b). While feeding, a female also may assess the nutritional value of the leaf, which may influence the decision whether to continue feeding and ovipositing or to leave (Bethke and Parrella, 1985). Because the larvae usually restrict their feeding to one leaf, the ovipositing adult female insect thus "determines" where, and therefore what food, her offspring will eat. The thesis of this chapter is an understanding of behaviour and aspects of biology of *Scaptomyza flava* regardless of its host plants.

REARING

MATERIALS AND METHODS

Rearing of adult *Scaptomyza flava* was carried out in a greenhouse at ambient temperature (about 20°C-uncontrolled temperature).

An initial stock of larvae was obtained from infested Chinese cabbage and turnip plants growing in the field at Palmerston North. Rearing colonies were maintained in terylene net cages over aluminium and wooden frames **(Plate 1).** Most larvae emerged from their mines and dropped to the floor of the rearing cage to pupate. Pupae were removed from the floor of the cage with a soft camel hair brush and soft forceps and placed in potting medium, and allowed to emerge.

[1] Some parts of this Chapter modified from a paper presented to XIX International Congress of Entomology. 1992. Beijing-China.

Plate 1: Rearing cages

water plus 10% honey solution imbibed in a cotton wool pad were provided as food for emerging flies. Host plants were placed in an oviposition cage (50 × 50 × 50 cm) and exposed to 100-200 flies. Potted plants of Chinese cabbage *Brassica rapa chinensis* group *(Brassica campestris* spp. *pekinensis)* and turnip *Brassica rapa L.* were used (plants were grown in pots in a greenhouse until they were 18-28 cm tall [about 1 month old] before use). After 3-4 days plants were exchanged for new ones. When it was necessary to replace plants, the oviposition cage was placed beneath a light or exposed to sunlight. The positively phototactic adults flew to the top of the cage when the plant was disturbed, enabling the old plants to be exchanged for new ones. Wild flies were sometimes added to this colony from field and nursery plantings of the respective hosts.

Plants with eggs were held in clean fine gauze cages (for approximately 2 weeks) until larvae had begun to form large blotch mines in the leaves. This occurred 2-3 days before the larvae dropped from the leaf to pupate in the potting mix or the cage substrate. After about two weeks new adults emerged.

Another method was sometimes used to rear adult insects from an infested plant by removing a leaf and placing it in a petri dish arena (9 cm diameter) containing either a piece of moist cotton wool or filter paper attached inside to the top and bottom. Most larvae from the host leaf pupated in the cotton. When adult flies emerged they were placed in an oviposition cage or used in experiments.

Larvae and adult insects were preserved in 70% ethyl alcohol in glass vials. Voucher specimens that have been collected from different plant species during two years (including weekly sampling of field plots) have been deposited in the insect collection of the Plant Science Department, Massey University, Palmerston North, New Zealand.

The life-cycle of *Scaptomyza flava* was determined under laboratory conditions with respect to the duration of larval instars, pupal and adult stages. Observations were also made on feeding, mating and egg laying behaviour.

MORPHOLOGY AND BEHAVIOUR OF INSECT

ADULT

The adult flies are small, about 3 mm long (tip of the head to the tip of the abdomen) with a wing spread of 6 mm (from wingtip to wingtip). The colour is very variable. Some are quite yellow (most insects reared in the laboratory and most spring and summer flies from the field) and some are greyish-brown or black (autumn and winter ones) **(Plate 2)**. Host and leaf selection is accomplished by the ovipositing female who cements eggs singly to the lower leaf surface. If the exposure period of plants for oviposition during rearing was prolonged, diminutive adult insects with wide variation in size resulted due to larval overcrowding.

Scaptomyza flava has been reared from the plants listed below collected in the Manawatu. Many specimens of an *Agromyzid* leaf miner were also reared from Cineraria and Sow thistle *(Sonchus oleraceus)*[1].

	Common name	**Botanical name**
1.	Turnip	*Brassica rapa ssp rapa*
2.	Chinese cabbage	*Brassica rapa chinensis* group
3.	Cauliflower	*Brassica oleracea var botrytis*
4.	Broccoli	*Brassica oleracea var italica*
5.	Radish	*Rhaphanus sativus*
6.	Wild turnip	*Brassica rapa ssp sylvestris*
7.	Wild radish	*Rhaphanus raphanistrum*
8.	Hedge mustard	*Sisymbrium officinale*

[1] Cineraria leaf miner, *Phytomyza atricornis* Mg., is the commonest leaf miner in New Zealand. It is of European origin and is almost worldwide in distribution (Wise, DSIR files). This pest also is active on sow thistle, chrysanthemum, pea, ragwort, groundsel, marigold, dahlia, dandelion, nettle, and scotch thistle (Wise, DSIR files).

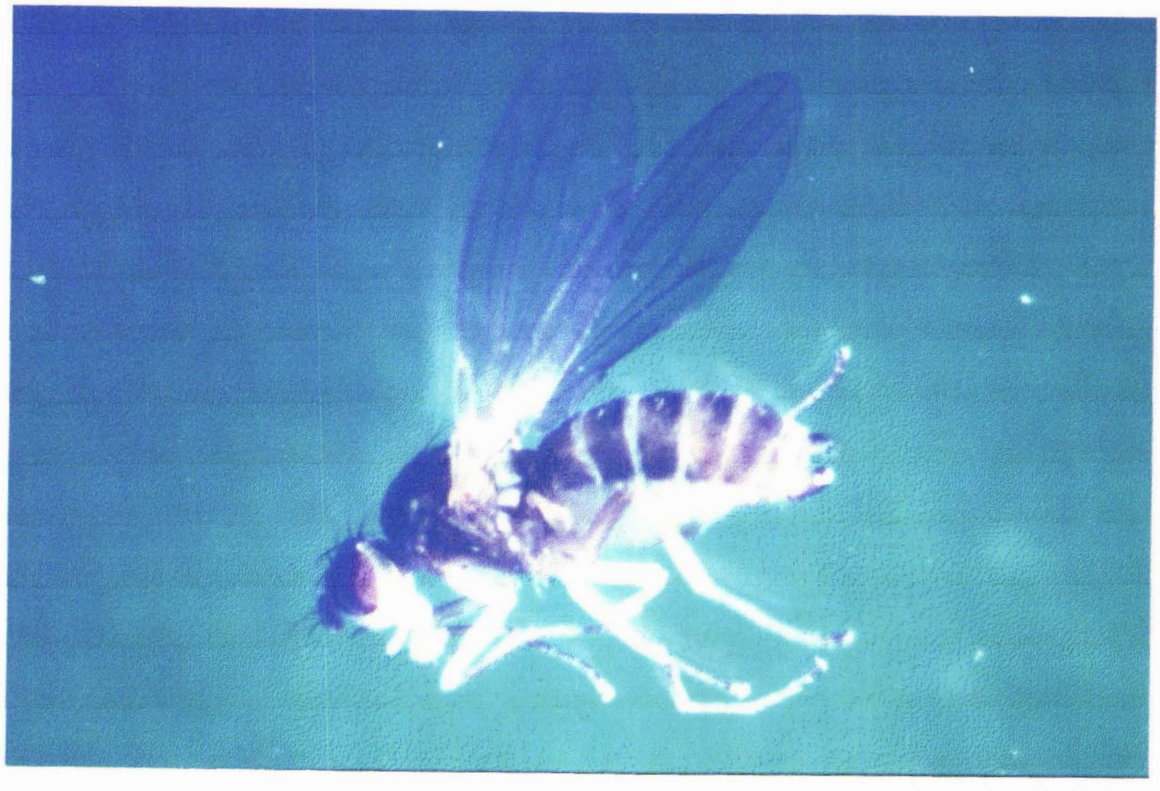


Plate 2: Adult female *Scaptomyza flava* (dark form)

EMERGENCE

To establish the time of emergence of the adults, large numbers of pupae (from the rearing cages) were checked hourly between 05.00 and 18.00 over a period of several days in December 1991 (sunrise: 05.42, sunset: 19.47). The pupae were placed in an environmental chamber at 20 ± 2°C uncontrolled humidity and natural daylength. Observations were started on day 10 following first formation of pupae.

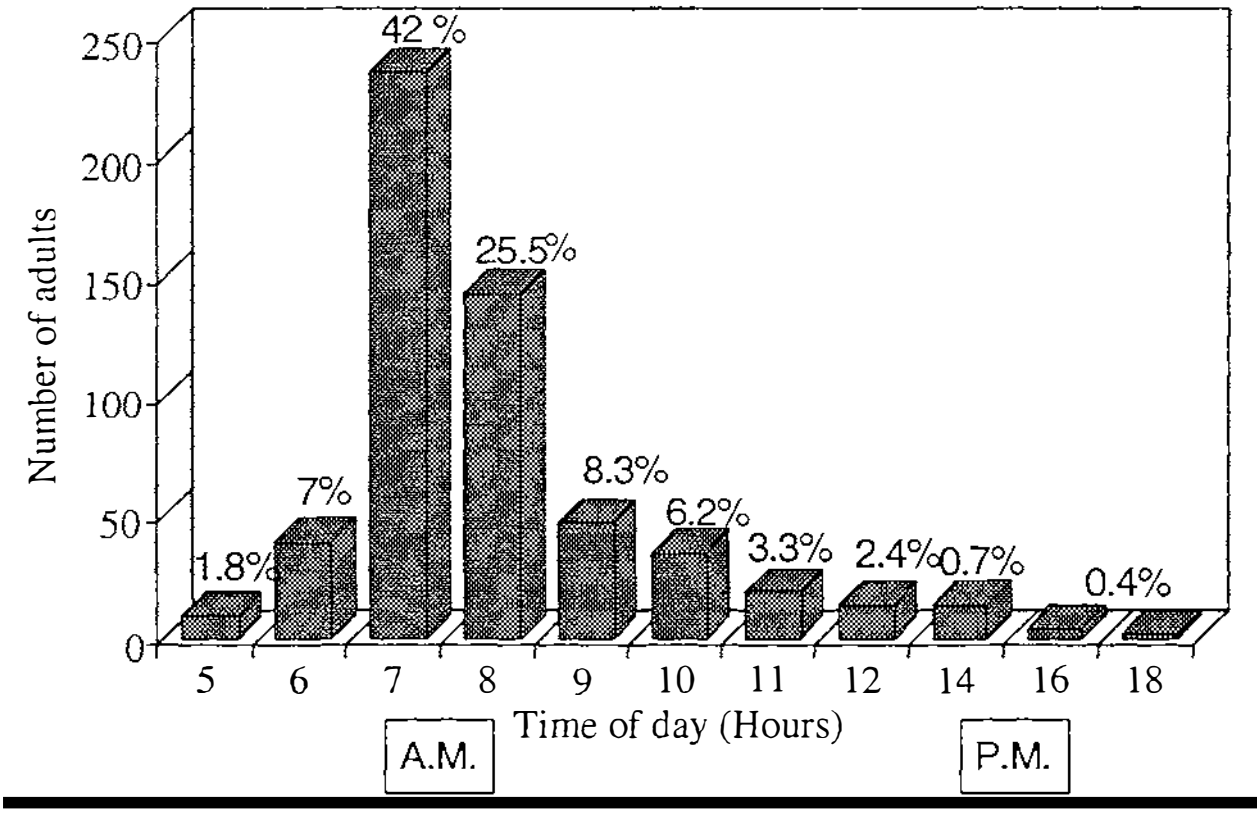
RESULTS

Adults emerge through the ventral anterior end of the puparium with the aid of the ptilinum. This process may take from 5 to more than 40 minutes.

Newly emerged adults exhibit a positive phototactic response and climb up the side of a cage or up the stalk of a plant where they remain quiescent for a period of approximately 30 min while expanding their wings and body. The body is fully sclerotized and coloured within 30 min-3 hr (personal observations). Emergence of both sexes occurs almost entirely during early daylight hours.

The data show that out of a total of 565 adults 545 (96.5 %), emerged between 05.00 and noon, with the largest proportion emerging (42 %) between 06.00 and 07.00. Fourteen of twenty adults which emerged in the afternoon emerged before 14.00. No emergence occurred between the hours of 18.00 and 04.00. The pattern of emergence is shown in **Fig. 3**. Adult females emerged before males (unrecorded data). Though this has been recorded for other species (*e.g., Spodoptera littoralis*) (Baker and Miller, 1974), the earlier emergence of males is more common (Singer, 1982). Earlier female emergence may be due to the length of time required for ovary maturation (Hamilton, 1986; Hamilton and Zalucki, 1991). In agro-ecosystems flies are likely to emerge near to host-plants, but under some circumstances distances to host plants may be greater (personal observations).

Fig. 3: *Time of emergence of S. flava adults under greenhouse condition*



SEX RATIO

The sex ratio is an important fitness character of any sexual reproducing organism. Sex ratios of animal species often approximate 1:1. The commonness of the 1:1 sex ratio was originally explained by the equal investment theory of Fisher (1930 cited by Ishihara and Masakazu, 1993), which is based on frequency-dependent selection. However, some species have been found to produce offspring with biased sex ratios. Several factors that may result in adaptive biased ratios have been suggested: local mate competition (Werren, 1980 cited by Ishihara and Masakazu, 1993), local resource competition (Clark, 1978 cited by Ishihara and Masakazu, 1993), and physiological condition dependent on maternal rank in a group (Clutton-Brock *et al.*, 1984 cited by Ishihara and Masakazu, 1993). Recent studies by Ishihara and Masakazu (1993) showed that secondary sex ratios in adults have also been found to deviate from 1:1 due to differential mortality during development, theoretically due to competition for resources, territories mates, *etc.*

Little has been published on the sex ratio of *Scaptomyza*. Mopper and Whitham (1992), mentioned that plant variety may strongly influence sex ratios, so insects were collected from Chinese cabbage from the laboratory colony and from the field.

MATERIALS AND METHODS

To determine the sex ratio of *Scaptomyza flava*, I checked 2 groups of insects, 400 puparia from the laboratory colony on Chinese cabbage (flies were sexed as they emerged from puparia kept in petri-dishes in the laboratory at room temperature [ca. 20°C]) and over 440 flies (typical morph) captured by sweep net from plots of Chinese cabbage in the field. Natural daylength (at a 15:9 [LD] hours photoperiod with photophase from 05.00 [sunrise] to 19.55 [sunset, summer time is not included]) was that in January 1992.

Flies were anaesthetized with carbon dioxide (CO^2) or ethyl acetate vapour to facilitate sexing (**Plate 3**). Flies were sexed using the end abdominal character. The pooled sex ratio was tested for conformation to a 1 : 1 ratio using the χ^2 statistic.

RESULTS

Results are summarized in the **Tables 1** and **2**.

Table 1: Sex ratio of *Scaptomyza flava* from laboratory colony.

Sample	Date	No. of puparia	No. of males	No. of females
1	1-7.6.91	100	52	48
2	1-7.7.91	100	51	49
3	1-7.8.91	100	56	44
4	1-7.9.91	100	55	45
Total		400	214	186
Mean percentage			53.5 %	46.5 %

The sex ratio of adults emerging from pupae in the laboratory did not deviate significantly from a 1:1 ratio (mean of 46.5% female and 53. 5% male for four samples) **(Table 1).** For field captured adults the corresponding values were 48.4% females and 51.6% males **(Table 2)**. Thus under greenhouse and field conditions males were about 7% and 3% more numerous than females respectively.

The Chi^2 statistic is calculated as:

$$\chi^2 = \Sigma (Ob-Ex)^2/Ex$$

Ob=Observation Ex=Expectation.

Table 2: Sex ratio of *S. flava* captured by sweep net in the field at Palmerston North from Chinese cabbage and turnip.

Sample Date	No. of flies	No. of males	No. of females
8.8.91	50	25	25
6.9.91	70	36	34
11.10.91	80	43	37
8.11.91	100	52	48
1.12.91	140	71	69
Total	440	227	213
Mean percentage		51.6%	48.4%

The value for chi-square at one degree of freedom, for the 5% level of probability is 3.841. This is not significantly different from expection of 50:50. Thus the sex ratio does not depart significantly from 50 : 50 in the laboratory and field data.

If one sex is more costly to produce than the other, then according to Fisher (1930) it is expected to be the less frequent sex. compared to balanced sex ratio, sex ratio biased inconsistent (non-significant) towards males should result in poor potential population fecundity in *Scaptomyza flava*, and this should be of deleterious in a species whose oviposition period is not restricted to a few days.

Plate 3: Anaesthetic operation tools

MATING, FEEDING AND OVIPOSITION

INTRODUCTION

Mating behaviour of adult leaf-miners has not been extensively studied. Leaf-miner matings may be single, at least for female Lepidoptera (Powell, 1980), but beetle matings are known to be multiple (Story *et al.*, 1979). Protracted copulation is known for both groups (Kirkendall, 1984; Pottinger and LeRoux, 1971; Story *et al.*, 1979), and post copulatory escort behaviour has been described for the hispine *Odontota dorsalis* (Kirkendall, 1984).

Among Diptera oviposition behaviour has been studied primarily for the Agromyzids *Phytomyza* on *Ranunculus* spp. in relation to egg and larval density (Sugimoto, 1980) and *Agromyza* on alfalfa (Quiring and McNeil, 1987). Both Agromyzids puncture the leaves with the ovipositor for both oviposition and for feeding; *Agromyza* females mark eggs with an oviposition pheromone (McNeil and Quiring, 1983) that can influence the outcome of larva-larva competition (Quiring and McNeil, 1984). In experimental choice situations, female *Agromyza* rank unexploited leaves above marked leaves or those with many nutrition holes above these with late-instar larvae (Quiring and McNeil, 1987). The average number of perforations made during the lifespan of the female alfalfa blotch leaf-miner *Liriomyza trifolii* was 3769 (Hendrickson and Barth, 1978).

The mating behaviour of insects is often very complex and varies greatly in different species. The factors that bring the sexes together may be chemical signals (sex attractants), acoustical signals, or visual signals (light flashing, dances and other courtship manoeuvers in many flies), and the high degree of specificity in this behaviour acts as an isolating mechanism to prevent the mating of different species (Southwood, 1975 cited by Stiling, 1988).

MATERIALS AND METHODS

Mating and oviposition behaviour of *Scaptomyza flava* were studied under laboratory conditions. I set up 10 small cages and released 1 pair of newly emerged adults in each, on one month old Chinese cabbage plants. cages were placed in a greenhouse under ambient lighting (L:12 D:12) photoperiod and ca. 18 ± 2°C temperature with 75 ± 10% RH (relative humidity). I observed insects and leaves under a stereo microscope hourly. Length and width of eggs were measured using an eyepiece micrometer.

To determine that *S. flava* females are polygamous, two preliminary experiments were established under greenhouse conditions:
In the first experiment, one female and three males were released onto plants in a cage. To distinguish them wings of two of the males were stained either green, blue or not stained. They were recaptured, by aspiration, several days after release and were subsequently identified and re-stained. During one week it was observed that the female mated with all three males. In a second experiment, a single pair of insects was released into a cage with a potted plant and each two days the male was replaced with a fresh one. The same female was observed to mate with three different males.

The potential frequency of mating in the male was determined by placing one newly emerged male and female in an oviposition cage. The following day the male was transferred to another oviposition cage with a new 1-day-old unmated female, and this was repeated daily until the male died. There were 24 replications.

RESULTS

Mating. The majority of males and females mate within 24-48 hr of emergence. The females are polygamous and copulate soon after emergence. Almost all females have mated within 48 hr. The sexes may remain coupled for as little as 5 minutes, but the norm is protracted copulation taking 20 min-1 hr, with maximum mating time about

2 hr. Males and females mate more than once. The males mated on average 4.88 times (range 1-12). One pair of adults mated on 5 consecutive days, and another pair was observed mating on 4 separate occasions within the same day. Still another pair was observed in copulation 10 different times over a period of 15 days. Mating was observed to take place at various times between 9 a.m. and 7 p.m., but more generally occurred during early morning hours.

During copulation, the male assumes a position behind the female at about a 60° angle above her body. In the more typical position, the male's forelegs clasp the mesothorax of the female, his middle legs clasp the female's abdomen, and his hind legs spread the female's wings. The wings of the male are folded in the normal resting position (held over the body), their tips touching the leaf. The male brings his abdomen forward to connect to the female genitalia as the male's hind legs move to rest on the substrate. This position is maintained throughout copulation. Aggressive behaviour between males of *Scaptomyza flava* during mating has not been observed in the laboratory under severely crowded conditions (about 2000 insects under one cage 50 × 50 × 50 cm). Sometimes females walk slowly forward during mating.

Feeding and oviposition. The behavioural repertoire of females included flying, alighting on leaves, arching of the body so that the tip of the abdomen touched the leaf surface. When a female initiates a leaf-puncturing sequence, the first event observed, regardless of host plant (turnip, Chinese cabbage, cauliflower, *etc.*), is a bending of the abdomen to position the ovipositor perpendicular to the leaf. The ovipositor contacts the leaf through a series of rapid thrusts. Once the ovipositor has penetrated the leaf surface, the thrusts becomes slower and more deliberate. At this point the female damages mesophyll cells (Parella, 1987). The females feed by using their ovipositor to make perforations of the epidermis (in the upper and underside surfaces of the leaves) **(Plate 4)**. The female of *Scaptomyza*, after producing a incision, quickly backs over the wound and sucks upon the exudation. Gravid females laid eggs more than once before leaving the leaf. Feeding punctures may be either scattered or concentrated in one area, while

the eggs are deposited more at random in the leaf. Sometimes eggs, and thus mines, were aggregated on leaves of host plants so that two or more mines coalesced. But eggs were limited to one at each discrete site or hole.

The time required to make a perforation averaged 22 seconds (range 6-65 sec, 20 observations), and the time used in feeding averaged 7 sec (range 5-10 sec, 12 observations). Eggs were laid within 20-32 sec (mean 25 sec, 30 observations) after the fly had alighted on the leaf. The punctures used for oviposition are made in practically the same manner as the ones used for feeding. The punctures used for oviposition were obviously bigger than others.

Females tend to make punctures and feed on a small area of a single leaf until disturbed. For example: one female made 44 pinholes in a 1 cm^2 area during 2 hr of observation. The average length and width of these feeding holes was 0.43 mm (range 0.3-0.5) and 0.27 mm (range 0.175-0.3) (25 observations) respectively; the area of a single pinhole was thus approximately 0.12 mm^2, but puncture size varies with the size of the adult female. In the field, the number of feeding punctures per leaf varies widely, but at times is sufficient to cause noticeable damage. For example, in one sampling (December 1991, 40 leaves) punctures ranged in number from 10 to 900 per leaf (the equivalent of ca. 1.2 to 108 mm^2 [$\approx$ 1 cm^2] of leaf), with an average of 86 (the equivalent of ca. 10 mm^2 of leaf). Thus under field conditions leaves with multiple attacks are quite common. Pinhole density on a leaf was counted under a binocular (magnification $\times$ 80). Feeding by adults before oviposition can thus be extensive and damaging to plants- both hosts and nearby plants. Leaf puncturing can reduce photosynthesis (Livene and Daly, 1966), growth and vigour of the whole plant (Hendrickson and Barth, 1978) and when leaf miner densities are high, host plant leaves can be completely girdled by mines that cause foliage to die and sometimes may kill young plants (laboratory and field observations, **Table 36)**. Dehiscence of leaves in response to adult feeding occurred when adult populations reached high levels (as seen in the laboratory). Eggs are deposited in a large percentage of leaf punctures.

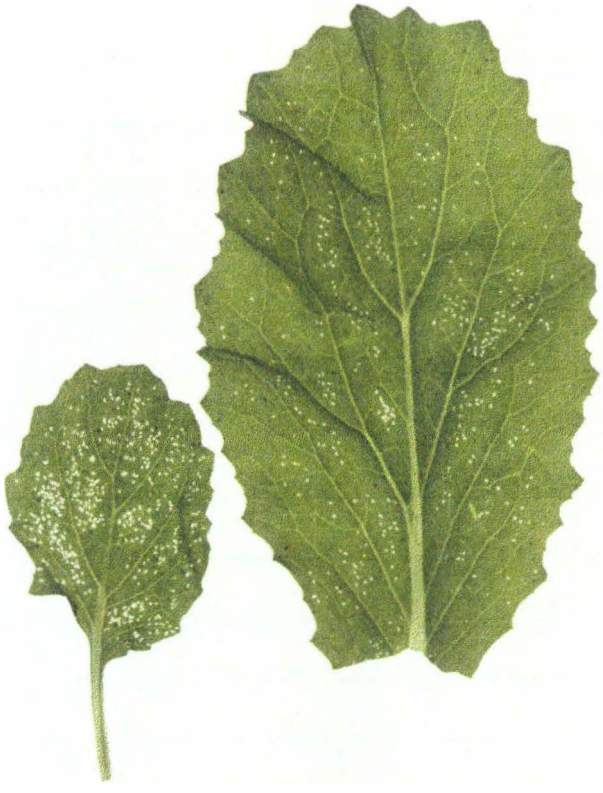


Plate 4: Feeding punctures of *S. flava* in leaves of Chinese cabbage

Observations during the scotophase indicated that the number of flies on the plants increased after natural darkness commenced (even under artificial light) but no feeding punctures were produced during darkness.

Under laboratory and greenhouse conditions, most gravid females began oviposition within 24-48 hr. after emergence. Eggs are deposited over several consecutive days (usually 2-15); the majority of eggs are laid between days 4 - 9 of adult life.

Eggs per female in constant association with males averaged 255 (range, 145-321) (on Chinese cabbage plant) (see **Table 16** in Chapter 3). On Chinese cabbage, cauliflower and turnip, eggs have been observed only on lower surfaces of leaves.

Aged females spent more time on the lower surfaces of the leaves, produced few feeding punctures, and apparently were more dependent upon plant exudations for food. Usually, just before death, the female (and male) adults were found on the cage floor where they exhibited weak and erratic movements when disturbed.

EGGS

The form of insect eggs varies considerably. Most Diptera eggs are elongate (Chapman, 1982). The whitish, translucent egg of *Scaptomyza flava* is deposited through the adaxial or abaxial leaf surface into punctures made by the ovipositor. The average length of the egg is 0.36 mm (range 0.3-0.45) and width 0.15 mm (range 0.1-0.2)(25 observations).

Eggs are laid singly, but often in close proximity to each other (though not in a cluster). The period of egg development (incubation) varies with temperature and averaged six days (range 2-8 days, 35 observations) under laboratory conditions. As the eggs develop they become opaque, and gradually the yellowish brown cephalopharyngeal

skeleton of the first instar larva can be seen. At eclosion, the larva is oriented with its anterior extremity, which contains the mouthhook, at the terminus of the egg furthest from the original oviposition puncture made by the female. *Scaptomyza flava* females laid a greater proportion of eggs on the edge of cauliflower leaves (against major veins and near leaf margins) but a greater proportion of eggs towards the centre of Chinese cabbage leaves. In cauliflower, because of leaf wax, eggs have never been observed on the dorsal surface of the leaves, the fly always laying on the lower surfaces. (personal observation, unrecorded data).

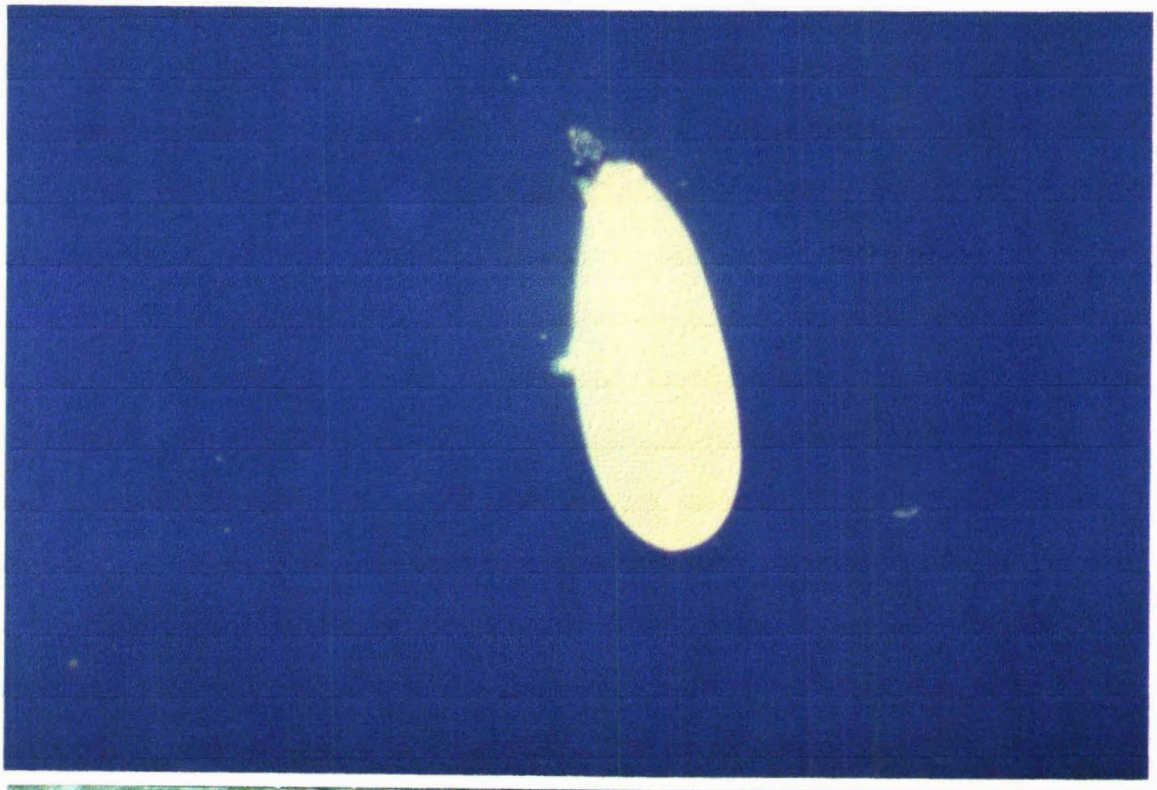
The egg is clearly seen through the epidermis of the leaf by means of a lens (under a stereo microscope) **(Plates 5** and **6)**.

LARVAE

Damage to plants by *Scaptomyza flava* is caused mainly by the larvae, which mine leaves and reduce yield or the aesthetic value of plants. The larva is somewhat cylindrical and typically maggot-like. The anterior end tapers and the posterior end is truncate **(Plate 7)**. The first instar larva begins feeding immediately after eclosion and feeds constantly to mine the leaves until it is ready to emerge from the leaf and pupate. It feeds in different areas of the leaf mesophyll layer, especially the parenchyma such that sometimes only the upper and lower transparent cuticular layers remain. On Chinese cabbage, oviposition punctures and hence larval mines are close to the main vein. In contrast on cauliflower, the majority of punctures and larval mines are around the leaf margin.

When larvae are forced to compete for resources because of crowding, they may tunnel into leaf stalks and into the main vein of leaves. Where more than one larva is present in the leaf, they usually come together near the main vein, but each larva of *Scaptomyza flava* preserves its own microecological niche. Larvae were not observed sharing a single mine.

Plate 5: Single egg of *Scaptomyza flava*



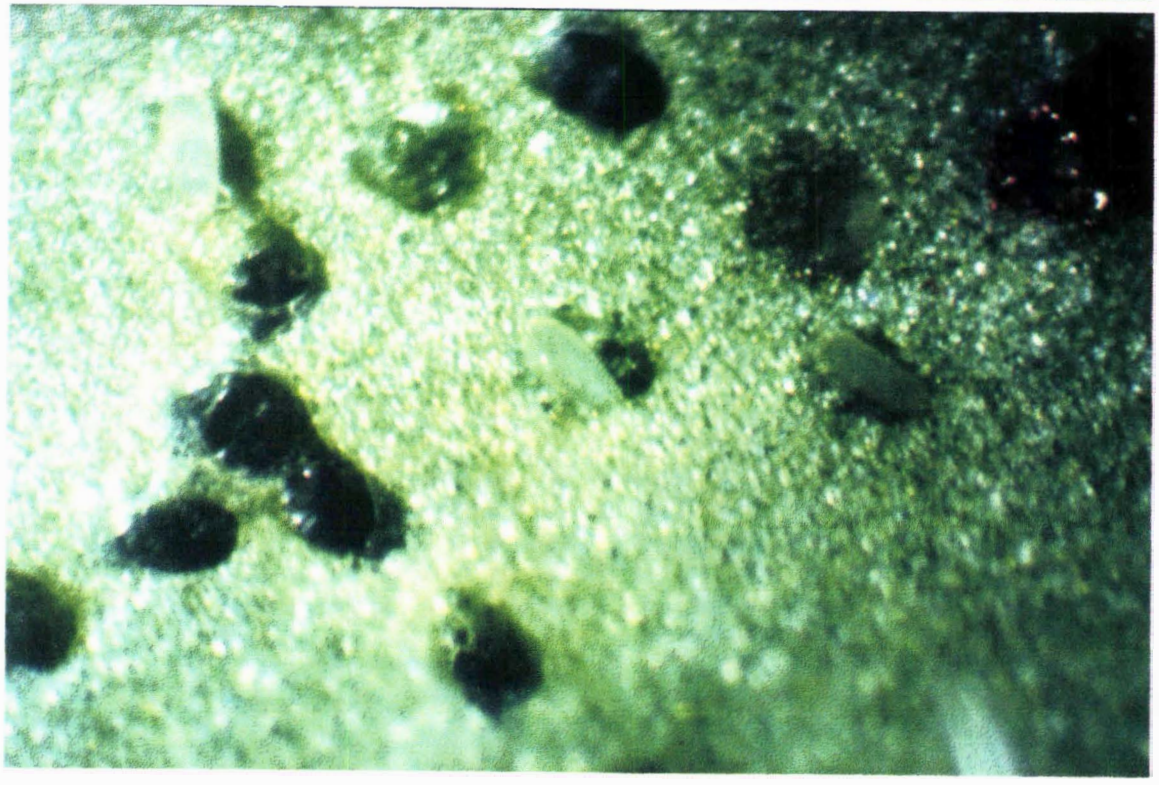


Plate 6: Eggs laid in leaf tissue

The first instar larva is transparent when newly emerged, soon becoming a faint green as it commences feeding on the leaf tissue. The second instar larva is light yellow-green, whereas the third instar larva becomes a rich yellow- green. The dark green chlorophyll-like matter in the intestines is clearly visible in this instar. The teeth of the black sclerotized mandibles, or mouth hooks, extend into the oral opening. The mandibles are united at the base and appear to work together as a unit. The mouth hooks are clearly visible in all instars.

After eclosion the larva forms a narrow translucent feeding channel. Starting from the point of hatching at the oviposition puncture, a thin pencil line-like mine denotes the trace of a L1 larva. This linear mine widens gradually from about 0.5 mm to 1.0 mm at the first moult. This is followed by long linear or serpentine and broader mines by second instar larvae (the linear mine gradually widens to about 5 mm at the second moult). The third instar larvae widen the mine gradually into an irregular blotch. The mine gradually expands and may cover ca. 100 mm^2 area (on big leaves) **(Plates 8** till **12)**. I observed up to seven fully developed mines on a single Chinese cabbage leaf. In such case, leaves are sometimes completely destroyed during 2 weeks (in the laboratory) or 3 weeks (in the field) (20 leaves observed in each case). Larval movement within the mines is of a peristaltic type. As the larvae increase in size, their dorsal and ventral sides contact the top and bottom of the mines, aiding them in their movements. In a heavily mined leaf, the larvae often have to move some distance to find green leaf tissue. This is particularly true of the third - instar larvae. In doing so they progress in the manner described, quickly eating any green tissue encountered. Larvae extrude frass through mines, where it adheres to the leaf and slowly accumulates; the larval faecal pellets are not very conspicuous as they are deposited at the side of the mine. Sometimes, because of severe damage by the larva to the whole plant, the plant may die (more than 100 observations). Larvae of *Scaptomyza flava* are unable to leave one leaf and enter another. But when removed from a mine and placed on a cut leaf surface, larvae of any size mine into the new leaf and begin feeding almost immediately (personal observation, unrecorded data).

Plate 7: larvae of *Scaptomyza flava*

Larvae move via peristaltic action of their hydrostatic skeleton. There are three moults and larval instars. The fourth instar occurs between puparium formation and pupation. A series of larvae were examined microscopically to determine the average size of the mouth hooks. Cephalopharyngeal skeleton lengths were measured to determine the number of larval instars. Measurements were made from a dorsal viewpoint. Sex of larvae was not determined. The data show that there are distinct mouth hook (cephalopharyngeal skeleton) sizes for each larval instar.

A knowledge of instar number is important for an understanding of the timing of population events, the effects of natural enemies, insecticides and the duration of damaging stages (Hamilton and Zalucki, 1991).

Larvae were dissected from the leaves of plant species on several dates and preserved in 70% alcohol for subsequent head-cephalopharyngeal skeleton length measurement. The average length of first instar larvae is 0.4 mm (range 0.375-0.450, 50 observations), the second instar is 2.3 mm (range 1.9-3.6, 50 observations), with the cephalopharyngeal skeleton about 0.25 mm in length. The third instar larva is 4.4 mm (range 3.5-5 mm, n= 50) and fourth instar is 5.5 mm (range 5.4-5.6 mm, n= 25). The mature fourth instar larva averaged 5.8 mm with a cephalopharyngeal skeleton about 0.50 mm long.

In a severe infestation (*e.g.*, about 60 larvae in each leaf) occasionally half of the body of a larva is inside and other half is outside of the leaf and sometimes larvae have been seen moving on the leaf surface.

Plate 8: Blotch mines on Chinese cabbage leaves

Plate 9: Increasing severity of damage on leaves of Chinese cabbage by *S. flava*

Plate 10: Blotch mines on cauliflower leaves

Plate 11: Blotch mines on turnip leaves

Plate 12: Plants of Chinese cabbage undamaged (left) and heavily damaged by *S. flava*

When a larva of *S. flava* is ready to pupate it cuts a semicircular slit in the leaf surface, usually at or near the end of the mine. This slit may be located on the upper or lower leaf surface, but depends on the mining location of the larva within the mesophyll. The larva emerges with characteristic peristaltic locomotion. Movement outside the mine is the same as within and is accompanied by a rolling motion, which usually forces the larva to fall from the leaf to the ground to form the puparium, after evacuating its gut. Larvae occasionally pupate within or on leaves or at the base of leaves or stalks. Larvae exit leaves during early daylight hours, with the majority of emergence occurring before 0900 hr.

Under laboratory and greenhouse conditions (room temperature in August and September 1991), mean development times of each stadium (calculated only for those individuals that reached adulthood) were : 1st instar 2 days, 2nd instar 2.4 days, 3rd instar 2.6 days and 4th 1 day (or third instar 3.6 days), a total time of 8 days as larvae. Despite the fact that the duration of L3 instar is only 1.3 times longer than L1, the volume of leaf tissue consumed by L3 is much greater than the L1. Mature larvae placed in a petri-dish pupate quickly (about one day).

PUPAE

At the end of the feeding phase the third instar departs from the food (host) and burrows into the soil (sometimes larvae enter diapause within their natal leaf [in the mine]) to pupate. When ready to pupate, the larva becomes shorter and thicker. The third-instar skin forms the puparium, in which the pupa stage is formed. The puparia are at first light yellow and within 24 hr. become brown **(Plate 13)**. The lateral sides of the pupa are subparallel and tapered rather sharply at the ends, flattened ventrally and arched dorsally. They average 3 ± 0.1 mm in length (n= 25). In the field most pupae are formed in soil crevices adjacent to host plants (personal observation, unrecorded data). Pupal development took on average 14 days (range 10-18 days, 50 observations) in November and December 1991 under laboratory conditions (no temperature control).

After the adult emerges, the empty puparium is a light brown, rather brittle structure, with a torn dorsal lid-like section left hanging open at the anterior end. A hyaline soft, pliable sac, which enveloped the developing adult, is left inside the puparium.

The entire life cycle can be completed in about 28 days at approximately 18 ± 2°C, natural daylength (under a 11L : 13D photoperiod), and 75 ± 3% RH (early spring).

Average duration of each stadium is:

- Egg: . . . . . 6 days, 20% of total development.
- Larval stage: . . . . . 8 days, 30% of total development.
- Pupa: . . . . . 14 days, 50% of total development.

Total development time: . . . . . 28 days, 100%.

Males and females required nearly the same time to develop (unrecorded data).

Plate 13: Pupa of *S. flava*

PRODUCTION IN TIME OF "FEEDING PUNCTURES" AND EGG LAYING BY *S. FLAVA* ON CHINESE CABBAGE

INTRODUCTION

Scaptomyza flava is unusual among phytophagous insects in that adult females make small punctures in leaves of host plants with their toothed ovipositor from which both sexes may feed on the exuding juices. Only a small proportion of these punctures is utilised for the deposition of eggs (see detail literature review and in the section "Comparison of plant species as hosts for *S. flava*"). It could be important to determine the sequence in time of the formation of punctures and the commencement of egg laying. An experiment was therefore undertaken using Chinese cabbage plants and individual pairs of insects to investigate this.

MATERIAL AND METHODS

Puncturing activity: To confirm that *Scaptomyza flava* females require additional nutrient for commencement of egg laying, a small experiment was undertaken under greenhouse conditions and with the following treatments:

1) Single pairs of newly emerged adult insects confined without plant material for first 24 hr.

2) Single pairs of newly emerged adult insects confined with plant material (potted Chinese cabbage plant) for first 24 hr.

In the subsequent three 24 hour periods insects in both treatments were provided with a fresh potted Chinese cabbage plant. There were 5 replications for each treatment. For each treatment and for each 24 hour period the number of feeding punctures and eggs were determined.

Time of feeding and oviposition: Observation suggested that feeding and oviposition by adults were crepuscular activities. To confirm the time of feeding and oviposition activity, two experiments were undertaken under laboratory conditions.

In the first experiment there were 14 sampling intervals (treatments) replicated 5 times in separate containers. Treatments (Hours): 05.00, 06.00, 07.00, 08.00, 09.00, 10.00, 12.00, 14.00, 16.00, 17.00, 18.00, 19.00, 20.00 and 21.00. At each time a single pair of 2 day old adult flies was placed in a gauze cage containing plant material (one potted Chinese cabbage plant) and removed after 1 hour. The numbers of feeding punctures and eggs were then counted.

The second experiment was conducted in a greenhouse conditions during November 1992. The greenhouse environment consisted of natural photoperiod (14L:10D) with ambient temperature of 13 to 19°C and 60 to 94% relative humidity. Single potted Chinese cabbage plants at the 3-4 leaf stage were placed in square cages 30 x 30 x 30 cm with fine mesh terylene net cloth screen ceiling and walls. Moist paper towels were placed on the floor of the cages. Individual pairs of newly emerged (1 to 2 hour old) unfed adult insects were introduced into each cage (flies had to be exposed to plants immediately after emergence to prevent excessively high initial feeding punctures and egg laying). Cages were restocked with a fresh plant every 4 hours until eggs started to be laid. Sequences and durations of activities were recorded and for each interval the number of eggs and punctures were determined by counting under a stereo microscope. In preliminary tests it had been established that eggs were not laid during the hours of darkness (though a few punctures were formed). Therefore plants were not renewed overnight. There were 10 replications each consisting of one pair of insects.

RESULTS The results of these experiments are summarised in **Tables 3, 4, 5,** and **6** and in **Figs. 4, 5** and **6.**

Table 3: Mean number of feeding punctures and eggs per female

Trt	1st 24 hours		2nd 24 hours		3rd 24 hours		Total means	
	Mean No. of holes[1]	Mean No. of eggs	Mean No. of holes	Mean No. of eggs	Mean No. of holes	Mean No. of eggs	No. of holes	No. of eggs
1	-	-	72	1.2	142	1.2	107	1.2
2	200	1.4	252	6	710	18	414	8.5

The results in **Table 3** show that insects deprived of plants during the first 24 hours after emergence laid fewer eggs over the subsequent two 24 hour periods compared to insects that had access to plants for the first 24 hours. In treatment 1, this delay may also be due to delay in mating (no host plant present for first 24 h). However, insects initially without access to plants also produced fewer leaf punctures, during the 2nd and 3rd 24 hours periods so may have been weakened by this deprivation.

The results of the second experiment **(Table 4)** showed that practically all of the feeding punctures were produced and eggs deposited between 6-10 a.m. and 5-8 p.m. (sunrise: 05.50, sunset: 20.45). Prior to 06.00 hours females that had mated showed little feeding and no egg laying activity but one hour later these activities had begun. By 10.00 hours, activities had reached a peak and means of 5.2 eggs and 42 feeding punctures occurred between 09.00 and 10.00. The frequency of feeding and oviposition declined subsequently to 14.00. The decrease in these activities was correlated with an increase in the temperature and light intensity. From 16.00 hours, feeding and oviposition activity increased from means of 12 and 2.3 per hour respectively to means of 42 and 5.4 per hour by 19.00. The pattern of feeding and oviposition activity in time is shown in **Figs. 4** and **5**.

[1] Holes: Feeding punctures

Table 4: Time of feeding and oviposition activity of *Scaptomyza flava* females under laboratory conditions

Numbers of egg laid and feeding punctures between indicated hours		
Hours	**Mean Number of feeding punctures**	**Mean No. of eggs per female**
05.00-06.00	10	0
06.00-07.00	34	3.1
07.00-08.00	35	4
08.00-09.00	38	3.9
09.00-10.00	42	5.2
10.00-11.00	9	1.6
11.00-12.00	4	0
12.00-14.00	3	0
14.00-16.00	8	1
16.00-17.00	12	2.3
17.00-18.00	40	5
18.00-19.00	42	5.4
19.00-20.00	21	4
20.00-21.00	2	0

Table 5: **Production in time of "feeding punctures" and egg laying by *Scaptomyza flava* on Chinese cabbage under greenhouse conditions**

Replication ↓	Time ☞	Day 1		
		08.00-12.00	12.00 - 16.00	16.00 - 20.00
1	No. of holes	5	36	99
	No. of eggs	0	0	0
2	No. of holes	50	20	300
	No. of eggs	0	0	0
3	No. of holes	25	25	37
	No. of eggs	0	0	0
4	No. of holes	3	6	40
	No. of eggs	0	0	0
5	No. of holes	50	0	11
6	No. of holes	Replicates 6 - 10 commenced at 16.00		110
	No. of eggs			0
7	No. of holes			105
	No. of eggs			0
8	No. of holes			60
	No. of eggs			0
9	No. of holes			150
	No. of eggs			0
10	No. of holes			30

Day 2				Day 3		
05.00 -0.800	**08.00- 12.00**	**12.00 -16.00**	**16.00 -20.00**	**05.00 -08.00**	**08.00 -12.00**	**12.00 -16.00**
80[1]	10					
5[2]	1					
8	2	10	25	50	0	45
0	0	2	0	0	0	5
30	10	0	10	110	11	88
0	0	1	0	0	0	6
39	11	1	15	150	0	80
0	0	0	0	0	3	
150	3	3	0	80	15	40
25	4	2	10	30	2	10
0	0	0	0	0	0	1
5	2	4	30			
0	0	0	2			
44	6	3	0	60	0	45
0	0	0	0	0	2	5
80	10	0	110	200	0	50
0	0	0	0	13	0	1
200	15	2	0	17	2	10

[1] No. of feeding punctures (holes).

[2] No. of eggs.

The results of the third experiment **(Tables 5, 6)** show that each female makes between 141 and 550 (mean 258) feeding punctures before commencing egg laying and that there is a period of approximately 24 hrs. after emergence before egg laying begins. Two pairs of insects (replications 5 and 10) did not produce any eggs but caused some feeding punctures.

Table 6: Mean number of feeding punctures and eggs per female in time

Time	**4**[1]	**8**	**12**	**17**	**22**	**26**	**30**	**34**	**42**	**46**	**50**	**54**
Holes	59	22	93	28	32	43	3.3	8	12	77	39	42
Eggs					0.1	0.5	0.6	0	0	2	1.2	4

DISCUSSION

All ten individual flies (**Tables 5-6,** the third experiment) commenced making leaf punctures within four hours after emergence and two out of ten females produced peak numbers of punctures within the first 12 hours and before egg laying commenced. With other individuals peak numbers of punctures did not occur until about the time that egg laying commenced. Where there was an early peak there was also a second peak once egg laying began. This is shown clearly in the mean values for all ten pairs of flies **(Fig. 6)**. Egg laying did not commence until at least 22 hours following emergence **(Table 5)**. This delay in commencement of egg laying and the pattern of feeding suggest that *Scaptomyza* females require additional nutrients for oviposition (pre-oviposition feeding). Additional nutrients to those obtained from host plant leaf juices are important to obtain maximum fecundity and they obtain these by feeding on leaf juices that are released by the puncturing activity of the ovipositor[2].

[1] hours from emergence.

[2] See results of the first experiment (puncturing activity test) in this section.

Fig. 4: *Time of feeding activity of S. flava females under laboratory conditions*

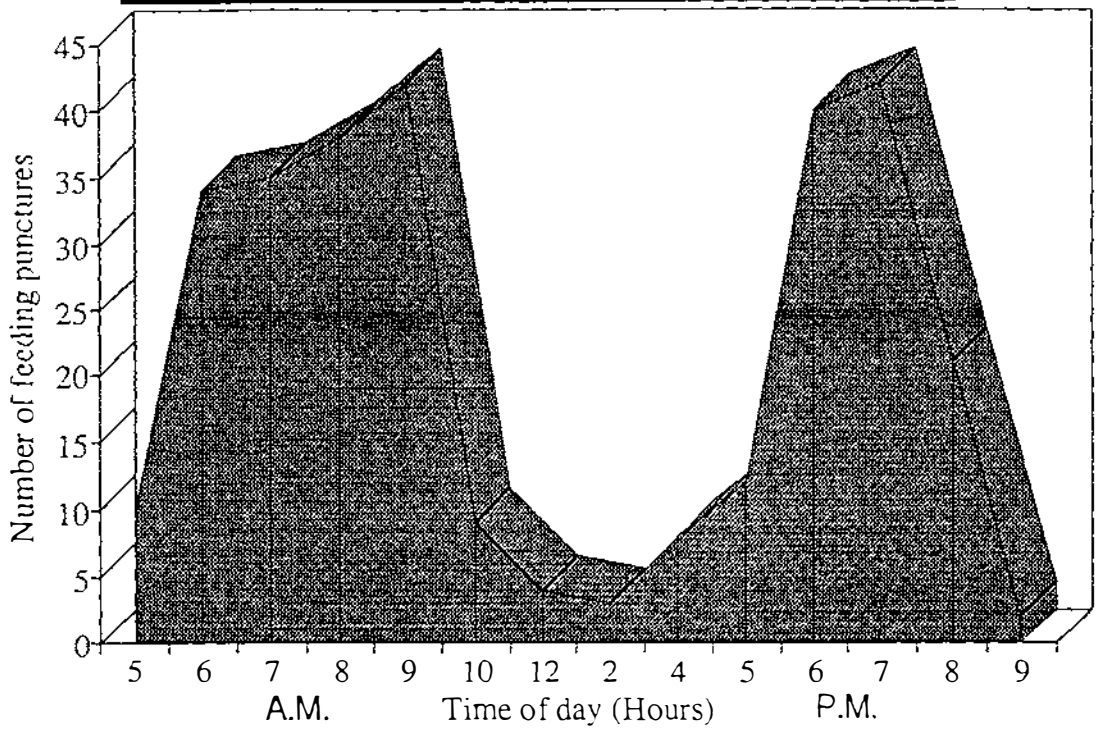


Fig. 5: *Time of oviposition activity of S.flava females under laboratory conditions*

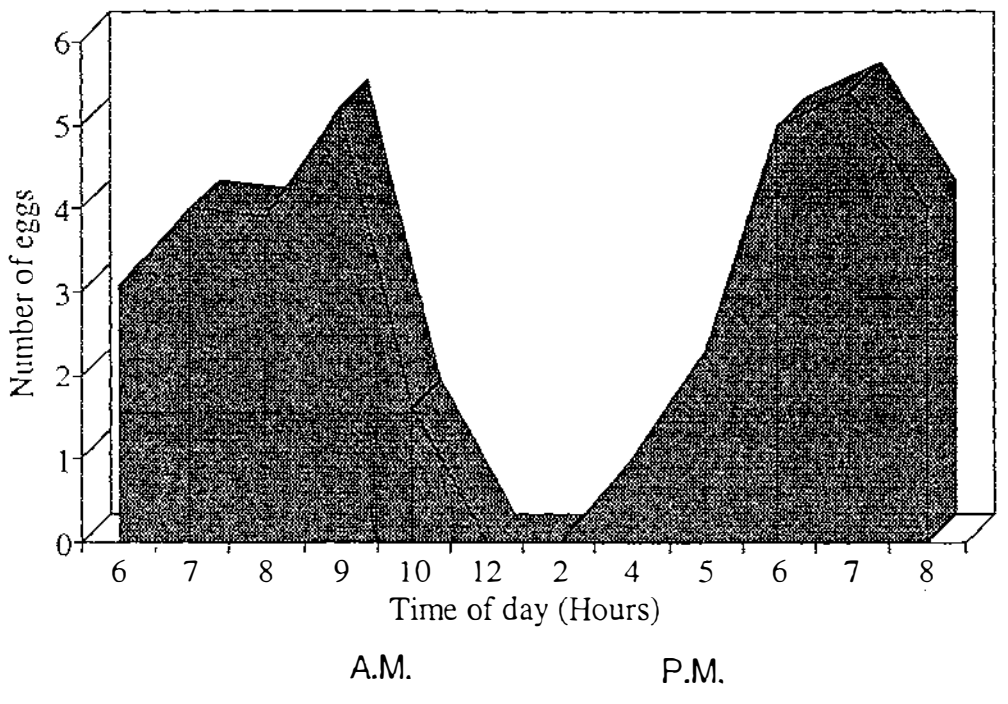
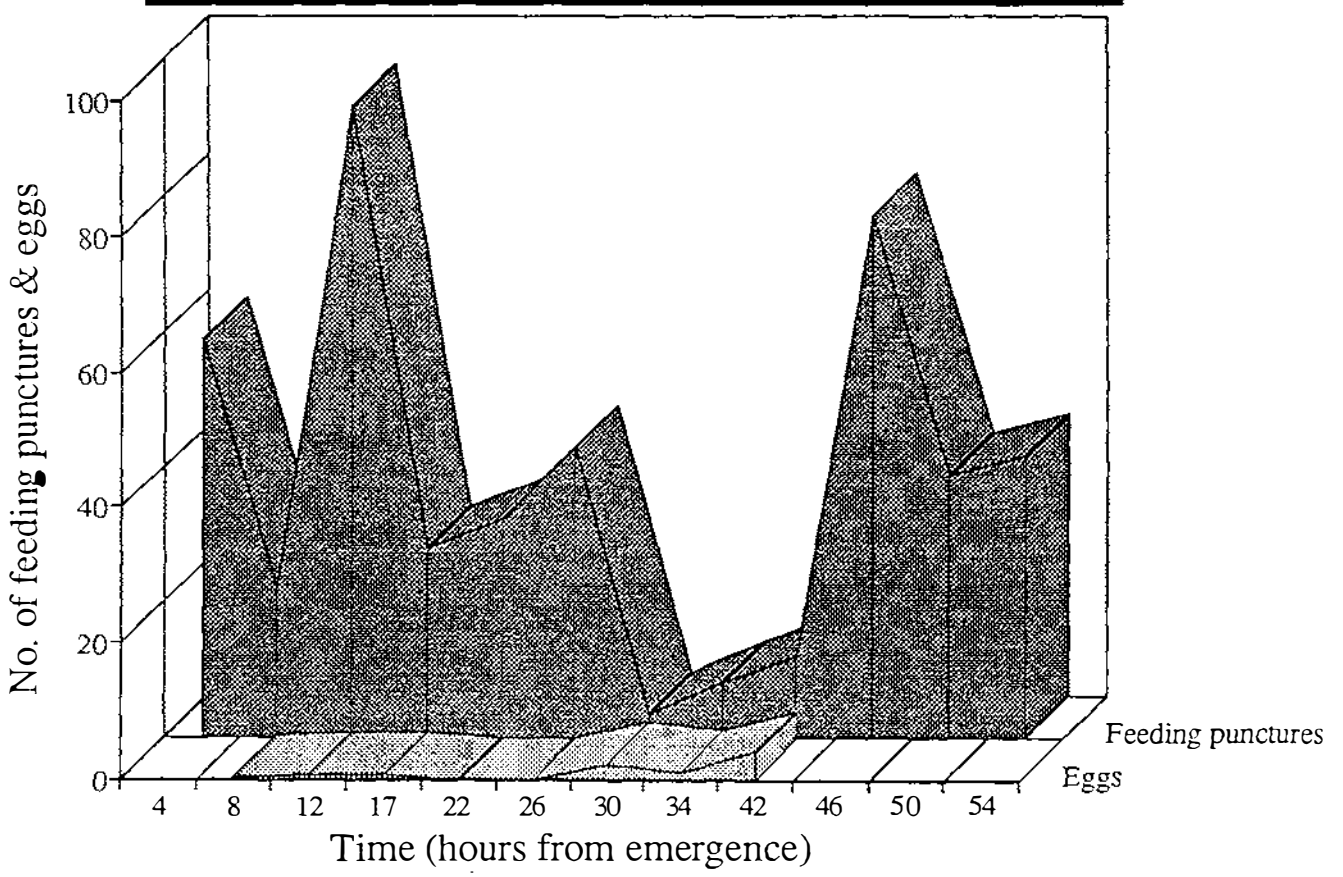


Fig. 6: *Mean no. of feeding punctures and ime to commencement of S. flava egg laying*



FEEDING AND FECUNDITY OF *S. FLAVA*

INTRODUCTION

The fecundity of an insect is determined by two major variables (Fenemore 1977). First, the number of eggs matured in the ovaries will depend on the insect's physiological condition, which in turn is influenced primarily by environmental conditions to which the individual, including its immature stage, has been exposed. Second, oviposition itself may depend for its maximum expression on suitable environmental conditions.

Fecundity has been measured for relatively few leaf miner species (Askew, 1979; Condrashoff, 1964; Martin, 1956; Miller, 1973) and depends on food resources (pre-oviposition feeding) for the adults in those cases examined. *Phyllonorycter blancardella* females produced an average of 44-67 eggs when offered sugar solution and 20-29 when offered water only (Pottinger and LeRoux, 1971). *Liriomyza trifolii* produced 78 eggs when aphid honeydew was available on tomato leaflets and only 12 on leaflets without honeydew (Zoebisch and Schuster, 1987). *Phyllocnistis* is reported to feed on foliar nectaries of *Populus tremuloides* in British Columbia, and Agromyzids have been seen feeding at extrafloral nectaries on *Byttneria* in Costa-Rica (Condrashoff, 1964).

My focus is on the relationship between feeding and oviposition of *Scaptomyza flava* adult females and food resources

MATERIALS AND METHODS

One experiment was undertaken to determine the relationship between food source and number of punctures per female. Treatments were as follows (4 treatments, each with 4 replications):

1. . . . . Provided with water and plant material[1]
2 . . . . . Provided with yeast, water and plant material
3 . . . . . Provided with 10% honey, water and plant material
4 . . . . . Provided with 10% honey, yeast, water and plant material

Chinese cabbage plants were utilized as hosts and were regularly replaced by fresh plants to maintain an adequate oviposition substrate and feeding source.

To confirm that the "feeding punctures" of *Scaptomyza flava* flies were made with the ovipositor rather than with the mouthparts, a preliminary test was undertaken under greenhouse conditions. Ten males and 10 females were caged separately over small Chinese cabbage plants. Puncture marks were produced only in cage with females (after several days), and none developed in cages with males. It was concluded that the feeding punctures were made with the ovipositor and that mouthparts were not involved.

Fecundity experiments were conducted in a semi - controlled environment (incubator room) at 20 ± 1°C. Artificial light was used to maintain a photoperiod of 12 L:12 D. The photophase occurred between 0600 and 1800 hours (light intensity, 4.2 W/m^2). RH was not controlled.

As *Scaptomyza flava* lays its eggs into slots cut in leaf tissue, some means of rendering eggs visible is necessary if they are to be directly counted. Several methods that have been reported as useful for other insects were tried, but none proved entirely successful, although I found that eggs are visible when the leaf is quite fresh. In experiments to determine fecundity it was decided to allow eggs to hatch and then to count larval mines at an early stage of development (majority in first instar) as a measure of number of eggs laid.

[1] Chinese cabbage.

Small cylindrical oviposition cages (15 cm in height, and 7.5 cm in diameter) **(Plate 14)** were constructed from transparent PVC acetate sheet (0.4 mm in thickness) and were ventilated by net cloth at the top. One 12 mm diameter circular hole was cut into the centre of the side of each cage, approximately 10 cm from the bottom and fitted with a cork stopper. This opening was used for the introduction of a syringe for watering the plant or to introduce adult insects into the cage. Flies used in experiments were about 25 to 40 generations removed from field populations. Data were analyzed with a general linear models procedure (SAS Institute, 1985).Where significant differences in the variables occurred, means were separated using LSD test ($P \leq 0.05$). There were 4 treatments with 8 replications.

Treatments were as follows:

1 ..... No additional food other than plant material
2 ..... Provided with yeast
3 ..... Provided with honey solution
4 ..... Provided with honey plus yeast

Two separate experiments were undertaken. In the first, one-month old potted Chinese cabbage plants were placed individually into cages from 0800 to 1000 hours containing 1 male and 1 female (newly emerged adults obtained from a colony reared on Chinese cabbage). Plants were placed in the controlled environment room and left for one week. New males were added if necessary. In a second experiment, the same procedure was followed, except the plant was left for one day only, then renewed regularly every three days during 10.00 - 12.00 hours. The procedure was continued until each female died.

After removal from the oviposition cage, plants were placed under a clean fine gauze cage for eclosion of larvae. In each case the plants were retained until leaf mines developed. Fecundity was estimated by daily counts of first instar larval mines.

Plate 14: Small cylindrical oviposition cages (foreground)

To prepare the yeast mixture the following method was used (as described by Roberts, 1986):

(i) 10 g of glucose; 10 g of dried yeast powder; and 2 g of agar in 100 ml of water.

(ii) Make the agar and yeast into a paste, boil the water add the glucose and paste.

(iii) Boil and simmer for 10 min.

(iv) Finally add Nipagin M (Nipagin and propionic acid 1 ml / 200 ml medium), dispense and seed with live yeast.

RESULTS

The results are summarised in **Tables 7, 8** and **Fig. 7.**

Table 7: Relationship between the number of feeding punctures and food source.

Treatment	**Water and plant**	**Yeast , water and plant**	**Honey , water and plant**	**Honey , yeast, water and plant**
Mean No. of feeding punctures	1632 a	1750 a	2044 a	2500 a

Treatments accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

Though the number of feeding punctures per female was about 1.5-fold greater when the female had access to honey (honey solution or honey solution plus yeast)

compared to females that were not able to feed on honey (yeast or water only), the difference was not significant.

Table 8: Fecundity of *S. flava* with different food availability

Treatment	Mean number of eggs laid per ♀[1]			
	Exp. 1[2]		Exp. 2[3]	
	Mean	Range	Mean	Range
Honey solution	181.32 a	(50 - 172)	102.25 a	(30 - 151)
Yeast and honey solution	165.98 a	(80-162)	117.12 a	(100-160)
Yeast	68.15 b	(16 - 125)	59.87 b	(05 - 118)
No additional food or water[4,5]	63.15 b	(33 - 99)	67.87 b	(35 - 110)

Treatments accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

[1] as estimated from first instar larval mines.

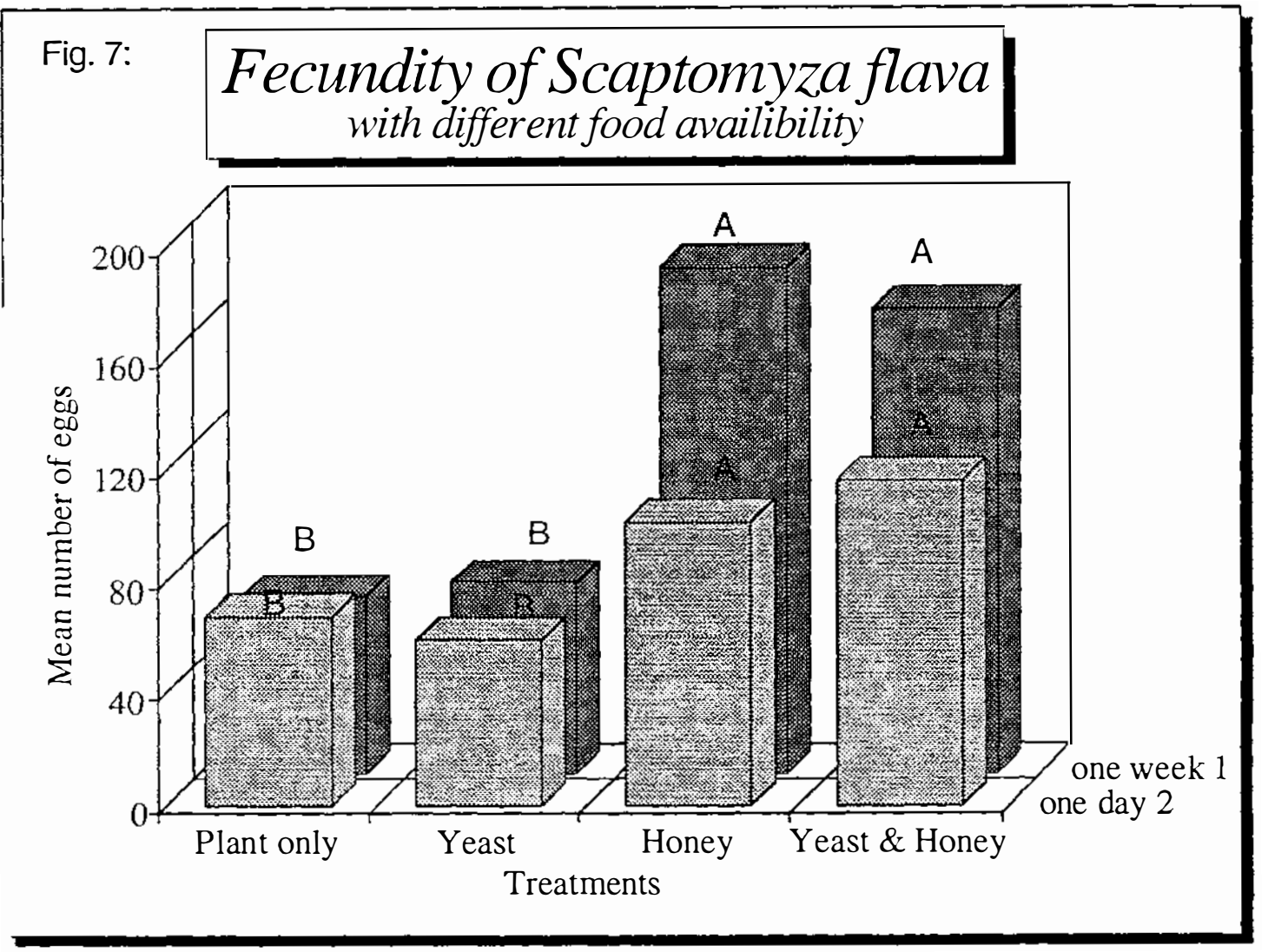
[2] Plants renewed weekly.

[3] Plants renewed after 1 day then every three days.

[4] No additional food or water other than plant material.

[5] As fresh Chinese cabbage plants were provided as oviposition substrate all adults were able to feed on leaf juices by normal feeding punctures.

Fig. 7:



[1] Exp. 1 Plants renewed weekly.

[2] Exp. 2 Plants renewed after one day then every three days.

DISCUSSION

In this work the term fecundity corresponds to the numbers of eggs laid during a certain period. These results provide strong evidence that nutrients additional to those obtained from host plant leaf juices are important to obtain maximum feeding punctures and eggs by *Scaptomyza* leaf miner flies. The fecundity ranged from a mean of 63.15 eggs for females with plant material only to 181.32 eggs for females additionally provided with honey solution (**Table 8** and **Fig. 7**). The availability of yeast did not increase fecundity for females provided only with plant material or those additionally provided with honey.

These results are in agreement with those of Charlton and Allen (1981) who observed that the feeding and fecundity of *Liriomyza trifolii* were augmented greatly when given honey. Dimetry (1971) also found that females of *Liriomyza congesta* provided with honey laid more eggs over a greater period of time than females provided with other foods.

Honey thus seems to provide necessary nutrients for high feeding puncture and egg production but the results leave unanswered the question as to which components present in honey are responsible for the increase. Food sources may affect feeding puncture and egg production by influencing adult longevity (Peng and Williams, 1991). Honeydew is a potential food source that can be encountered in the field and that may greatly increase oviposition of insects. Charlton and Allen (1981) suggested that floral nectars could increase leaf miner populations. Because of the diversity of plant hosts that the leaf miner exploits, it is probable that in the field aphid honeydew or floral nectar may be encountered by adults on crop plants or alternative hosts. Even if females have access to honey for a short time (24 hr), oviposition still would be increased.

It is difficult without further work to decide which components present in honey are responsible for these effects on oviposition.

LONGEVITY OF *S. FLAVA*

INTRODUCTION

Adult longevity varies among species depending on life history; for example, Buprestids of the genus *Taphrocerus* overwinter as adults (Chapman, 1923 cited by Hespenheide, 1991) as does *Rhynchaenus fagi* (Bale, 1979,1981). Longevity also depends on access to food in some species that have been studied: *Phyllonorycter blancardella* females lived 8-14 days with access to sugar solution and 4-7 days with water only (Pottinger and LeRoux, 1971). Charlton and Allen (1981) reported that *Liriomyza trifolii* females survived 2- to 3-fold longer when an alternative food source was available; namely these females lived 2.4 days on glass, 4.3-5 days on tomato leaflets without honeydew, and 9.7 days when aphid honeydew was available (Zoebisch and Schuster, 1987).

Hollingsworth and Burcombe (1970), reported that different species of *Drosophila* survive much longer when sugar or honey are added to their diets. Numerous papers have been published on the utilization of sugars, honey and yeast by insects (reviews: House, 1974; Wyatt, 1967). There has been no work reported on effect of food availability on the longevity of *Scaptomyza.*

Survival rate is usually related to fecundity in that species with high potential natalities (potential natality is the reproductive rate of individuals in an optimal environment) tend to have relatively low survival rates and vice versa.

Experiments were undertaken to determine the lifespan of *Scaptomyza flava* adults offered different foods.

MATERIALS AND METHODS

To determine longevity, single pairs (1 ♀ and 1 ♂) (10 pairs total) of newly emerged adults (flies on the day of eclosion were designated as 0-day-old) were sexed and removed from the rearing colony. Flies were anaesthetized with either carbon dioxide or ethyl acetate vapour to facilitate sexing and handling when setting up tests. They were transferred to individual cages in the laboratory (without plant material but with moist paper towels on the cage floor), and subjected to one of the following treatments:

1 . . . . . Confined on glass plates and starved[1]
2. . . . . Provided with water only.
3. . . . . .Provided with yeast[2] plus water.
4. . . . . Provided with 10% honey solution plus water.
5. . . . . Provided with 10% honey solution, yeast and water.

The experimental containers were placed in an environmental chamber, maintain at 20 ± 2° C during the light (L) period and 13 1° C during the dark (D) period, uncontrolled humidity and natural daylength (illuminated at a L16:D8 photoperiod). Observations were started on day 2 following release of insects and then repeated daily (sometimes at 2-d intervals) until the adult insects had died. Water, honey solution and yeast were renewed as required. The experiment was of factorial design and data analyzed accordingly. Dead flies were counted daily, and were retained for sex determination. Observations were continued until 100% flies had died on each food source. Data were analyzed with a general linear models procedure (SAS Institute, 1985).Where significant differences in the variables occurred, means were separated using LSD test ($P \leq 0.01$).

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[1] no food or water [moist paper towels.

[2] Type of yeast is specified in section concerned with fecundity. One slice of yeast preparation (approximately 10 g) was placed per cage in yeast treatments.

RESULTS AND DISCUSSION

The results are given in **Table 9** and **Fig. 8.**

Table 9: The longevity (survival) of adults of *S. flava* with different food availability[1] (without plant material).

Treatment	Mean life span in days	
	males (♂)	females (♀)
Starved (No water or food)	≤ 1.00 C[2]	
Honey solution, yeast and water	16.30 A (5.5-24.5)	19.70 A (16.5-24.5)
Honey solution plus water	8.70 B (3.5-11.5)	17.90 A (11.5-22.5)
Yeast plus water	7.70 B (7.5-8.5)	7.90 B (7.5-9.5)
Water only	3.70 B (2.5-5.5)	6.50 B (4.5-9.5)

Values with the same letter do not different significantly ($P \leq 0.01$).

[1] Overall mean life span (all treatments with food) of males was 9.17 days and of females 13.08 days (significantly different $P \leq 0.01$).

[2] Sexes not separated, so data for the two sexes were pooled.

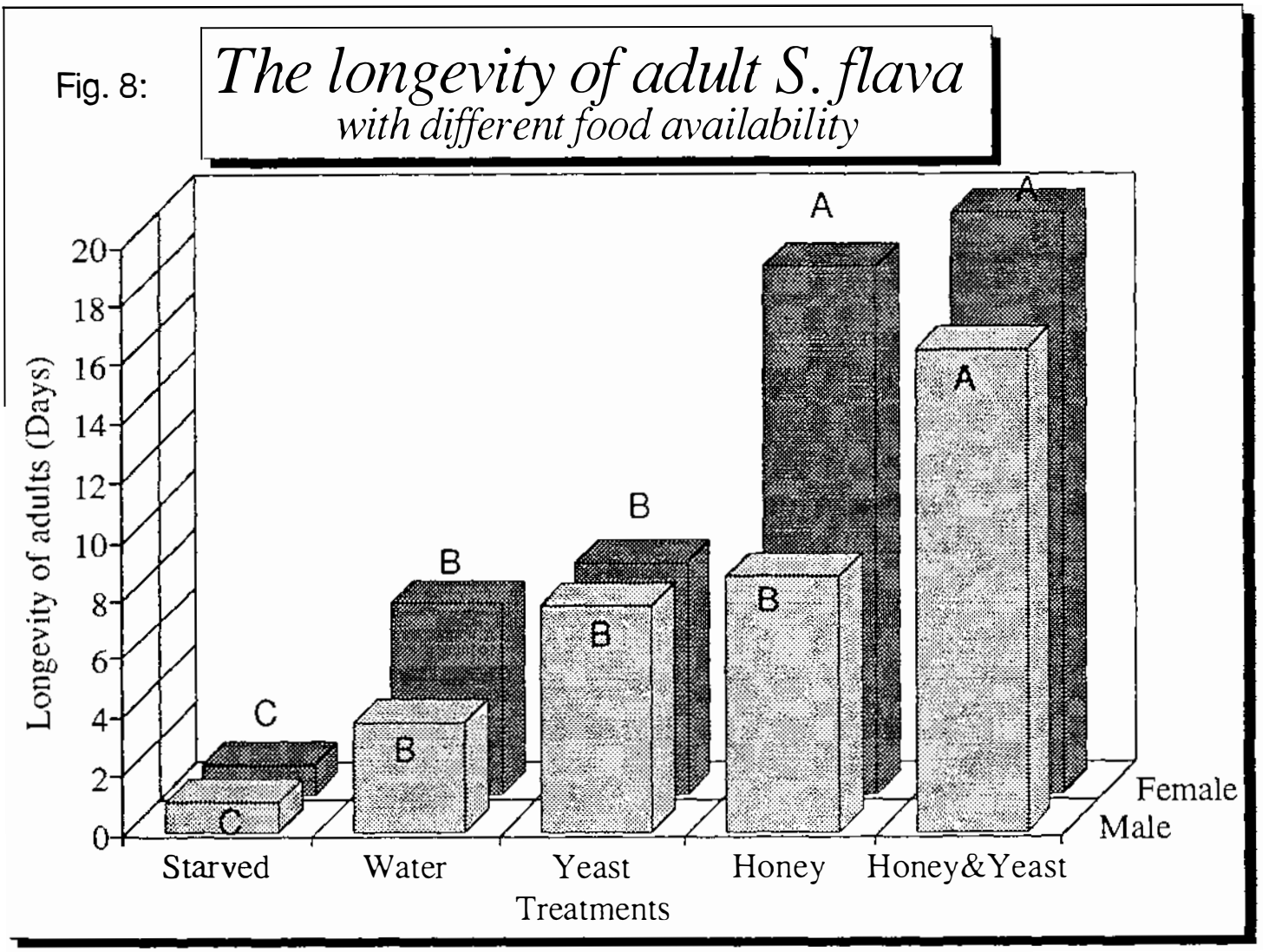
The profile of longevity between treatments was quite different. When starved all insects died within 24 hours. For both sexes, the differences in mean longevity between long-lived and short-lived is affected by food source. When adult flies had access to water but no food, the lifespan averaged 3.7 days for males and 6.5 days for females but this difference was not significant ($P \leq 0.01$). When the flies had access to a food source females survived significantly longer (13.08 d) than males (9.17 d). Females survived >3 times as long with honey and males with honey solution survived >4 times as long compared to those that had access only to water. The greatest lifespan was for those fed honey solution with water and yeast also available **(Table 9, Fig. 8)**.

There was no significant difference between the lifespan of leaf miners provided with water only and yeast plus water, but for males there was significant improvement in lifespan when yeast was available as well as honey solution. Similar results were obtained for *Liriomyza trifolii* species by Dimetry (1971), Zoebisch and Schuster (1987), Pedigo (1989), Kircher and Al-Azawi (1985), House (1974), Wyatt (1967) and Hollingsworth and Burcombe (1970).

Honey apparently provides necessary nutrients to increase longevity significantly. It may also be concluded that access to water allows mobilisation of food reserves not available to starved flies (Hollingsworth and Burcombe, 1970), but that maximum longevity requires additional nutrients provided by honey solution. Further studies are required to determine which components present in honey are responsible for the effects on longevity observed in this study.

The results suggest that longevity may be greater in the field if carbohydrate food sources are available. Nectar is such a potential food source and more field observations are needed to determine if female leaf miners exploit nectar from crop or weed flowers. The presence of aphid infestations on either crop plants or weeds associated with Chinese cabbage and turnip plants may also provide food for adult leaf miners via their honeydew, thus increasing their biotic potential.

Fig. 8:


The longevity of adult S. flava
with different food availability
Longevity of adults (Days)
0
2
4
6
8
10
12
14
16
18
20
C
C
B
B
B
B
A
A
Female
Male
Starved
Water
Yeast
Honey
Honey&Yeast
Treatments

LIFESPAN OF MATED AND UNMATED ADULT *SCAPTOMYZA FLAVA*

INTRODUCTION

"Costs of reproduction occur when an increase in current reproductive rate leads to a drop in lifespan or in future fertility" (Partridge and Fowler, 1990). It is well known that sexual activity reduces longevity in *Drosophila* (Service, 1989). Virgin females (Smith, 1958; Partridge *et al.,* 1986 cited by Service, 1989) and virgin males (Partridge and Andrews, 1985 cited by Service, 1989) live longer than mated flies. However, the deleterious effects of sexual behaviour on longevity are reversible: when the sexual activity of mated flies is terminated, their death rates become similar (after a short time lag) to those of same-aged virgins (Partridge *et al.,* 1986). Thus, sexual activity appears to represent a short-term risk or hazard with respect to survival. This pattern of effects has been interpreted as evidence that mating does not cause an acceleration of senescence and that the shortening of lifespan by sexual activity does not involve the ageing process, *i.e.*, somatic deterioration (Partridge and Andrews, 1985 cited by Service, 1989). Based on their observations of the effects of mating on male lifespan, Partridge and Andrews (1985) have argued that selection for increased longevity in *Drosophila melanogaster* (Rose and Charlesworth, 1981; Luckinbill *et al.,* 1984; Rose, 1984 cited by Service, 1989) may in fact be selection for reduced sexual activity or, more generally, for reducing short-term mortality risks. Differences in female lifespan appear to be associated with changes in age-specific fecundity (Service, 1989).

The results of several studies have implied that egg-production is costly to female insects, by reducing their survival. For instance, the lifespan of female *Drosophila subobscura* is increased after sterilization by high temperatures (Smith, 1958 cited by partridge *et al.,* 1987) or by X-irradiation (Lamb, 1964). In these examples a strong case for an effect on lifespan of egg-production *per se* was made by the demonstration that the lifespan of mutant *ovaryless* females was unaffected by the same experimental

treatments (Partridge *et al.,* 1987).

In contrast to these findings, a study of the lifespan and egg-production rates of female *Drosophila melanogaster* whose exposure to males was experimentally varied suggested that the reduced longevity of females kept with males could not be caused by variation in egg-production rates (Partridge *et al.,* 1986). Exposure of females to males may affect female longevity directly (Partridge *et al.,* 1987). Unlike *Drosophila subobscura* females, *Drosophila melanogaster* females regularly remate (Newporty and Gromko, 1984), and this or some other consequence of exposure to males may result in reduced longevity.

Partridge *et al.* (1987) manipulated egg-laying rate environmentally. Flies that laid fewer eggs lived longer, but differences in total body weight between experimental groups were not consistent with the hypothesis that increased fecundity caused greater mortality through reduced somatic investment. Thus, higher egg-laying rates may also represent an increased short-term hazard, similar to that associated with mating activity, rather than an acceleration of somatic deterioration. If this is the case, then the increased longevity obtained in selection experiments may result from a reduction in the short-term risk attributable to egg laying. According to this interpretation, females in long-lived populations are exposed to lower levels of risk (early in life) because they have reduced fecundity.

The aim of the present study was to investigate whether mating and egg-production reduce longevity of *Scaptomyza flava.*

MATERIALS AND METHODS

An experiment was conducted to determine the lifespan of virgin and mated female and male *Scaptomyza flava* under greenhouse conditions and natural daylength (April 1993, 13 h light : 11 h dark cycle). All experimental transfer of insects was done

using minimal carbon dioxide anaesthesia (after passage through water to maintain humidity) **(Plate 3)** on flies not less than three hours from eclosion. This procedure has been shown to be without significant effect on *Drosophila* female fertility or longevity (Partridge *et al.,* 1986). During this study, ambient temperature ranged from 8 to 15°C and relative humidity from 65 to 98%. Sample size was 10 adult flies per treatment.

Two one-month old (at the 3-4 leaf stage) potted Chinese cabbage plants were placed in each of 4 cages, which contained:

1. - 10 unmated females.
2. - 10 mated females.
3. - 10 unmated males.
4. - 10 mated males.

All cages were provided with free water. Clean white paper was placed on the floor of each cage.

To obtain unmated flies, two methods were used:
1) they were collected at eclosion (less than four hours old from a colony reared on Chinese cabbage. Because adults do not mate until they are >1 day old [Chapter 2], there was no opportunity for females to mate within rearing cages),
2) pupae were separated individually into small glass tubes and emerged flies were removed daily.

For supplying fertilized females, flies after emergence were housed in groups with males in cages with Chinese cabbage plants for 3 days to ensure they were inseminated (preliminary laboratory and greenhouse observations indicated that most males mated within 24 to 48 hours after emergence). Thereafter mated females remained isolated in their cages for the remainder of their lives. Mated male flies were obtained two days following emergence.

As virgin and mated females produce punctures on leaves plants were renewed every four days until all flies had died. No leaf punctures were observed in the cages in which males were held **(Plate 15)** so plants in these cages were not renewed. Cages were checked daily and the number of dead insects recorded until all had died. Deaths were recorded and dead flies removed from the cages at the same time each day.

Based on reports of Picard (1913, cited by Partridge *et al.*, 1986) and Attia and Mattar (1939, cited by Partridge *et al.*, 1986) that unmated females of some insects deposit a limited number of eggs, plants which were exposed to unmated females were checked for eggs.

Data were analyzed with a general linear models procedure (SAS Institute, 1985). Where significant differences in the variables occurred, means were separated using LSD test ($P \leq 0.01$).

Plate 15: Comparison between feeding punctures with male and female *S. flava*

Left. Leaf exposed to female flies

Right. Leaf exposed to male flies

RESULTS AND DISCUSSION

Results are summarized in **Table 10.**

Table 10: Life span of *Scaptomyza flava* under greenhouse conditions (with plant material)

Treatment	Mean life span (Days)	Range (Days)
Unmated female	17.5 B	5 - 46
Mated female	17.1 B	8 - 26
Unmated male	26.3 A	14 - 56
Mated male	8.5 C	4 - 14

Means in each column accompanied by the same letter are not significantly different at $P \leq 0.01$ (ANOVA followed by LSD (lsd = 0.65) test for separation of means).

Surprisingly, the effect of mating on lifespan of female was opposite from my predication on survivorship of *Scaptomyza flava.* The increased lifespan in my experiments of virgin males compared to virgin females was unexpected. A shorter lifespan in mated males of *Busseola fusca* was observed by Usua (1970). Some (unfertilized) eggs were laid by unmated females (mean 5 per female) but neither I nor Usua (1970) have observed any development in eggs laid by such virgin females. All such eggs laid by virgin females collapsed within two days and failed to develop.

Unmated males lived significantly longer (26.3 days) than all other groups ($P \leq 0.01$) and about 3 times as long as mated males (8.5 days). However, virgin females (17.5 days) did not live significantly longer than mated females (17.1 days). Taken the results of the experiment suggests that exposure to females may be potentially more

damaging to male survival.

Contrary to my expectation, mating and egg production by females did not increase female death rate. The results overall therefore are equivocal with respect to Partridge and Andrews (1985) results, as in some species of *Drosophila* mating and egg laying do lower survival (Partridge *et al.,* 1987). The difference in longevity between male and female could be attributed to different amounts of body fat. Luckinbill *et al.* (1988) also found that mating had a more pronounced effect on male longevity than on female longevity in some *Drosophila* species.

In natural, these may be an interaction between the two effects, both because elevated egg-laying rates have been shown to lead to more frequent re-mating by female (Gromoko and Gerhart, 1984 cited by Partridge *et al.,* 1987). For female flies, the difference in mean longevity between virgin and mated ones is unaffected by mating status, as shown by the absence of statistical interactions between them.

NUMBER OF ADULT INSECTS EMERGING FROM A SINGLE LEAF OF CHINESE CABBAGE

MATERIALS AND METHODS

Ten infested leaves of Chinese cabbage obtained from the rearing colony were placed individually with their stems into small water containers and covered with small PVC acetate sheet cages until all eggs hatched, larvae fed and pupated and new adults emerged.

The experiment was set up under greenhouse conditions. Ambient temperature approximated 20°C, 70 (±3)%RH and natural daylength was about 14 hours. The experiment was set up between 0800 and 1000 hours. At the end of the experimental period numbers of emerged adult flies were recorded.

RESULTS

Results presented in **Table 11** show that from each leaf between 1 to 5 adults emerged.

Table 11: Number of adult insects from ten leaves of Chinese cabbage

Leaf	Area of leaf (cm^2)	No. of emerged adults
1	60	5
2	55	4
3	54	4
4	53	3
5	45	3
6	44	1
7	41	1
8	40	2
9	39	1
10	35	2
Mean	46.6	2.6

THE ABILITY OF *SCAPTOMYZA FLAVA* TO DEVELOP IN DEAD AND DECAYING LEAF MATERIAL

INTRODUCTION

Pomace flies or small fruit flies (Drosophilidae) are generally found around decaying vegetation and fruits. The larvae of most species occur in decaying fruits and leaves (Borror *et al.,* 1981). As *Scaptomyza flava* is taxonomically placed within the Drosophilidae in contrast to most other leaf mining Diptera, two experiments were conducted to determine whether this species can breed in dead and decaying leaf material.

MATERIAL AND METHODS

Environmental chambers were maintained at 14:10 L:D photoperiod, and relative humidity of 40 - 70%. Data were collected daily. In the first experiment, several Chinese cabbage plants were exposed to newly emerged adult flies in a cage until some eggs were laid. The leaves were then cut from the plants and placed into separate cages. Moist tissues were placed under the leaves and watered each day. After 2-3 days the leaves were well decayed. In the second experiment, 10 pairs of newly emerged male and female *S. flava* were confined in a cage. Some decayed leaves of Chinese cabbage were placed in the cage for 3 days then removed.

RESULTS AND DISCUSSION

In both experiments larvae of *Scaptomyza flava* developed in the decaying leaf material, pupated and produced adult insects. The number of adults from the first experiment was 80 and from the second experiment 25. From this brief experiment it is apparent that *Scaptomyza flava* will lay eggs and larvae can develop in decaying leaves of Chinese cabbage. However, the number of emerging adults was greater when the flies first laid their eggs in live leaves.

Chapter 3

HOST PLANT RELATIONSHIPS OF *SCAPTOMYZA FLAVA*[1]

COMPARISON OF PLANT SPECIES AS HOSTS FOR *SCAPTOMYZA FLAVA*

INTRODUCTION

One of the most crucial events in the life cycle of phytophagous insects is the selection of a suitable site for oviposition. Newly hatched larvae of many insects are relatively immobile (*e.g.*, leaf miners), and depend on the ability of their mother to find the best source of food for their successful growth and development. The driving forces affecting host finding and acceptance or rejection of a host are governed largely by surface (*e.g.*, polar extracts, nonpolar compounds [Renwick and Chew, 1994]) and nutritional qualities of the plant, competition, and coincidence of favourable conditions that ensure success of offspring (Capinera, 1993).

Host selection by phytophagous insects can be considered as "choice behaviour" with the choice being made at different stages in the sequence leading up to host acceptance (Browne, 1977 cited by Visser, 1988). Some insects "choose" solely after contact with the plant. Here the frequency with which different plants, hosts and nonhosts, are visited depends only on their apparency and relative abundance. Other insects perceive plant characteristics at a distance and initially "choose" according to these impressions (Visser, 1988). However, in this case, after this initial choice is made,

[1] Some parts of this Chapter modified from a paper published in *Entomologia experimentalis et applicata.* 1994. pp.

it should be noted that the insect probably continues to "choose" as it proceeds through the sequence leading up to oviposition (Harris, 1994 personal communication).

Plant chemistry almost certainly provides cues for location of the host as well as poses problems for the larvae after hatching. However, other plant characteristics, such as morphology, may influence the interaction of insects with their host plants (Vaugun and Hoy, 1993). Cruciferous plants have a distinctive biochemistry, characterized by the presence of one or more enzymatic hydrolysis products of glucosinolates (mustard oil glucosides) (Kjaer, 1976) a group of naturally occurring anionic compounds whose known number totals almost 100 (Pivnik *et al.,* 1992). These are hydrolysed by enzymes (*e.g.,* enzyme myrosinase) within the plant cell to produce volatile chemicals including isothiocyanates (Cole, 1976) or mustard oils, nitriles and other compounds, depending upon pH and other conditions (Chew, 1988). Some hydrolysis probably takes place during normal catabolysis, particularly during early seedling development. It also occurs rapidly when plant tissue is damaged (Pivnik *et al.,* 1992). Glucosinolates are secondary plant substances which are believed to have evolved as a chemical defence against herbivores (Rhoades and Cates, 1976; Feeny, 1976 cited by Nottingham, 1988). Insects that are specialized to feed on cruciferous plants are able to detoxify these chemicals (Nottingham, 1988) and in many cases use them as host-finding cues and feeding and oviposition stimulants (*e.g.*, Nottingham, 1988). However, a number of insect species feed primarily or exclusively on plants containing glucosinolates. Many of these insects are known to suffer no adverse effects from naturally occurring concentrations of glucosinolates and isothiocyanates. It has been well documented that at least some crucifer-specialist insects are also attracted by one or more of the isothiocyanates (Chew, 1988). For example, gravid female cabbage root flies use isothiocyanates as host-finding cues and glucosinolates as oviposition stimulants (Hawkes *et al.,* 1978 cited by Nottingham, 1988). Host preference is associated with higher oviposition rates, increased female longevity, shorter developmental time, and higher survival in all life stages (van Lenteren and Noldus, 1990).

Many studies have investigated the interactions between insects and host plant species but the relationship between *Scaptomyza flava* and its host plants has not been reported other than the general observation that it is usually found associated with Cruciferous plants. As neonate larvae of *Scaptomyza flava* are incapable of moving from plant to plant, the choice of feeding sites of larvae is determined entirely by ovipositional preference of the adult female. Because *Scaptomyza flava* had not been studied in regard to its oviposition behaviour, I was unable to predict which plants might be especially suitable for survival and reproduction. Therefore, a study was initiated to determine host-feeding behaviour using a range of common plants from the family Brassicaceae compared to plants from other families. The strong correlation between the presence of glucosinolates and the host range of some insect such as cabbage butterflies has led to numerous studies based on the assumption that these compounds are responsible for host recognition (Renwick and Chew, 1994).

In this study I first examined selection by *S. flava* for feeding and oviposition between 8 plant species including 5 species within the family Brassicaceae. The specific objectives of this study were to (1) determine if *S. flava* will accept plants other than *Brassicaceae* and (2) compare a range of brassicas as host plants for *S. flava.*

MATERIALS AND METHODS

The experiments were conducted under ambient greenhouse conditions in the Plant Growth Unit (PGU), Massey University. Feeding and oviposition preferences of adult females were determined for eight plant species (five cruciferous, one composite and two grasses). Preference was measured by the number of feeding punctures and by the number of eggs laid on the plants in choice and non-choice tests. Temperature in the experimental chamber was maintained at 14 ± 2°C [night] and 22 ± 2°C by day. Natural daylength (at a 10:14 [L:D] hours photoperiod with photophase from 07.15 [sunrise] to 17.15 [sunset]) was that in July 1993. The experiments began between 09.00 and 11.00 hours when the flies were introduced to the test arenas.

The following plant species were evaluated **(Table 12)**:

Table 12: Plant species used in studies of host discrimination by *S. flava*

Common Name	Scientific Name	Family
1- Turnip	*Brassica rapa*	(Brassicaceae)
2- Hedge mustard	*Sisymbrium officinale*	(Brassicaceae)
3- Chinese cabbage	*Brassica chinensis*	(Brassicaceae)
4- Radish	*Rhaphanus sativus*	(Brassicaceae)
5- Cauliflower	*Brassica oleracea var botrytis*	(Brassicaceae)
6- Lettuce	*Lactuca sativa*	(Compositae)
7- Wheat	*Triticum aestivum*	(Gramineae)
8- Prairie grass	*Bromus willdenowii*	(Gramineae)

All plants were raised from seed in a greenhouse with the exception of hedge mustard which was collected from the field (plants about 10-15 cm high) and placed into pots. Seeds were germinated in greenhouse media (peat, sand, pumice, dolomite, superphosphate and lime) in plastic pots (20 cm diameter) in an outdoor growth chamber (controlled environment with 20 ± 1°C temperature and 70 ± 10% RH) with enough light and fertilizer for plant growth to continue. Except for wheat and prairie grass seedlings were transplanted at cotyledon opening into pots (10 cm diameter) . A single transplant was planted in each pot except for wheat and prairie grass where plants were not transplanted and each pot contained a group of plants (5 plants for prairie grass and 10 for wheat). Plants were overhead watered on alternate days for the first 4 weeks and were also kept moist by capillary matting and perforated plastic film on the bench. Plants selected for choice and non-choice experiments were mostly at the 3-4 true-leaf stage (26 - 30 days after sowing, ca. 24 cm tall).

Newly emerged adult *S. flava* used in choice and non-choice experiments were

treated identically before exposure to test plants. Flies were sexed under a binocular microscope after being anaesthetized by CO_2. The insects used in experiments were about 50 to 60 generations removed from field populations and were from a laboratory colony raised on Chinese cabbage. When the experiments were terminated, plant foliage was examined for the presence of feeding punctures and eggs with transmitted light under a dissecting microscope. To measure oviposition I divided each leaf into four quadrants by marking four segments equidistant along the midvein, then drawing a line perpendicular to the midvein. The number of eggs (or feeding punctures) occurring in each quadrant were then counted. Test plants were stored in a coolroom (4°C) until assessments could be made.

Choice tests:

In these tests, experiments were conducted in the test chamber described above, in five arenas (cylindrical cage, 85 cm in diameter and 90 cm in height made from net fine cloth) **(Plate 16)**, each of which contained eight potted plants (one of each plant species) arranged at random in a circular formation 10 cm apart and 14 cm from the cage walls. Groups of four male-female pairs of newly emerged adult *S. flava* were introduced into each cage and left for four days (19.7.1993 - 23.7.1993) to permit mating, feeding and egg laying. The flies were then removed, and the distribution of feeding punctures and eggs among leaves was recorded.

The experimental design was a randomized complete block. The strata of variation were between the five blocks (cages) and between the 8 treatments within blocks. The experimental "whole treatment" units were pots of one plant and the allocation of treatments (different plant species) within blocks was randomised and their order was changed for each replicate. The results were subjected to two-way analysis of variance. When the analysis of variance showed significant treatment effects ($P \leq 0.05$), Fisher's protected least significant difference (LSD) test was used to separate means at $P \leq 0.01$ (Milliken and Johnson, 1984). Regression analysis (SAS Institute, 1985) was used to evaluate the relationship between numbers of feeding punctures and eggs per leaf.

Plate 16: Cylindrical cage used for choice tests

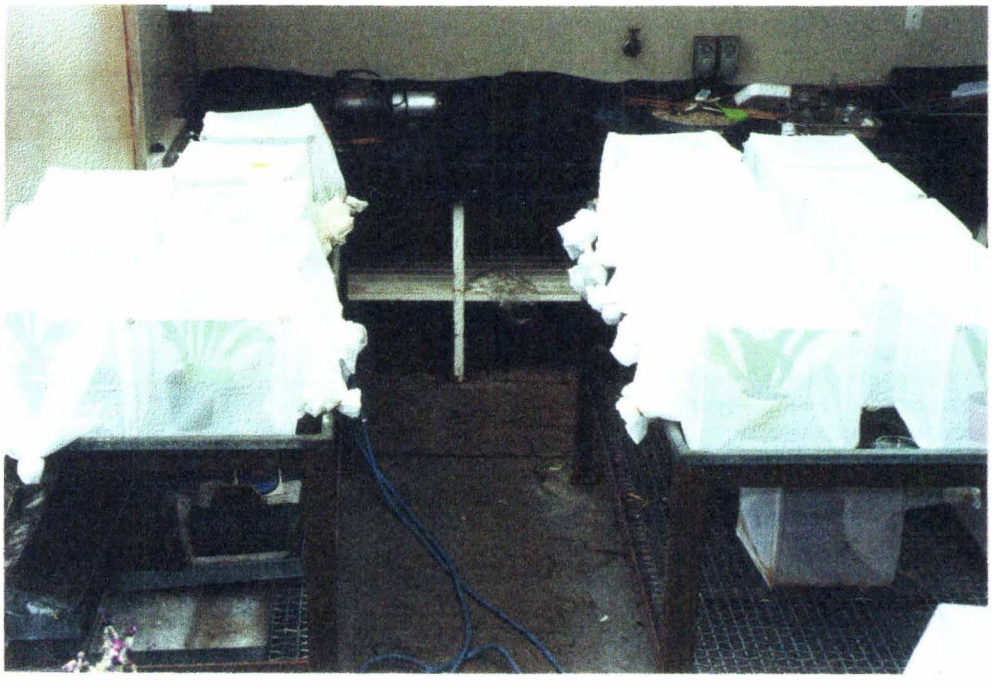


Plate 17: Square cage used for non-choice tests

Non-choice tests:

In the non-choice test, eight single pots of each plant species were placed separately in each test arena (square cages [30 by 30 by 30 cm] of terylene net). There were three arenas (replications) for each species. The arenas were assigned at random to positions in the greenhouse **(Plate 17)**. The flies were sexed and paired up at random. Four newly emerged (3 hours old) male + female adult flies were placed in each cage and left for 4 days.

RESULTS

The results of choice tests are presented in **Table 13** and of non-choice tests in **Table 14**. **Figures 9** and **10** compare the numbers of feeding punctures and of eggs in choice and non-choice tests respectively.

Choice tests:

In a choice situation, on the basis of feeding punctures and of eggs laid, plant species fell into three groups:

1. turnip, hedge mustard, Chinese cabbage and radish with large number of feeding punctures and moderate numbers of eggs;
2. cauliflower with few feeding punctures and fewer eggs than the first group;
3. lettuce, wheat and prairie grass (*i.e.*, non-Brassicaceous plants) with no feeding punctures and no eggs.

There were significant differences in total number of feeding punctures on the cruciferous plant species; most for radish, least for cauliflower and intermediate for turnip, hedge mustard and Chinese cabbage. Some differences between species within this group in the total number of eggs laid were also significant. Turnip received significantly more eggs than radish and cauliflower, and cauliflower received fewer than all other species. There was no significant correlation between number of feeding

punctures and eggs deposited **(Table 13; Fig. 9)**.

I have observed that *S. flava* selected intact leaves of Chinese cabbage and turnip over damaged leaves (by rust, aphids and white flies) for oviposition (uninjured plants received increased feeding and were always chosen over injured plants, regardless of species or age).

Table 13: Number of feeding punctures and eggs on eight plant species in choice tests with *Scaptomyza flava*

Plant species	Mean No. punctures per pot	Mean No. eggs per pot	Percentage of punctures with eggs
turnip	229.5 b	7.2 a	3.1
hedge mustard	181.3 bc	4.5 ab	2.5
Chinese cabbage	132.4 c	4.0 ab	3
radish	347.5 a	2.5 b	0.7
cauliflower	15.5 d	1.0 c	6.4
lettuce	0 d	0 c	-
wheat	0 d	0 c	-
prairie grass	0 d	0 c	-

Treatments accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD [$lsd_{punctures} = 53.87$; $lsd_{eggs} = 6.29$] test for separation of means).

Non-choice Tests:

Two major differences occurred between the non-choice tests and choice tests. First, radish received significantly fewer punctures than turnip, hedge mustard and Chinese cabbage, and was not significantly different from cauliflower. Secondly, an appreciable number of feeding punctures were made on wheat (significantly more than cauliflower) and eggs were deposited in 2.5% of these. Numerically per pot (10 plants per pot), wheat received as many eggs as cauliflower, hedge mustard and radish.

No significant difference ($P > 0.05$) occurred between turnip and Chinese cabbage for feeding or oviposition but there was a significantly higher number of feeding punctures on hedge mustard, Chinese cabbage and turnip compared to cauliflower **(Table 14; Fig. 10)**. Approximately 1.3-fold and 3.5-fold more eggs were deposited on Chinese cabbage than on turnip and cauliflower respectively.

When the percentage of punctures with eggs was calculated for each species (column 4, **Tables 13, 14**) cauliflower had by far the highest value at 6.4% and 28% in choice and non-choice tests respectively. For all other species on which eggs were laid it was less than half this.

In the presence of radish or lettuce only (non-choice test), 40 and 6 feeding punctures per pot were made by *S. flava* compared with 347 and 0 respectively when those and other plants were provided simultaneously (choice test).

On Chinese cabbage, most eggs were laid near the midrib of the leaf. In contrast on cauliflower, the majority of feeding punctures were around the leaf margin.

Table 14: Number of feeding punctures and eggs on eight plant species in non - choice test with *Scaptomyza flava*

Plant species	Mean No. punctures per pot	Mean No. eggs per pot	Percentage of punctures with eggs
turnip	202 B	11.3 A	6
hedge mustard	331.8 A	2.2 B	0.6
Chinese cabbage	269.7 AB	14.6 A	5.4
radish	40.3 CD	3.1 B	7.7
cauliflower	15.1 D	4.2 B	28
lettuce	6 D	0 B	0
wheat	85.4 C	2.1 B	2.5
prairie grass	0 D	0 B	-

Treatments accompanied by the same letter are not significantly different at $P \leq 0.01$ (ANOVA followed by LSD [$lsd_{punctures} = 66.54$; $lsd_{eggs} = 4.31$] test for separation of means).

Fig. 9: *Comparison of plant species for feeding punctures by Scaptomyza flava*

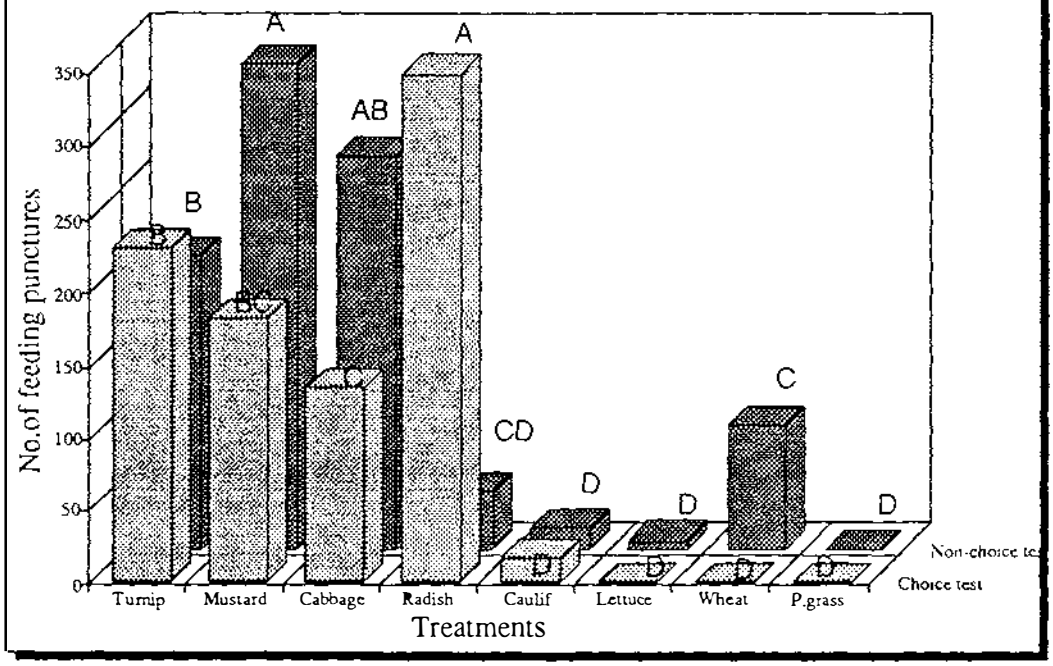
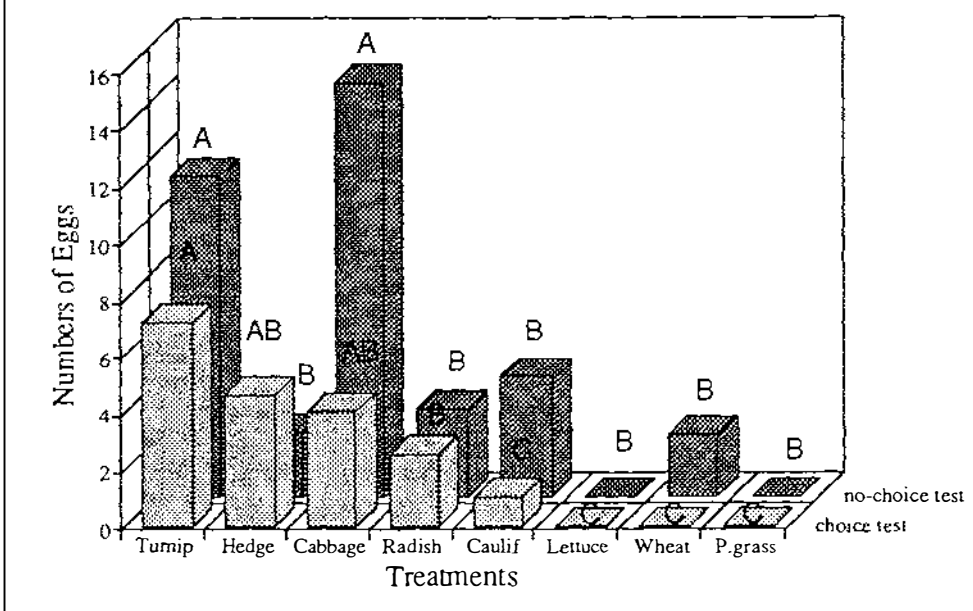


Fig. 10: *No. eggs laid by Scaptomyza flava in choice & n -ch ice tests*



DISCUSSION

My results argues that apart from some anomaly plant, *Scaptomyza flava* female accepted only plant from Brassicaceae family. In the choice experiment reported here *Scaptomyza flava* typically selected only plants from the family *Brassicaceae* for feeding and egg laying. However, under non-choice conditions poor and moderate acceptance of lettuce and wheat respectively also occurred. The eggs on the leaves of these non-host plants collapsed within a day or two and failed to develop.

Thus, in accordance with field records of plant species affected (Michalska, 1973; Szwejda, 1974; and Pol, 1974), *S. flava* showed clear preference for plants within the *Brassicaceae* based on number of feeding punctures and of eggs laid. On Chinese cabbage, the majority of feeding punctures were void of eggs (3% and 5.4% of punctures with eggs in choice and non-choice tests respectively). In contrast on cauliflower, 6.4% and 28% punctures contained eggs in choice and non-choice tests respectively. Thus although the leaves of cauliflower appear to be less suitable than other *Brassicaceae* for feeding, they are well accepted for egg laying.

Scaptomyza flava showed very similar feeding and ovipositional preference for Chinese cabbage and turnip in both choice and non-choice tests with numerical differences not significantly different.

In non-choice tests, *S. flava* produced significantly more feeding punctures on hedge mustard than on turnip. However, when able to choose between hedge mustard and turnip the difference was not significant. In contrast, radish was preferred over other *Brassicaceae* for feeding in choice tests but received few feeding punctures in non-choice tests and not significantly greater than cauliflower.

When insects exist in an ecosystem provided with several host species, they may prefer to feed and oviposit on some hosts more than the others (Dethier, 1954; Holdren

and Ehrlich, 1982; Carolina *et al.,* 1992). Insects may be expected to be more selective and show strong preferences given a choice between host and nonhost plant species. However, in the absence of highly preferred hosts, a nonpreferred plant may be accepted (Carolina *et al.,* 1992).

In these experiments (Chapter: 3, Effect of adult experience on oviposition preference) *S. flava* flies preferred cauliflower least of the five *Brassicaceae* offered. There is no obvious reason for this but turnip and Chinese cabbage have a much softer leaf than cauliflower and may be easier to puncture with the insect's ovipositor. On the other hand, selection of plants for oviposition is determined both by the physical nature of their surfaces and by chemical factors which are detected only on contact (Fenemore, 1988). Surface texture of substrates may play an important role in oviposition preference of *Scaptomyza flava.* Soft or wax-textured surfaces, *i.e.*, leaves of cauliflower (cauliflower leaves have a very different leaf wax structure from turnip and Chinese cabbage) were less suitable than other Brassicaceae for feeding, but they were accepted for oviposition sites. Although percentage of punctures with eggs on cauliflower was relatively high, damage to leaves was relatively low. No data are available to explain this but it could be due simply to physical condition of cauliflower leaves compared with Chinese cabbage and turnip. General morphology of leaves may also influence oviposition preference. However, leaf hair density does not appear to have an effect on feeding and oviposition of *Scaptomyza flava*; relatively high leaf hair densities of turnip compared to Chinese cabbage do not apparently inhibit penetration of the leaf surface for feeding and egg-laying.

Of the three non-Cruciferous plant species evaluated, flies fed and infertile eggs were laid on wheat under non-choice conditions. This suggests that, under extreme conditions, *S. flava* may oviposit on plants other than *Brassicaceae.*

Non-choice tests addressed several questions unanswered by choice tests. In choice tests, reduced number of eggs laid on cauliflower could have resulted from (a) fewer females accepting treatments, (b) females accepting treatment but laying fewer

eggs, or (c) some combination of these factors. The first possibility begs the question of why even a small number of females would accept altered treatments, when the more host plants were available. A possible explanation in that some females were less discriminating because they (a) had matured eggs more rapidly than other females and, therefore, were showing behaviour effects of "time-dependent responsiveness"(Papaj and Rausher, 1983) or (b) were stimulated to oviposit on the unaltered host, but reacting to proximity of other treatments or crowding on the unaltered cauliflower (or wheat), laid eggs on what would normally be a less stimulately treatment (Singer, 1971).

CONCLUDING REMARKS

All five Brassicaceous plant species tested may be regarded as acceptable adult hosts because sustained feeding occurred on each though to a much lower extent on cauliflower than the other species. One non-Brassicaceous plant (wheat) can also be considered as marginally acceptable for adult feeding and perhaps would be oviposited on to a small degree if females had no other choice of plants. No measurable feeding or oviposition occurred on prairie grass or lettuce even under non-choice conditions. Therefore, these species should not considered as hosts for *Scaptomyza flava. Scaptomyza flava's* distinct preferences between species within the family Cruciferae *(= Brassicaceae)* suggests that development of host plant resistance might be a possible control strategy for this pest in the future. Also these results support the hypothesis that host preference of ovipositing females is an important factor in the utilization of cruciferous crops by *S. flava* flies. It is possible that some populations of *S. flava* have broadened their host range beyond cruciferous plants. A factor conducive to host plant expansion is limited access to preferred hosts (Singer, 1971; Miller and Miller, 1986). The absence of other leaf miners on Chinese cabbage, turnip, radish and cauliflower in the Manawatu area has allowed *S. flava* to exploit this niche without competition.

In summary, I have found that oviposition of *S. flava* adult is considerably more complex than early studies. Further studies are needed to quantify the fitness of *S. flava* (both larvae and adults) developing on Cruciferous plant species compared with others.

EFFECT OF HOST PLANT SPECIES ON BODY WEIGHT OF ADULT *SCAPTOMYZA FLAVA*

INTRODUCTION

The body weight of newly-emerged adults depends on the diet regime and host-plant species on which the insect developed (Borrer, 1981). For leaf miners this is related to the food quality of host leaves within species. Physical changes in the morphology or toughness of leaves or shoots can also be important (Potter, 1989).

Body weight (and size) is the most comprehensive predictor of male fitness in *Drosophila* (Pitnick, 1991). In laboratory *Drosophila melanogaster* populations larger males inseminate more females during the first 2 weeks of life (Partridge and Farquhar, 1981, 1983 cited by Pitnick, 1991). In some insects, males transfer fecundity-enhancing, sperm-associated nutrients to females during copulation (Butlin *et al.,* 1987 cited by McLain *et al.,* 1990). Because a larger male may transfer a greater quantity of nutrients, female fecundity may also covary with mate size (McLain *et al.,* 1990). In contrast, female size and weight are positively correlated with fecundity (the number of eggs produced) in some insects (McLain *et al.,* 1990).

Fecundity of females is known to vary with adult size (weight) in many insects, and the nutritive value of different larval food plants might influence the final body weights of larvae, and hence of pupae and adults (Fenemore, 1977). Many authors have shown a positive correlation between adult weight and fecundity (Chutter, 1970; McCreadie and Colbo, 1990). Meisner *et al.* (1974) recorded fecundity of potato moth, *Phthorimaea operculella* differing widely according to the larval food. The purpose of the present experiment was to elucidate the effect of three larval food plants on adult body weight of *Scaptomyza flava.*

MATERIALS AND METHODS

Potted plants of turnip, Chinese cabbage and cauliflower were placed into separate cages containing adult insects and left for 3 days (6/8/1993 - 9/8/1993). There were 20 males and 30 females per cage and each cage contained 10 plants. After eggs were laid the flies were removed. The infested plants were held separately under clean fine gauze cages for eclosion of larvae, formation of pupae and emergence of the new generation of adult flies.

In order to weigh adults, individual insects were sucked up by an aspirator, and placed in a plastic cup with a lid (diam 5 mm by 40 mm) of a known weight. The cups plus insects were weighed on a microbalance Mettler AE 163 (Mettler Instrument Corporation, Highstown, N. J.), and mean weights for males and females were calculated. Data were analyzed with a general linear models procedure (SAS Institute, 1985). Where significant differences in the variables occurred, means were separated using LSD test ($P \leq 0.05$).

RESULTS

Adult male and female weights, as affected by host are shown in **Table 15**. Greater adult weights for males resulted when insects developed on turnip or Chinese cabbage compared to cauliflower. For females the trend was the same as that for males, with the heaviest females developing on turnip and Chinese cabbage and lower weight when raised on cauliflower. Males and females weighed 21.7% and 22.3 % more, when reared on turnip than on cauliflower and Chinese cabbage respectively. Combining host types, adult males weighed an average of 33 % less than adult females **(Table 15)**.

Fecundity of *Scaptomyza flava* is positively correlated with female body weight (compared Tables 15 and 16) and this is the common pattern among insects (Gwynne, 1981).

Table 15: Mean weights of adult *S. flava* according to sex and host.

Host	Weight of adult insect in mg			
	n	♂♂	n	♀♀
Turnip	55	0.92 a (range: 0.71-1.12)	49	1.39 a (range: 1.22-1.57)
Chinese cabbage	49	0.90 a (range: 0.82-1.00)	55	1.30 ab (range: 1.21-1.47)
Cauliflower	50	0.72 b (range: 0.53-0.86)	50	1.08 b (range: 0.84-1.04)
Total	154	84.6	154	125.6

Means within a column followed by the same letter are not significantly different ($P \leq 0.05$).

LIFE SPAN, NUMBER OF FEEDING PUNCTURES AND NUMBER OF EGGS PRODUCED BY *SCAPTOMYZA FLAVA* ON THREE PLANT SPECIES

INTRODUCTION

The host plant is a very important factor in determining a leaf miner's lifespan. Many leaf miners are quite specific in their host preferences. The host plant of a leaf miner may affect it in many way: its growth, development, reproduction (certain leaf miners require specific types of host plant before they can lay eggs), behaviour and lifespan (Auerbach and Simberloff, 1984). To determine how adult longevity, feeding and reproduction varies between different host plant species an experiment was conducted with Chinese cabbage, turnip and cauliflower.

MATERIALS AND METHODS

The experiment was undertaken under greenhouse conditions. Temperature was not regulated (range 10 - 18 °C by day, mean 14°C). Natural daylength was that in April 1993 (sunrise:06.40, sunset:18.10). Tests were run between 14 - 28 April. Plants were raised from seed in pots in a greenhouse. Plants selected for experimental use were about the same size and age, and were at the 3-4 leaf stage. There was a single plant per pot for each plant species. Plants were exposed in square cages (30 × 30 × 30 cm) to groups of 2 males + 1 female of newly emerged adult *S. flava* (=1 replicate). The insects were about 50 to 60 generations removed from field populations and were raised in a glasshouse on Chinese cabbage and turnip. Plants in each cage were replaced with a fresh one every 3 days until the female insect had died. Because fecundity may be influenced by access to males, any males that died were immediately replaced so that the female would always have access to two males. There were 10 replications of each treatment. For each interval the mined leaves were assessed for the number of punctures and eggs using a zoom stereomicroscope with a magnification range of X10-20. To

estimate average daily egg deposition, I divided total fecundity over the lifespan by the lifespan in days to yield the mean number of eggs per female per day. Data were analyzed with a general linear models procedure (SAS Institute, 1985) to examine the relationships between adult longevity, daily egg deposition and lifetime fecundity. Where significant differences in the variables occurred, means were separated using LSD test ($P \leq 0.01$).

RESULTS AND DISCUSSION

Results are summarised in **Table 16** and **Figures 11** and **12.**

Table 16: **Mean life span, number of feeding punctures and number of eggs produced by *Scaptomyza flava* (during entire life span) on three plant species**

Plant species	Life span of female (days)	Mean No. of feeding punctures / female	Mean No. of punctures/ day	Mean No. of eggs/ female	Mean No. of eggs/day
Turnip	12.2 A (7-17)	1158 A (650-1800)	95	255 A (145-321)	20.9
Chinese cabbage	10.7 B (7-14)	800 B (392-1100)	75	165 B (32-286)	15.4
Cauli-flower	10.8 B (7-14)	394 C (220-907)	36	48 C (12-105)	4.4

Means in each column accompanied by the same letter are not significantly different at $P \leq 0.01$ (ANOVA followed by LSD test for separation of means).

The lifetime totals of feeding punctures on plants, were significantly different between the three plant species; most for turnip, least for cauliflower and intermediate for Chinese cabbage ($P \leq 0.01$). There were also significant differences in the total number of eggs laid on the plant species with the same rank as for feeding punctures ($P \leq 0.01$).

The area of a single pinhole was ca. 0.12 mm^2. Therefore average total leaf area destroyed by the feeding of one adult female was 139, 96 and 47 mm^2 for turnip, Chinese cabbage, and cauliflower, respectively. The life span of *S. flava* females was significantly longer on turnip than on Chinese cabbage or cauliflower but there was no difference between Chinese cabbage and cauliflower. Average fecundity according to host plant ranged from 48 to 255 eggs deposited over the total life span. The number of eggs laid on turnip was >5 fold as many as on cauliflower and the number of eggs laid on Chinese cabbage was slightly more than half of the total number on turnip.

The majority of feeding punctures on Chinese cabbage, turnip and cauliflower were made between days 3-11, 7-11 and 3-7 of adult life respectively and the majority of eggs on Chinese cabbage and turnip were laid between days 4-9 of adult life but peak oviposition on cauliflower occurred 2-4 days following emergence and had declined to low levels by age 9 days **(Fig. 12)**.

Fig. 11: *Patterns of feeding by Scaptomyza flava on three host plants*

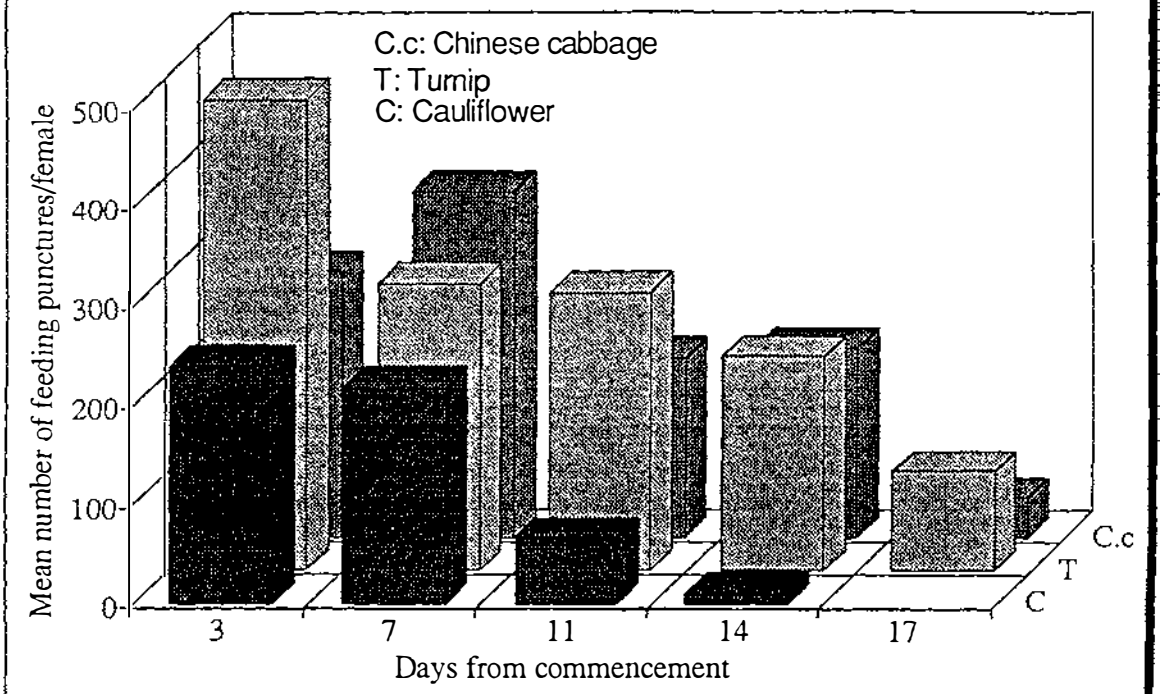
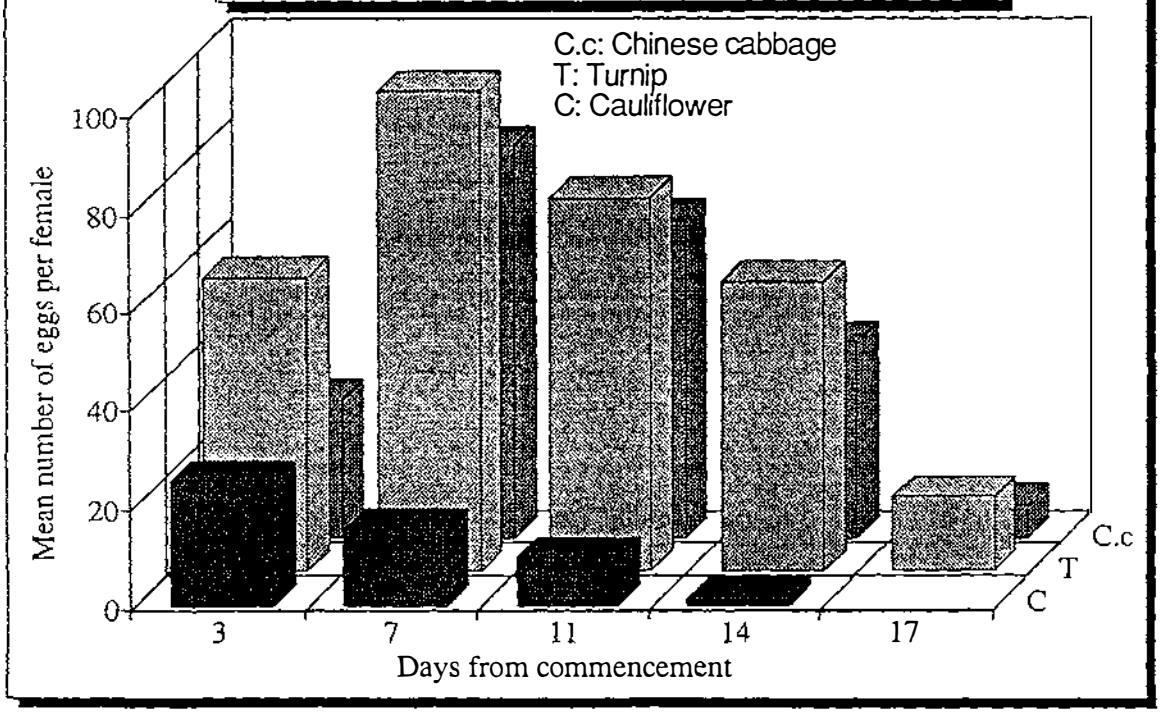


Fig. 12: *Patterns of egg laying by S. flava on three host plants*



HOST EFFECTS ON THE SURVIVAL AND DEVELOPMENTAL TIME OF *SCAPTOMYZA FLAVA*

INTRODUCTION

Development time is one of the fitness components least often analyzed in competition experiments. It plays a decisive role in the reproductive success of any individual by determining the age at first reproduction (Candelas *et al.,* 1990).

The adults of endophagous insects such as leaf miners choose the feeding sites of their offspring by choosing oviposition sites (Hering, 1951; Miller, 1973; Whitfield *et al.,* 1985). Selective pressures should result in females ovipositing in leaves which promote increased larval development and survival (Mitchell, 1975; Wiren and Larsson, 1984 and Larsson *et al.,* 1986). Therefore, larval occurrence and damage should reflect qualitative and quantitative differences in plant quality detectable by the ovipositing female (Chew, 1977; Rausher, 1979). Mandibular and ovipositor chemoreceptors exist in many insect species, including Diptera, which are sensitive to characteristic host plant chemicals and primary nutrients (Collinge, 1988). Adult females of some leaf-mining species appear to sample plant quality. For example, some Agromyzid females puncture holes in the leaf cells with their ovipositor and then "test" the sap (Dureseau and Jeandel, 1977); it is not clear whether female are merely sampling the leaf tissue or are actually feeding. *Scaptomyza flava* has the same habit of puncturing leaves.

Survival and duration of egg incubation, larval growth rate, and duration of pupal stage, which together determine total time from egg laying to adult emergence, may vary on different plant species (Pittara and Katsoyannos, 1992). In this study, my objectives were to quantify the influence of host type on several of these parameters for *Scaptomyza flava.* Three host plants were used: Chinese cabbage, turnip and cauliflower. The following parameters were measured: number of feeding punctures, number of eggs, times to first appearance of 1st instar larvae, mature larvae, pupae, and emergence of adult flies, and hence overall time from egg laying to adult emergence.

Unfortunately non have attempted to determine the bases of food quality and optimum requirements of nutritional ingredients for *Scaptomyza* species have not been reported. Thus the present work attempted to investigate the significance effected host plant on a particular stage such as larval development, pupal period, fecundity and adult lifespan of *Scaptomyza flava*.

MATERIALS AND METHODS

This experiment was conducted under greenhouse conditions. Three pairs of freshly emerged adult insects (within 12 h. of expected commencement of oviposition) were caged over individual plants (one month old 3-4 leaves, potted Chinese cabbage, turnip and cauliflower plants) for 72 hours from 8.1.1991. Leaf area can be critical to herbivore survival (Tuomi *et al.*, 1981), so for this experiment I selected plants with closely similar leaf area[1] to ensure that differences in miner survival were not simply due to leaf size differences. Experimental cages were made from PVC acetate sheet. Holes were cut on opposite sides and covered with net cloth for ventilation. Filter paper was placed in the bottoms of the cages to aid in the detection and recovery of pupae. At the end of the experimental period numbers of feeding punctures and eggs were recorded. Plants were then transferred to greenhouse benches. The duration of larval, pupal and adult stages from egg hatch to adult death was determined. Ambient temperature approximated 22°C, 60 ±5%RH and natural daylength was about 15.30 hours in January. Data for feeding punctures and eggs were recorded each day as this provided a more accurate record of feeding and ovipositional trends.

Overall egg-to-adult developmental time was determined by counting the number of eclosed flies at regular intervals (once or twice a day), until all flies had emerged. The beginning of the first larval stage was taken as the day or which larval were first observed and similarly for the commencement of the pupa stage. Data were analyzed

[1] Total leaf area and leaf area mined were measured by an Area Meter MK2 (Webb, 1989).

with a general linear models procedure (SAS Institute, 1985). Where significant differences in the variables occurred, means were separated using LSD test ($P \leq 0.05$).

RESULTS AND DISCUSSION

Results are presented in **Tables 17-18.**

Table 17: Mean numbers of punctures, eggs and adults of *Scaptomyza flava* and leaf area mined per plant

Host	No. of punctures/ plant	No. of eggs/ plant	No. of new adults emerged	Leaf area mined (cm^2)	Leaf area mined (cm^2)/ egg
Chinese cabbage	780 A	39 A	30 A	79 A	4
Turnip	400 B	41 A	33 A	86 A	2.9
Cauliflower	60 C	14 B	3 B	10 B	2.5

Treatments accompanied by the same letter are not significantly different at $P \leq 0.01$ (ANOVA followed by LSD test for separation of means).

Table 18: The mean durations (days) of the egg stage, the three larval instars, the pupal period and total time from egg laying to adult death on three plant species

Phase	Turnip	Chinese cabbage	Cauliflower
From egg laying to hatch of 1st instar larva	3 a	3 a	4 a
From 1st larva to 3rd larva stage	4.5 a	5 a	3 b
From 3rd stage to pupa	5 ab	3.7 b	8 b
From pupa to adult emergence	8 b	9 b	15 a
From egg to adult emergence	20.5 b	21 b	30 a
From adult emergence to adult death (lifespan)	10.5 b	13 a	11 b
From egg to adult death	31 b	33.7 b	41 a

Means in each row accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

Significant differences in developmental time to first instar larvae occurred only between flies reared on cauliflower compared to Chinese cabbage and turnip, but there were differences in development time to third instar larvae and to the pupa stage between the three hosts. Development was most rapid on Chinese cabbage, slowest on cauliflower and intermediate on turnip. Because of these differences errors may be made in field studies if generalisations about the biology of *Scaptomyza flava* are based on studies of populations on a single host even though multiple hosts may be present, *e.g.*, population dynamics may not always be generalised from host to host. There were no significant differences ($P > 0.05$) in number of eggs laid and adults emerged between Chinese cabbage and turnip, but cauliflower received significantly fewer eggs and produced fewer adults ($P \leq 0.01$). Very low number of eggs were laid in this experiment for unexplained reasons. Incubation time of eggs laid on cauliflower and duration of the pupa stage was longer than on turnip and Chinese cabbage. This combined with markedly fewer punctures, and slightly lower survival on cauliflower suggests that this is a less suitable host plant for *Scaptomyza flava* than turnip or Chinese cabbage. Mortality from egg to adult emergence was apparently low for all 3 plant species, though numbers of eggs observed was low. This low mortality could be due to the absence of predators under greenhouse conditions and to the low density of larvae. Lower survival may occur under field conditions. Which physical or chemical factors of these three Cruciferous host affect *Scaptomyza flava* development rate are unknown but differences in nutritional composition of host plants may well influence rate of development.

PREFERENCE FOR FEEDING AND EGG LAYING BY *SCAPTOMYZA FLAVA* WITH RESPECT TO LEAF AGE AND LEAF SIZE OF CHINESE CABBAGE

INTRODUCTION

Various factors influencing leaf selection by ovipositing leaf miners have been identified. For example, leaf size, leaf age, position, and as well as previous herbivore damage, affect leaf selection for oviposition by some adult leaf miners (Auerbach and Simberloff, 1989). Because leaf miners and gallers spend a major portion of their lives attached to one site on the host (Mitchell, 1983 cited by Clancy *et al.*, 1993), the size of the leaf often provides a good index of the resource available to the herbivore and thus enables one to quantify the subset of resources used by each to estimate the influence of leaf size on the fecundity and survival of the herbivores (Whitham, 1978; Van Driesche, 1983; Price, 1992 cited by Clancy *et al.*, 1993). The size and age of leaves or other plant parts is typically an important factor influencing oviposition choice, survival, and pupal or adult biomass of sedentary herbivorous insects such as leaf miners and gall formers (Clancy *et al.*, 1993).

Leaf phenology has been suggested to play an important role in the demography and population dynamics of herbivorous insects (Connor *et al.*, 1994). Apart from phenological effects on ontogenetic changes in the chemistry, moisture content, toughness and pubescence of leaves and their potential effects on insect growth, survival, reproduction and host selection, two distinct aspects of leaf-phenology have been proposed to affect populations of herbivorous insects: the timing of leaf production and the timing of leaf fall (Connor *et al.*, 1994).

In some leaf miners (*e.g., Lithocolletis quercus*), females strongly prefer young leaves but their discriminatory powers are not perfect (Pittara and Katsoyannos, 1992). Besides leaf age, the other cue related to leaf selection is leaf size. The size and shape

of a potential oviposition site is of great importance (Pittara and Katsoyannos, 1992).

Results of studies on several different leaf miners have demonstrated that some (but not all) species select bigger leaves or shoots over smaller ones (Clancy *et al.*, 1993). For example Mopper and his co-workers (1984 cited by Clancy *et al.*, 1993) found that leaf area was positively correlated with the density of microlepidopteran leaf miners on sand live oak. In general, other leaf miner studies have also found positive relationships between leaf size and mine density (*e.g.*, Hileman and Lieto, 1981; Tuomi *et al.*, 1981; Simberloff and Stiling, 1987; Sato, 1991 cited by Clancy *et al.*, 1993). Leaf size apparently influences how females disperse eggs and the probability of survival for their offspring (Faeth, 1991).

Often, leaves are also selected according to leaf nitrogen content (McNeil and Southwood, 1978; Mattson, 1980; Scriber, 1984). In this case, a leaf of high quality is defined as a leaf containing much nitrogen. Some authors (*e.g.*, Hanna *et al.*, 1987; Minkenberg and Fredrix, 1989) claim that the variation in nitrogen level among leaves may explain the distribution and growth of leaf miner populations to some extent.

I therefore performed a series of experiments to examined the selection of leaves of Chinese cabbage by *Scaptomyza flava* according to leaf age, area and nitrogen content. I hypothesized that such choice should be critical for this leaf miner.

MATERIALS AND METHODS

Ten individual naive females, each with two 3-day-old males, were caged in enclosed arenas over individual Chinese cabbage plants (4-5 leaf stage). Plants were placed in a greenhouse under ambient and artificial lighting (L14:D10) photoperiod with the photophase between 0600 and 20.00, and ca. 18 ± 2°C temperature with 80 ± 4% RH. Light was provided by three fluorescent tubes of the daylight type and during most

of the photophase also by natural daylight entering from windows. The light intensity (irradiance), at the level of the cages with the flies, varied between 4 and 15 W/m^2, depending on the outdoor illumination. The nuptial chambers (square cages 30 × 30 × 30 cm) were large enough so that the insects could fly freely around the plants. The insects were provided with honey solution and left for 72 hours from 9/2/1993 when plants were removed from cages. At the end of this period, the number and position of all feeding punctures and eggs were recorded for each individual leaf within each plant, starting with the outer (older) leaves, and working progressively to the smallest and youngest leaf in the centre of the plant. The area of each leaf was also measured. Samples of undamaged leaves were taken for N analysis.

Analysis of leaf nitrogen :

Nitrogen content may vary with the age of the plant, the age of the leaf and growing conditions. Thus leaf samples for analysis leaf nitrogen content were taken on 12/2/1993 from plants grown at the same time under similar conditions and same leaf age as those I used for experiments with insects. Leaves were removed and immediately taken to the laboratory. Leaf samples were dried at 60°C (in an oven) for 3 days before extraction. Before commencing digestion of leaves, tubes were weighed and tube weights recorded. All glassware used for analysis was first acid-washed in 2 M HCL (made with deionised water). To prepare the samples for analysis the following method was used (as described by Mahimairaja *et al.*, 1990). Nitrogen was determined by Kjeldahl method (McKenzie and Wallace, 1954) (Kjeldahl digestion solution allows measurement only of organic N and NH_4 -N): 250 g K_2 SO_4, 2.5 g Selenium powder, 2.5 litres Conc. H_2 SO_4.

- In digestion tube weigh approximately 0.1 g of dry herbage accurately and add 4 mls digestion solution.
- Heat to 350 °C for 4-5 hours, or until solution clears.
- Make up to 50 mls using distilled water.

- Shake and pour into numbered vial
- Store in fridge.
- Measurements were made using an autoanalyser.

The effect of leaf size on the leaf nitrogen was examined by analysis of variance and comparison of means.

RESULTS

Four of the ten females produced no leaf punctures or eggs. Results are presented in **Table 19** and **Figs. 13, 14** and **15**, for the remaining six.

Table 19: Mean leaf area, number of punctures, eggs and nitrogen content according to leaf age

Leaf age	Leaf size ($cm^{2)}$	No. of punctures	No. of punctures per cm^2	No. of eggs	No. of eggs/ cm^2	Nitrogen content Mmol/kg
First (oldest)	79 a (68-88)	330 a (20-450)	4.3 a	23 a (1-60)	0.3 a	3948 a
Second	60 b (55-87)	292 a (40-800)	4.1 a	9 b (1-21)	0.15 b	4378 a
Third	58 b (43-78)	203 a (20-550)	3.5 a	4 b (1-11)	0.06 bc	5422 a
Fourth	37 c (21-45)	74 b (10-180)	2 b	5 b (0-25)	0.13 b	4670 a
Fifth (youngest)	13 c (5-20)	2 c (0-8)	0.15 c	0 c	0 c	4678 a

Treatments accompanied by the same letter are not significantly different at $P \leq 0.05$.

The questions addressed in this study were: Is feeding or oviposition affected by leaf size? Do flies prefer (in sense of Singer [1986]) leaves of certain nitrogen level, for feeding and oviposition?

The results show that nitrogen content was not related to leaf age. Although all leaf sizes (ages) were accepted by the insects (with the exception of the smallest leaves for egg laying), the number of feeding punctures and eggs per cm^2 leaf decreased with decreasing leaf size (age). Thus younger leaves were not favoured for feeding or egg laying **(Table 19, Figs. 13, 14** and **15)**.

DISCUSSION AND CONCLUSIONS

Based on findings for other leaf miners (Hering, 1951; Whitham, 1978; Mopper *et al.,* 1984; Bultman and Faeth, 1986a; Craig *et al.,* 1989, 1990; Clancy *et al.,* 1993), I predicted that *Scaptomyza flava* would select larger Chinese cabbage leaves for feeding and oviposition. My results support this prediction. *Scaptomyza flava* spent considerably more time on older leaves than on younger ones (personal observation, unrecorded data) in my experiment, which supports the conclusions of Vaughun and Hoy (1993) that host preference can change with host age and leaf type. In contrast to these results some workers found that some insects selected young leaves for oviposition over old ones (see detail in the introduction).

Thus leaf size appears to be correlated with preference for feeding and oviposition by *S. flava.*

Scaptomyza flava females feed on sap that exudes from leaf punctures. It is possible that increased numbers of punctures on older leaves are associated with the increased difficulty of extracting sufficient nutrient from older leaves. However, as a choice of leaf age was freely available, this explanation is not likely.

Leaf size apparently influences how females disperse eggs and the probability

of survival for their offspring (Faeth, 1991). It is likely that variation in leaf sizes exerts the greatest influence on pattern of density and dispersion at the time of colonization via reduced oviposition and aggregated dispersion of eggs. That mean leaf size of cruciferous explains a significant amount of variation in density of *Scaptomyza flava.*

The positive relationship observed between leaf area and within-leaf miner density supports Mopper *et al.*'s (1984) findings on the selection of large leaves for oviposition. Murai (1974) suggested that ovipositing lepidopteran miners tend to avoid laying eggs on small leaves, or on leaf regions with previously deposited eggs. In a developing field situation plant phenology may also be important (Collinge, 1987), because the lower leaves are the first available and are present at the time of oviposition. Some lower leaves die before the average leaf miner completes development.

While these results show that *Scaptomyza* has preference for certain leaf ages, the mechanism by which discrimination occurs is unclear. Although I cannot currently resolve these uncertainties, some of above mentioned hypotheses cannot be eliminated without considerably more work.

Fig. 13: *Relationship between nitrogen content of leaf and leaf age of Chinese cabbage*

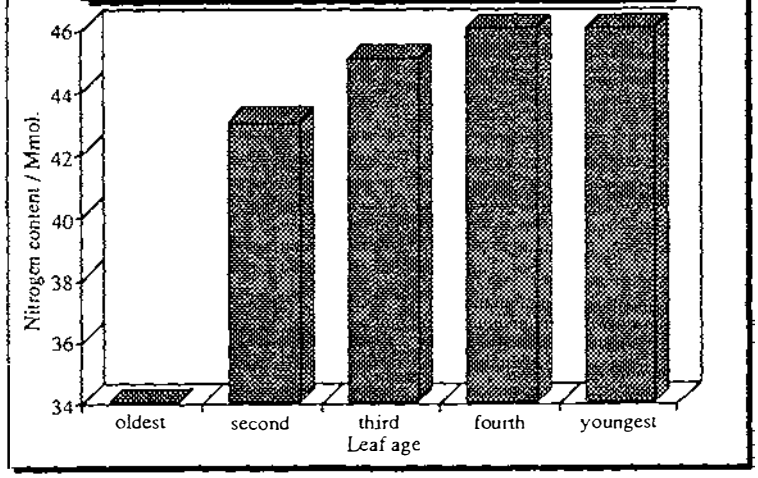


Fig. 14: *Relationship between number of feeding punctures of S. flava and leaf age*

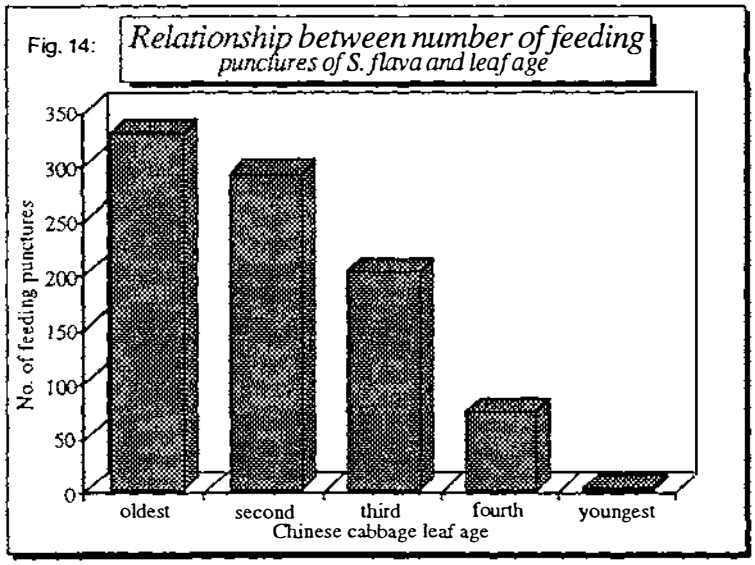
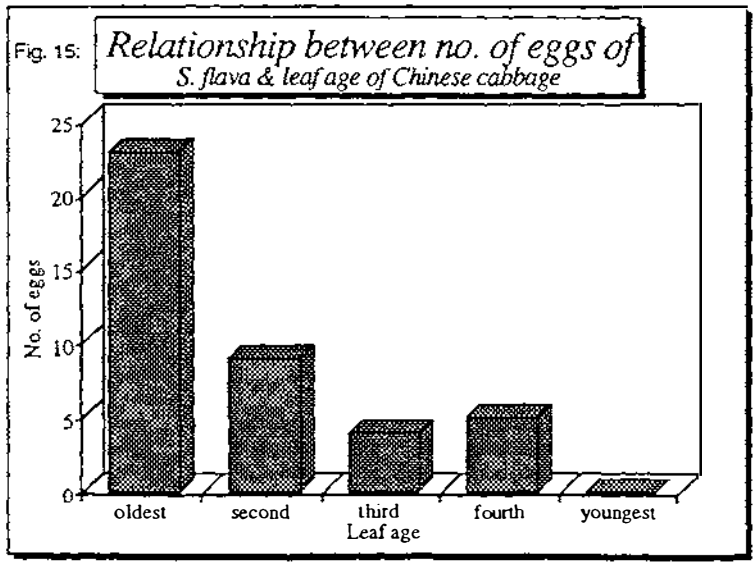


Fig. 15: *Relationship between no. of eggs of S. flava & leaf age of Chinese cabbage*



EFFECT OF LARVAL FOOD PLANT ON ADULT EGG LAYING PREFERENCE

INTRODUCTION

According to Hopkins' Host Selection Principle (Hopkins, 1917), the selection of a plant species for egg laying by adult female insects is influenced by the plant species on which the females developed in the larval stage. Hopkins' Host Selection Principle has been controversial since it was first put forward in 1917 (Hopkins, 1917) and there is little published data in its support.

> "A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behaviour..... With habitat and food selection - behavioral phenomena playing a major role in the shift into new adaptive zones, the importance of behaviour in initiating new evolutionary events is self-evident" (Mayr, 1963).

To determine whether Hopkins Host Selection Principle applies to *Scaptomyza flava*, an experiment was undertaken with three host species, Chinese cabbage, turnip and cauliflower.

MATERIALS AND METHODS

Scaptomyza flava was reared on 3 plant species, Chinese cabbage, cauliflower, and turnip. Plants were chosen to be about the same size and age (3-4 leaf stage).

In the first phase, plants of the 3 species were placed into separate cages containing adult insects (newly emerged unfed adults were obtained from a colony reared on Chinese cabbage) and left for 4 days (22/3/1993 - 26/3/1993). There were four males and four females per treatment. After eggs were laid the flies were removed. The infested plants were held separately under clean fine gauze cages for eclosion of larvae,

formation of pupae and emergence of the new generation of adult flies.

In the second phase, 8 males and 4 females obtained as described above from rearing on each of the three plant species were released into cylindrical cages (85 cm diameter, 90 cm high) (n=3), each containing 2 plants of the 3 plant species arranged randomly in a circular formation. Seventy-two hours later the numbers of feeding punctures and eggs on each plant were counted. Three replications were run over the next four weeks. A one-way analysis of variance (ANOVA) was undertaken. Comparisons among treatment means were subjected to LSD test ($P \leq 0.05$).

RESULTS

Results are presented in **Table 20** and **Figures 16** to **21**.

Table 20: Influence of larval food plant on adult feeding and egg laying preference

1) Adult insects raised as larvae on **cauliflower**[1]:

Plant	Mean no. of punctures	Percentage of punctures	Mean no. of eggs	Percentage of eggs
Cauliflower	5 c	1.5%	1 b	9%
Chinese cabbage	250 a	70.5%	6 a	55%
Turnip	100 b	28%	4 a	36%
Total	355	100%	11	100%

[1] Within a column, treatments accompanied by the same letter are not significantly different at $P \leq 0.05$.

2) Adult insects raised as larvae on **Chinese cabbage**[1]:

Plant	Mean no. of punctures	Percentage of punctures	Mean no. of eggs	Percentage of eggs
Cauliflower	95 b	3%	39 ab	32%
Chinese cabbage	1700 a	49%	60 a	49%
Turnip	1650 a	48%	24 b	19%
Total	3445	100%	123	100%

3) Adult insects raised as larvae on **Turnip**[1]:

Plant	Mean no. of punctures[2]	Percentage of punctures	Mean no. of eggs	Percentage of eggs
Cauliflower	61 C	4%	19 b	32%
Chinese cabbage	485 B	34%	14 b	23%
Turnip	866 A	62%	27 a	45%
Total	1412	100%	60	100%

[1] Within a column, treatments accompanied by the same letter are not significantly different at $P \leq 0.05$.

[2] Within a column, treatments accompanied by the same letter are not significantly different at $P \leq 0.01$.

4) Mean total numbers of feeding punctures and eggs from insects raised as larvae on each plant

Plant	Feeding punctures	Eggs
Cauliflower	118.33 c	3.58 c
Chinese cabbage	1148.3 a	41.3 a
Turnip	478.17 b	20.4 b

Within a column, treatments accompanied by the same letter are not significantly different at $P \leq 0.05$.

DISCUSSION

In terms of total feeding punctures and eggs laid, flies reared on Chinese cabbage produced significantly more than those reared on turnip, which in turn produced more than those reared on cauliflower. This suggests that Chinese cabbage is the better quality host plant. Flies reared on turnip produced significantly more feeding punctures ($P \leq 0.01$) on turnip than on Chinese cabbage or cauliflower **(Table 20[3]).** Also they deposited significantly more eggs on turnip ($P \leq 0.05$) compared with Chinese cabbage and cauliflower.

Flies reared on Chinese cabbage produced an equal number of feeding punctures on Chinese cabbage compared to turnip, but showed a distinct preference for Chinese cabbage for egg laying. However, flies reared on cauliflower showed no preference for cauliflower and made most feeding punctures and laid most of their eggs on Chinese cabbage.

Thus, although there was significant preference for both egg laying and feeding on turnip in the case of insects raised on that plant and similar slight preference in the case of Chinese cabbage, this was not the case at all for cauliflower where rearing on that plant induced no preference.

The results from the present experiment appear to support the principle in the case of Chinese cabbage and turnip, though not for cauliflower. However, the results should be viewed with caution due to the limited number of insects used and the fact that the laboratory colony, from which the test insects were drawn, had been maintained for a considerable number of generations on Chinese cabbage.

Further experiments with large numbers of insects of field origin would be desirable before it can be claimed that this is a true case of Hopkins' Host Selection Principal.

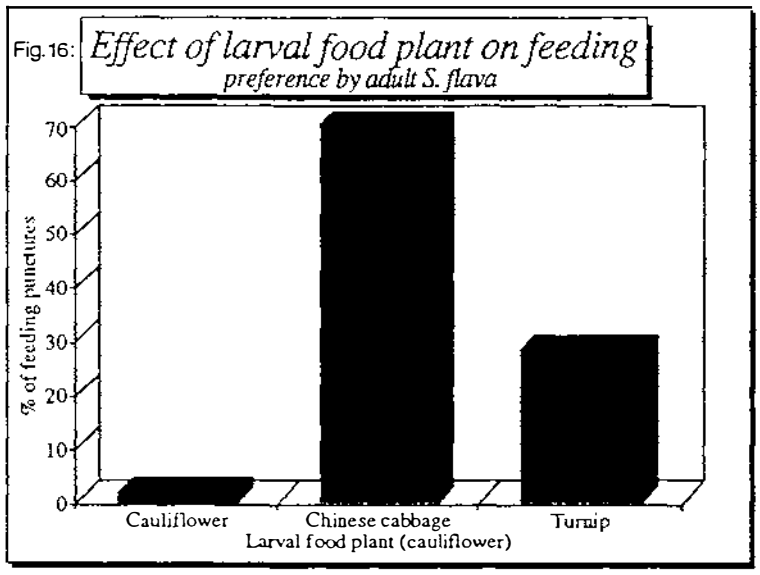


Fig.16: Effect of larval food plant on feeding preference by adult S. flava
% of feeding punctures
0
10
20
30
40
50
60
70
Cauliflower
Chinese cabbage
Turnip
Larval food plant (cauliflower)

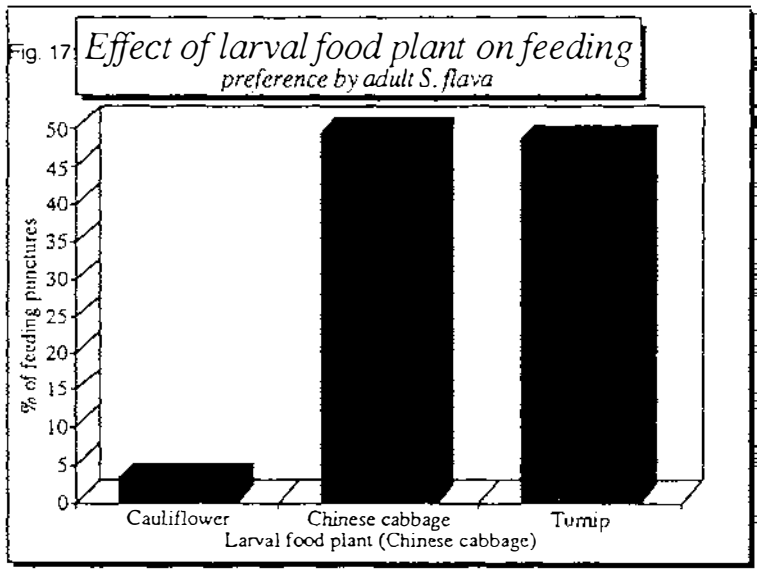


Fig. 17: Effect of larval food plant on feeding preference by adult S. flava
% of feeding punctures
0
5
10
15
20
25
30
35
40
45
50
Cauliflower
Chinese cabbage
Turnip
Larval food plant (Chinese cabbage)

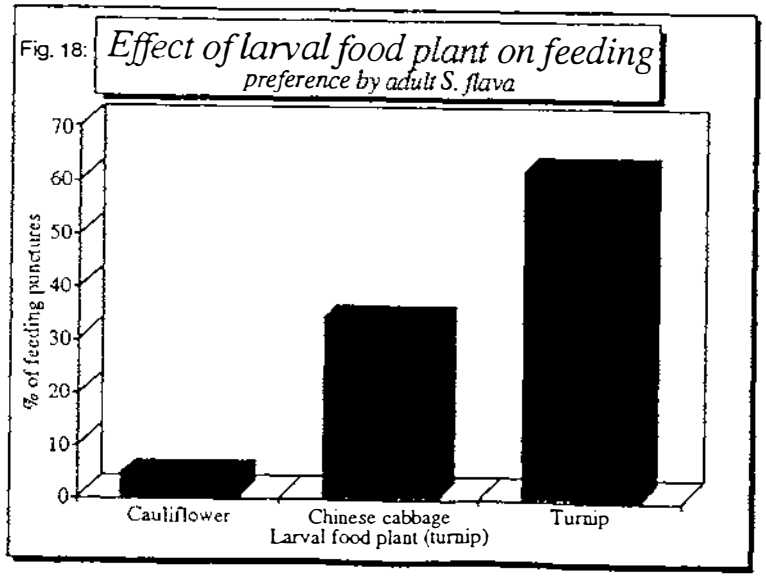


Fig. 18: Effect of larval food plant on feeding preference by adult S. flava
% of feeding punctures
0
10
20
30
40
50
60
70
Cauliflower
Chinese cabbage
Turnip
Larval food plant (turnip)

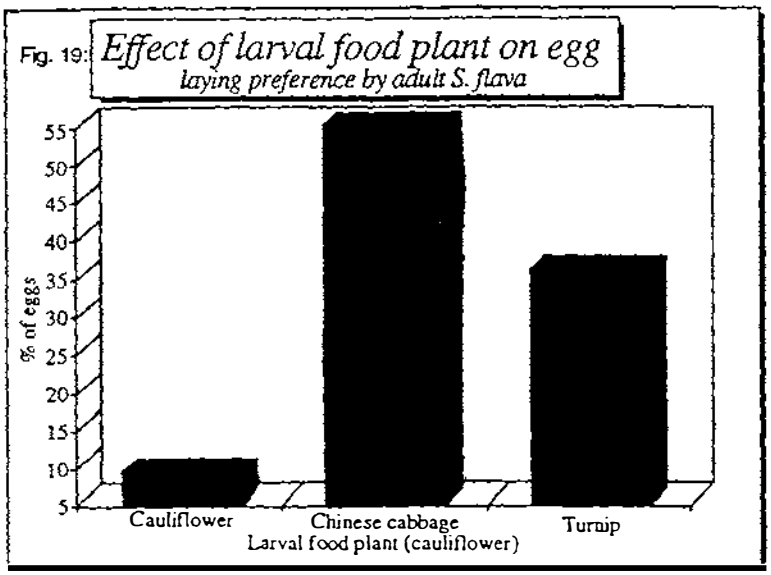


Fig. 19:
Effect of larval food plant on egg laying preference by adult S. flava
% of eggs
55
50
45
40
35
30
25
20
15
10
5
Cauliflower
Chinese cabbage
Turnip
Larval food plant (cauliflower)

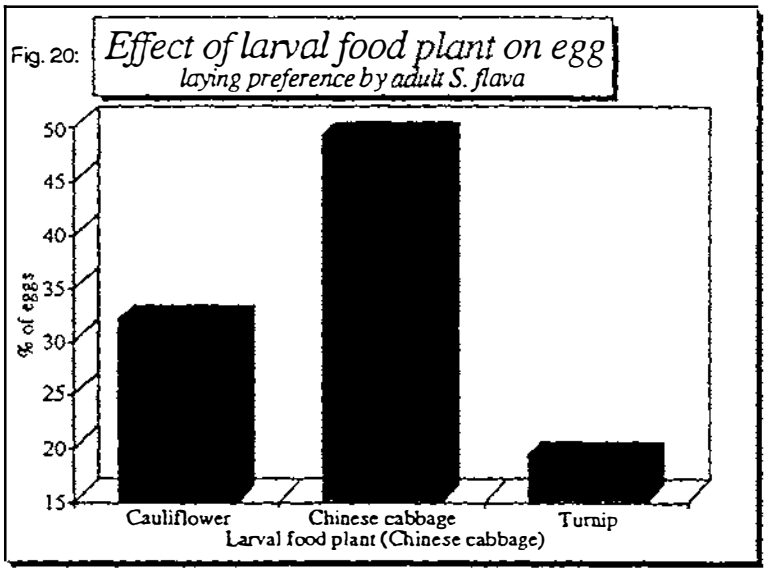


Fig. 20:
Effect of larval food plant on egg laying preference by adult S. flava
% of eggs
50
45
40
35
30
25
20
15
Cauliflower
Chinese cabbage
Turnip
Larval food plant (Chinese cabbage)

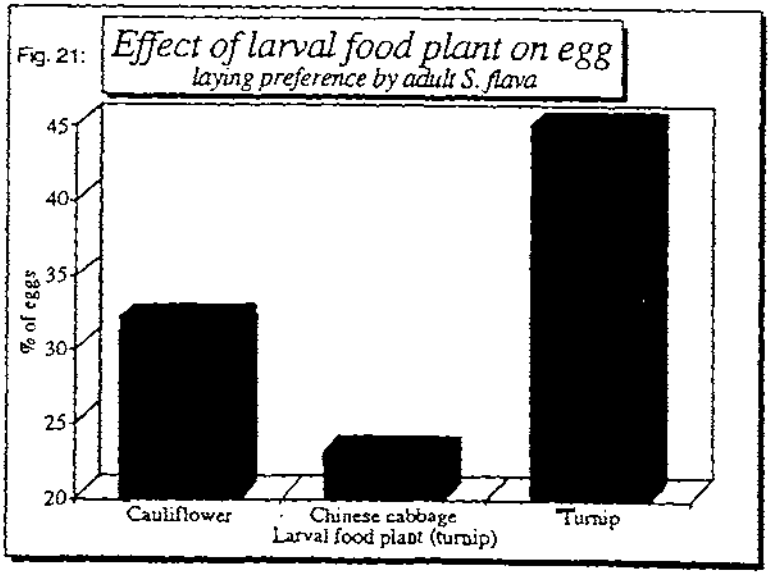


Fig. 21:
Effect of larval food plant on egg laying preference by adult S. flava
% of eggs
45
40
35
30
25
20
Cauliflower
Chinese cabbage
Turnip
Larval food plant (turnip)

EFFECT OF ADULT EXPERIENCE ON OVIPOSITION PREFERENCE

INTRODUCTION

The role of learning in host selection by phytophagous insects has received a good deal of attention over the last few years (see reviews by Jermy, 1986; Papaj and Prokopy, 1989; Lee and Bernays, 1990; Papaj and Lewis, 1993). Much of this attention has focused on what is commonly known as induction of preference, that is, increased preference for a plant food as a result of feeding experience with the food.

A number of recent laboratory and field studies on insects have demonstrated that early experience of adult insects with host plants can affect subsequent responses to hosts (Prokopy *et al.*, 1982; Papaj, 1986 cited by Hoffmann, 1988). Most studies have reported positive experience effects, where insects show a tendency to be attracted to, or oviposit on, the host to which they were exposed. Positive experience effects are usually interpreted as evidence that insects can learn to remain associated with particular hosts (show habitat fidelity). However, negative experience effects (where insects avoid the host they were previously exposed to) have been found in some cases (Hoffmann, 1988; Blaney and Simmonds, 1985).

The larval environment does not appear to strongly affect host preferences in phytophagous insects and relevant adult experience can only occur in the period between eclosion and departure from the larval host. The length of this period will depend on the dispersal behaviour of the young adults and the extent to which hosts of the same type are aggregated. Experience effects in recently eclosed adults have been studied particularly in experiments with *Drosophila* (Jaenike, 1982, 1983; Hoffmann, 1985 cited by Hoffmann, 1988). A limitation of some of these studies has been that the experimenter rather than the insect determined the length of exposure to a host. Adults were held on hosts in confined containers for at least 3 days, and it is unknown whether

recently eclosed individuals would stay near their larval environment for so long. Forced exposure to a host can also lead to changes in host response unrelated to learning. For example, insects may become starved as a consequence of confinement on a nutritionally poor host, and apparent positive learning effects may result if the starved adults are less discriminating than individuals kept on a high quality host (Hoffmann, 1988).

For this experiment three plant species were chosen which in previous experiments had shown high numbers of eggs (**Chinese cabbage**), intermediate numbers (**turnip**) and low numbers (**cauliflower**).

MATERIALS AND METHODS

Five, recently eclosed female *Scaptomyza flava* plus 10 males from the laboratory rearing colony (on Chinese cabbage) were released at 08.30 hours into screen mesh square cages (30 × 30 × 30 cm). Three potted plants were placed in each cage spaced 20 cm apart. There were four treatments:

1. all three plants of cauliflower (non-choice experience).
2. all three plants of Chinese cabbage (non-choice experience).
3. all three plants of turnip (non-choice experience).
4. one plant each of cauliflower, Chinese cabbage and turnip (choice experience).

The insects were allowed to feed on the plants for 24 hours. During this time no eggs were laid (plants were checked for possible eggs). The following day, between 08.30 and 09.00, the insects (two males and one female from each cage) were removed from the cages by aspirator and transferred to cages of the same size, each containing one plant of the three species. The experimental design was a randomized complete block with four treatments and eight replications (single females). After 48 hours the numbers of feeding punctures and eggs on each plant were recorded. A video camera (Panasonic F15) was set up on a dissecting microscope with zoom lens for counting punctures and eggs on a television screen.

RESULTS

The results obtained are given in **Table 21** and **Figures 22** and **23.** Insects first allowed to choose between the three plant species (**Table 21,** treatment 4) preferred Chinese cabbage for feeding and egg laying over turnip and cauliflower in the second phase of the experiment. No eggs at all were laid on cauliflower. The same order of preference was shown when insects were first exposed to cauliflower (**Table 21,** treatment 1). When insects first fed on Chinese cabbage (**Table 21,** treatment 2) there was an unexpected preference for turnip. However, when insects first fed on turnip (**Table 21,** treatment 3) there was no difference subsequently between turnip and Chinese cabbage, either for feeding or egg laying. In all treatments, including first exposure to cauliflower, cauliflower was the least preferred species.

Table 21: Effect of first adult feeding on plant preference

1) Adult insects first fed on **cauliflower**:

Plant	Mean No. of punctures per plant	Percen-tage	Mean No. of Eggs per replication	Percen-tage
Cauliflower	22 b	5%	1.5 b	13.6%
C. Chinese	285 a	67%	6 a	54.4%
Turnip	118 b	28%	3.5 b	32%
Total	425	100%	11	100%

2) Adult insects first fed on **Chinese cabbage**:

Plant	Mean No. of punctures per plant	Percen-tage	Mean No. of Eggs per replication	Percen-tage
Cauliflower	8 b	3.5%	0.25 b	3%
C. Chinese	60 b	26%	1.87 ab	30%
Turnip	162 a	70.5%	4 a	67%
Total	230	100%	6	100%

3) Adult insects first fed on **Turnip**:

Cauliflower	12 b	2.5%	1 b	7%
C. Chinese	226 a	48%	7 a	50%
Turnip	234 a	49.5%	6 a	43%
Total	472	100%	14	100%

4) Adult insects first allowed to select between cauliflower, Chinese cabbage and turnip **(control treatment)**:

Cauliflower	4 c	1%	0 c	0%
C. Chinese	226 a	62%	15.6 a	67%
Turnip	135 b	37%	7.6 b	23%
Total	365	100%	23.2	100%

5) Mean total numbers of feeding punctures and eggs from insects first fed on each plant

Plant	Feeding punctures	Eggs
Cauliflower	141.6 a	3.6 bc
Chinese cabbage	76.72 b	2.01 c
Turnip	157.3 a	4.6 b
Control treatment	120.9 a	7.9 a

Within a column, treatments accompanied by the same letter are not significantly different at $P \leq 0.05$

DISCUSSION

Little is yet known about the role of learning in host selection by Drosophilidae insect species. Lewis and van Emden (1986) discussed examples of the effects of previous feeding experience on an insect's subsequent preference for host plants and a number of studies have documented induced feeding preferences in insects (Jermy *et al.*, 1968; Wiklund, 1973; Phillips, 1977; Barbosa *et al.*, 1979; Jermy *et al.*, 1982; Ferguson *et al.*, 1991). In this experiment, previous feeding experience of adult *Scaptomyza flava* on cauliflower and Chinese cabbage did not enhance feeding and egg laying preference for these hosts.

Considering the total numbers of leaf punctures produced after exposure to each plant species, insects allowed to feed on cauliflower for 24 hours produced the lowest number of punctures. This is in agreement with the results of the experiment "Comparison of plant species as hosts for *Scaptomyza flava*". The total number of punctures was highest after exposure to turnip.

Egg numbers overall were low especially after exposure to cauliflower. It is possible that the 48-h period over which the experiment was conducted was not long enough to allow full expression of fecundity.

The general conclusion from this experiment is therefore that exposure of adult *S. flava* for 24 hours to one plant species did not increase preference for that species for production of feeding punctures. The extent to which the host fidelity occurs in the field may depend on the nature of the resources that *Scaptomyza flava* flies encounter after eclosion. Rather than occurring because of adult experience, host fidelity may occur if individuals encounter fresh plants of the same type as their larval or adult host near the eclosion site (non-choice situation) (Hoffmann, 1988).

Fig. 22: *Effect of adult experience on feeding preference by S. flava adult flies*

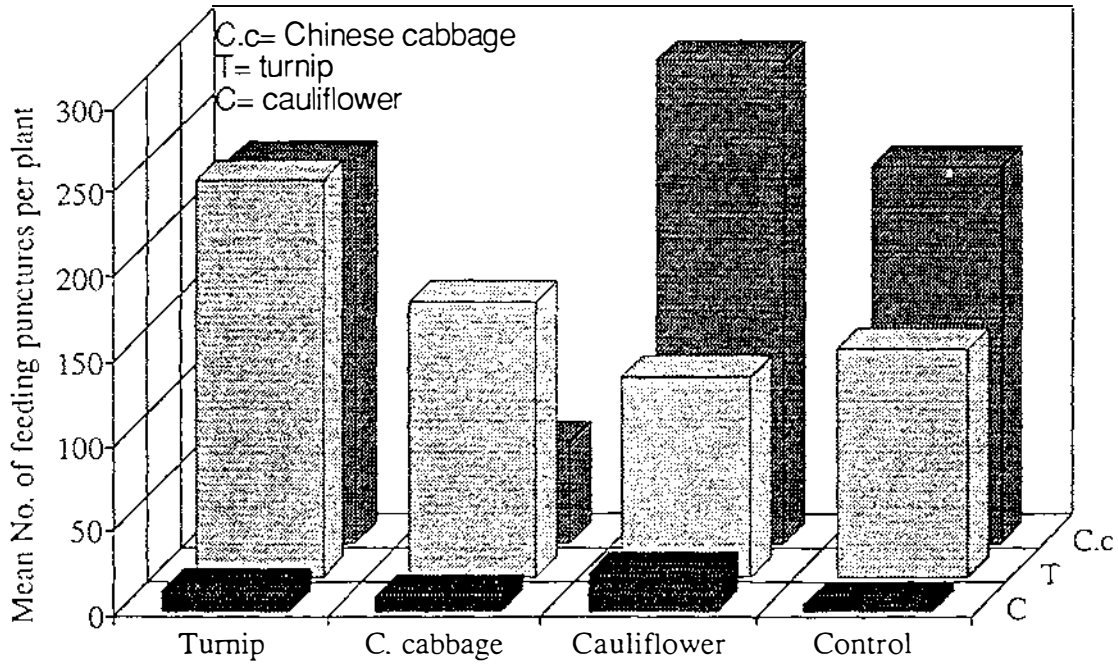
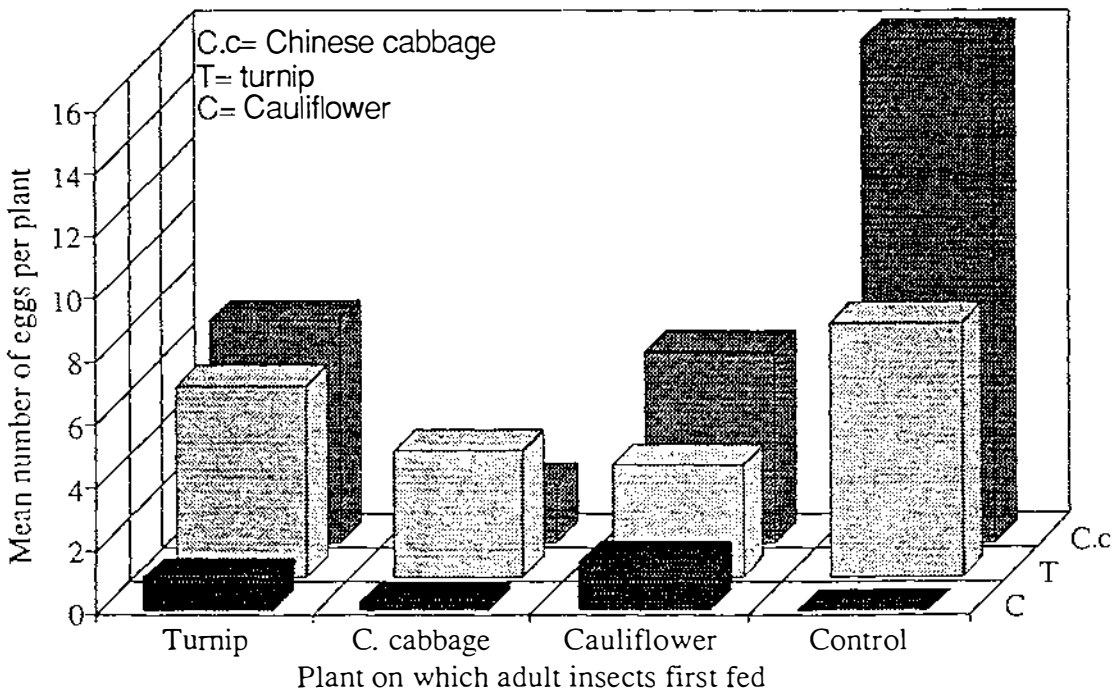


Fig. 23: *Effect of adult experience on oviposition preference by S.flava flies*



Chapter 4

SEASONAL LIFE CYCLE AND POPULATION DEVELOPMENT OF *SCAPTOMYZA FLAVA*

INTRODUCTION

Many population studies reported in the literature considered key-factors and density-dependent processes which govern insect population dynamics, but only a few species of two-winged flies have been studied in this respect (Hövemeyer, 1992). *Scaptomyza* leaf miners appear to have been little studied previously, and life cycle data on *Scaptomyza flava* in New Zealand, are lacking probably because the insect was considered to be a minor pest. The need for basic biological studies on *Scaptomyza flava* has been enhanced by the increasing importance of this leaf miner as a pest of cultivated *Brassicaceae.*

Studies by Minkenberg (1990) showed that the host plant and its growing conditions and temperature have a considerable effect on the life history of some leaf miners (*e.g.*, Agromyzid flies). A few studies have addressed the effects of temperature on the development and reproduction of the leaf miner *Liriomyza bryoniae* (Minkenberg and Helderman, 1990).

STUDY SITE

Studies of the seasonal life cycle and biology of *Scaptomyza* spp. were carried out on Massey University Plant Growth Unit land (PGU) at Palmerston North, Manawatu, New Zealand over a 2-year period from October 1990 to September 1992. The study site was located in a 5 ha. field in grass and mixed vegetable cultivation. The climate of the area is classified as humid temperate with no distinct summer dry season. In order to gather information on the prevailing temperature and precipitation during the

leaf-miner survey, the meterological data of agroclimatic station in the region was provided. Mean annual rainfall at the nearest weather station (AgResearch Grasslands) approximately one km away is 1240 mm (mean of 30 years. December has the most rain [110 mm] and February the least [70 mm]). Mean temperatures of the hottest (February) and coldest (July) months at that station (mean of 30 years) are 18°C (65°F) and 6°C (43°F), respectively. The site was on a silt loam soil at an altitude of 30 metres, longitude of 175°.37′E and latitude of 40°.23′S. **Figures 24** and **25** summarize the weather pattern over the two year study period.

A small area was repeatedly sown with Chinese cabbage *Brassica rapa chinensis* group *(Brassica campestris* spp. *pekinensis)* and turnip *Brassica rapa L.* plants at approximately 2 monthly intervals from June 1990 to June 1992 (vegetative growth of Chinese cabbage and turnip extend throughout the year). Two rows each of approximately 25 metres length were sown of each plant species on each date.

SAMPLING METHODS

Sampling is an integral part of any seasonal population determination programme. The number of samples required is determined by the degree of precision required plus other factors such as sample variability, and distribution and abundance of the pest population. An estimate of the pest population that has a standard error within 25% of the mean is considered acceptable for crop protection entomology (Southwood, 1978; Stewart and Sears, 1989).

The seasonal field population trends of *Scaptomyza flava* were followed in the field area during 1990 - 1992 by sampling at weekly intervals.

Sampling of each sowing commenced once a number of mature sized leaves had developed on each plant. Once plants become overmature and started to flower sampling

was transferred to a new sowing of younger plants.

In order to obtain abundance estimates two life stages were sampled : (i) adults and (ii) larvae (which were still within their mines).

A: SAMPLING FOR ADULT FLIES

Three collection methods were tried for determining numbers of adult *Scaptomyza* present within the planted area:

i) Sticky traps
ii) Water traps
iii) Sweep netting

I) STICKY TRAPS

Sticky traps provide a simple method of obtaining relative measurements of insect populations. Sticky traps can also detect early pest infestation more efficiently than intensive unit area sampling because they serve to collect and fix the insects within the trap area (Southwood, 1978; Heinz *et al.,* 1992).

Sticky traps consisted of yellow cylinders of approximately 25 cm height × 15 cm diameter mounted on a post approximately 1 metre above soil level. Each cylinder was covered with a removable acetate sheet smeared with insect trapping grease. Sticky traps were operated over October and November 1990.

II) WATER TRAPS

Two yellow plastic buckets (30 cm diameter) part filled with water plus a little detergent were used as water traps and were partly sunk into the ground between rows.

Water traps were operated and examined weekly for 12 months from late November 1990 through November 1991.

III) SWEEP NETTING

The sweep net is one of the most common methods used for sampling insects on cruciferous plant species. However, the sweep net gives only a relative estimate of the actual population density. Factors such as row spacing, insect developmental stage, plant growth characteristics (plant height being the most important factor), and time of day may affect efficacy of sweep net sampling (Studebaker *et al.,* 1991).

Sweep net samples were taken usually between 0900 and 1000 hours weekly throughout the study period from November 1990 to September 1992. Only during very heavy rain was sampling suspended. A net of 38 cm diameter (generalized insect sweep net) was used to make 10 arm length sweeps brushing lightly through the foliage of the plants while walking along a row and covering a strip of about 100 m by 70 cm. Netted samples were transferred to clear plastic bags in the field, sealed, and brought back to the laboratory for counting, sorting and identification. After killing by ethyl acetate vapour or anaesthetizing by CO_2, specimens of *Scaptomyza* were separated from the rest of the catch and identified to species (*S. flava, S. fuscitarsis* and *S. elmoi*). Voucher specimens have been deposited in the insect collection of Massey University of New Zealand. Student's t-test (SAS Institute, 1985) was used for comparison of numbers of adult *Scaptomyza flava* swept from Chinese cabbage compared to turnip.

B: SAMPLING FOR LARVAE AND FOR LEAF MINING INJURY

In 1991, to determine populations of larvae, random samples of 10 Chinese cabbage and 10 turnip leaves were taken each week from the centre rows of the plots (in order to avoid edge effects) throughout the year. Larvae were dissected free from mines under a stereomicroscope, counted, then killed and preserved in 75% ethanol.

At fortnightly intervals from November 1991 to December 1992 five Chinese cabbage and five turnip plants were taken at random (according to table of random numbers) from the centre area of the plots. In this programme for Chinese cabbage and turnip whole-plant samples were used to obtain estimates of larval population density. Plants were cut off at ground level and returned to the laboratory for close inspection. Measurements were made on each plant to determine leaf area (area of each leaf and total leaves), area mined, height of plant from crown to the tip of the highest leaf, number of leaves, and number of larvae. I also compared mean leaf area of the two host plants to ensure that any variation in miner density was not simply due to leaf size differences. To determine total leaf area and mined area (in cm^2) a MKII leaf area meter was used **(Plate 18)**.

RESULTS AND DISCUSSION

The results are summarised in **Tables 6**, **7** and **9** of **Appendix 7** and **Figures 26** to **31** and are discussed under four headings:

1. comparison of sampling methods for adults,
2. relative numbers of adults on Chinese cabbage compared to turnip,
3. seasonal changes in abundance of adults and larvae on Chinese cabbage, and
4. numbers of *Scaptomyza elmoi* and *Scaptomyza fuscitarsis*.

1. Comparison of sampling methods for adults

Sticky traps caught 8 *Drosophila* adults during the 6 weeks that they were operated but no *Scaptomyza* were captured and traps were abandoned for further sampling.

Numbers of adult *Scaptomyza flava* caught each week by sweep netting and water trapping on Chinese cabbage for the 12 months from November 1990 are shown

in **Fig. 26**. Similar data for turnip is shown in **Fig. 27**. Generally, peaks and troughs in numbers were paralleled by the two sampling methods but sweep netting caught consistently higher numbers. As the effectiveness of water traps is dependent on flight activity of insects, and as this in turn may be affected by prevailing weather conditions it was decided to cease water trapping after 12 months and to base comparisons over the 2 year study period on sweep net sampling data.

2. Relative numbers of adults on Chinese cabbage compared to turnip

The fluctuations in numbers of adults from Chinese cabbage and turnip, both by water trap and sweep net sampling, were closely similar over 12 months from November 1990 (**Figs. 26** and **27**). However, numbers swept from turnip for the period were somewhat higher than from Chinese cabbage (but differences were not significant, *t-test:* $t = 1.83$, $P > 0.05$) especially over the winter months of June, July and August.

3. Seasonal changes in abundance of adults and larvae on Chinese cabbage

Seasonal changes in numbers of adults on Chinese cabbage as determined by sweep netting and of larvae from leaf sampling are shown on **Fig. 28** for the period November 1990 to November 1991 and in **Fig. 29** for adults only for 24 months from November 1990.

Adults and larvae were present throughout the year with no evidence of diapause or aestivation. However, there was considerable variation in numbers from month to month. There is a pattern of higher numbers of flies during spring and early summer (October - December) and again in autumn to early winter (May - July) with lower numbers in early autumn (March - April) and early spring (September - October). Numbers of larvae paralleled and slightly preceded the peaks and troughs in numbers of adults **(Fig. 28).**

Prevailing weather conditions and stage of growth of the host plant, in addition to overall seasonal temperature changes, may play a major role in determining numbers. There was particularly heavy rainfall in February 1992 **(Fig. 24)** and this was followed by low numbers of adults in March and April. The same pattern is apparent to a lesser extent in January/February 1991 (high rainfall) followed by low numbers of adults in April.

Although I have no any reason to believe that my 2 year-study was in any way atypical. Data were obtained on adult flies and larval activity from traps operated over 2 year period, the results do not enable firm conclusions to be drawn as to dates of generation number. From the above results, I draw the following conclusions:
(1) *Scaptomyza flava* leaf miner population in Brassicaceae field varied as the season progressed; (2) *S. flava* were more aggregated at the earlier part of the summer and winter; (3) with no evidence of cease over the winter or summer months.

Observations indicated that the infestation was generally heaviest in the plants along the edge of the planted area (unrecorded data). The reasons for this are not known but within the planted area adults can disperse to host plants in any direction, but at the edges, because of their close relationships with the host, they have only a 180° range for such movement.

4. Numbers of *Scaptomyza elmoi* and *Scaptomyza fuscitarsis*

Small numbers of the closely related species *Scaptomyza elmoi* and *Scaptomyza fuscitarsis* were collected in sweep net samples from both Chinese cabbage and turnip. Data for the 12 month period from November 1991 is presented in **Fig. 31** (and **Table 8** of **Appendix 7**). Laboratory experiments (**Appendix 6**) showed that *S. elmoi* is saprophagous in habit and does not oviposit or develop in living leaves (of Chinese cabbage). The insects captured by sweep netting in the field are therefore unlikely to have developed from the turnip or Chinese cabbage plants.

Fig. 24: *Seasonal Rainfall & Relative Humidity*

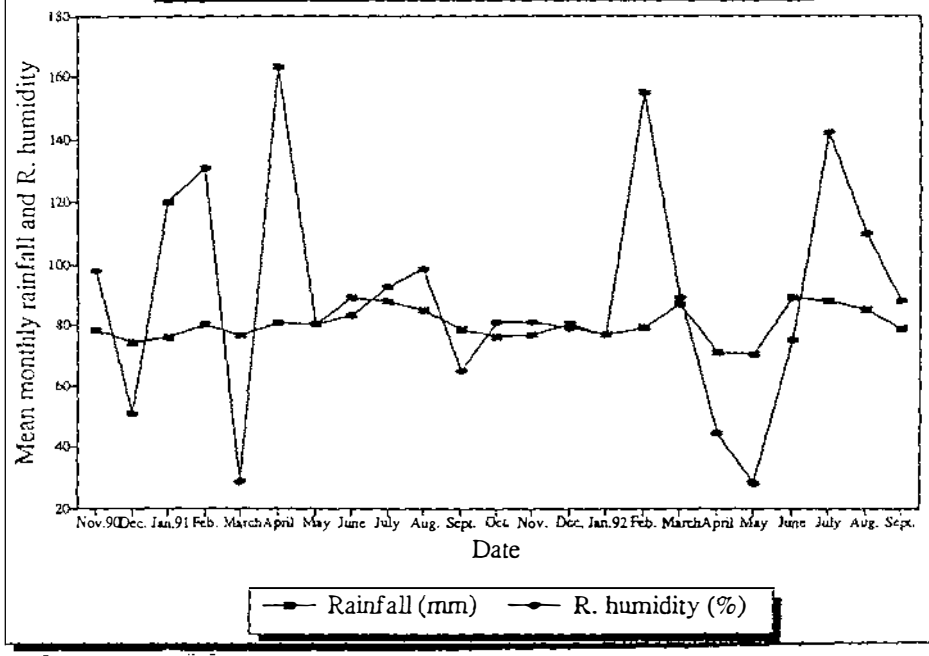


Fig. 25: *Seasonal Temperature (Max., Mean, Min.)*

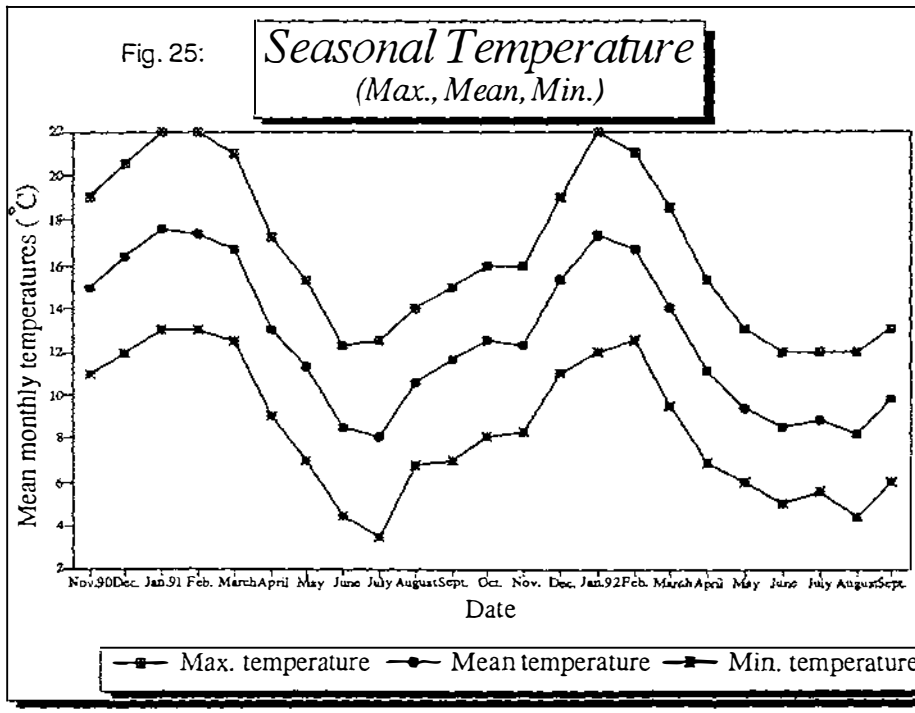


Fig. 26: *Weekly Sampling of S. flava on* Chinese cabbage by two sampling methods

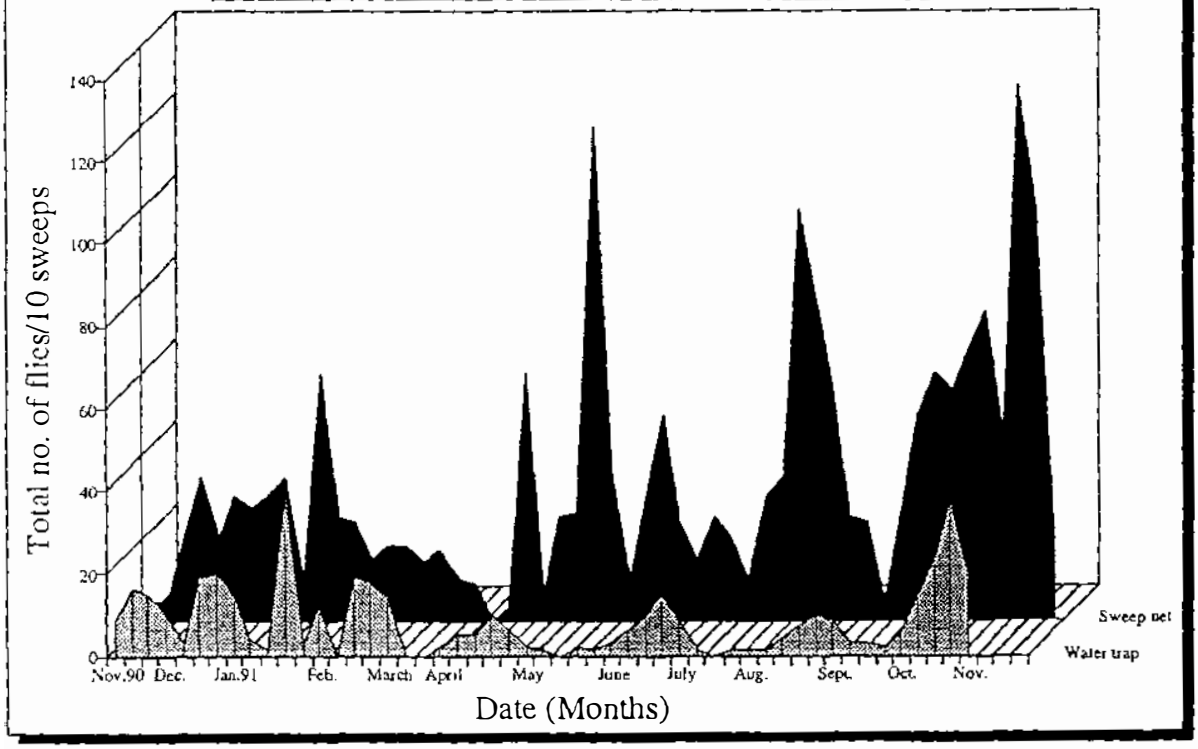


Fig. 27: *Weekly Sampling of Scaptomyza flava on turnip by two sampling methods*

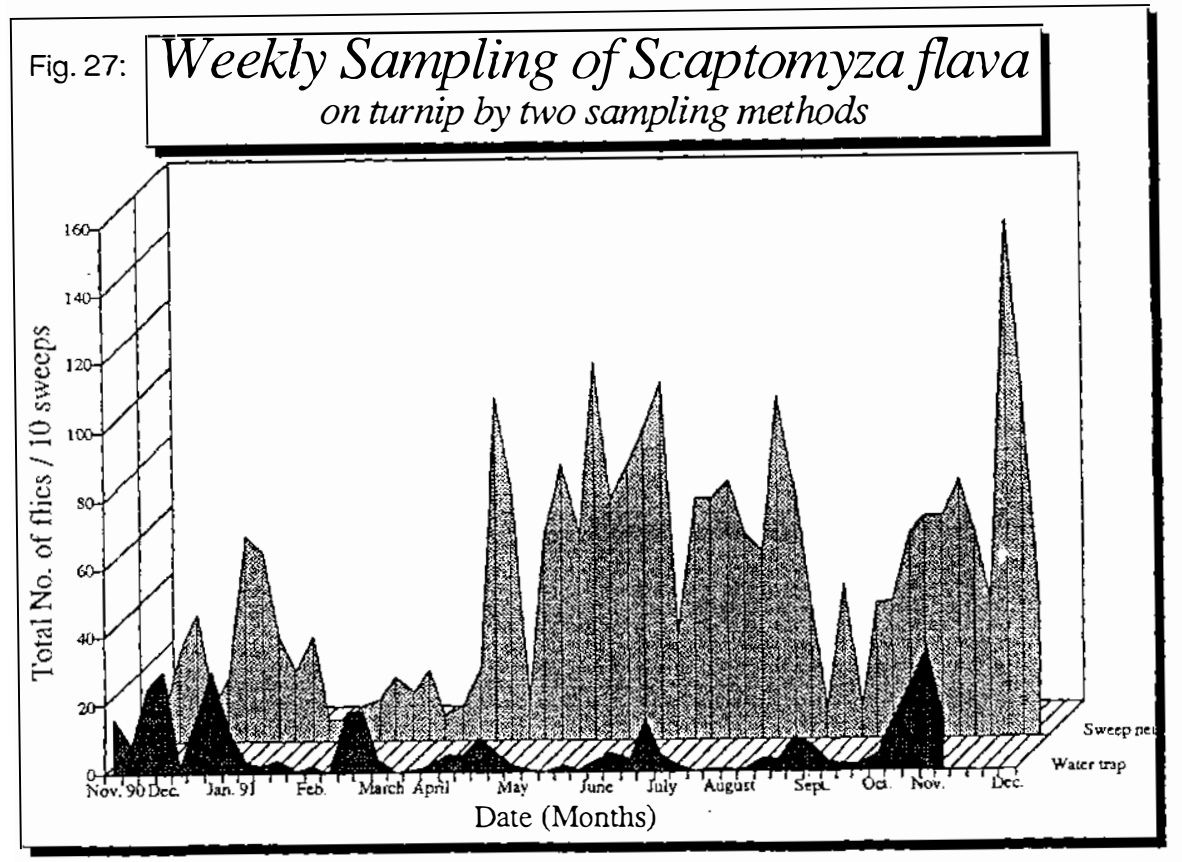


Fig. 28: *Weekly Sampling of Scaptomyza flava*
adults and larvae on Chinese cabbage

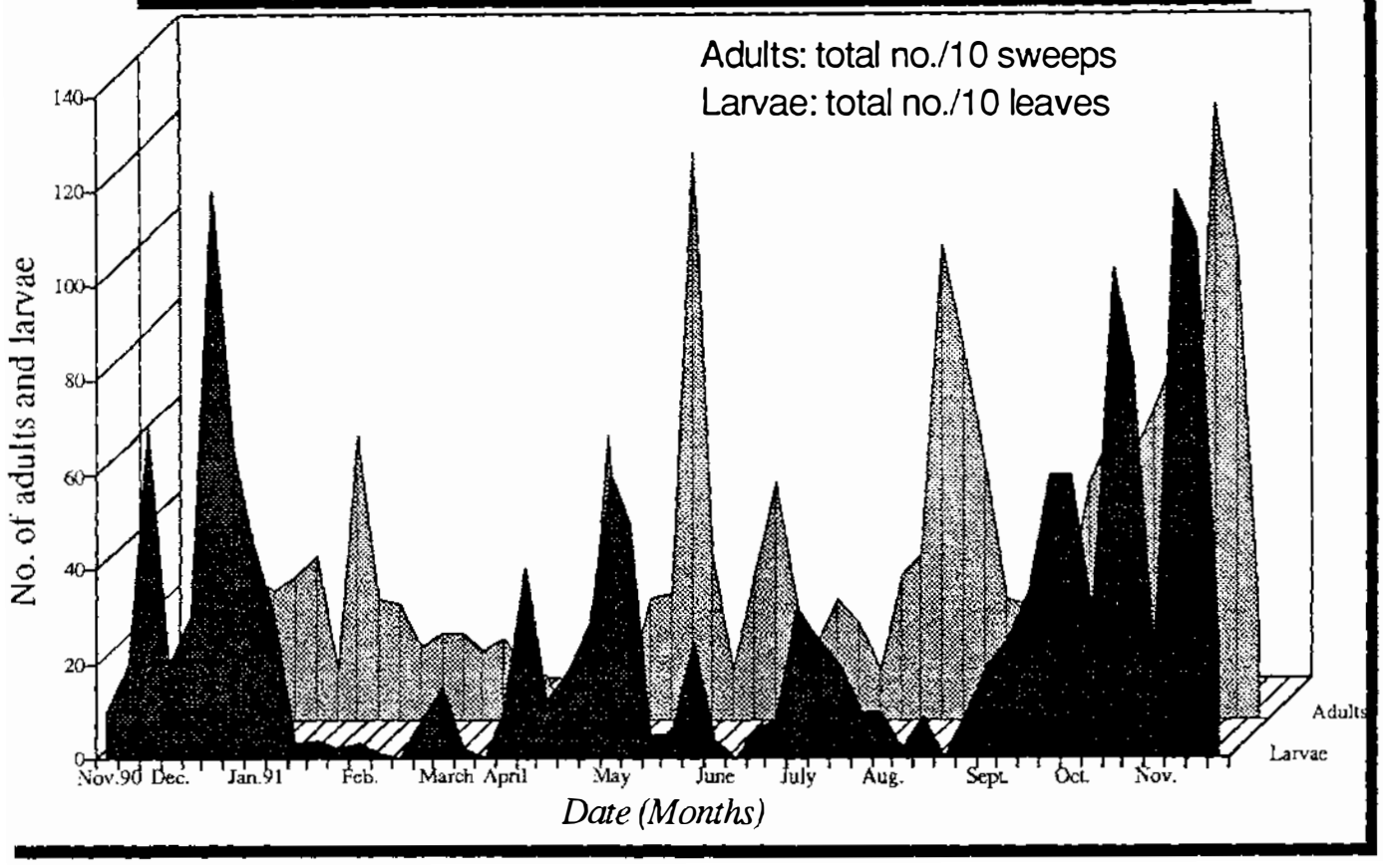


Fig.29: *Weekly Sweep Net Sampling of S. flava on Chinese cabbage*

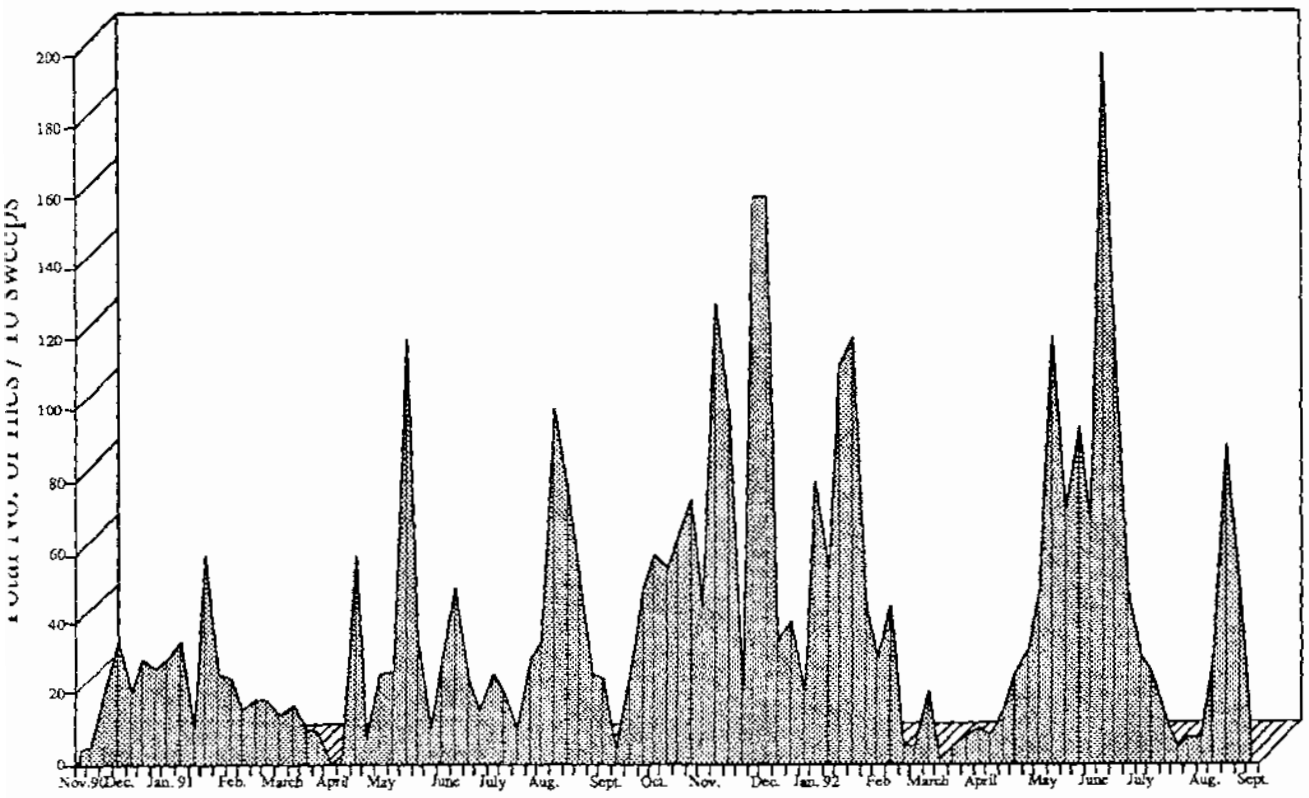


Fig. 30: *Percentage of leaf area mined for Chinese cabbage by Scaptomyza flava*

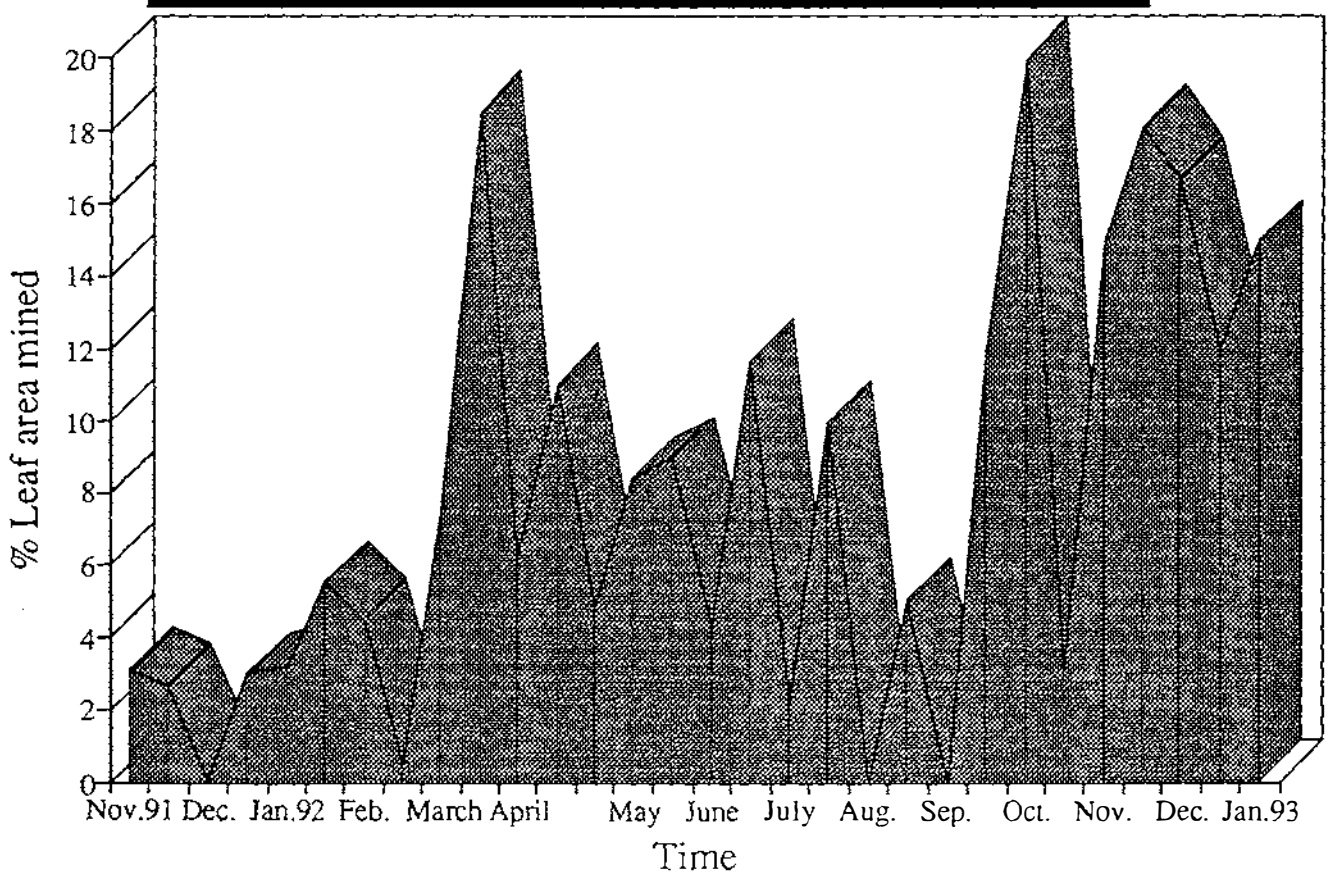
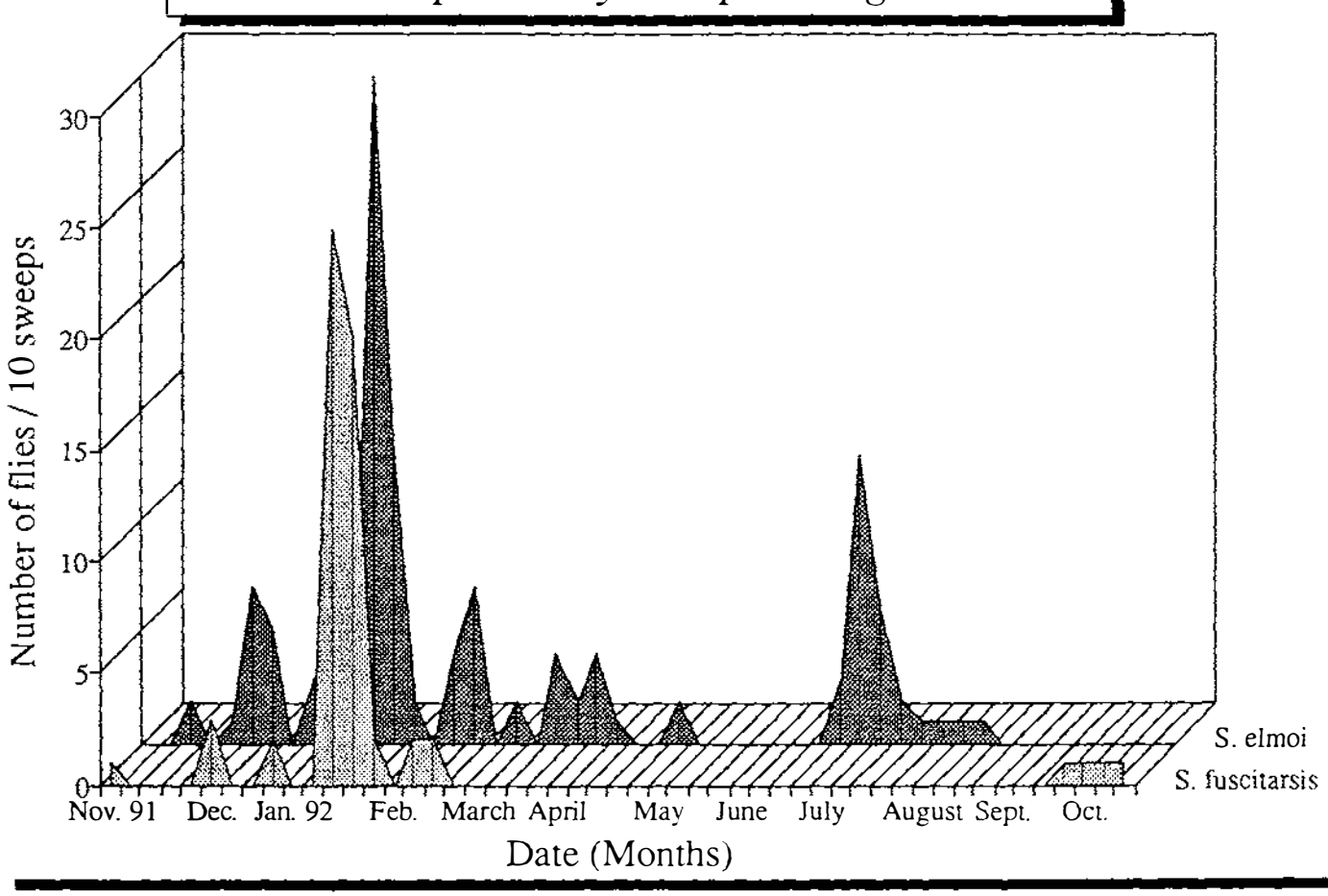


Fig. 31: *No. of S. elmoi and S. fuscitarsis captured by sweep netting*



Chapter 5

DAMAGE ASSESSMENT EXPERIMENTS IN LABORATORY AND FIELD WITH *SCAPTOMYZA FLAVA* [1]

INTRODUCTION

Scaptomyza flava is a dipterous leaf miner that commonly infests many cruciferous vegetables especially in the young plant or seedling stages. It is common throughout New Zealand but no damage assessment experiments have previously been reported. It has multiple generations per year with no distinct dormancy. Adult flies feed on leaf tissue of host plants, creating small pinholes in the epidermis which affect the marketability of leafy cruciferous crops such as Chinese cabbage and water cress. Larvae create irregular blotch mines in leaves and may affect growth and yield of plants.

Insect damage in cabbage crops can be the result of injury to the leaves during the preheading stages, or of injury to the head. The first type of injury can cause the formation of a smaller head, thus a lower weight of yield (quantitative yield reduction); the second type generally gives cosmetic damage (qualitative yield reduction) (Wit, 1985). Criteria to estimate the damage thresholds for qualitative yield reduction are generally very subjective and dependent on long and short term market situations. Whether quantitative damage occurs or not depends on the type of crop, the growing stage, the amount of insect injury, and growing factors (Wit, 1982). Straka (1979) found economic damage (above 3%) when 8.9-10.4% of the leaf area was destroyed in early cabbage, and 10.7-13.7% in late cabbage.

[1] Modified from a paper published in Proceedings of the 46th New Zealand Plant Protection Conference. 1993. pp. 45-49.

In order to assess the ability of *Scaptomyza flava* leaf miner to affect the growth and yield of two cruciferous vegetables (Chinese cabbage and turnip), several experiments were conducted in the laboratory and field.

Chinese cabbage was chosen because it is a leaf vegetable the tops of which are harvested and utilized; thus any leaf mining injury will directly affect the product. In contrast turnip was selected as it is a root vegetable the leaves of which are not normally harvested for human use. Any leaf mining injury would therefore be indirect in its effect on the harvested part, the bulb root.

A: LABORATORY EXPERIMENT

MATERIALS AND METHODS

Turnip seed *Brassica rapa* L. and Chinese cabbage *Brassica rapa chinensis* group *(Brassica campestris* spp. *pekinensis)* seeds were sown in seed boxes in a glasshouse on 15 November 1991.

Ten days after sowing, the seedlings were transplanted individually into plastic flower-pots (10 cm diam.) which were kept in a growth room at 20 ± 1°C during the day (about 16 hours of light) and 15 ± 2°C during the night (about 8 hours darkness). After 20 days in the growth room (one month old plants), 1-2 day old adult *Scaptomyza flava* obtained from the rearing colony were released onto the plants, which were kept individually under small cages. At this stage the average number of leaves per plant for turnip was 5 and for Chinese cabbage 4.5.

There were six treatments as follows, each replicated four times, in a completely randomized design:

1) plants without any insects (control plants).
2) plants with one pair of adult insects per cage.
3) plants with two pairs of adult insects per cage.
4) plants with three pairs of adult insects per cage.
5) plants with four pairs of adult insects per cage.
6) plants with six pairs of adult insects per cage.

After 1 day, the plants were removed from the cages and mines allowed to develop. When larvae were fully fed and had pupated (8 weeks after sowing), plants were harvested by cutting off at ground level (16 days after infestation).

The following were measured for each plant;

a) fresh weight of tops (whole plant cut off at ground level),
b) total leaf area,
c) leaf area mined for each leaf, and
d) fresh weight of the bulb root (for turnip only after lifting washing and drying).

RESULTS

Results for Chinese cabbage and turnip respectively are summarised in **Tables 22** and **23. Figures 32-33** illustrate the effect of *S. flava* on the amount of leaf area mined and fresh weight of leaves of Chinese cabbage and turnip. Also **Fig. 33** shows the effect of leaf miner on weight of bulb root of turnip.

Table 22: **Results of laboratory experiment to assess the effects of *Scaptomyza flava* on Chinese cabbage**

Pairs of adults per plant for 24 hr.	Total leaf area (cm^2/plant)	Leaf area mined (cm^2/plant)	Leaf area mined (%)	Fresh weight of leaves (g/plant)
0	586.75 a	0.00 a	0	40 a
1 pair	465.25 ab	18.50 ab	4	28 ab
2 pairs	362.00 b	15.00 ab	4	22 b
3 pairs	414.75 ab	20.25 b	4.8	26.5 b
4 pairs	454.25 ab	30.25 b	6.6	27.7 b
6 pairs	502.25 ab	80.07 c	16.4	24 b

Within a column, means with the same letter are not significantly different ($P \leq 0.05$).

Table 23: **Results of laboratory experiment to assess the effects of *Scaptomyza flava* on turnip**

Pairs of adults per plant for 24 hr.	Total leaf area (cm^2/plant)	Leaf area mined (cm^2/plant)	Leaf area mined (%)	Fresh weight of leaves (g/plant)	Fresh weight of bulb root (g/plant)
0	531.75 a	0 a	0	26.77 a	7.25 a
1 pair	450.25 ab	8.50 bc	1.9	25.20 abc	3.72 ab
2 pairs	428.75 b	10.00 cd	2.3	26.10 ab	4.30 ab
3 pairs	441.75 b	12.25 cd	2.8	22.97 abc	2.82 ab
4 pairs	390.50 b	3.25 ab	0.8	17.75 c	1.40 b
6 pairs	463.25 ab	15.75 d	3.4	18.15 bc	2.02 b

Within a column, means with the same letter are not significantly different ($P \leq 0.05$).

DISCUSSION

The results for Chinese cabbage and turnip are discussed separately.

Chinese cabbage: The degree of injury to the plant was closely related to the density of the leaf miners. The area of leaf mined for Chinese cabbage **(Table 22)** increased with increasing numbers of adult insects released but not in direct proportion. For example one pair of adults resulted in 18.50 cm^2 (3.9 %) of leaf mined but four pairs of adults produced only 30 cm^2 (6.6 %) of leaf mined rather than an expected 73 cm^2.

This could be due to interference between females during oviposition with increasing numbers confined to relatively small plants. Also at high pest density interference between individual larvae may occur and closely adjacent injuries to the leaf may exert less effect than ones widely spaced. Even six pairs of adults per plant resulted in only 80.07 cm^2 of leaf area mined or approximately 16.4% of total leaf area at the termination of the experiment.

Nevertheless, all treatments, with the exception of one pair of adults per plant, significantly reduced total leaf weight; however, there were no differences between treatments with increasing adult insect densities. Total leaf area, including that mined, showed no significant differences compared to untreated except for an anomalous reduction associated with two pairs of adults per plant.

Turnip: The area of leaf mined for turnip **(Table 23)**, except for an anomalous figure with four pairs of adults, increased in about direct proportion to numbers of adults but there was not a close linear relationship (r^2= 0.69). Regarding fresh weight of leaves and bulb roots, there was a significant difference between the control plants and treatments with 4 pairs and 6 pairs of adults. Significant reduction of bulb root occurred only with 4 or 6 pairs of adults per plant.

Fig. 32: *The effects of Scaptomyza leafminer on C.cabbage & turnip in the laboratory*

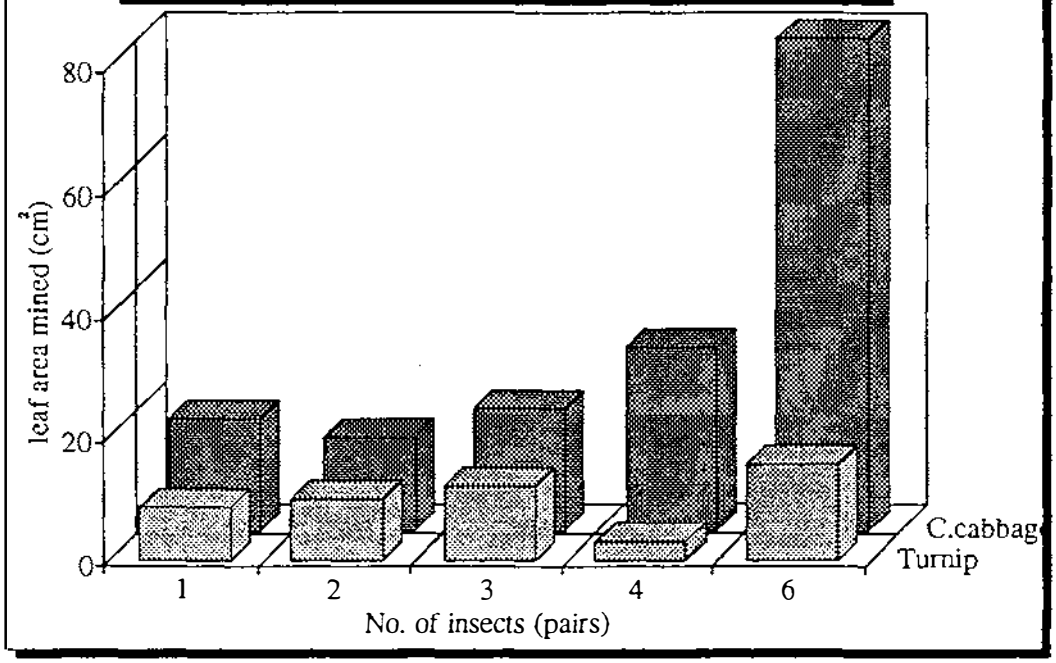
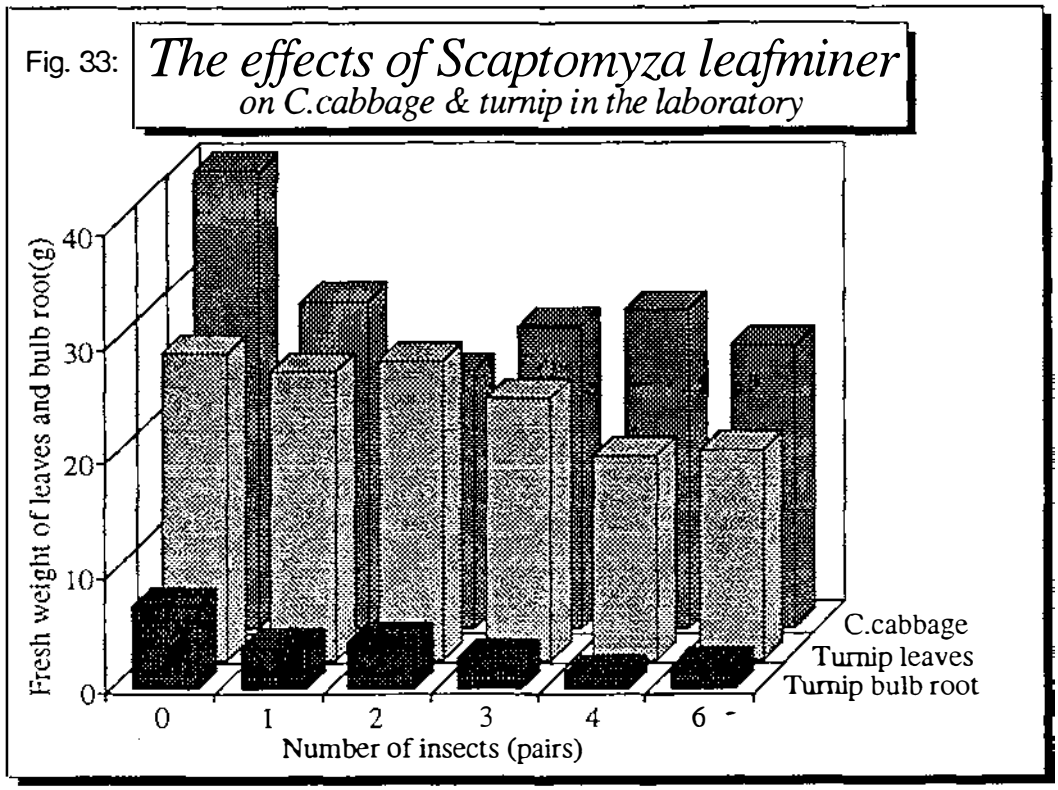


Fig. 33: *The effects of Scaptomyza leafminer on C.cabbage & turnip in the laboratory*



It seems that turnip may compensate to a considerable extent for damage from larvae to leaves. This compensatory growth prevented significant loss of root weight for treatments with up to 3 pairs of adults per plant. A single pair of adult insects per plant gave a bulb root weight little more than half that of untreated control, but the difference was not significant due to high variability.

It is apparent from these results that plant compensation in turnip is an important factor that must be considered when determining pest control actions. It is likely to be a dynamic process which will vary throughout the growth of the plant.

Taylor (1968) has reported that only injury to the older leaves of turnip plants affects root weight, perhaps because in turnip, older leaves are more important than young ones in exporting photosynthetic assimilates to the roots. In the experiment with *Scaptomyza flava* larvae fed mainly on the older leaves, some of which were badly injured. However, attacked plants mostly retained their older leaves as long as unattacked ones (except for severely damaged leaves that dropped before maturity).

B: LEAF MINER DAMAGE ASSESSMENT FIELD TRIAL

INTRODUCTION

In damage assessment experiments a common approach is to alter the pest density with chemicals, by applying different kinds, concentrations, times or number of applications of insecticide. There can be a problem of interplot interference due to pest movement between pesticide-treated plots. There is the added complication of possible movement of pesticide by drift or run-off or of unplanned repellency if plots are too close or movement is not prevented by careful choice of the droplet size or consideration of the wind direction. Yields are measured on plots receiving different treatments, with different degrees of pest infestation and yield / infestation regressions calculated.

The control of leaf mining pests is generally difficult, as the insects are protected for a major part of their life cycles by the leaves they are attacking. A spray must either penetrate the leaves to kill the young insect in the mine during they leave the mines during a later stage of their life cycles. It is difficult to find a spray which will penetrate leaves in sufficient quantity to kill the insects but not damage the plant. To kill the insects after emergence from the mines it would be necessary to know the life history in detail and then attempt to find a spray that would be effect give in killing the insects at some unprotected stage (Hill, 1987). Chemical control involves the use of insecticides with penetrate action in order to kill the larvae *in situ*, and some systemic chemicals are also effective. To other alternative is to use insecticides against the adult flies on the plant foliage prior to oviposition and this method requires very careful timing.

The objective of the trials was to create different levels of leaf miner attack during the growth of Chinese cabbage and turnip by the application of different insecticide treatments and to determine harvested yields in relation to the degree of leaf miner injury earlier in crop life.

MATERIALS AND METHODS

Experiment 1: 1991 / 1992

Chinese cabbage (*Brassica rapa* spp. *chinensis* group), variety "Chi-Hi- Li", and turnip (*Brassica rapa* spp. *rapa*), variety "Snow ball" , were sown in field plots with 40 cm spacing between rows on December 5th 1991. Plots were four 3 m rows. The seedlings were thinned to about 15 cm spacing between plants.

Insecticide was applied with treatments designed to provide different levels of leaf miner suppression. On commercial Brassica crops *Scaptomyza* is probably normally controlled by insecticides applied for control of other pests such as white butterfly, diamondback moth and aphids. Each treatment was replicated four times in a randomized complete block design for both turnip and Chinese cabbage. Data were analyzed by linear regression analysis (General linear model SAS) and a two-way ANOVA and treatments compared using LSD test at 0.05 level.

The treatments[1] were as follows:

1. Control, no insecticide applied (*Scaptomyza* allowed to develop freely).
2. Permethrin (Ambush 50 EC) (a contact insecticide) applied at full label rate of 100 ml Ambush 50 EC / ha. as a dilute spray.
3. Permethrin applied at 1/2 label rate (50 ml Ambush 50 EC / ha.)
4. Pirimicarb (a contact / systemic insecticide) applied at full label rate (250 g Pirimor 50 EC / ha) for the first application plus acephate (Orthene 75 EC at 1kg / ha) for the second application.

[1] Insecticide treatments were selected on the basis of results from laboratory tests (see Appendix 5).

Sprays were applied with a knapsack sprayer at approximately 700 l water per ha. Prior to each spray application ten plants were selected at random from the centre rows of each plot and total leaf area and leaf area mined measured.

At maturity the effects of leaf miner attack were determined by taking random samples of 10 plants from the centre rows of each plot (in order to avoid edge effects) and recording gross fresh weight of plants after cutting at ground level, and net weights after damaged leaves were removed. In addition for turnip, the fresh weight of washed bulb roots was recorded.

The timetable of sowing, sampling and spraying was as follows:

Sowing date	05.12.1991
Seedlings thinned	16.12.1991
First sampling (before first spraying)	24.12.1991
First spraying	24.12.1991
Second sampling	07.01.1992
Second spraying	09.01.1992
Third sampling (Turnip only)	10.02.1992
Harvest: Chinese cabbage	29.01.1992
Turnip	10.02.1992

Total leaf area and leaf area mined were measured by an Area Meter MK2 (Webb, 1989). The great advantage of this system is that the measured areas are seen on the monitor so that discrimination between different areas can be controlled before the measurements are made. Areas of different tone on the same object can be measured independently by adjustment of the threshold control of this machine. For measurement of irregular blotch mines, the blotch areas may be measured as a proportion of the whole for a single leaf, or as a direct percentage if required **(Plate 18).**

Plate 18: Area Meter MK2

Experiment 2: 1992 / 1993

A similar experiment was established. Chinese cabbage variety "Chi-Hi-Li", and turnip variety "Snow ball" were sown in field plots with about 50 cm spacing between rows. The plants were thinned to about 20 cm spacing between plants. Plots were 4 rows x 3m. The treatments were as follows:

1. Control; no insecticide applied. (*Scaptomyza* allowed to develop freely).
2. Permethrin (Ambush 50 EC) (a contact insecticide) applied at full label rate of 100 ml Ambush 100 EC / ha.
3. Permethrin applied at 1/2 label rate (50 ml Ambush 50 EC/ha.).
4. Permethrin applied at 1/4 label rate (25 ml Ambush 50 EC/ha.).

Sprays were applied with a knapsack sprayer at approximately 700 l water per ha.

The timetable of sowing, sampling and spraying was as follows:

Sowing date	24.11.1992
Seedling thinned	15.12.1992
First spraying	28.12.1992
First sampling	06.01.1993
First sweep netting	07.01.1993
Second spraying	08.01.1993
Third spraying	14.01.1993
Second sampling	18.01.1993
Second sweep netting	19.01.1993
Fourth spraying	20.01.1993
Fifth spraying	28.01.1993
Sixth spraying (turnip only)	04.02.1993

Third sweep netting 02.02.1993
Harvest: Chinese cabbage 02.02.1993
Turnip 17.02.1993

The experiment was a randomized complete block design with four replications. The results were subjected to two-way analysis of variance (ANOVA). Multiple regression analysis (SAS) was used to evaluate the relationship between gross weight and net weight per plant of Chinese cabbage (comparisons among treatment means were subjected to LSD test [SAS Institue, 1985] for separation of means at 0.05 level).

On 1st and 2nd sampling dates, 5 plants were picked from the middle row of each plot and total leaf area and leaf area mined measured by Area Meter MK2 (Webb, 1989).

At maturity the effects of leaf miner attack were determined by taking random samples of five plants from each plot and recording gross fresh weight of plants after cutting at ground level, and net weights of Chinese cabbage after a cohort of mined leaves were removed from the experimental plants. For turnip the fresh weight of bulb roots was recorded in addition to leaf weight.

To compare populations of adult insects, sweep net samples were taken (10 arm length sweeps brushing lightly through the foliage the Chinese cabbage and turnip plants while walking the length of rows) on three dates *ie.,* one or two days before spray applications.

RESULTS

The results of the two field experiments are summarised in **Tables 24** to **33.**

Table 24: **Mean total leaf area, leaf area mined and percentage leaf area mined of Chinese cabbage on two sampling dates. 1991/92 field experiment.**

Treatment	Leaf samples 24/12/91			Leaf samples 7/1/92		
	Total leaf area (cm^2)	Leaf area mined (cm^2)	Leaf area mined (%)	Total leaf area (cm^2)	Leaf area mined (cm^2)	Leaf area mined (%)
Untreated	144.58 a	1.17 ab	0.75	95.45 a	13.07 a	13
Permethrin 50 g ai/ha	138.72 a	2.65 a	2	97.45 a	01.6 c	2
Permethrin 25 g ai/ha	121.20 a	0 b	0	99.82 a	0.72 c	0.75
Pirimicarb 125 g ai/ha + Acephate 750 g ai/ha	128.82 a	0 b	0	97.50 a	06.55 b	7

Figures in each column accompanied by the same letter are not significantly different at P≤ 0.05 (ANOVA followed by LSD test for separation of means).

Table 25: Gross and net weights of Chinese cabbage at harvest

Treatment	Weight of head at harvest	
	Gross weight (g)	**Net weight (g)[1]**
Untreated	149.74 a	118.01 a
Permethrin 50 g ai/ha	145.79 a	135.05 a
Permethrin 25 g ai/ha	134.92 a	116.09 a
Pirimicarb 125 g ai/ha + Acephate 750 g ai/ha	134.10 a	112.22 a

Within each column, means with the same letter are not significantly different ($P \leq 0.05$).

[1] After removal of outer leaf miner damaged leaves.

Table 26: Mean total leaf area, leaf area mined and percentage leaf area mined of turnip on two sampling dates. 1991/92 field experiment[1]

Treatment	Leaf samples (24/12/91)			Leaf samples (9/1/92)		
	Total leaf area cm^2	Leaf area mined cm^2	Leaf area mined (%)	Total leaf area cm^2	Leaf area mined cm^2	Leaf area mined (%)
Untreated	149.35 a	0 a	0	160.30 a	38.45 a	24
Permethrin 50 g ai/ha	167.00 a	0 a	0	148.7 ab	3.67 c	2
Permethrin 25 g ai/ha	152.15 a	1.22 a	0.75	128.05 b	4.17 c	3
Pirimicarb 125 g ai/ha + Acephate 750 g ai/ha	159.20 a	0 a	0	160.72 a	18.02 b	11

Figures in each column accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

[1] Continued on Page 191

Table 26 (Continued from page 190):

Treatment	Leaf sample (10/2/1992)		
	Total leaf area (cm^2)	**Leaf area mined (cm^2)**	**Leaf area mined (%)**
Untreated	206 b	8 ab	4
Permethrin 50 g ai/ha	272 a	3.5 b	1.5
Permethrin 25 g ai/ha	250 a	5 b	2
Pirimicarb 125 g ai/ha + Acephate 750 g ai/ha	208 b	13 a	6

Figures in each column accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

Table 27: Mean weights of leaves and bulb roots of turnip on 7/1/92 and at harvest

Treatment	Plant sample 7/1/92		Weight of leaves at harvest 10/2/92		Weight of bulb root (g) 10/2/92
	Weight of leaves (g)	Weight of bulb root (g)	Gross weight (g)	Net weight (g)[1]	
Untreated	31.4 c	3.8 b	81.95 b	61.57 c	132.3 bc
Permethrin 50 g ai/ha	51.4 ab	8.4 a	131.7 a	121.1 a	230.3 a
Permethrin 25 g ai/ha	52.5 a	7.7 a	115.1 a	92.70 b	193.8 ab
Pirimicarb 125 g ai/ha + Acephate 750 g ai/ha	39.0 bc	5.4 b	81.35 b	59.25 c	118.4 c

Within each column, means with the same letter are not significantly different at the 5% level of probability.

[1] After removal of outer leaf miner damaged leaves.

Table 28: Mean total leaf area, leaf area mined and percentage leaf area mined of Chinese cabbage on two sampling dates. 1992/93 field experiment

Treatment	6/1/93			18/1/93		
	Mean total leaf area per plant (cm^2)	Mean leaf area mined (cm^2)	Leaf area mined (%)	Mean total leaf area per plant (cm^2)	Mean leaf area mined (cm^2)	Leaf area mined (%)
Untreated	139 a	4 b	2.9	433 b	13.7 b	3.2
Permethrin 50 g ai/ha	164 a	0 a	0	536 a	0.3 a	0.05
Permethrin 25 g ai/ha	172 a	3.7 ab	2.15	501 ab	7.5 ab	1.5
Permethrin 12.5 g ai/ha	154 a	0.6 ab	0.39	506 ab	1.0 ab	0.2

Treatments accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

Table 29: **Mean total leaf area, leaf area mined and percentage leaf area mined of turnip on two sampling dates. 1992/93 field experiment**

Treatment	6/1/93			18/1/93		
	Mean total leaf area per plant (cm^2)	Mean leaf area mined (cm^2)	Leaf area mined (%)	Mean total leaf area per plant (cm^2)	Mean leaf area mined (cm^2)	Leaf area mined (%)
Untreated	115.6 a	5 b	4.5	294.8 a	10.7 b	4.2
Permethrin 50 g ai/ha	132.2 a	1.1 a	0.85	268.3 ab	6.3 ab	2.5
Permethrin 25 g ai/ha	142.8 a	0.5 a	0.35	258.2 a	0.9 a	0.3
Permethrin 12.5 g ai/ha	154.3 a	0.9 a	0.99	235.7 b	2.5 ab	1.2

Figures in each column accompanied by the same letter are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

Table 30: **Mean number of adult *Scaptomyza flava* captured by sweep netting on Chinese cabbage on three sampling dates**

Treatment	7.1.1993	19.1.1993	2.2.1993
Untreated	40.6 c	32 b	33 a
Permethrin 50 g ai/ha	5.2 a	17.2 a	35 a
Permethrin 25 g ai/ha	15.3 b	17.5 a	50 b
Permethrin 12.5 g ai/ha	14.5 b	27.8 ab	67 c

Within a column, means with the same letter are not significantly different ($P \leq 0.05$).

Table 31: **Mean number of adult *Scaptomyza flava* captured by sweep netting on turnip on three sampling dates**

Treatment	7.1.1993	19.1.1993	2.2.1993
Untreated	24 a	20 b	29 a
Permethrin 50 g ai/ha	22 a	10 a	22 a
Permethrin 25 g ai/ha	22 a	17 b	28 a
Permethrin 12.5 g ai/ha	23 a	9 a	27 a

Within each column, means with the same letter are not significantly different ($P \leq 0.05$).

Table 32: Gross and net weights of Chinese cabbage at harvest

Treatment	Weight of head at harvest	
	Mean gross weight (g/plant)	Net weight (g)
Untreated	218 a	152.4 b
Permethrin 50 g ai/ha	381.5 a	300.7 a
Permethrin 25 g ai/ha	348.4 a	238.6 ab
Permethrin 12.5 g ai/ha	367.5 a	221.9 ab

Within each column, means with the same letter are not significantly different($P \leq 0.05$).

Table 33: Mean weights of leaves and bulb roots of turnip at harvest

Treatment	Weight of head at harvest	
	Mean gross weight (g/plant)	Net weight (g)
Untreated	112.5 a	225 a
Permethrin 50 g ai/ha	124.7 a	242 a
Permethrin 25 g ai/ha	124.2 a	267.8 a
Permethrin 12.5 g ai/ha	113 .1 a	231 .5 a

Within each column, means with the same letter are not significantly different($P \leq 0.05$).

DISCUSSION

The results for Chinese cabbage and turnip are discussed separately.

Chinese cabbage: The leaf area mined on untreated control plants was less than on turnip in both seasons, reaching a maximum of 13% in January 1992. Permethrin at full label rate gave the most effective suppression of leaf miner **(Tables 24, 28)**.

Based on gross weights of heads at harvest, leaf miner had no effect on yield in either season **(Table 25)** but in 1992/93 net weight of heads **(Table 32)**, after removal of leaf miner damaged outer leaves, was significantly lower for untreated control plants compared to the full permethrin treatment. This difference was not significant in 1991/92.

The number of adult insects captured by sweep netting of Chinese cabbage on 7.1.93 and 19.1.1993 was significantly greater on the untreated control plants compared to other treatments **(Table 30)**.

Turnip: Percentage leaf area mined reached a peak of 24% on untreated control plants in January 1992 but had declined to 4% by harvest. The contact insecticide (permethrin) at full label rate gave the most effective suppression of leaf miner and percentage area mined on sprayed plants at no time exceeded 2% **(Table 26)**.

The gross weights of leaves and of bulb roots of untreated control plants were significantly less than at the full rate of permethrin **(table 27)**.

In 1992/93 (Experiment 2) **(Table 29)**, due presumably to poor weather conditions, leaf miner infestation was at a low level and did not exceed 5% leaf area mined on unsprayed control plants. There were no significant differences at harvest between treatments in gross weight of leaves or of bulbs **(Table 33)**.

CONCLUSION

It is concluded that *Scaptomyza* can reduce the yield of both turnip and Chinese cabbage, in the case of the former by reducing effective leaf area and thus indirectly affecting yield and with the latter by directly damaging outer leaves of the head, which then require removal at harvest. In the Manawatu such effects are unlikely to occur every year based on two season's experience.

SIMULATED INSECT DAMAGE

INTRODUCTION

Clipping treatments have been used to simulate the effects of herbivory in numerous studies. The adequacy of this approach has been reviewed by Baldwin (1990) with mixed conclusions. The fidelity with which clipping reproduces the effects of damage by insects depends on the particular plant variable and the specific pairing of plant and herbivore. The final conclusion by Baldwin (1990) was that clipping more frequently than not does not adequately simulate real herbivory.

However, as Baldwin (1990) also discussed, the advantages of using artificial clipping techniques are numerous and not easily discarded. Use of real herbivory within large manipulative experiments has proven difficult because of logistical problems associated with managing a large population of herbivores. If clipping represents a good model for herbivore damage, then increased replication, more precise placement of damage, and tighter timing of a defoliation event are possible (Welter, 1991).

Another compelling reason to use artificial clipping techniques instead of real herbivory is the need in some experiments to uncouple plant susceptibility from plant tolerance to herbivory. Susceptibility refers to plant characteristics that influence the amount of damage from herbivory sustained by a plant. Tolerance refers to characteristics that influence a plant's ability to sustain damage without significant changes in the marketable portion of the crop. Susceptibility to herbivory can vary with many different treatments including plant cultivar, abiotic stress factors, or other biotic stress agents such as nematodes. If plants differ in their relative susceptibility, then exposure to equal numbers of herbivores does not result in equal levels of damage. Therefore, use of clipping techniques, where appropriate, may allow particular experiments to be concluded that would be logistically impossible otherwise (Welter, 1991).

The effects of pest attack on crop yield are often investigated by attempting to cause similar injury artificially to plants by partially or completely removing heads or leaves. The main difficulty associated with this approach is that of exactly simulating natural pest attack, which often has most effect on yield at a critical stage in crop growth. The recovery of the crop after damage in the field may be different to that in experiments. Plant compensation and growing conditions may also be different under field conditions. In all cases the amount of damage should be monitored in terms of leaf area or dry weight in order to compare artificial with natural damage.

Although many studies have documented an increase in plant yield after either actual or simulated damage caused by herbivorous insect populations (Southwood and Norton, 1973; Kolodny- Hirsch and Harrison, 1982), relatively few studies have demonstrated the basis of plant compensation for such injury. In studies where increased cell division has been demonstrated in response to damage, the potential for compensation by leaves was related to the stage of leaf development at the time of injury; growth from meristemic tissue ceased when immature leaves reached 25 - 75% of mature size (Bardner and Fletcher, 1974). Any additional growth then occurred in response to cell enlargement (Wall and Berberet, 1979). Palisade mesophyll tissue removed from mature leaves of *Phaseolus lunatus* (L) by the leaf-mining herbivore *Liriomyza trifolii* was replaced with photosynthetically active cells, permitting virtually complete recovery from injury. Decreases in photosynthesis did not exceed 10% for leaves with approximately one-fourth of the leaf area mined (Martens and Trumble, 1987).

As part of my programme to investigate the effects of *Scaptomyza* on vegetable brassicas quantitative yield reduction in Chinese cabbage was investigated. In this experiment insect injury to the leaves was simulated by partial defoliation in comparison with *Scaptomyza flava* damage.

MATERIALS AND METHODS

Leaf miner damage to potted Chinese cabbage plants was compared to artificial simulation of damage by removing different amounts of leaf area. The experiment was executed according to a completely randomized design with 3 treatments, each replicated four times. The Chinese cabbage plants were one month old at the commencement of the experiment. Treatments were as follows:

1. Control plants: No insects released on them, no leaf area removed.

2. Real herbivory: 10 pairs (10 ♀ and 10 ♂) of adult ≥ 72 h old *Scaptomyza flava* (obtained from the rearing colony) were released onto the plants and removed after 2 days (22/2/1992 to 24/2/1992).

3. Simulated damage plants: After the larvae which developed on plants of treatment 2 were fully grown (immediately before pupation), the area mined on each leaf was measured by an Area Meter MK2 (Webb, 1989). Holes were then punched in leaves, to an equivalent leaf area using scissors and a cork borer.

The holes were made alongside the midrib (because most leaf mines were concentrated near the midrib of Chinese cabbage leaves). Care was taken not to damage the midrib. The percent area damaged by either *Scaptomyza flava* larvae or the clipping regime was confirmed with the leaf Area Meter. The plants were protected from insect infestation.

About 2 weeks after insects of treatment 2 had pupated new adults began to emerge and were removed. The plants were considered mature just before flowers became apparent (about two months old). Twenty-one days after defoliation treatment, all plants were harvested by cutting off at ground level and measured (overall length of head) and weighed. The results were subjected to analysis of variance. Photoperiod throughout the experiment was 14:10 (L:D).

RESULTS

The mean lengths and weights of the Chinese cabbage heads from each treatment are given in **Table 34**, together with significance values.

Table 34: Results of actual and simulated damage to Chinese cabbage

Treatment	Mean length of head (cm)	Fresh weight of head, mean total per plant(g)
Untreated control	25.50 a	87.75 a
Simulated damage plants	25.50 a	67.50 ab
Plants exposed to insects	24.50 a	43.00 b

Treatments accompanied by the same letter in each column are not significantly different at $P \leq 0.05$ (ANOVA followed by LSD test for separation of means).

Measuring the length of a Chinese cabbage head essentially measures the length of the longest leaf. Under the conditions of this experiment, simulated herbivory and leaf mining activity by *Scaptomyza flava* had no effect on mean length of heads as shown in **Table 34**.

However, the fresh-weight of heads from plants subject to leaf miner injury was significantly ($P \leq 0.05$) lower (less than half) that of uninjured control plants.

DISCUSSION

Artificial simulation of injury did not produce the same effect as actual leaf miner injury. Although the artificial treatment removed a similar amount of leaf area to

that caused by leaf mining larvae, the injury was imposed at a time when leaf mines were fully developed. This could account for the decreased effect.

These results agree in part with Welter (1991). He found that total dry-weight was reduced significantly for increasing levels of defoliation by artificial herbivore and by tobacco hornworm.

A variety of physiological mechanisms are likely to play a role in plant compensation for herbivore damage (McNaughton, 1979; Martens and Trumble, 1987). Thus the effect of insect feeding depends not only on the amount eaten, but also on other factors such as the time when it occurs and the method of feeding. Leaf miners feed primarily in the palisade parenchyma tissue (Parrella *et al.*, 1985), leaving a continuous band of frass at the top, sides, or, more commonly, the bottom of the mine (Martens and Trumble, 1978).

Artificial simulation of such injury is likely to be much more difficult (or impossible) compared to biting / chewing insects.

MEASUREMENT OF LEAF AREA DAMAGED BY A SINGLE LARVA

INTRODUCTION

A number of laboratory and field studies have reported the proportion of a leaf mined by a single miner: *Agromyza*, 27% (Guppy *et al.*,1988) of alfalfa; *Coptodisca*, 7.6% of vegetative and 47% of floral leaves of *Chamaedaphne* (Hileman and Lieto, 1981). New (1976, 1979) has calculated the actual weight of leaf consumed by individual miners *(Acrocercops plebeia).*

Guppy (1981) reported that the area consumed by a single larva of alfalfa blotch leaf miner *Agromyza frontella* (based on a sample of 25 alfalfa leaves) during its life span ranged from 0.20 to 0.78 cm^2, average 0.39 cm^2. The range in area consumed is large; however, mine size may depend on thickness of the leaf. Hendrickson and Barth (1978 cited by Guppy, 1981) have pointed out that one larva consumed an average of 0.64 cm^2 of alfalfa leaflet; however, their results were based on more tender laboratory-grown plants.

MATERIAL AND METHODS

In order to determine the area of leaf that is damaged by an individual *Scaptomyza flava* larva one pair of newly emerged adult insects were released onto each of 4 Chinese cabbage plants for 24 hr then removed. As soon as the eggs hatched, all except one larva on each leaf were killed by pricking with a pin. There were 5 such leaves for each plant. When the larvae were fully fed and had pupated, the leaf area affected by each larva was measured.

RESULTS AND DISCUSSION

Results are presented in **Table 35.**

Table 35: Leaf area damaged by a single larvae of *Scaptomyza flava*

Plant	Mean leaf area damage per larva (cm^2)
1	7.2
2	7
3	5
4	1.2
Mean	5.1

The mean leaf area consumed by each larva during its life time was 5.1 cm^2 but with a wide range from 1.2 to 7.2 cm^2 (20 observations). This represents ca. 12% of the Chinese cabbage leaf area. These differences in leaf area damaged may be due to differences in either leaf size (ranged from 10 to 65 cm^2, averaging 40.8 cm^2), or size, age (larval stage) and sex of larvae, though all developed from eggs laid over a 24 hr period. Further studies are required to determine the reasons for this wide variation.

WHAT DENSITY OF LEAF MINER (*SCAPTOMYZA FLAVA*) MAY KILL PLANT SEEDLINGS?

INTRODUCTION

Sometimes in the field and under laboratory conditions dead leaves and even small dead plants were observed due to damage by *Scaptomyza* leaf miner. Thus an experiment was undertaken to determine what density of leaf miner is capable of killing seedlings of Chinese cabbage under laboratory conditions.

MATERIALS AND METHODS

On 27th April, 1992 different numbers of adult *Scaptomyza flava* were released onto seedling Chinese cabbage plants (4-6 leaf stage) in individual containers in the glasshouse (one plant per pot). Each pot was covered with an inverted transparent plastic cylinder from which the bottom had been removed. The pot and cylinder were joined with sticky tape. Either 5, 10, 15, 20 or 30 pairs of adult *Scaptomyza flava* were introduced into pots and the open tops closed with a piece of mesh cloth (for ventilation), held in place by a rubber band. After either 1, 2, or 3 days the flies were removed. Treatments were as follows (15 treatments each with 4 replications):

1. 5 pairs of adult insects released for . . . . . 1 day
   . . . . . 2 days
   . . . . . 3 days

2. 10 pairs of adult insects released for . . . . . 1 day
   . . . . . 2 days
   . . . . . 3 days

3. 15 pairs of adult insects released for . . . . . 1 day

. . . . . 2 days
. . . . . 3 days

4. 20 pairs of adult insects released for . . . . . 1 day
. . . . . 2 days
. . . . . 3 days

5. 30 pairs of adult insects released for . . . . . 1 day
. . . . . 2 days
. . . . . 3 days

In each case after removal from the oviposition cage, plants were placed under a clean fine gauze cage for eclosion of larvae. Plants were retained until leaf mines developed and there were established pupae. The number of dead leaves and seedlings in each container were recorded.

RESULTS AND DISCUSSION

The results are shown in **Table 36**. It seems that the period of time that plants are exposed is more important than the number of insects with respect to plant injury. For example when plants were exposed to five pairs of insects for three days, almost all leaves on the plants were killed, but 20 pairs of insects for 1 day killed only half of the leaves **(Table 36)**.

The results confirm that high levels of *Scaptomyza flava* attack can kill all leaves of small plants, and hence whole plants, of Chinese cabbage.

Table 36: Number leaves damaged by different number of *S. flava* adults

Treatment (No. pairs adult insects released)	Total leaves per plant	Day(s) the plants were exposed to insects	Mean no. of dead leaves per plant	Mean no. of severely damaged leaves per plant
5	6	1	4	1
	5	2	2.5	0.5
	5	3	4.5	0.5
10	6	1	4	0
	5	2	3.5	0
	4	3	3	1
15	6	1	3	1
	6	2	5	0
	5	3	3.5	1
20	4	1	3	2
	5	2	4.5	1
	5	3	4	1
30	6	1	4	1
	5	2	5	0
	5	3	5	0

Chapter 6

GENERAL DISCUSSION

In New Zealand the genus *Scaptomyza* occurs as a complex of four closely related known species, one of which (*Scaptomyza flavella*) has been recorded only from a small island locality (Mokohinau Is.). The other three species occur sympatrically but do not occupy similar feeding niches as *Scaptomyza flava* is considered to be a herbivore, and feeds by mining leaves whereas *Scaptomyza elmoi*, and *Scaptomyza fuscitarsis* are saprophytic. The genus *Scaptomyza* is placed taxonomically within the Drosophilidae. Most other leaf mining Diptera are in the family Agromyzidae.

In this study several aspects of the biology, ecology, reproductive behaviour and pest status of *Scaptomyza flava* were investigated.

Scaptomyza flava females are polygamous and mate more than once. Multiple matings can have two effects on the fitness of female insects; they increase fertility, and also increase fecundity (Lawrence, 1990). *S. flava* is unusual among phytophagous insects in that adult females make small punctures in the leaves of host plants with their toothed ovipositor from which both sexes may feed on the exuding juices. A similar habit is exhibited by some Agromyzidae. Only a small proportion of these punctures is utilised for the deposition of eggs. Flies commence making leaf punctures within 4 hours after emergence and there is a delay of approximately 24 h. before egg laying commences. This delay and the pattern of feeding suggest that *Scaptomyza* females require additional nutrients for oviposition and that they obtain these by feeding on leaf juices that are released by the puncturing activity of the

ovipositor. Pre-oviposition feeding therefore greatly enhances reproductive capacity.

High levels of *Scaptomyza flava* larval attack can kill all leaves of small small plants. The period of time that plants are exposed to adult females is more important than the number of *Scaptomyza flava* insects with respect to plant injury. The extent of damage is linked with the number of feeding punctures and the intensity of mining by larvae in the host plant's leaves. My results show that such mining activities reduce considerably the lifespan of primary cabbage leaves. In the laboratory quite often the less heavily attacked plants survive.

Pre-oviposition feeding by adults can thus be extensive and damaging to plants- both hosts and nearby plants. Leaf puncturing can reduce photosynthesis (Livene and Daly, 1966), growth and vigour of the whole plant (Hendrickson and Barth, 1978) and when leaf miner densities are high, host plant leaves can be completely girdled by feeding punctures that cause leaves to die and/or young plants to die (laboratory and field observations). Dehiscence of leaves in response to adult feeding occurred when adult populations reached high levels (in the laboratory).

Maximum oviposition varied between different host plant species. The total fecundity of some females was as high as 320 eggs on turnip over a lifespan of about 12 days and as low as 12 eggs on cauliflower. Oviposition is dependent on the presence of a suitable host plant. *Scaptomyza flava* attacks living plants but also lays eggs on, and larvae can develop in, dead and decaying plant material. However, the number of emerging adults was greater when the flies first laid their eggs in live leaves. The facultative saprophytic habit of *Scaptomyza flava* means that abundance of adults in a crop environment may not necessarily reflect a population arising from the crop itself. It would be

interesting to know what proportion of a population develops saprophytically and what factor (s) determine this. The species is evidently capable of surviving in the absence of a living host if suitable rotting plant material is available. In contrast to *S. flava; S. elmoi* and *S. fuscitarsis* cannot feed, leaf mine or develop on Chinese cabbage. Also I have been unable to find any literature reference to other genera in the family Drosophilidae as pests of cruciferous plant species.

A detailed Knowledge of an insect's host finding and oviposition behaviour can suggest ways of modifying behaviour to man's advantage. Understanding the factors affecting feeding and oviposition of *S. flava* would be important for the development of cruciferous crop varieties that are resistant to this insect, so I discuss various factors that could be involved in host plant discrimination. *S. flava* is clearly oligophagous, host plants being restricted to the Brassicaceae. Some feeding/oviposition on non- Brassicaceae plants occurred in non-choice tests but eggs failed to hatch and may have been infertile.

Glucosinolates are a group of compounds found in all cruciferous plants and their principal volatile hydrolysis products are isothiocyanates, sometimes referred to as mustard oils (van Etten and Tookey, 1979). Isothiocyanates are insect attractants (Matsumoto, 1970; Read *et al.,* 1970; Eckenrode and Arn, 1972; Free and William, 1978) and feeding stimulants (Tanton, 1977) for many crucifer-feeding insects. Glucosinolates are known to stimulate feeding (David and Gardiner, 1966; Nault and Styer, 1972; Tanton, 1977; Larsen *et al.,* 1985) and oviposition (Ma and Schoonhoven, 1973; Nair and McEwen, 1976; Nair *et al.,* 1976; Renwick and Radke, 1983) in a number of insect species that feed exclusively on Crucifers (Reed *et al.,* 1989). At the same time, though, glucosinolates are feeding deterrents and toxins for many polyphagous insects. Changes in glucosinolate composition of plants might reduce the attractiveness of the crop to Cruciferous specialists (Butt and Lamb, 1990). Sang *et al.,*

believed that the types of glucosinolates vary in different plants and change rapidly as seedling plants develop (McGregor, 1989).

As larvae of *S. flava* cannot move from plant to plant (or even from leaf to leaf) host selection is entirely by the egg laying female. Factor (s) responsible were not investigated in this study but for some other oligophagous insects restricted to Brassicaceae *e.g.,* diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), oviposition is known to be regulated by plant chemicals restricted to the Brassicaceae (Reed *et al.,* 1989).

Although it seems obvious that adult female insects should select individual host-plants, or part(s) of host-plants on which their larvae do best, the empirical evidence is equivocal: sometimes they do (Rausher, 1979; Rausher and Papaj, 1983; Quiring and McNeil, 1978; Damman and Feeny, 1988; Preszler and Price, 1988), but sometimes they do not (Auerbach and Simberloff, 1989). Intraspecific variation in host-plant suitability seems to be much greater for leaf-miners than for free-living insects (Mattson *et al.,* 1988). Adult female *S. flava* not only oviposit in Cruciferous plant leaves, but also host-feed, creating characteristic feeding punctures in the leaf. I cannot say whether females select plants on which to feed themselves (thereby enhancing fecundity, *e.g.,* Minkenberg and Fredrix, 1989) and simply stay to oviposit; or whether host-feeding provides them with information about the suitability of plants for oviposition. Both may be involved.

S. flava flies must have one or more means of recognizing Cruciferous plants. The presence of attractants/stimulants must be accompanied by the absence of deterrents. This is analogous to diamondback moth where, for example, rutin and coumarin are known to deter oviposition (Tabashnik, 1985). Host plant ranges are known to be wider in laboratory trials when plants are

offered individually compared to the field situation with relatively unlimited supply of one or few preferred hosts. Insects will eventually become more selective given a choice but when insects exist in a habitat provided with several host species, they may prefer to feed and oviposit on a select number of hosts. On the other hand, in the absence of highly preferred host plants, what are generally nonpreferred plants may now be accepted.

If we postulate that *Scaptomyza flava* are attracted to isothiocyanates found in Cruciferous plants, it is likely that dead plant material acceptable to *S. flava* for feeding and egg laying must also be from Brassica plants.

Eggs laid by *Scaptomyza flava* on wheat in non-choice experiments did not hatch, presumably because they were unfertilized. This suggests that courtship and mating did not occur on wheat leaves. It has been hypothesized that in some insect species (*e.g., Drosophila conformis*) the most successful males are those that occupy the centre of leaves (Shelly, 1989). This observation has led to the suggestion (Wiley, 1978) that territory (site = leaves) position itself may serve as an important cue to females in selecting a mate. Territory selection by both males and females could depend, not only on a leaf's position within a plant, but also on overall characteristics of the plant. Wheat leaves are narrow in contrast to wide broad leaves of Cruciferous plants and thus leaves of wheat have no distinct and facile centre as Brassica leaves have. Thus based on this hypothesis, leaf form alone, without consideration of plant chemistry, could account for *S. flava* choosing Cruciferous leaves for mating.

In choice and non-choice tests *S. flava* adult flies fed and oviposited on all Cruciferous plants but showed distinct ovipositional preferences for some species. When *Scaptomyza flava* were given a simultaneous choice of seven plant species for feeding and oviposition, there was a distinct hierarchical

ordering in their ovipositional preference, with turnip and then Chinese cabbage and hedge mustard being highly preferred over all others. These results support the hypothesis that host preferences area factor in utilization of cruciferous crops by this leaf miner.

The results of the non-choice tests were somewhat surprising in that wheat was more readily accepted for feeding than cauliflower. Flies did not feed or oviposit on prairie grass in choice or non-choice tests, and clearly this species is a nonhost. Numbers of feeding punctures recorded from lettuce were too low to reach firm conclusions.

Choice tests, non-choice tests and observations of individual ovipositing females yield different insights into the ovipositional behaviour of *S. flava*. Choice tests permit rapid screening for effects of diverse stimuli and would thus aid the search for more resistant Cruciferous plants.

Leaves of turnip, hedge mustard and Chinese cabbage gave higher fitness indices based on larval growth rate and survival and were the most preferred for egg laying while cauliflower, and radish gave the poorest performance and were the least preferred.

In holometabolous insect herbivores, the main oviposition sites are not necessarily the main feeding sites for the adult. For example *Scaptomyza flava* flies preferred to feed on wheat compared to cauliflower but wheat was not a suitable plant for oviposition and vice versa.

For some insects selection of plants for oviposition is determined both by the physical nature of their surfaces and by chemical factors which are detected only on contact (Fenemore, 1980). For potato moth (*Phthorimaea operculella*) apparently surface texture was the principal cue. Surface texture of substrate also

may play a role in oviposition preference of *S. flava*. Heavily wax-textured surfaces *e.g.*, leaves of cauliflower were not suitable compared to other Brassicaceae for feeding, but were relatively well accepted for oviposition. In addition to differences in leaf surface wax, Chinese cabbage and turnip have a much softer leaf than cauliflower and may be easier to puncture with the insect's ovipositor. Such puncturing is essential in order for feeding to take place.

The literature on the feeding of *S. flava* under field or laboratory conditions is very scarce. The effect of the non-host plants was lost if they were grown more than 0.5 m. from the brassica rows (Tukahirwa and Coaker, 1982 cited by Nottigham, 1988). The non-host plant might also have acted as a physical barrier to oviposition (Nottigham, 1988).

Scaptomyza leaf miner development in the Manawatu area is limited by the absence of host plants in peripheral areas (by bush, mountain and river). On the other hand, the absence of other leaf miner species on Brassicaceae plants allows *S. flava* to exploit this niche without competition.

Knowledge of larval food quality as determined by plant species and cultivar could assist in formulation of total population management strategies for *S. flava*. The developmental time of *S. flava* was significantly affected by host plant. Of the plants tested, turnip gave the best biological performance as expressed by the biological fitness[1]. Insects reared on turnip required the least time and those reared on cauliflower the most time from egg to adult death. Overall survival was also better on turnip. On cauliflower only 20% of the eggs of *Scaptomyza flava* developed and produced adults in contrast to 77% and 80% on Chinese cabbage and turnip respectively. Unfortunately the results do not to

[1] Biological fitness i.e., no. of eggs laid per female, percent of hatch of eggs, duration of larval and pupal development (day), percent pupation and weight of pupae.

explain the mechanisms underlying these differences in growth rate or fecundity of *S. flava.*

Oviposition by leaf mining insects is frequently non-random because ovipositing females prefer and/or avoid certain leaves or egg arrangements within leaves (Heads and Laeton, 1983; Potter, 1985; Bultman and Faeth, 1986; Simberloff and Stiling, 1978 cited by Auerbach and Simberloff, 1989). One might expect oviposition site preference to be under strong selective control for insects such as *Scaptomyza flava* whose larval feeding location is determined solely by egg placement. Oviposition patterns among and within leaves should reflect enhanced probabilities of survival relative to alternative arrangements.

Comparison of my results of *Scaptomyza flava* with those of Minkenberg *et al.* (1989) for *Liriomyza trifolii* indicate that age of leaf influences fecundity independently of nitrogen.

Good to poor correspondence between oviposition preference and offspring performance on different species of plants has been observed for a variety of insect taxa (*e.g.,* Copp and Davenport, 1978; Valladares and Lawton, 1991). A major working hypothesis on the evolution of oviposition behaviour is that females will choose plant species that maximize larval survival and growth. Most studies of Lepidoptera analysing the preference/performance hypothesis have focused on survival, growth rate, and pupal mass in the absence of natural enemies of eggs, larvae, and pupae (Thompson, 1990).

Several hypotheses may explain lack of concordance between adult host-selection behaviour and offspring performance: *e.g.,* performance could be influenced by plant characteristics. A lack of-correlation between oviposition preference and larval performance can also result from at least five other factors: First, the preferred plant may be rare. Second, a plant commonly chosen for

oviposition but poor for larval growth may be a recent addition to habitat. Third, a host plant may be favourable for larval growth under some conditions, but it may sometimes grow in a habitat unfavourable for flight of ovipositing females or for larval growth. Fourth, females may oviposit preferentially on plants that allow their offspring to sequester particular secondary plant compounds for defense, even if those plants result in lower growth of larvae. Fifth, in species whose larvae feed as grazers and move among several plants during development, rather than feed as parasites on an individual plant selection may not consistently favour females that oviposit on a certain plant species (Thompson and Pellmyr, 1991).

I observed that (unrecorded data) within a plant, both sexes (but particularly females) appeared to settle preferentially on the larger leaves. The same pattern has been observed by Shelly (1987). He has demonstrated that two positional features of a male's territory strongly influence the likelihood of visits of *Drosophila conformis* females. First females usually visited the lowest leaves within a plant. In addition, females appeared to preferentially visit territories in large leaves over those in smaller ones. This preference for larger leaves may have evolved as a behavioural mechanism to facilitate mate choice. By visiting larger leaves, females encountered larger "samples" of males and therefore may have benefited from the increased number of possible comparisons among potential mates (Alexander, 1975).

Recent work on *Plantago zelicaon* and *P. oregonius* showed that oviposition preference is genetically independent of larval performance in these species, at least with respect to the physical linkage of loci (Thompson, 1990).

Female *Scaptomyza flava* consistently laid more eggs on older than younger leaves in all experiments. This result is support by several pieces of evidence from work with other insects (*e.g.,* Murai, 1974). Leaf size could be

a factor determining which leaves were selected. While my results show that *Scaptomyza* has preference for certain leaf ages, the mechanism by which discrimination occurs is unclear. The role of nitrogen could be further investigated by manipulating plant nitrogen content.

Previous larval feeding experience on turnip and Chinese cabbage influenced adult host plant oviposition preference, but adult host plant preference was not influenced by previous feeding experience as larvae on cauliflower. These results are only partly consistent with findings from previous experiments on the effect of adult experience in *Drosophila* on oviposition, where the experimenter determined the exposure time to resources. Positive effects were found in small containers (Jaenike, 1983), including experiments where apple and orange media were used (Hoffmann, 1985). However, negative or non-significant experience effects were found in other oviposition experiments in large cages (Hoffmann, 1985) that are similar to the cages I used. The reasons for these inconsistencies (non-significant effects) are unclear. One possibility is that effect of experience on oviposition is different from its effect on host attraction. Another possibility is that the resources used in the experiments differed.

Hoffmann and Turelli (1985) reported non-significant experience effects for *Drosophila* females, and they also found inconsistent experience effects in releases with several fly stocks and pairs of alternative resources. The extent to which host fidelity documented in the laboratory experiments occurs in the field depends on the relevance of these experiments to field behaviours and the nature of the resources that flies encounter in the field after eclosion.

On the other hand, inability to move from one food resource to another is a constraint in leaf miner larvae, so aversion learning has no relevance for them (Bernays *et al.*, 1992). The relative aversion of *Scaptomyza flava* to

cauliflower may to be due to a nutritional deficiency rather than any toxic effect (aversion learning has been demonstrated for some insects *e.g.,* learned aversion of the polyphagous grasshopper *Schistocerca americana* to spinach [Papaj and Lewis, 1993]). Avoidance learning by fly larvae is controlled by the same genes as avoidance learning in adult flies (Aceves-Pine and Quinn, 1970).

The general conclusion from these experiments is that larval or early adult experience of *Scaptomyza flava* to one plant species did not increase preference for that species for feeding or egg-laying with the part exception of Chinese cabbage and turnip.

Effective control of pests in integrated programmes normally requires regular field samples to estimate pest population levels. Methods for estimating field densities of *Scaptomyza flava* have not been thoroughly evaluated. Unfortunately, little is known about factors that might affect the variability of field samples of Drosophilid species. In addition to time of day (Fisher *et al.,* 1982), within-field dispersion patterns of *Scaptomyza flava* may be influenced by wind direction and speed, and field size. It is likely that these factors would, in turn, affect sampling variability. However, their influence on the daily or weekly pattern of *Scaptomyza flava* dispersion has not been quantified.

Unbaited sticky traps were used for detection of adult *Scaptomyza flava* abundance but flies were rarely captured on such traps. Water traps were superior to sticky traps and were easy to service.

I used whole-plant samples to obtain estimates of larvae and of leaf mining injury. Samples that include only a portion (*e,g.,* certain leaves) of individual plants could reduce the effort required to reach a control or management decision (Stewart and Sears, 1989).

In the field adults and larvae of *S. flava* were present all year round with no winter dormancy. Abundance of *S. flava* varied considerably from month to month and year to year and it was observed that at certain times Chinese cabbage leaves abounded with mines, whereas at the same time in another year they did not (the spring and summer of 1992/1993 was exceptionally cool and wet). This could be a reflection of seasonal weather variability or of different stages of plant development. However, the numbers of adult flies caught showed distinct peaks during spring and early summer, and again in autumn to early winter. This pattern was reflected in the results from larval sampling. The large numbers of flies caught in early summer and early winter must be mostly progeny from the first spring and autumn generation of larvae.

Were differences in infestation levels between the two plants in field experiments (turnip and Chinese cabbage) simply a consequence of females staying, feeding and laying more eggs on turnip. From laboratory experiments turnip leaves appear more suitable for oviposition of *Scaptomyza flava* than Chinese cabbage leaves.

Weather does seem to play a major role in determining seasonal abundance but females were present and oviposited at all times during the 2-year observation period. There remains the question of whether *Scaptomyza flava* is likely to be a more serious problem in warmer, *i.e.,* more normal years. Although seems individual meterological parameters (*e.g.,* rainfall) show significant correlation with catches flies. High rainfall in particular showed significant correlation with low catches of flies especially in January / February and March. Several mechanisms have been proposed to explain the effect of precipitation upon the *Scaptomyza flava* populations. Eveleens (1966) suggested that the shedding of mined leaves during the rainy reason could reduce the population of the leaf miner by curtailing larval development. Crowe (1964) proposed that he higher leaf miner mortality is due to larvae drowning inside

overflowed mines in which the dead epidermis became lacerated by the physical damage provoked by rain-drops, or by the penetration of water through the pupation holes of older larvae in mines containing mixed ages of larvae. In addition, rain has been proposed as a mortality factor of leaf-miner eggs, which seem to have a greater chance of survival when the leaf surface is dry (Nestel *et al.,* 1994). In this context, it should be noted that female *Scaptomyza flava,* as some other leaf miner adults (Hovemeyer, 1992), may survive hidden in the litter layer for quite a long time when the weather is cold or rainy, and that they may resume oviposition activity after such adverse periods. Overall though the factors determining survival and reproductive success in *Scaptomyza flava* females in the field are poorly understood.

For the most part, leaf-mining Drosophilidae do not appear to be economically important in New Zealand. This may be because economic injury levels are difficult to assess and data in not available. McGregor (1989) considered that parasitoids already present in New Zealand may restrict populations of potentially damaging Drosophilid leaf miners but I found no evidence of parasitism in *Scaptomyza flava.*

As with many other species of leaf miners, the larval mine is conspicuous, but actual damage from *S. flava* is often slight in terms of yield reduction. For many field crops where the damage consists of leaf mining, it is neither necessary nor really feasible to consider applying control measures. However, the effect of *S. flava* on some leafy vegetable brassicas such as Chinese cabbage is more serious and for a few where appearance is all important, *e.g.,* watercress, this is particularly the case.

Although my results show that *S. flava* can reduce the yield of both turnip and Chinese cabbage, it is apparent that plant compensation in turnip (because injury is indirect) is an important factor that would need to be

considered when determining pest control actions. Compensation is likely to be a dynamic process which will vary throughout the growth of the plant. Furthermore adult *S. flava* flies are susceptible to a range of contact insecticides. In Manawatu, brassica leaf miner populations did not reach pest levels, so, not necessary prompted action towards control of the insect. On commercial brassica crops *S. flava* is probably normally controlled by insecticides applied for control of other pests such as white butterfly, diamondback moth, and aphids.

This research has highlighted our limited knowledge of the biology and damage potential of *Scaptomyza* spp. as leaf miners of vegetable brassicas. It should also have made clear the desirability of dialogue with researchers on the behaviour and host relationships of other Drosophilidae. It is hoped that this thesis will aid in developing such dialogue.

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Appendices

Appendix 1

TAXONOMICAL NOTES ON THE GENERA *SCAPTOMYZA* HARDY (1814) AND *DROSOPHILA* WITHIN THE FAMILY DROSOPHILIDAE

The relation between the genera *Scaptomyza* and *Drosophila*

(Diptera: Drosophilidae)

Family Drosophilidae

Several diagnoses of the family Drosophilidae have been given by various authors. One of the most extensive is that of Duda (1924), after which the following is modified by Bock (1976).

Head with 2 or (usually) 3 (fronto-)orbital bristles of which 1 is proclinate and remaining 1 or 2 reclinate; postvertical bristles large to minute (parallel to convergent, or absent; outer and inner vertical bristles usually present; antennae decumbent, 3rd segment more or less elliptical; arista micropubescent or plumose, if plumose usually with several short medial hairs in addition to larger dorsal and ventral rays; vibrissae usually present. Mesonotum rarely bare, acrostichal hairs usually in 2-10 more or less well defined longitudinal rows; 1, (usually) 2, 3 or 4 pairs of dorsocentral bristles present; prescutellar acrostichals developed or undeveloped; thorax usually with 1 pair of humeral bristles, 2 notopleurals, 2 supra-alars and 2 postalars; mesopleuron bare; sternopleuron usually with 2 or 3 bristles ('sternopleurals') above and several small bristles below; disc of scutellum usually bare; scutellar margin with 4 bristles (anterior and posterior scutellars), anterior pair reduced in some genera; preapical bristles usually present on tibiae.

Costa of wing with proximal and distal breaks, costa reaching end of 3rd or 4th longitudinal vein; 1st longitudinal vein terminating at distal costal incision; auxiliary vein obsolete apically or fused with 1st longitudinal vein; anterior and posterior crossvein present; discal and second basal cells separated by 3rd crossvein in some genera. With very little loss of accuracy, the diagnosis of the family may be considerably condensed to the following essential features:

Head with 1 pair of proclinate and 1 or 2 pairs of reclinate orbital bristles; postvertical bristles, when present, parallel or convergent; mesopleuron bare; costa twice broken; auxiliary vein not reaching costal margin.

The separating characters

Hackman (1982) has discussed characters for separating *Scaptomyza* and *Drosophila* as follows:

The **"external morphological characters"** generally used for separating the genus *Scaptomyza* Hardy from *Drosophila* Fallen are the following:

The head nearly square in profile and the greatest eye dimension more or less oblique in *Scaptomyza.* In *Drosophila* the head is usually higher than long and the greatest eye dimension is more or less vertical. Arista with one or no ventral branch in addition to the end fork in *Scaptomyza* and with two or more ventral branches in *Drosophila.* Mesonotum usually dull in *Scaptomyza,* usually shiny in *Drosophila.* Acrostichal rows of hairs 2—4 in *Scaptomyza, 6—8* in *Drosophila.*

The *Scaptomyza* subgenera often have characteristic features in the male terminalia, but no key characters have been found for separating the entire genus from *Drosophila.* Prominent dentate egg-guides occur in the *Scaptomyza* species with leaf-mining larvae. Leaf-miners are rare in *Drosophila.* On the other hand, sclerotized egg-guides with dense marginal dentation often occur in both genera and these structures

have a function in copulation (Nater, 1953). Some *Scaptomyza* subgenera tend to have very weakly sclerotized egg-guides (cf. Hackman, 1959).

Inner anatomical characters, such as the shape of the spermatheca, testes, vasa deferentia, paragonia, ejaculatory apodemes, and Malphigian tubules, have been used as important characters by Throckmorton (1962, 1966) in studies of the phylogeny in the entire *Drosophila* complex (including related genera) and for separation of endemic Hawaiian *Drosophilas* and *Scaptomyzas*. The inner anatomy of *Scaptomyza* species from other parts of the world is poorly known (see further). Characters of the eggs, larvae and puparia have also been used to some extent in the taxonomy of the *Drosophila* complex (Throckmorton, 1962). The egg-filaments are usually short in *Scaptomyza* and long in *Drosophila*. Okada (1968b) gives much information about the developmental stages of *Drosophila,* but too little is known about *Scaptomyza*.

The subgenera of Scaptomyza

The origin of the *Scaptomyza* genus is a little more than 40 million years ago (Lewin, 1985).

Sixteen subgenera have been distinguished in *Scaptomyza* (Hackman, 1959; Okada, 1973; Tsacas, 1972; Tsacas and Cogan, 1976). The subgenera are comparatively distinct and separated by combinations of about 10 characters of external morphology. Two endemic species from New Zealand (described by Harrison, 1959) and some African species are still unplaced. Most of the subgenera are comparatively distinct from *Drosophila* and a general *Scaptomyza* type can be recognized, but there is considerable overlap of characters between the Hawaiian "Drosophiloids" and "Scaptomyzoids" (Throckmorton, 1966; Carson *et al*., 1970). Before the borderline between *Scaptomyza* and *Drosophila* can be discussed further, however, there is a taxonomic and nomenclatorial matter to be cleared up.

The borderline between *Scaptomyza* and Drosophila

Several cases of adaptive radiation can be traced in the evolution of the *Drosophila* complex (Throckmorton, 1975), but the most impressive and unique example is provided by the Hawaiian Drosophilidae, in which nearly 500 endemic species have been described. The majority of them have been placed in *Drosophila* or in new endemic genera derived from *Drosophila* and these are all called "Drosophiloids" by Throckmorton (1966). The rest are the "Scaptomyzoids", which comprise the *Scaptomyza* species and the species of the derived genus *Titanochaeta* Knab, in all 131 described species. A detailed investigation made by Throckmorton (1966), including extensive study of internal organs, showed that there is considerable overlap of characters between the Scaptomyzoids and the Drosophiloids. There are species groups, and even a subgenus, which are more or less intermediate between the genera. Throckmorton (1966) observes that "the simplest and most parsimonious conclusion" is that the Scaptomyzoids originated in Hawaii from the same stock as the Drosophiloids. According to him the alternative conclusion that founder Drosophilids were introduced twice into Hawaii is less likely in view of the improbable parallelism that this would involve. As a corollary of the first alternative, he puts forward the theory that the entire genus *Scaptomyza* had its origin in Hawaii, from which it spread out all over the world, undergoing adaptive radiation as it did so. Though not incompatible with the age of the Hawaiian Islands (see further Carson *et al.*, 1970), the theory is rather hard to believe. Let us therefore consider the question whether *Scaptomyza* is a monophyletic taxon or not.

Máca (1972) has described the genus *Scaptomyza* Hardy as follows:

"The genus *Scaptomyza* comprises at the present time about 90 described species; it is cosmopolitan. The most conspicuous characters of the genus are as follows: Arista branching, most often with only 1 lower branch situated distally, acrostichal setae usually in 2-4 rows. The anterior sternopleural seta is longer than the medial one. Apart from the cleaning apparatus (on 1st and 3rd tibiae and metatarsi) there are no conspicuous groups of hairs on legs. The body is slender, and the wings are narrower

than in *Drosophila* Fall. (the ratio of the wing length to width is 2.4—2.6 in palaearctic species), with sensillae on the base of r (radial vein) and with one sensilla on the posterior transverse vein. Inner organs, as far as they were studied, did not show too marked difference from the genus *Drosophila*".

Preimaginal stages of only a few species have been described so far. Eggs are finely rugose, without projections or with 2—4 short filaments. In the mining species, the eggs are laid in pits hollowed in the leaf parenchyma with the ovipositor; saprophagous species lay them on the surface of substrate. Larvae are elongate, with several rows of tiny spines in the basal part of each segment. Above the mouth cavity there are three pairs of sensory organs. The buccal armature with mouth hooks bearing minute teeth in prevalently saprophagous larvae, in the phytophagous species these teeth are unequal and very strong. Usually there are four of them. In the first instar the anterior part of buccal armature is connected with the pharyngeal sclerite and the teeth on the mouth hooks are less conspicuous. The mouth hooks of each new instar are without teeth when they are being formed. In this phase there is dark chitinous matter between the mentum and the mouth hooks, from which new sclerites are formed. The dental sclerite of *Scaptomyza,* s. str. is horseshoe-shaped in the first instar **(Fig. 10)**.

In the pharynx of larvae of saprophagous as well as phytophagous species there are longitudinal furrows (fanoni pharyngei — Vimmer, 1931); the oesophagus is longer than the pharynx. The proventriculus bears sac-like appendages. The mesenteron and proctodaeum are broad and straight. The tracheal system corresponds to that of the genus *Drosophila.* Anterior spiracles are lacking in the 1st instar, in the 2nd they are small and without any processes, in the 3rd instar they have 6—9 processes. In the subgenus *Parascaptomyza* their stem is projected. Posterior spiracles are conical, on short stems protruding from a common base; each spiracle is distally tripartite.

At present the genus *Scaptomyza* is divided into 13 subgenera, two of which *Parascaptomyza* and *Scaptomyza,* s.str. occur in Central Europe.

A key to the species of the genus *Scaptomyza* according to the phallic organ **(Figs. 1—4)**: (Máca, 1972)

1 Aedeagus not forked, only slightly emarginate distally with minute sensillae. Gonites (submedial processes of the caudal margin of hypandrium) as long as the aedeagus without apodeme or longer . . . . . *S. pallida* (Zett)

— Adeagus forked almost down to its base, gonites shorter than aedeagus 2

2 Gonites narrow, distally more or less spiked. Submedial setae present aedeagus with sensillae. . . . . *S. flava (apicalis) Hardy*

— Gonites broad and rounded or almost lacking. Submedial setae undeveloped. aedeagus without sensillae 3

3 Gonites slightly indicated, not elongate. The length of hypandrium (from the cranial end of the ventral phragma to the outer corner of the caudal margin) less than 0.25 mm . . . . . *S. griseola* (Zett)

— Gonites digitate. Hypandrium longer than 0.27 mm . . . . . .*S. graminum* (Fall)

For the identification of larvae, Maca suggests a key according to the shape of posterior spiracles **(Figs. 7—9)**. (Usually they can be distinguished by their host-plants; see Hering, 1957).

1 Posterior spiracles with setae arranged in a ring on the apex. Mouth hooks narrow, usually with 4 weak teeth . . . . . *S. pallida* (Zett)

— Posterior spiracles sclerotised, without setae near the apex. Mouth hooks robust, with 4 unequal, strong teeth 2

2 Posterior spiracles dark, with approximately round apices **(Fig. 7)** . . . . . *S. graminum* (Fall)

— Posterior spiracles light, with elongate, parallel apices **(Fig. 8)** . . . . . *S. flava (apicalis)* Hardy

Scaptomyza (Parascaptomyza) pallida (Zetterstedt, 1847)

(Figs 1, 9, 11, 12)

The analysis of the morphology of this species, supplemented by anatomical characters, was published by Okada (1956).

Wings: See **Fig. 11. s** = medium quadratic divergence $=\sqrt{\sum d^2/N-1}$, N = number of specimens examined, d = divergence from the arithmetical mean.

Depicts a wing: costal index (C-index), A/B; fourth vein index (4v-index), D/C; 5x-index, F/E; 4C-index, B/C.

Wing length: ♂♂ -2.49 mm (s = 0.18 mm); ♀♀ — 2.74 (s = 0.17 mm).

C-index : ♂♂ - 3.26 (s = 0.28); ♀♀ — 3.43 (s = 0.29).
4v-index : ♂♂ - 1.58 (s = 0.14); ♀♀ — 1.48 (s = 0.04).
5x-index : ♂♂ - 1.55 (s = 0.22); ♀♀ — 1.55 (s = 0.17).
4C-index : ♂♂ - 0.70 (s = 0.07); ♀♀ — 0.66 (s = 0.04).

Subgenus *Scaptomyza, s.str.*

Scaptomyza graminum (Fallen, 1823)

(Figs. 2, 7, 11, 12)

The principal characters of this species have been pointed out by Duda (1935) and, in particular, Okada (1956). According to Okada (1956) the legs of Japanese specimens (♂ ♀ ?) are sometimes dark. The scutellar index of the central European specimens is approximately 1.6, and that of Japanese specimens 1.55.

Wings. Wing length: ♂ ♂ 2.26 mm (s = 0.15 mm); ♀ ♀ 2.47 mm (s = 0.19 mm).

In northern Europe the wing length does not reach 2.7 mm (Hackman, 1955); in central and southern Europe individuals with longer wings are found. In a population sample from Bily Kriz (the Beskydy, Doskocil Igt.) containing 12 specimens, 9 of them have wings longer than 2.7 mm (maximum 2.92 mm in a male and 3.27 mm in a female). Identification was revised by Hackman.

C-index : ♂♂ - 3.31 (s = 0.24); ♀♀ — 3.36 (s = 0.32).
4v-index : ♂♂ - 1.47 (s = 0.13); ♀♀ — 1.48 (s = 0.09).
5x-index : ♂♂ - 1.48 (s = 0.26); ♀♀ — 1.54 (s = 0.15).
4C-index : ♂♂ - 0.67 (s = 0.07); ♀♀ — 0.65 (s = 0.05).

Phallic organs (Fig. 2): The average length of hypandrium is 0.29 mm. *Scaptomyza norica* Hackman (1955) with genitalia resembling those of S. *graminum* (differing from it by a small forceps and a supernumerary orbital seta, sometimes also present in S. *graminum)* is probably a mere monstrosity of *S. graminum.* This form has also been found in Czechoslovakia.

Development: Egg similar to that of S. *apicalis;* length 0.35 mm. The morphology of larva was described by Okada (1968). It can be distinguished from the larva of *S. apicalis* by the shape of posterior spiracles. Length of mouth hooks: 0.03 mm; 0.06 mm; 0.08 mm. Length of the buccal armature: 0.14 rdm; 0.29 mm; 0.44 mm. Length of the sclerotized part of the posterior spiracle: 0.03 mm; O.O6 mm.

Larval bionomics: The larvae always make mines. Specimens were collected (by Buhr, 1941) from the following families of host-plants: *Silenaceae, Chenopodiaceae, Amaranthaceae* and *Viciaceae (Anthyllis vulneraria).* In addition, Buhr (1941) recorded *Mesembryanthemaceae,* and Hering (1957) *Portulacaceae.* Information on the family *Scrophulariaceae* (Hering, 1957) must be checked as well as all data given by Frost (1923). Artificially transferred larvae can develop on a wider range of plant families (Buhr, 1937). The occurrence on Brassicaceae mentioned by Stary (1930) (mines only have been preserved in a herbarium) probably concerns the grey form of *S. apicalis*; see Zavrel (1967).

Imaginal bionomics: Adults are found in habitats similar to those of *S. pallida*, being almost as abundant.

Experiments with both pair mating and mass mating of *S. graminum* were made (by Buhr, 1941). Larvae were collected on *Malachium* and the emerged adults (about 40 ex.) were divided into 1 lt to 3 lt vessels with potted plants: *Malachium, Lupinus, Phaseolus, Pisum, Trifolium, Antirrhinum,* and *Tussilago,* respectively. The ♀ ♀ hollowed pits without eggs into leaves of all these plants, but only on *Malachium* was further development observed. Specimens removed after some time from the "sterile" plants to *Malachium* bred normally on the latter plant. Data on the length of development (at about 18°C): 3. V. to 10.V. 1971 moulting adults from the collected larvae; adults without opportunity to copulate lived till 1. VI.

Several specimens *S. graminum,* from larvae collected on *Anthyllis,* were reared on *Malachium* quite easily. If the leaf of *Malachium* is too damaged by larvae, it is best to cut it and put it on to the leaf of a sound plant and to let larvae move through.

Juvenile adults are rather light in colour. The ♀ ♀ have light-coloured, ovipositor plates (those of older ♀ ♀ are dark brown); the ♀ ♀ could be, in the extreme cases, similar to the light form of *S. apicalis.*

Graph of seasonal dynamics **Fig. 12.** Doskocil (1963) mentions 2—3 maxima of occurrence in his paper. Hering (1957) states 3 generations a year according to his study of larvae. Some aberrations can be brought about by quiescence which appears in a part of the population with the lack of moisture. In sheltered places larvae can develop in winter as well. Daily dynamics as in *S. pallida.*

Larvae are rarely parasitized by a braconid, *Dacnusa (Rhizarcha) faeroensis* Roman (Capek det.); puparia are sometimes infected by a mould. When rearing *S. graminum, Dacnusa* emerged about 7 days later than the host.

Scaptomyza griseola (Zetterstedt, 1847)

(Figs: 3, 5, 11)

Most of the authors considered this species to be only a form of *S. graminum.* Both species are closely related and *S. griseola* differs mainly in the coloration of the thorax and legs and in some details of the male genitalia (Hackman, 1955).

Wings: Wing length: ♂♂ - 2.07 mm (s = 0.18 mm); ♀♀ — 2.24 (s = 0.10 mm).

C-index : ♂♂ - 3.02 (s = 0.22); ♀♀ — 3.12 (s = 0.17).
4v-index : ♂♂ - 1.49 (s = 0.15); ♀♀ — 1.41 (s = 0.11).
5x-index : ♂♂ - 1.36 (s = 0.14); ♀♀ — 1.19 (s = 0.12).
4C-index : ♂♂ - 0.71 (s = 0.07); ♀♀ — 0.68 (s = 0.05).

Scaptomyza flava (Fallen, 1823)

=

Scaptomyza (s. str.) *apicalis* (Hardy, 1849)

(Figs. 4, 6, 8, 10, 11)

Wheeler and Takada (1966) use the name S. *apicalis* only for palaearctic forms of this species, because they could not compare European and American specimens. Maca examined several specimens collected by Wheeler near Pasadena (California), but he did not find any difference from European ones.

Scaptomyza ? montana sensu Basden, 1954 (peristomal setae remote from the margin of eye, wing length 2.7—3.6 mm, dark, narrowing lamellae of the ovipositor) also belongs, in Maca's view point, to the variability range of *S. apicalis.* Maca examined several specimens, males as well as females, collected by Basden near Mortonhall (Scotland), and several similar individuals in the Czechoslovak material. The phallic organs show no difference from *S. apicalis.*

S. apicalis displays great variability of colour, but there are no morphological differences between dark and light forms. Probably the coloration depends on the temperature at which the larva develops (similarly as in *S. pallida*, see Stalker, 1945, and to a lesser degree in other species as well). An analysis of the morphological characters of *S. apicalis* was made by Hendel (1928).

Wings: Wing length: ♂♂ - 2.52 mm (s = 0.21 mm); ♀♀ — 3.01 (s = 0.20 mm).

C-index : ♂♂ - 3.18 (s = 0.27); ♀♀ — 3.33 (s = 0.25).
4v-index : ♂♂ - 1.48 (s = 0.11); ♀♀ — 1.44 (s = 0.08).
5x-index : ♂♂ - 1.60 (s = 0.14); ♀♀ — 1.47 (s = 0.20).
4C-index : ♂♂ - 0.69 (s = 0.05); ♀♀ — 0.65 (s = 0.05).

Phallic organs (Fig. 3): The density of sensillae on the aedeagus is quite variable, irrespective of the body colour.

Anatomy. ♂♂ : Bulbus ejaculatorius with a pair of long, folded appendages. Ejaculatory apodeme transparent, tetragonal, with a short stem.

♀♀: Ovaria white, spermatheca slightly wider than long. Parovaria larger than the spermatheca, with an elliptical knob. Ventral receptacle coiled approximately five times **(Fig. 5).**

Development: Egg **(Fig. 10).** Larvae: 3rd instar and puparium were described by Hendel (1928). Posterior spiracles of all instars light coloured, with an elongate apex **(Fig. 8).** Mouth hooks: 0.04 mm; 0.07 mm; 0.10 mm. Buccal armature—length:0.18mm; 0.38 mm; 0.62 mm. Sclerotized part of posterior spiracle: 0.02 mm; 0.04 mm; 0.06 mm.

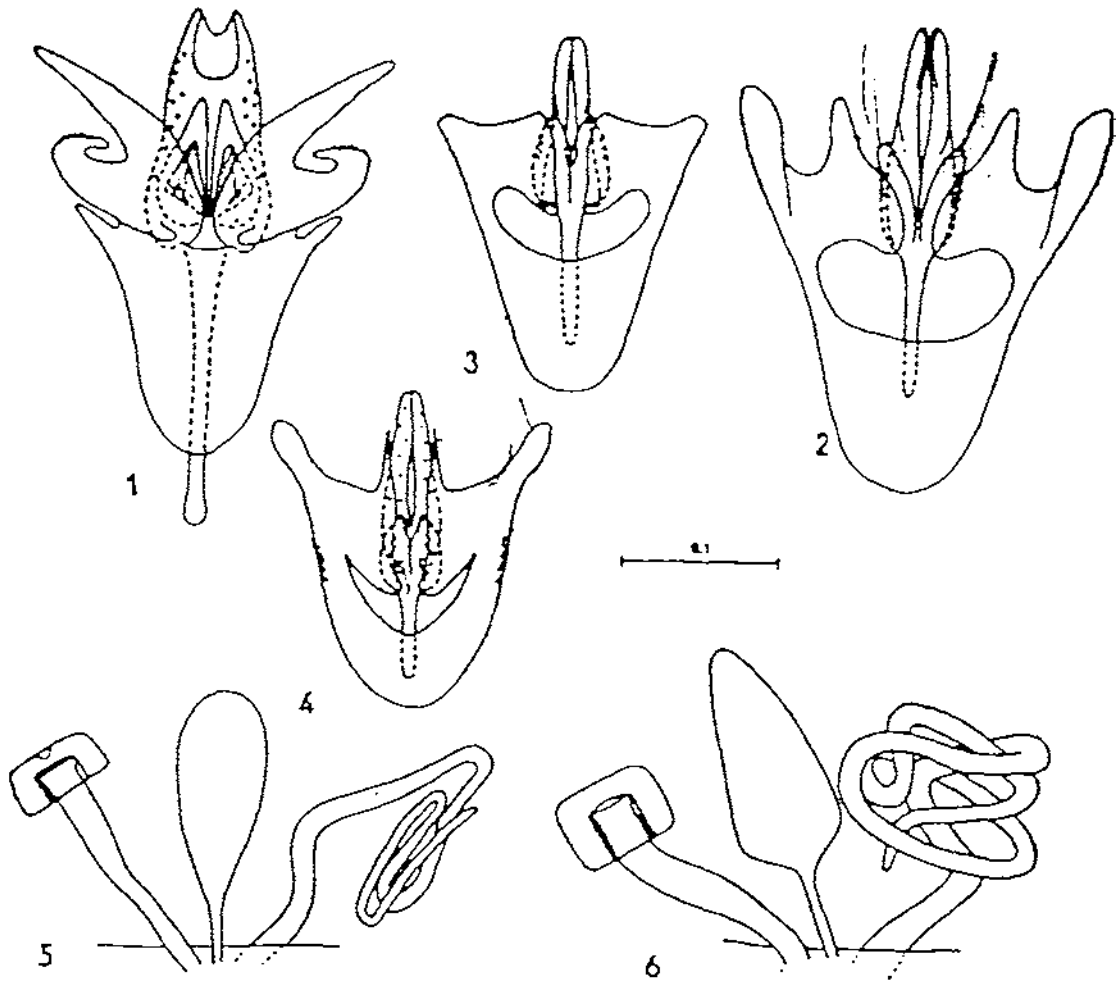
Larval bionomics: Larvae usually mine in leaves, exceptionally in the leaf-like widening fruit of *Thlaspi arvense*—Brassicaceae (Coll. Buhr), in the stem of *Caylusea abyssinica*—Resedaceae (Coll. Buhr) or in the seed-leaves of *Raphanus sativus*—Brassicaceae (Maca lgt.). The families of host-plants— Brassicaceae, Resedaceae, Capparidaceae, Tropaeolaceae, Asteraceae *(Rhodanthe manglesii*—larvae in Coll. Buhr), Viciaceae *(Pisum sativum)*—given by various authors were ascertained by Maca (1972), too. Other data: Papaveraceae (Herling, 1957). Buhr (1937) found that artificially transferred larvae can develop on plants of certain other families as well. Most of the host-plants have a high content of thioglycosides.

Imaginal bionomics: Only sporadic occurrence on non-cultivated land, more frequent in gardens and in the fields of brassicaceous monocultures. *S. apicalis* is easily reared in a vessel with a potted host-plant. Two couples of the yellow form reared in this way, both having emerged from puparia on *Brassica rapa,* produced together 43 adults of **F1** generation (the progeny of one couple was reared on *Brassica rapa,* of the other on *Pisum sativum*). All **F1** adults were yellow. Length of their development (at 18°C): 1 st instar 2—3 days, 2nd instar 3—4 days, 3rd instar 8 days on the average, puparium 12 days. Oviposition about 10 days after emergence (Buhr, 1941).

Buhr (1941) has pointed out that all adults reared from mines collected in the field (about 80 specimens) were yellow. Their development was completed at 16—18°C. 20 larvae in mines collected in July 1969 on *Brassica* spp. and *Pisum sativum* were reared at an average temperature of 12°C. All adults were yellow, a few displayed transition to brown colour. Only 1 grey-brown male emerged from the larvae in mines collected in September, 1970 on *Brassica* spp. and reared at a temperature ranging between 5° and 15°C.

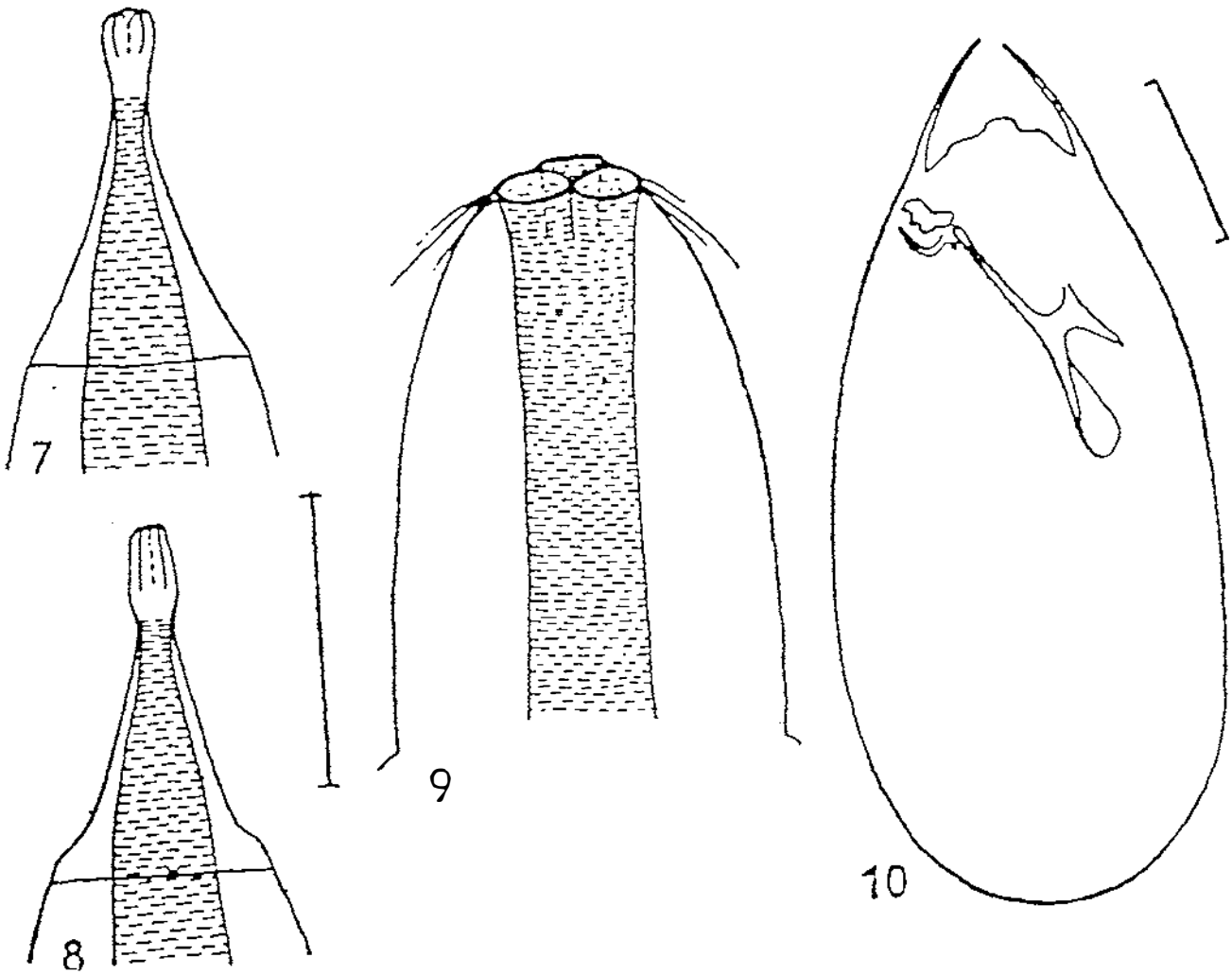
Hering (1957) stated 3 generations a year. It is not always easy to determine in which generation adults belong, as at insufficient humidity (or by means of some other stimulus?) larvae and puparia enter quiescence and the puparial stage can then last up to 300 days (Buhr, unpublished).

Distribution: *S. apicalis* occurs throughout the holarctic region.



Figs. 1-4: Phallic organs of the *Scaptomyza* species. **1**. *S. pallida, 2. S. graminum, 3. S.griseola, 4. S. apicalis (flava).*

Figs. 5-6: Spermatheca, parovarium, ventral receptacle (each of the first two organs is paired). **5.** *S. griseola,* **6.** *S. apicalis (flava).* Scale in mm. (Máca, J. 1972).



Figs. 7-10: Posterior spiracles of 3rd instar larvae. **7**. *S. graminum,* **8**. *S. apicalis (flava),* **9**. *S. pallida.* **10**. *S. apicalis (flava)*; Egg (1st instar buccal armature showing through). Scales: 0.05 mm for Figs. 7-9; 0.1 mm for Fig. 10 (Máca, J. 1972).

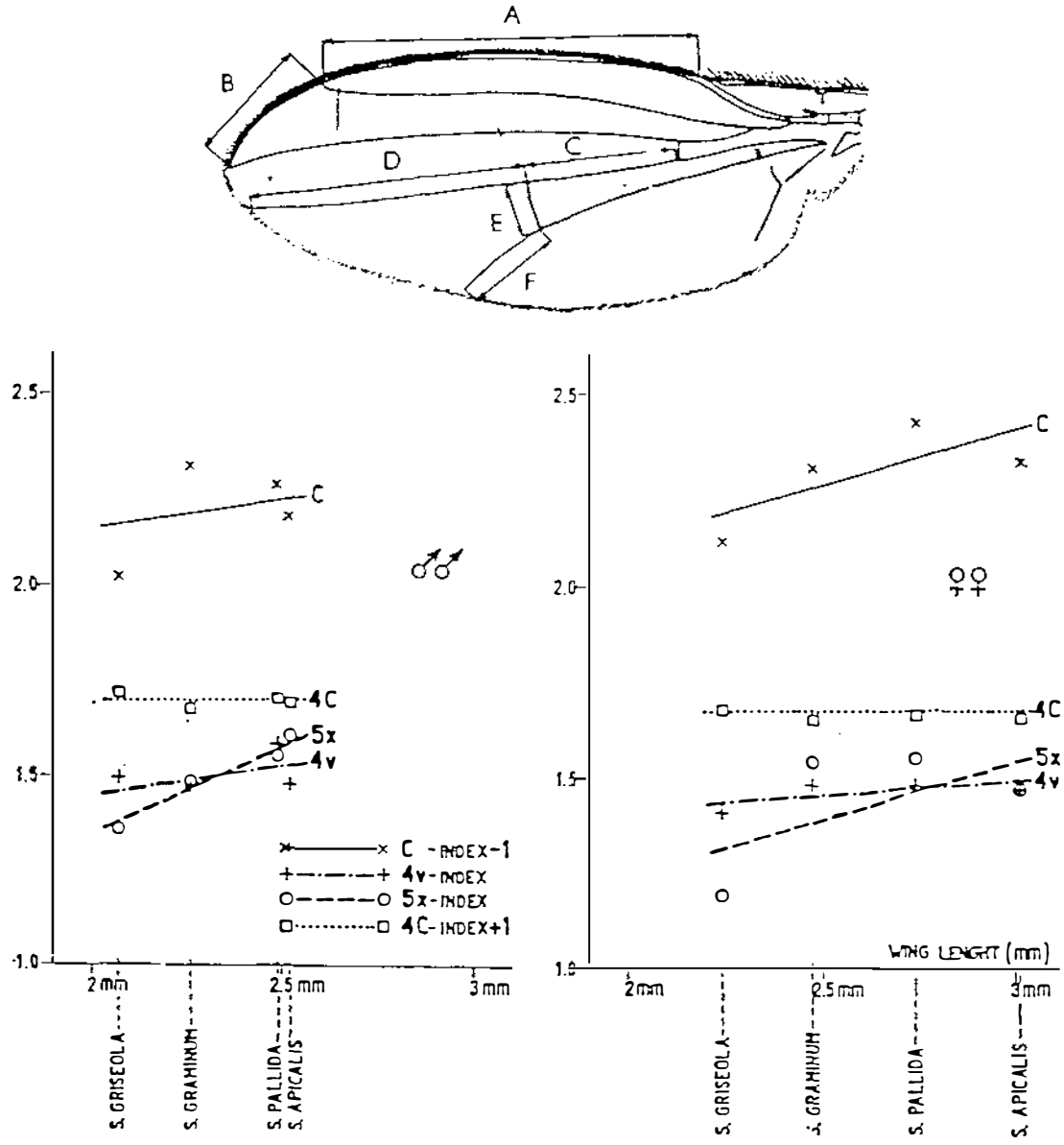


Fig. 11: Wing indices of *Scaptomyza* and their dependence on the wing length. A : B = C - index; D : C = 4v - index; F : E = 5x - index; B : C = 4C - index (Máca, 1972).

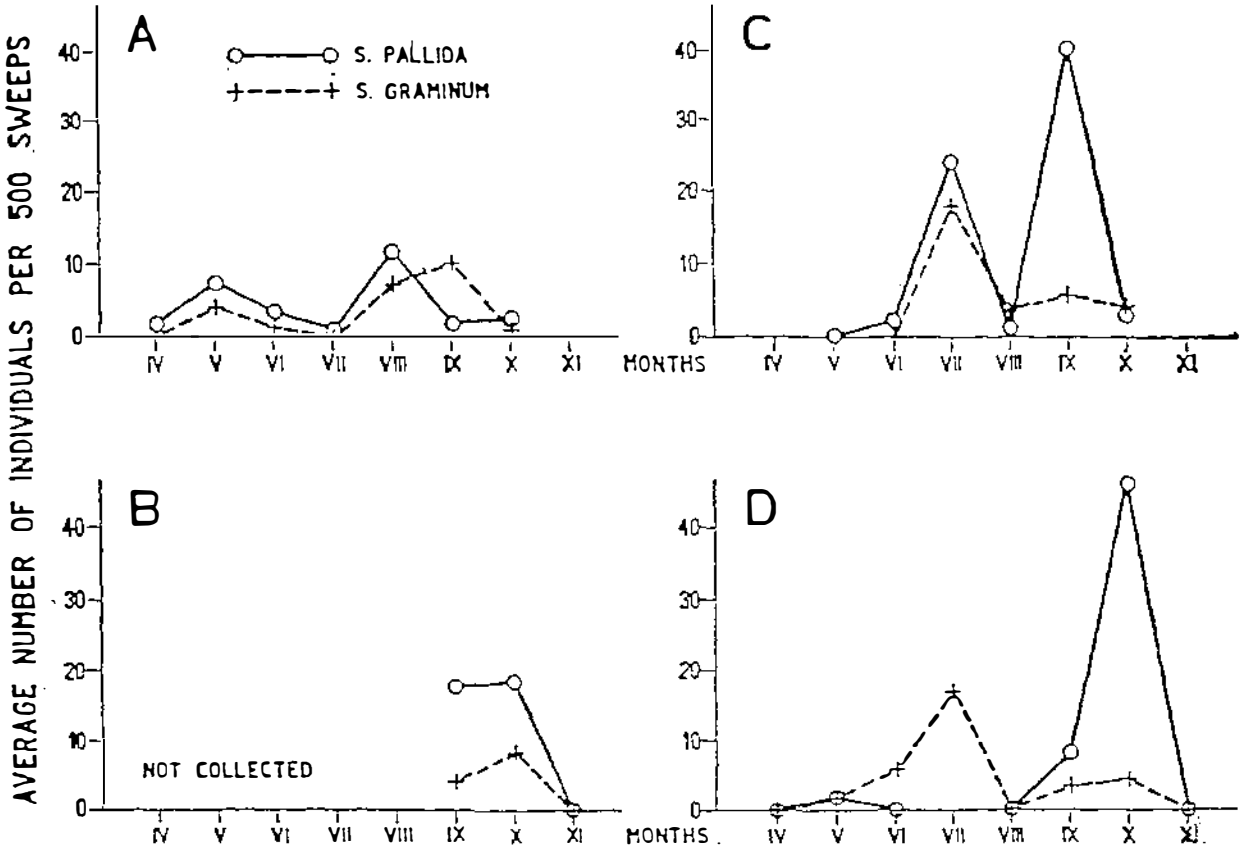


Fig. 12: Frequency of *Scaptomyza pallida* and *S. graminum* during collecting periods. A: Veself n. Luz., 1966, B: Praha-Šàrka, 1966, C: Veself n. Luž., 1967, D: Praha-Šàrka, 1967 (Máca, 1972).

Duda (1935, p. 49) separates *Parascaptomyza* and *Scaptomyza* in his key to the subgenera of *Drosophila.* Hackman (1982) finds in Duda's key that the size relation of the humeral bristles (h) and the number of rows of acrostichal hairs (a.Mi) are used as the main separating characters for the two genera. The key characters for the two genera are then as follows:

Acrostichals in 2 or 4 rows. One prominent humeral bristle, the upper one. The lower humeral bristle represented by a fine hair or, if a true bristle, not longer than half the upper one. Male genitalia as a rule (except in subg. *Trogloscaptomyza)* with conspicuous paired lobes between the anal plates (cerci) and the forcipes (see **Figs. 13—17**). These lobes, called paralobes by Frey (1954), are provided with one or more strong teeth or setae and are probably derived from the anal plates. The latter are usually small and not protruding below. Ovipositor usually weakly chitinized and provided with short teeth at the margin. Larvae usually feeding on vegetable debris, at least not obligate leaf-miners . . . . *Parascaptomyza* Duda.

Acrostichals in 4 rows, rarely in two (S. *subsplendens* Duda). Two humeral bristles, usually of nearly the same size, or the lower one at least half as long as the upper one. Male genitalia without paralobes (sensu Frey). Forceps with a dense marginal (rarely interrupted) row of stout and usually blunt teeth. Ovipositor usually with coarse marginal dentation (see **Fig. 33**). Includes obligate leaf-mining species . . . . *Scaptomyza* Hardy.

The genera *Parascaptomyza* and *Scaptomyza* are, as was already pointed out by Duda (1935, p. 61), closely allied to the *fenestrarum* group in the genus *Drosophila.* A nomenclatorial question concerns the species which Collin (1953) records from England under the name *Scaptomyza flaveola Meig.* 1830. This species is described by Hardy, 1849 under the name *Scaptomyza apicalis.* Meigen's type specimen of *flaveola* is probably lost and the identity cannot be verified.

There is, on the other hand, no special reason to doubt the synonymy of these two

names, and Hackman has used here the name *flaveola* Meig. for the species. Fallen names *flava* (1823), as already pointed out by Collin (op.c.), is not available.

Parascaptomyza disticha Duda is easily distinguished from the Finnish *Scaptomyza* species in having only 2 rows of acrostichals. For identification of *Scaptomyza* species the key is as follows:

1. Upper humeral bristle much stronger and sometimes nearly double as long as the lower one. Hind trochanters beneath with a short black spine-like bristle. Ground colour of mesonotum decidedly rufous 2
— Upper humeral bristle not much stronger than the lower one, or both equal in size. Trochanters beneath with hair-like bristles not contrasting in colour. Mesonotum yellow-brown or grey in ground colour 3
2. Male with a dark spot at the apex of the wing . . . . . *unipunctum* Zett.
— Wings (♀,♂) not spotted . . . . . *trochanterata* Collin.
3. A minute bristle, sometimes present, sometimes absent, on the frontal orbits between the upper reclinate orbital and the vertical bristles. If absent, body entirely yellow with dark anal cerci 4
— No bristle between the upper reclinate orbital and vertical bristles. Greyish species 5
4. Body yellow. Male cerci dark and rounded, not drawn out to a point *flaveola* Meig.
— Body always grey. Male cerci drawn out to a point . . . . . *montana* Wheeler.
5. Palpus with one strong dark apical bristle, the other bristles more hair-like *similis* n.sp.
— Palpus with two or more dark apical bristles 6
6. In the male genitalia the teeth of the forceps margin are remarkably elongated in the ventral direction; the caudal margin of hypandrinm with a deep median notch. Penis apodeme stout (see **Figs. 39-40**). Wing length in both sexes as a rule more than 2.7 mm . . . . . *teinoptera* n. sp.
— Marginal teeth of forceps almost equal in size, short and blunt; caudal margin of hypandrium with a narrow median split or a less deep notch **(Figs. 41-44)**. Penis apodeme slender. Wing length in both sexes as a rule less than 2.7 mm 7

7. Male cerci large with a broadly rounded free ventro-caudal margin **(Fig. 42)** and only partially covered with microscopically small short hairs. In both sexes the brown stripes on the mesonotum distinctly contrasting with the light grey ground colour . . . . . *graminum* Fall.

— Male cerci small, completely covered with microscopic hairs **(Figs. 43—44)**. In both sexes and especially the female the brown stripes on the mesonotum are only faint, if present at all . . . . . *griseola* Zett.

Scaptomyza unipunctum Zett. (Figs. 18-19)

Scaptomyza trochanterata Collin (Figs. 20-21).

Scaptomyza flaveola Meig. (Figs. 29-30).
A leaf-mining species represented in the Australianm Museum's collection.

Scaptomyza montana Wheeler (Figs. 31-32).
This species, has been reared from leaf-mines on both *Pisum* and *Brassica.*

Scaptomyza consimilis n.sp. (Figs. 27-28).

Scaptomyza teinoptera *n.sp.* (Figs. 39-40).

Scaptomyza clavata Okada

Scaptomyza tistai (Kumar and Gupta, 1992)

Scaptomyza graminum Fall. (Figs. 41-42).

The males of this species can be recognized by the large rounded cerci (visible in dried specimens even without dissecting the abdomen). The females can be separated from *griseola* by the distinct thorax pattern and in most cases from *teinoptera* by the

difference in wing length. According to Basden (1954), imagines of this species can be trapped on apple baits. The larva is leaf-mining and feeds on Caryophyllaceous plants. Some of the food plants mentioned in the literature may refer to other grey species of *Scaptomyza,* but there is reliable record at least for *Stellaria media* (Basden op. C.).

Scaptomyza griseola Zett. (Figs. 43-44).

Scaptomyza norica *n.sp.* (Fig. 34).

Scaptomyza terminalis Loew (Fig. 23).

Scaptomyza apieata Thomson *(S. terminalis* Wheeler 1952, nec Loew) (Figs. 24,26).

Scaptomyza hsui *n.sp.* (S. *terminalis* Hsu 1949, nec Loew) (Figs. 22,25).

Scaptomyza atlantica n.sp. (Figs. 35-36).

Scaptomyza (Exalloscaptomyza) caliginosa Hardy: flower breeding Drosophilids (Montague, 1989).

Scaptomyza mateola sp. nov. :from the flowers of cultivated Cucurbitaceae in Mauritius (McEvey 1990).

Scaptomyza exilis sp. nov. :from *Crinum* sp. in Madagascar (McEvey 1990).

Scaptomyza tistain n.sp. (Kumar, A. and Gupta, J.P. 1992).

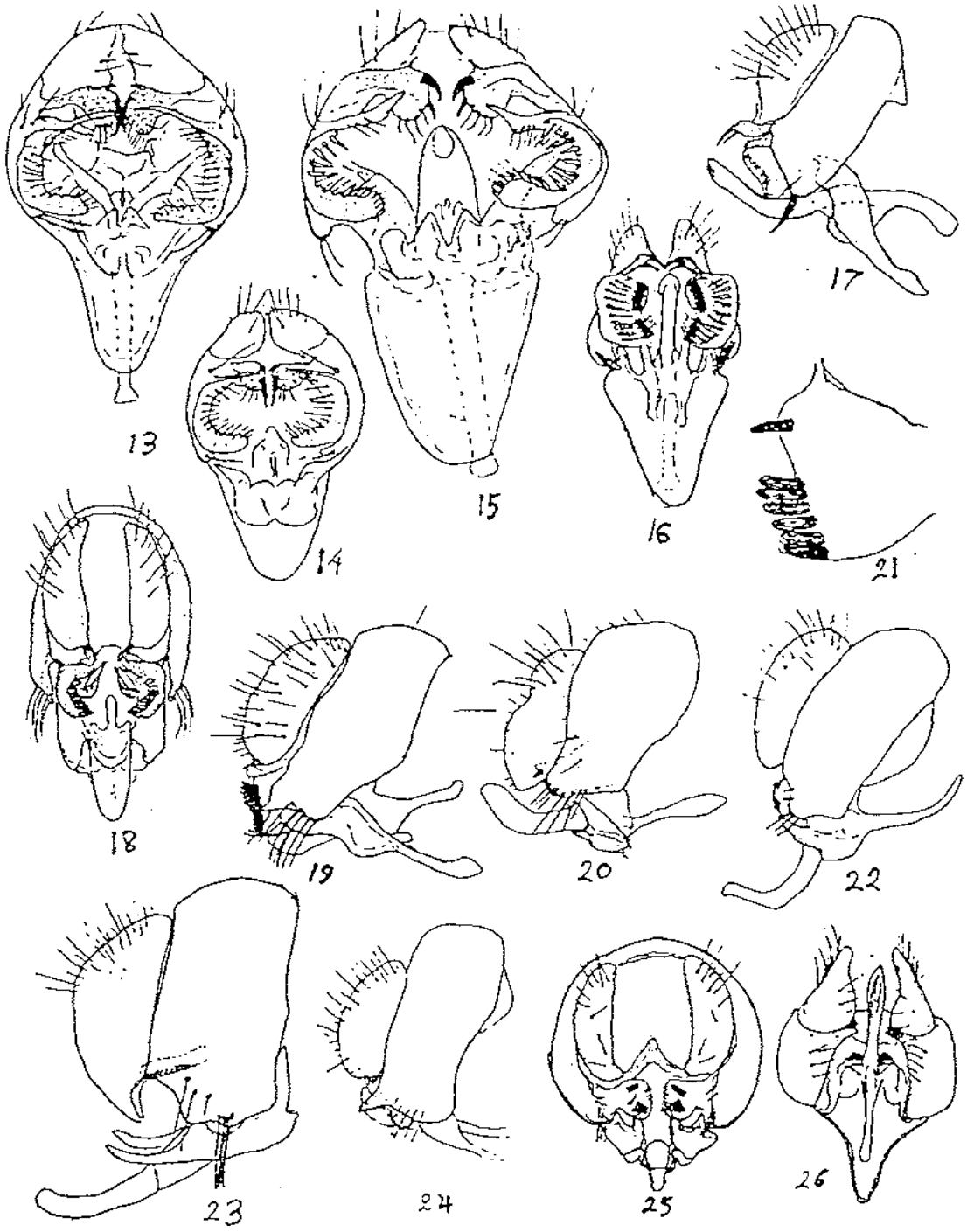
Scaptomyza clavata Okada (Kumar, A. and Gupta, J.P. 1992).

Scaptomyza (Bunostoma) australis

(Figs. 45-48)

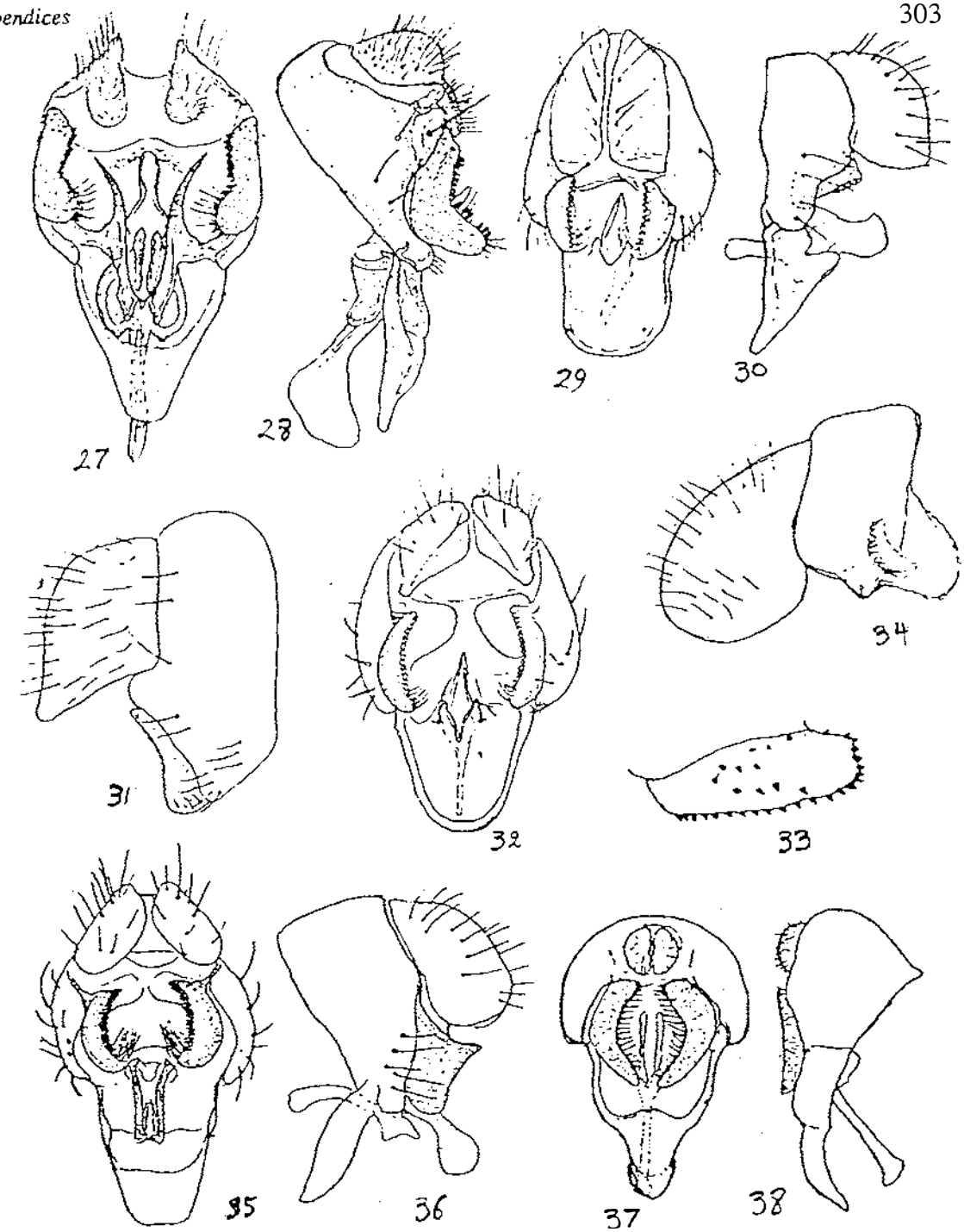
In his large monograph treating the Australian Drosophilid fauna, Bock (1977) documented numerous records of *Scaptomyza australis,* ranging from Western Australia to Queensland. He also mentioned that the species is an ecological generalist, and is found in most habitats. Later, he reported a large series from Norfolk Island, a possession of Australia about 500 miles south of New Caledonia and about 1000 miles northeast of Sydney (Bock, 1986).

Bunostoma presently includes the following species or groups of species: *bicolor* Malloch (Samoa), *boninensis* Okada (Bonin Is.), *philipensis* Bock (Norfolk and nearby Philip Island), *flavifacies* (Malloch) (Marquesas Is.), 8 species from Hawaii (Hardy, 1965), and perhaps *flavella* Harrison and *fuscitarsis* Harrison (both from New Zealand). Grimaldi (1990), like Hackman, has not examined the two New Zealand species, and Harrison's descriptions are based only on the external male genitalia, not the internal ones. Wheeler (1981) placed these two species in *Scaptomyza* subgenus incertae *sedis,* but Hackman (1982) indicated (on dubious morphological grounds) that they may be *Bunostoma.* Still, the undisputed sister species of *Scaptomyza australis* is *S. philipensis,* based on male genitalic features. The male genitalia of these species are remarkably similar to that of *S. anomala* from Hawaii (Grimaldi, 1990).

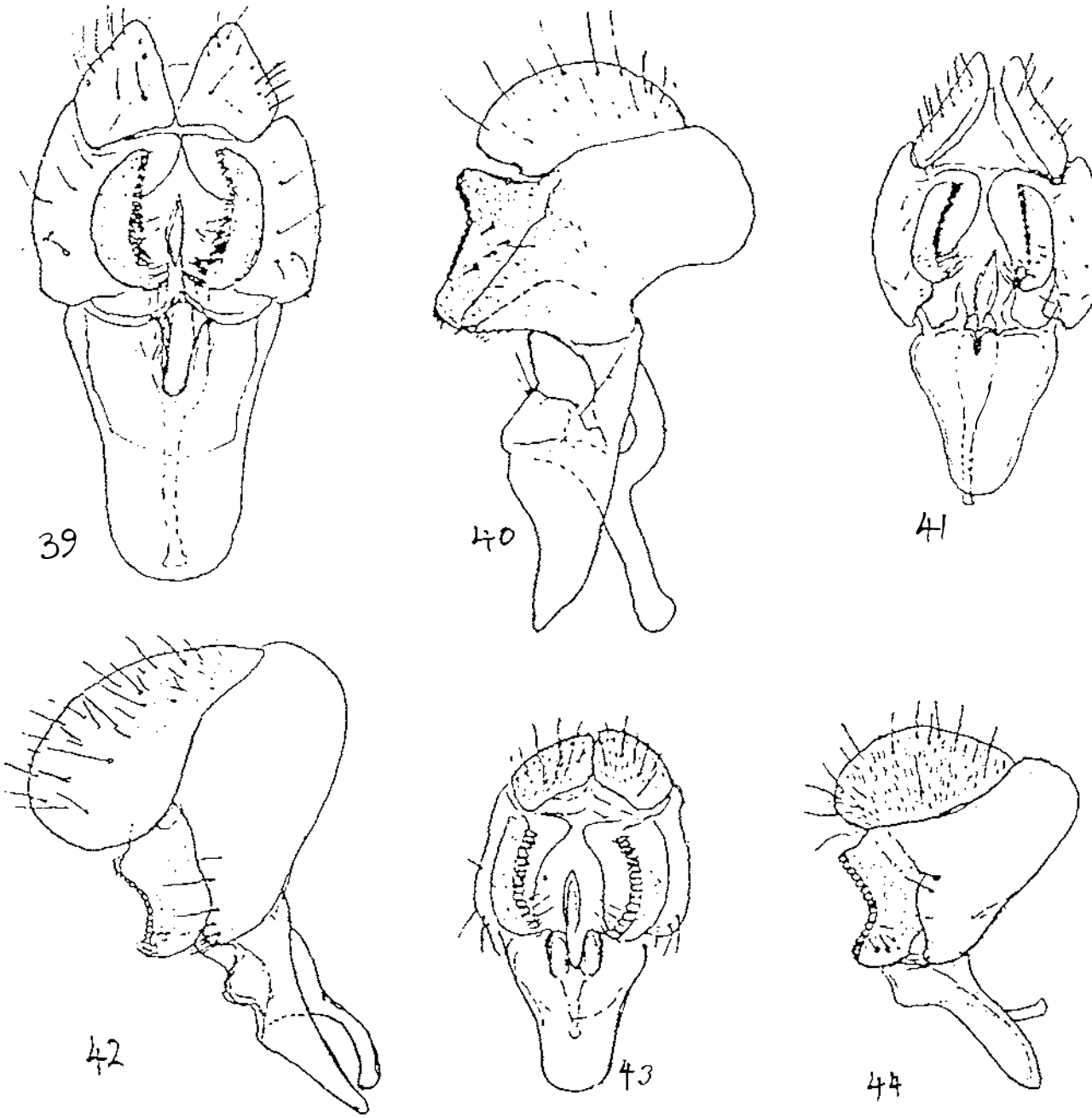


Figs. 13-17: Male genitalia of *Parascaptomyza* species. **13.** *Parascaptomyza disticha,* ventral view. **14.** *Parascaptomyza substrigata.* **15.** *Parascaptomyza impunctata* **16.** *Parascaptomyza adusta,* ventral view. **17.** The same species, profile.

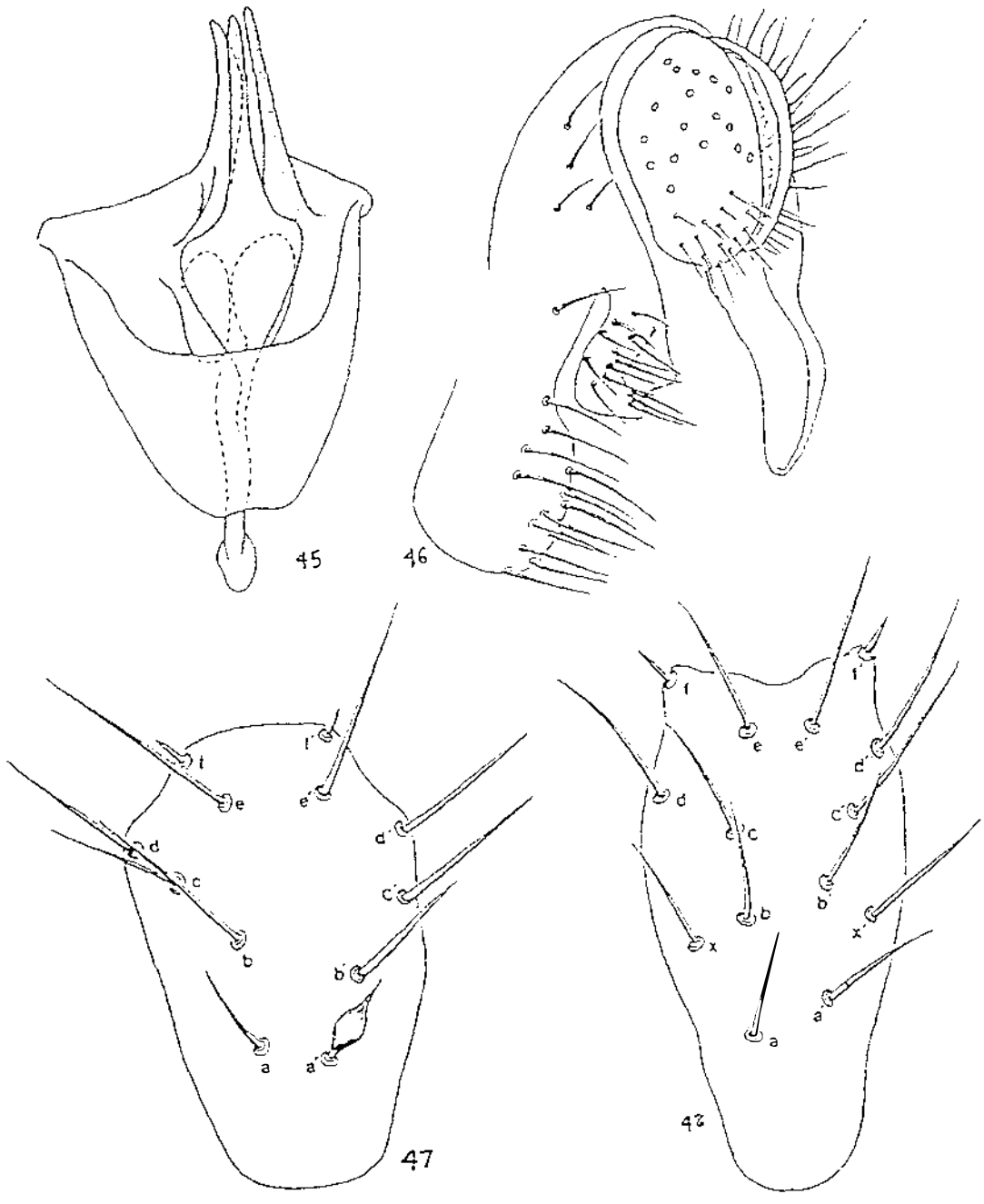
Figs. 18-26: Male genitalia of *Scaptomyza* species. **18.** *S. unipunctum,* ventral view **19.** The same, profile. **20.** *S. trochanterata.* **21.** Forceps of the same. **22.** *S. hsui* n.sp., profile. **23.** *S. terminalis.* **24.** *S. apicata* **25.** *S. hsui* ventral-caudal view. **26.** *S. apicata,* ventral view (Hackman, 1955).



Figs. 27-38: Male genitalia of *Scaptomyza* species. **27.** *S. consimilis* n.sp., ventral view. **28.** The same, profile. **29.** *S. flaveola*, ventral view. **30.** The same species, profile. **31.** *S. montana*, profile. **32.** The same species, ventral view. **33.** Ovipositor of the same species. **34.** *S. norica* n.sp. Genital arch and cerci of the male. **35.** *S. atlantica* n.sp., ventral view. **36.** The same profile. Figs. **37-38**: Male genitalia of *Drosophila forcipata* ventral and side view (Hackman, 1955).



Figs. 39-44: Male genitalia of *Scaptomyza* species. **39-40.** *S. teinoptera* n.sp., ventral and side view. **41-42.** *S. graminum*, ventral and side view. **43-44.** *S. griseola*, ventral and side view (Hackman, 1955).



Figs. 45-48: Genitalia of *Scaptomyza australis* from newly discovered distributions. **45**. Male: hypandrium, aedeagus, and associated structures, dorsal view (Pitcairn Is.). **46**. Male: epandrium, cercus, oblique terminal view (same specimen as in Fig. 45). **47**. Female: sternite 8 (Pitcairn Is.). **48**. Female: sternite 8 (Vanuatu) (Grimaldi, 1990).

Harrison (1959) described New Zealand species as follows:

" Family D R O S O P H I L I D A E "

Arista plumose, pectinate, or pubescent. Third antennal segment rounded or oval. Front with conspicuous bristles. Postvertical convergent. Face with distinct antennal fossae and a carina. Vibrissa present. Costal twice broken; subcosta vestigial; first vein short; discal and second basal cells united; anal cell present.

Distinguished and separated from other families by having two costal breaks, discal and second basal cell united, subcosta vestigial, anal cell present, arista usually plumose with ray dorsally and ventrally on main axis, and convergency postverticals.

Genera occurring in New Zealand:

Drosophila Fallen

Scaptomyza Hardy

Hutton (1901) first recorded and described New Zealand representatives of the family and Harrison (1952) described the domestic species of the genus *Drosophila* in New Zealand. None of species considered up to 1952, with the possible exception of *D. marmoria* Hutton, is endemic. Endemic species are recorded here for the first time.

A species of *Leucophenga* was recorded by Miller (1921). This is shown below to be a *Drosophila* and as yet no true member of *Leucophenga* has been found in New Zealand. *Scaptomyza* has been not previously recorded from New Zealand.

Species additional to those recorded below are present in New Zealand but as they are represented in collections by few specimens and have not been examined in the live state, their description is postponed until further material is available. The subgenus *Pholadoris* and the *obscura* group of species appears to be represented in the undescribed material. In most New Zealand collections *Drosophilidae* are poorly represented. Compared with other families these flies are rarely taken in the sweep net

and it is only when special collecting procedures are practised, such as the use of banana-baited traps, that large numbers are obtained. Such collecting has been confined, so far to the Auckland district. When trapping can be extended in other area of New Zealand a more complete picture of the fauna will be optained.

KEY TO GENERA OF *DROSOPHILIDAE* IN NEW ZEALAND

(Harrison, 1959)

Two or 4 rows of acrostichal hairs . . . . . *Scaptomyza*

At least 6 rows of acrostichal hairs . . . . . *Drosophila*

Genus *SCAPTOMYZA* HARDY

Occiput distinctly convex. 2 or 4 rows of acrostichal hairs in front of transverse suture, 2 between dorsocentral bristles; prescutallars always absent. Thorax, abdomen and wings slender.

Species occurring in **New Zealand**:

Scaptomyza flavella sp.n.

S. fuscitarsis sp.n.

S. graminum (Fallen)

Not previously recorded from New Zealand. *S. graminum* is the most widespread species in the genus and has probably been introduced to New Zealand through commerce. The other 2 species are possibly endemic.

KEY TO SPECIES OF SCAPTOMYZA IN NEW ZEALAND

1 Entirely yellow species . . . . . **flavella**

Brown to black species 2

2 Dorsal surface of scutellum almost flat . . . . . **graminum**

Dorsal surface of scutellum distinctly convex . . . . . **fuscitarsis**

Scaptomyza flavella sp.n.

(Figs. 51, 54 and 56)

Male and female

Head (Fig. 56): Arista with 7 branches, two below in addition to the terminal fork; axis dark brown with basal segment light yellow. Antenna yellow; 3rd segment longer than 2nd segment, covered with fine white pile; 2nd segment with 2 strong black bristles and small black hairs. Front yellow, over half width of head at vertex; ocellar triangle small, enclosing ocelli and ocellar bristles and hairs, whitish-grey dusted; area between ocelli distinctly raised above level of front, ocelli clear; orbits light greyish-brown, pollinoses. Postverticals cruciate; ratio of length of fronto-orbitals, anterior to posterior, 3: 2: 4; anterior reclinate bristle much closer to proclinate than to posterior reclinate and lateral to it; one small hair on frontal orbit anterior to orbitals; about 8 small black hairs near anterior median margin of front. Face yellowish-white. Carina wedge shaped, broad and prominent below; not sulcate. Cheeks yellowish-white. Vibrissa strong; 2nd oral bristle equal to vibrissa; 3 prominent bristles at lower posterior angle of cheek. Occiput yellow, bunch of black hairs immediately above foramen. Eyes dark red in pinned specimens; covered with short, whitish pile. Vertical diameter of eye about 5 times width of cheek in same axis. Proboscis yellow; palpi light yellow with 2 apical fine bristles, one longer than the other, and a few fine bristles on anterior margin.

Thorax: Yellowish-brown; scutellum yellowish-brown, flat disc. Acrostichal hairs in 2 rows; 2 enlarged hairs anterior to anterior- dorsocentrals; basal scutellars divergent, equal in length to apical scutellars, both pairs strong; 1 strong humeral and 1 strong hair close to it; 2 enlarged hairs medial to presutural, 2 prominent sternopleurals, 1 enlarged hair dorsal to posterior bristle; sterno-index about 0.63.

Legs: Yellowish-brown; apical segments of tarsi light brown. Apical bristle on 1st and 2nd tibiae; preapicals on all three tibiae.

Wings: Clear; veins light brown. Costal ending at apex of 4th vein but weaken between 3rd and 4th veins; third costal section with heavy bristles on basal three-fifths; pair of strong bristles at distal costal break. Wing indices: costal about 3.5-3.7; 4th vein about 0,6; 5x about 1.8. Halteres yellowish-brown.

Abdomen: Yellowish-white. Strong bristles on posterior margin of tergites, small black hairs elsewhere on tergites.

External male genitalia: Genitalia arch lightly chitinised, parallel sided, with about 6 bristles near middle on either side; anal plate brown posteriorly, about 20 strong bristles and a cluster of fine short bristles at ventral margin; clasper with row of about 8 very strong black teeth and a subapical row of about 8 shorter stout black teeth with fine bristles between these teeth and between the row of teeth.

Scaptomyza graminum (Fallen).

(Figs. 50, 53)

A small light brown to greyish species. Body length 2.0-2.25 mm., wing length 2.0-2.75 mm.

Male and female

Head: Arista with about 7 branches, usually only 1 below in addition to the terminal fork; axis dark brown, basal segment light brown. Antenna light brown; 3rd segment dark on outer margin; 2nd segment darker on outer margin, with 2 bristles and smaller black hairs. Front brown posteriorly and medianly, yellowish-brown anteriorly; about half width of head at vertex; area between ocelli almost black in some specimens and raised above level of front; ocelli clear; frontal orbits greyish-blown about bristles, yellowish-brown anteriorly. Ratio of length of orbitals; anterior to posterior, about 7:3:9; anterior reclinate lateral to and just anterior to or level with proclinate; 1 or 2 small hairs on frontal orbit anterior to orbitals; a few minute hairs on median anterior region of front. Face yellowish-brown. Carina brown, narrow, ridge shaped, but slightly broader

and nose-like below. Cheeks light yellow. Vibrissa strong; 2nd oral bristle about half length of vibrissa; 3 or 4 prominent bristles at lower angle of cheek. Occiput grey to dark purplish-grey. Eyes dark red in pinned specimens; Covered with dense light-coloured pile. Vertical diameter of eye about 6 times width of cheek in same axis. Proboscis yellowish-brown; palpi with 1 strong apical bristle and some smaller black hairs.

Thorax: Light brownish-grey, dusted dorsally, sometimes lighter laterally, and yellowish-brown ventrally; broad light-coloured stripes on mesonotum extending from acrostichal rows through dorsocentral row to 1st row of hairs outside of the dorsocentral row; scutellum greyish-brown, almost flat disc. Acrostichal hairs in 2 rows; 2 enlarged hairs anterior to anterior dorsocentrals; basal scutellars divergent, equal in length to apical, both pairs strong; 1 strong humeral; 2 prominent sternopleurals, 1 enlarged hair dorsal to posterior bristle, sterno-index about 0.5.

Legs: Yellowish-brown; tarsi faintly but not distinctly darkened towards tip; preapical bristles on all tibiae; apical on 1st and 2nd only.

Wings: Clear; veins light brown. Costal ending at apex of 4th vein; third costal section with heavy bristles on its basal third; pair of strong bristles at distal costal break. 3rd vein with a slight bend posteriorly near apex, thus narrowing the 1st posterior cell somewhat. Wing indices: costal about 3.2; 4th vein about 1.7; 4c about 0.75; 5x about 1.3. Halteres yellowish-greyish-brown.

Abdomen: Varies from light brown to blackish-brown, shining. Lightest areas occur about median region of anterior tergites, apical tergites the darkest and often almost completely black. Sternites light yellow.

External male genitalia: Genitalia arch narrow dorsally, heavily chitinised, anteriorly and posteriorly on dorsal half, ventral margin concave and produced posteriorly and anteriorly, 2 strong bristles at postero-ventral and antero-ventral regions;

anal plate normal and oval on dorsal half and with bristles over most of this surface, ventral half modified to a posteriorly directed auxiliary clasper with row of about 4 very strong apical teeth and a cluster of small bristles above them; clasper crescent shaped and fitting into ventral margin of arch, apical margin with strong teeth and bristles.

Distribution in New Zealand: Waitakere Ranges, Auckland, Pukekohe, Christchurch, the Brothers Islands (July, August, October, December, January, March, May, June).

Remarks: Separated from *S. fuscitarsis* by having the scutellum almost flat dorsally and from *S. flavella* by its smaller size, darker colour, and lower costal index.

Scaptomyza fuscitarsis sp.n.

(Figs. 49,52 and 55)

A slender shining fly, usually black but varies from brown to black. Body length 1.75-2.25 mm., wing length 1.75-2.5 mm.

Male and female

Head: Arista with 7 branches; 2 below in addition to the terminal fork; axis black, basal segment light brown. Antenna yellowish-brown, occasionally reddish-brown; 3rd segment somewhat pointed apically and about equal in length to 2nd segment; 2nd segment with 2 bristles and some minute black hairs. Front light yellowish-brown to dark brown occasionally tinged with red, dark and, in some lights, grey dusted at vertex; anterior region frequently light brown; orbits grey to dark brown, lighter anteriorly; area between ocelli dark brown to black and raised above level of front; ocelli clear. Ratio of length of orbitals, anterior to posterior, 2 : 1 : 3; anterior reclinate lateral to and level with or just posterior to proclinate; usually 1 small hair on frontal orbit anterior to orbitals; a few minute black hairs on median anterior region of front. Face yellowish brown, occasionally light yellow. Carina ridged, not sulcate, sometimes with a brown stripe on ridge. Cheeks yellowish-brow, black posteriorly. Vibrissa strong; 2nd oral

bristle usually distinct from other hairs and third to half length of vibrissa; 3 prominent bristles at lower angle of cheek. Occiput brown or greyish-black with lightly dusted bands extending from vertex, at either side of ocelli to foramen. Eyes dull red in pinned specimens; covered with dense whitish pile. Vertical diameter of eye about 6 times width of cheek in same axis. Proboscis light yellowish-brow; palpi with 1 strong apical and 2 or 3 small bristles on anterior margin of apical third.

Thorax: Brown to purplish-black with much grey dusting dorsally and laterally, light ventrally, no pattern of stripes expect lighter specimen have indications of yellowish-brown area between the ventrally acrostichal and dorsocentral rows anteriorly; scutellum same colour as mesonotum, with distinctly convex disc. Acrostichal hairs in 2 rows; 2 enlarged hairs anterior to dorsocentrals; basal scutellars divergent and equal to longer than apical scutellars, both pairs strong; 1 humeral and often, 1 enlarged hair 2 sternopleurals, sterno-index about 0.5.

Legs: Light yellowish-brown; anterior tarsus with apical three segments dark brown to black; other tarsi darkening gradually towards apices. Preapical on all tibiae; apical on 1st and 2nd tibiae only.

Wings: Clear; veins light brown. costal ending at apex of 4th vein; but weakened between 3rd and 4th vein; third costal section with heavy bristles on its basal two-thirds; pair of strong bristles at distal costal break. Wing indices: costal about 2.5-3.1; 4th vein about 1.9; 4c about 0.9; 5x about 1.6. Halteres light yellow, darkened basally.

Abdomen: Shining blackish-brown with lighter areas anteriorly. In the light-coloured specimens the anterior tergites may be brown, or even yellowish-brown dorsally, but apical segments and lateral regions of anterior segments are always dark brown.

External male genitalia: Genitalia arch broad and parallel sided, about 3 bristles near middle of posterior margin, cluster of short bristles along ventral margin; narrow

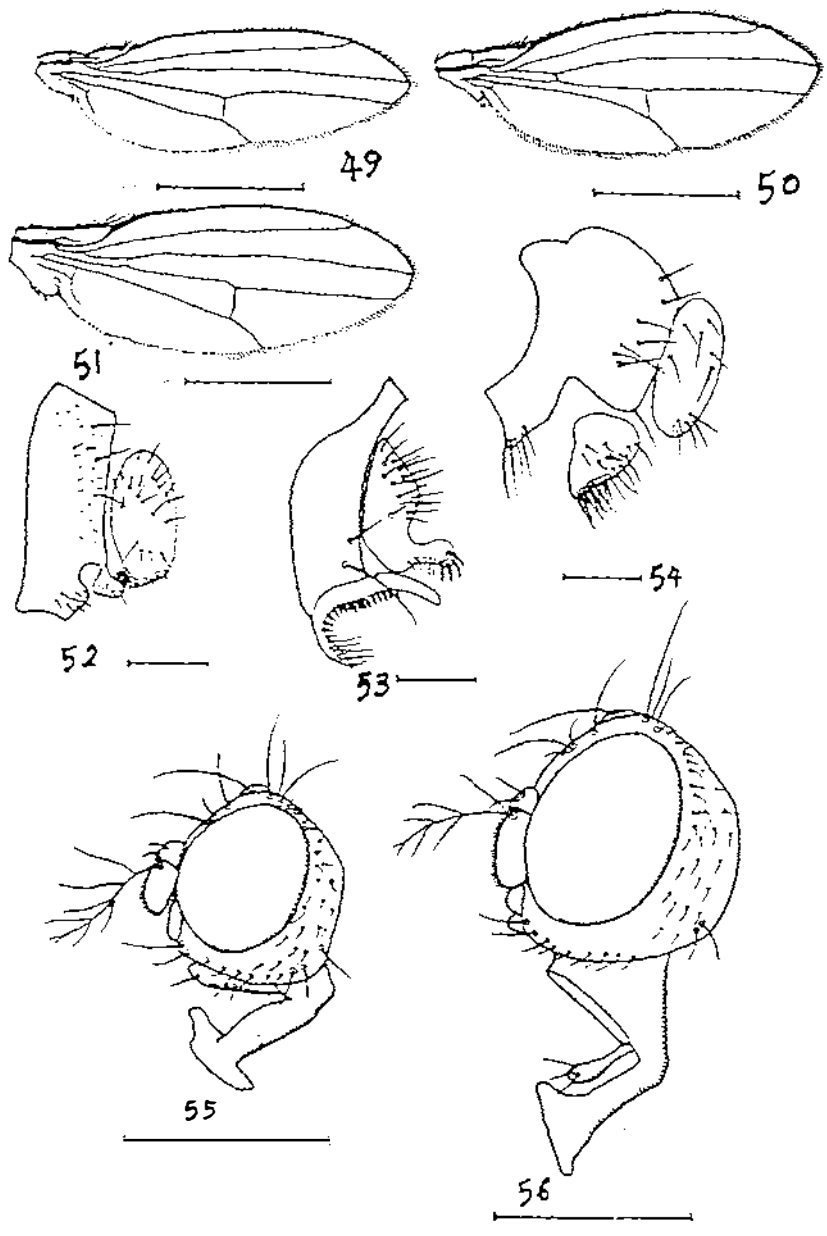
posteriorly directed arm arising near postero-ventral corner; anal plate ovoid, bristles over most of surface, expect at middle; shorter and thicker bristles clustered about ventral margin; clasper small with very short almost tooth-like bristles on ventral margin.

Paratypes: Auckland: Browns Bay, swept off *Leptospermum* foliage. Palmerston North: flying around rotting swedes.

Additional Specimens: Palmerston North: flying around rotting swedes, on new swede area.

Distribution: Auckland, Pukekohe, Palmerston North, Christchurch, Banks Peninsula, Okarahia, Roxburgh. (All the year).

Remarks: Readily separated from *S. graminum* and *S. flavella* by the distinctly convex scutellum.



Figs. 49 - 54: Wings of the *Scaptomyza* species. **49.** *S. fuscitarsis.* 50. *S. graminum.* **51.** *S. flavella.* **Figs. 52 - 54:** External male genitalia of the *Scaptomyza* species. **52.** *S. fuscitarsis.* **53.** *S. graminum.* **54.** *S. flavella.*

Figs. 55 - 56: Head of the *Scaptomyza* species. **55.** *S. fuscitarsis.* **56.** *S. flavella.* Scale: Figs. 49-51, 1.0 mm.; Figs. 52-54, 0.1 mm.; Figs. 55-56, 0.5 mm. (Harrison, 1959).

Holloway (1990) believed what Harrison identified as *S. graminum* was in fact *S. elmoi.*

Key to *Scaptomyza* species occurring in New Zealand

(Figs. 57-60 and Plates 1-5)

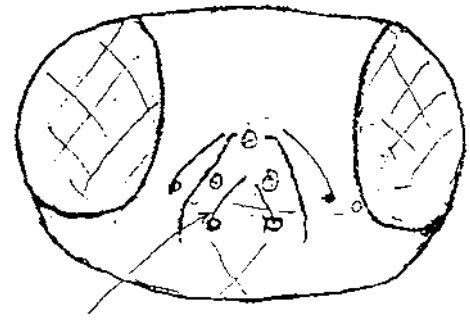
Prepared by B.A. Holloway, 1990

1. Four longitudinal rows of acrostichal setae in front of anterior dorsocentral bristles ..... *S. flava*
- Two longitudinal rows of acrostichal setae in front of anterior dorsocentral bristles 2

2. Scutellum convex dorsally ..... *S. fuscitarsis*
- Scutellum flattened dorsally 3

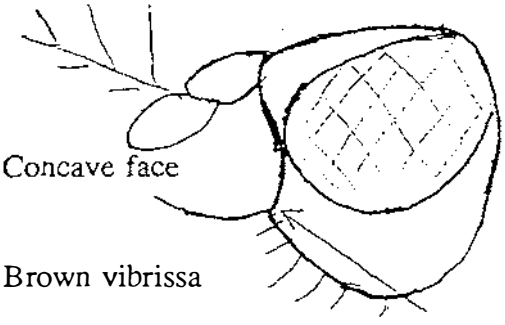
3. Arista of antenna with 1 ventral ray in additional to terminal fork . . . *S. elmoi*
- Arista of antenna with 2 ventral rays in additional to terminal fork . *S. flavella*

Post vertical bristles



P v s convergent

Face profile

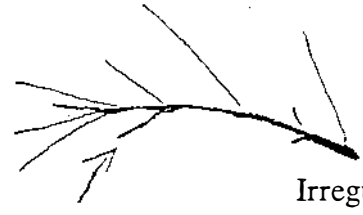


Concave face

Brown vibrissa

Vibrissa angle

Antennal arista



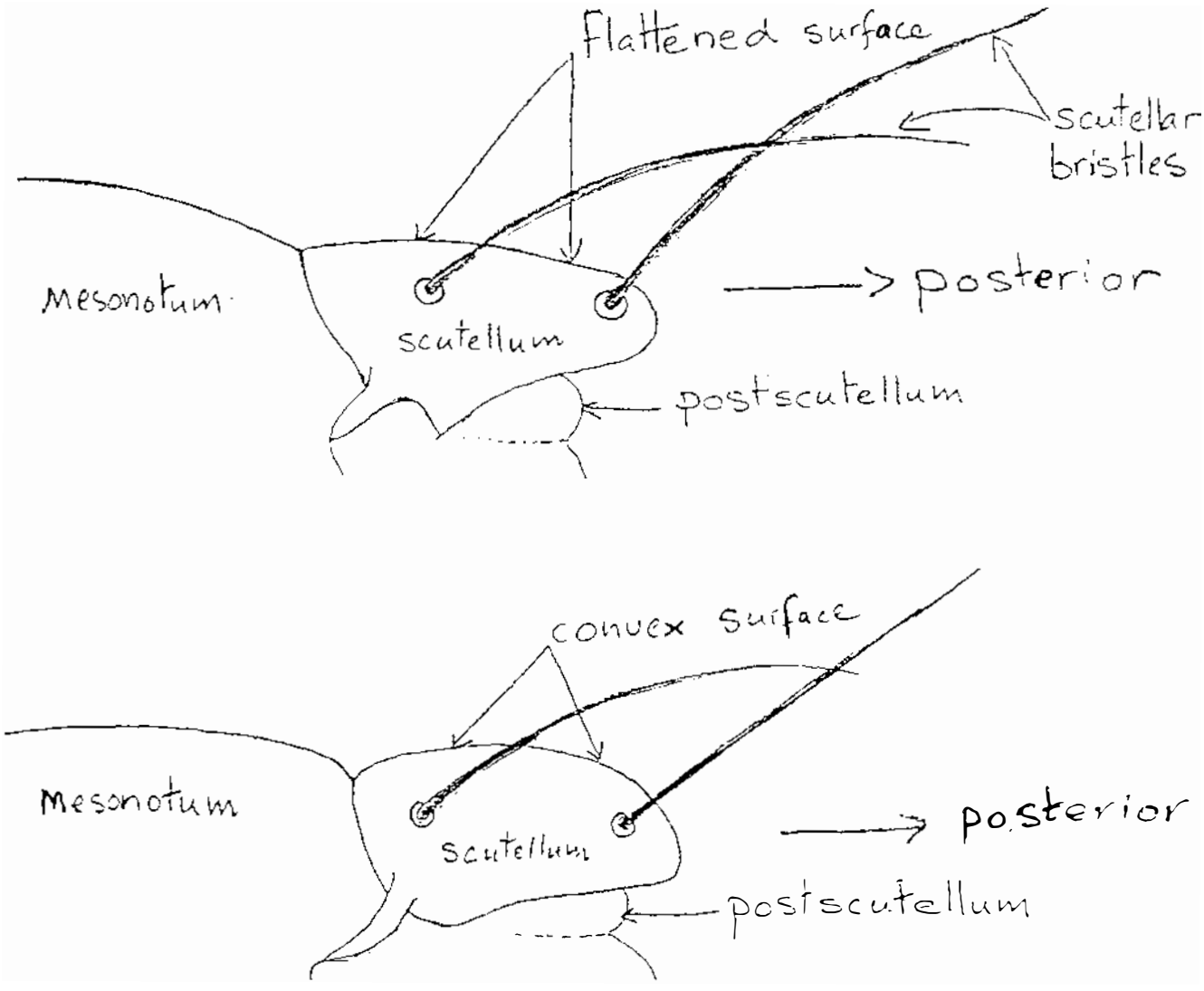
Branches also on this side

Irregular lengths

No spine

Fig. 57: Some characters of the family Drosophilidae (Holloway, 1990).

Scaptomyza flavella

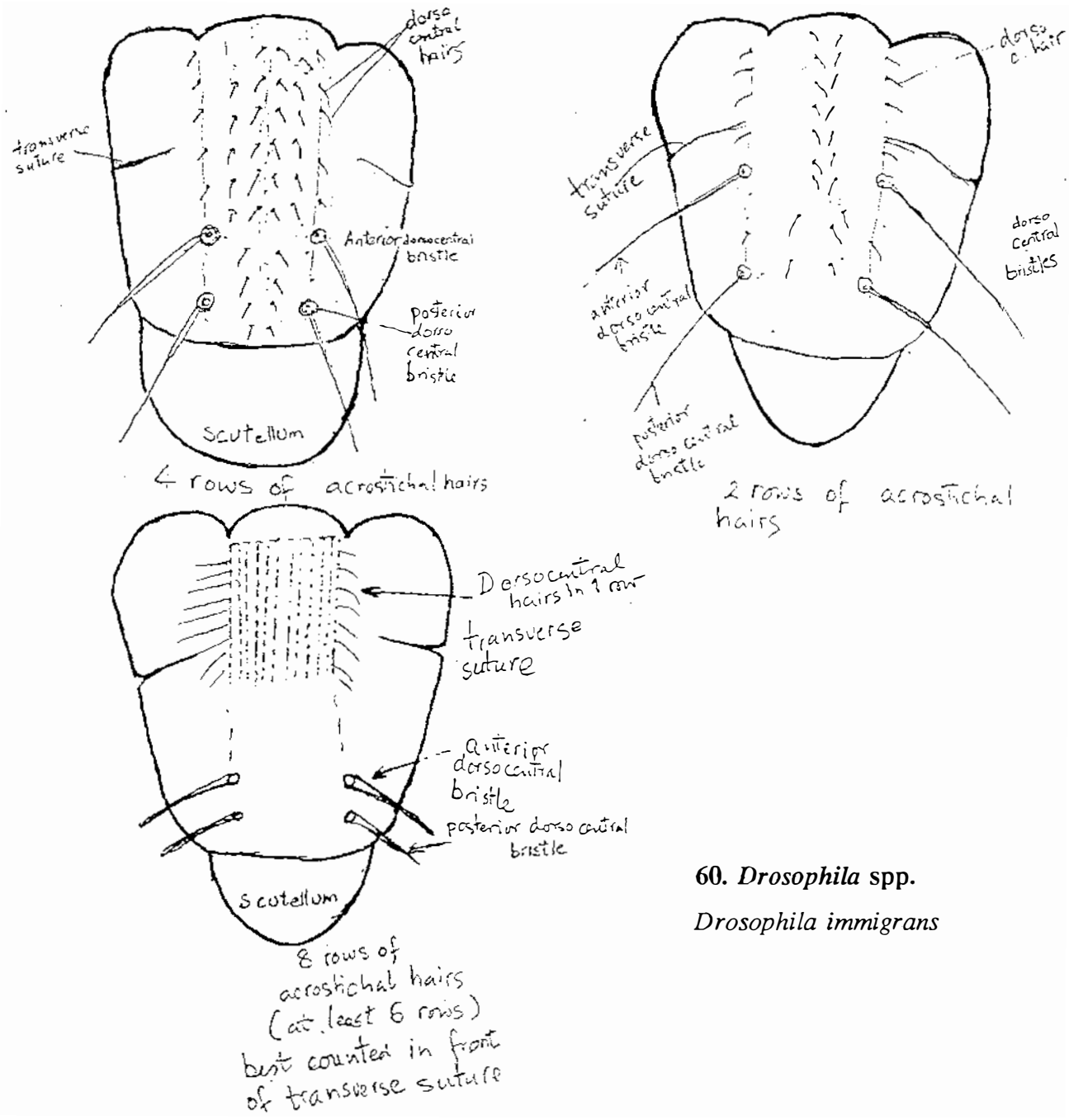


Scaptomyza fuscitarsis

Fig. 58: Profile of scutellum (from the left side) of the *Scaptomyza* species. *S. fuscitarsis* differs from all the other *Scaptomyza* spp. in New Zealand in having a strongly convex, rather than flattened, dorsal surface on the scutellum (Holloway, 1990).

59. *Scaptomyza* spp.

a: *S. flava* b: *S. fuscitarsis*



60. *Drosophila* spp.

Drosophila immigrans

Figs. 59-60: Acrostichal hairs on thorax of the *Scaptomyza* species compared with *Drosophila* species (Holloway, 1990).

Plates 1-2: Ovipositor of female *S. flava*

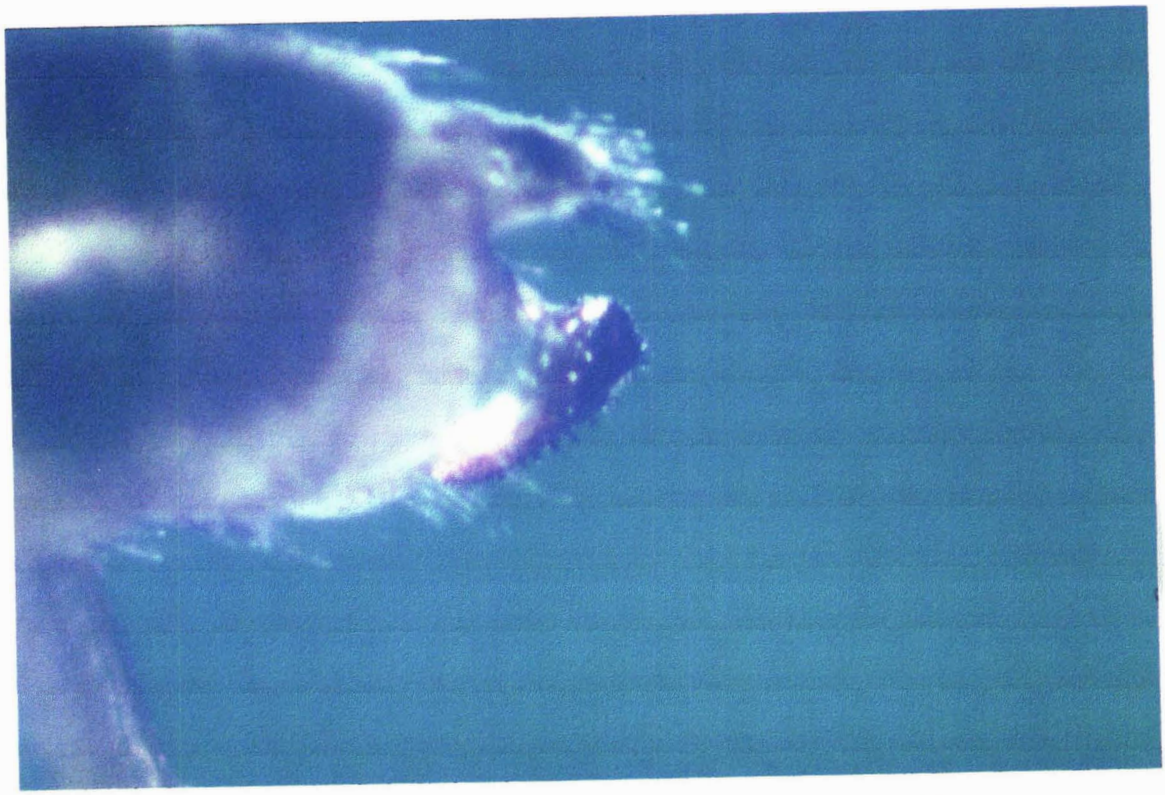


Plate 3: External male genitalia of *S. flava*

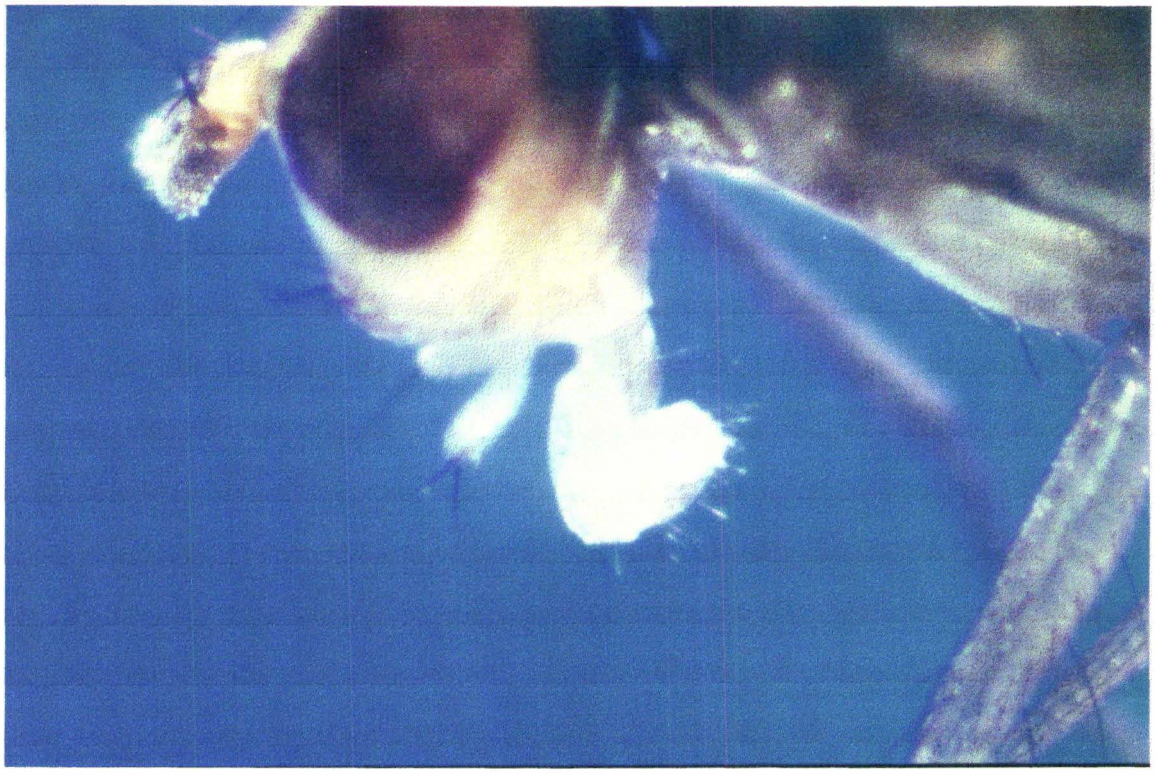


Plate 4: Proboscis of adult *S. flava*

Plate 5: Longitudinal rows of acrostichal bristles *S. flava*

THE PHYLOGENY OF *SCAPTOMYZA*

Among the Hawaiian species of *Drosophila* and *Scaptomyza* the most obvious overlapping of characters are found in the subgenus *Engioscaptomyza* Kaneshiro. For practical reasons this subgenus was retained in *Drosophila,* but its internal characters suggest that it belongs to the Scaptomyzoids (Hardy, 1966; Kaneshiro, 1969). The "white-tip-scutellum group" among the Drosophiloids also show several Scaptomyzoid characters (Throckmorton, 1966).

It seems most probable that the same ancestral stock in Hawaii has given rise to the Drosophiloids and at least the Scaptomyzoids belonging to the big subgenus *Elmomyza,* subg. *Rosenwaldia,* subg. *Alloscaptomyza,* subg. *Tantalia* and the genus *Titanochaeta.* Okada (1973) places the endemic Hawaiian *Scaptomyza* subgenus *Exalloscaptomyza* Hardy on the same branch of a phonogram as *Hemiscaptomyza* and *Scaptomyza (s.* str.) keeping it quite separate from the other Hawaiian *Scaptomyza* subgenera. Okada's phonogram is based on a dozen external characters, including the seven used in Hackman's old hypothetical system of the *Scaptomyza* subgenera (Hackman, 1959). No *Exalloscaptomyza* species has been found outside Hawaii and the similarity with *Hemiscaptomyza,* a subgenus not found in the Pacific area, is probably due to parallelism. *Exalloscaptomyza* Hardy may be a strongly differentiated off-shoot of the Scaptomyzoid branch. The spermatheca **(Fig. 81)** depicted for several species by Throckmorton (1966) are of a rather aberrant type, but the same type is also found in *Titanochaeta contestata* Hardy from Hawaii. It seems more difficult to clarify the origin of the subgenus *Bunostoma,* described by Malloch (1932) as a genus and with endemic species in Hawaii, other island groups in the Pacific and in Australia. Though not typical Scaptomyzas in general appearance, the *Bunostoma* species have been included in *Scaptomyza* because of some key characters (see **Table 1** and Hackman, 1959). The spermatheca of the Hawaiian species are of the same general type as in several *Scaptomyza* species (see **Figs. 68 - 74**). In Okada's phonogram (1973) *Bunostoma* is a sister group of the other Hawaiian subgenera excluding *Exalloscaptomyza.* The male genitalia differ distinctly in type from those in *Elmomyza* and the Drosophiloids near the branching-off point of the Scaptomyzoids. It therefore seems uncertain that *Bunostoma*

has its origin in Hawaii and the possibility exists that it was introduced separately from some other part of the Pacific, where the subgenus is widely distributed (Bonin Is., Marquesas).

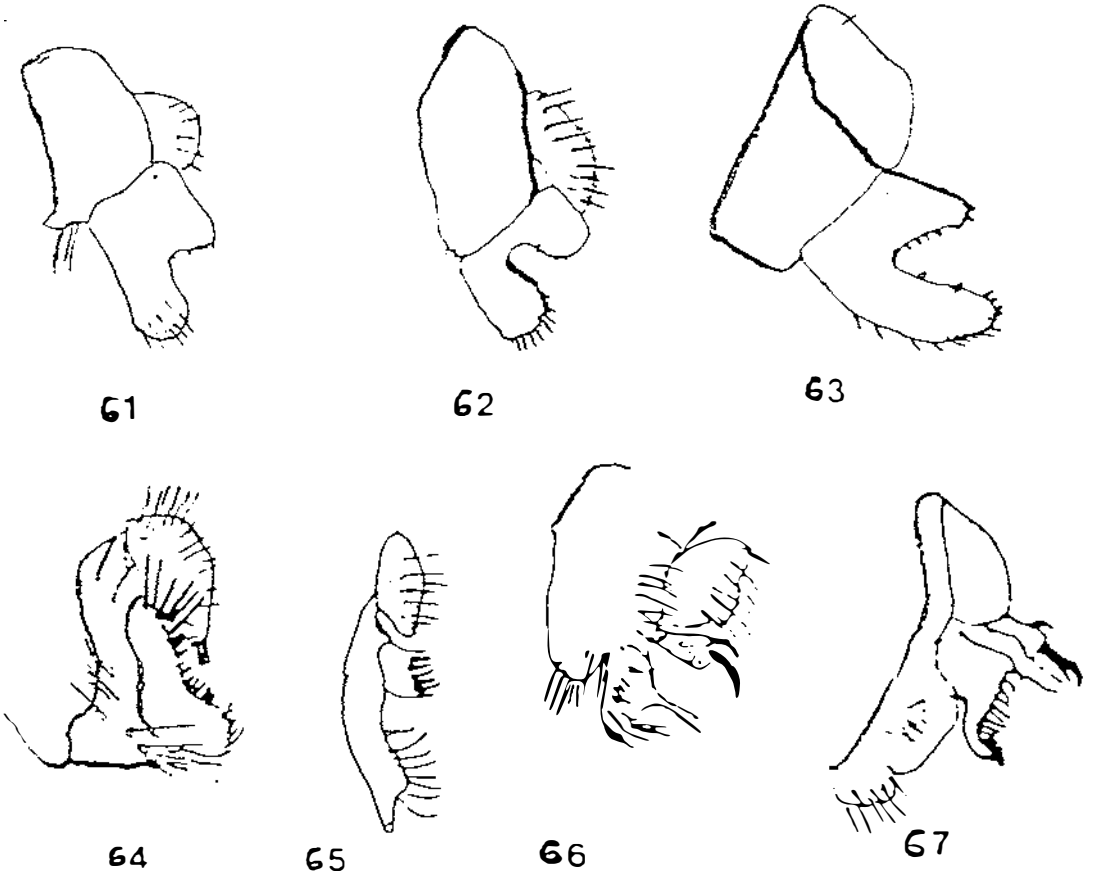
The *Bunostoma* species show some external similarity to the *Drosophila* subgenus *Lordiphosa* Basden, which has not been considered in Throckmorton's (1962 / 1966) studies on the *Drosophila* complex. Lastovka and Maca (1978), who revised the European species of *Lordiphosa,* insert this small but widely distributed subgenus as an isolated branch near *Sophophora* and *Chymomyza.* A comparison of *Bunosoma* and *Lordiphosa* is made here in **Table 1.** He has also included in the table 1 unplaced endemic *Scaptomyza* species from New Zealand because they may have something to do with *Bunostoma* (data from Harrison's [1959] descriptions of the species).

As shown in the table, *Bunostoma* differs from *Lordiphosa* in the number of humeral bristles and number of sternopleural bristles, and in having a small clasper **(Fig. 65)** of another type than in *Lordiphosa* **(Fig. 64).** On the other hand, there are certain similarities to the two New Zealand species.

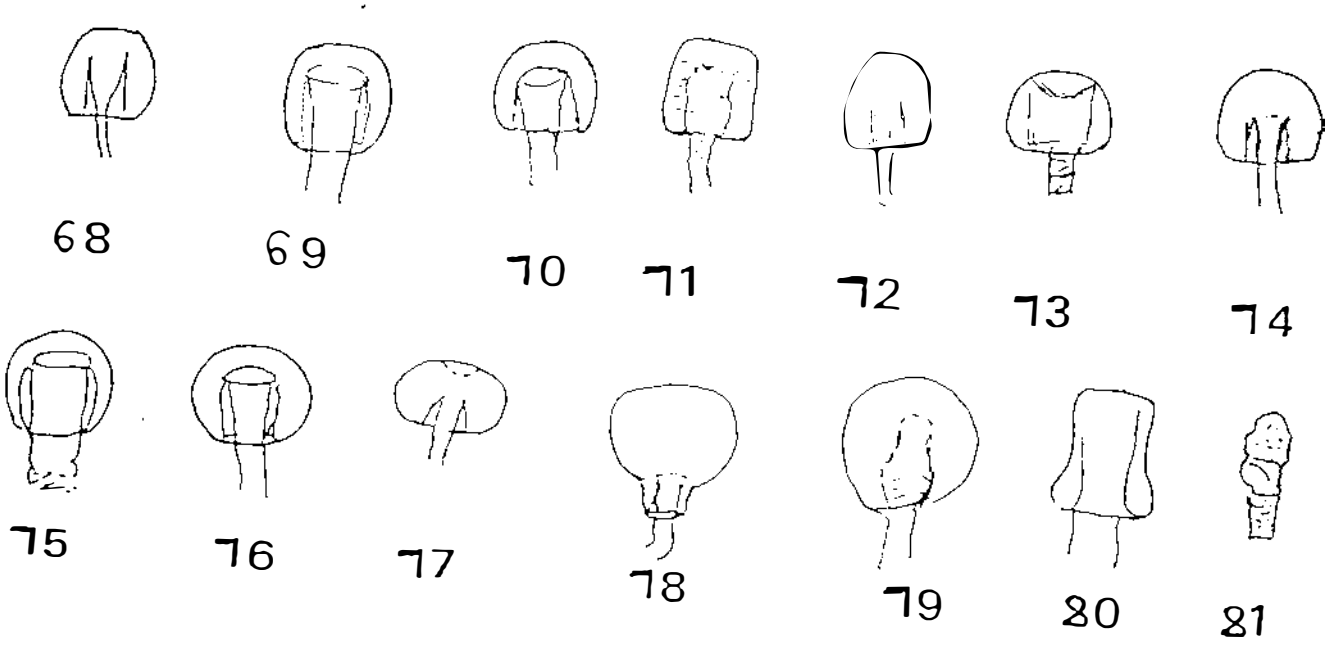
The stout dentate clasper characteristic of most *Lordiphosa* species shows similarity to that of the less far evolved Hawaiian Drosophilidae (mentioned above) and of *Trogloscaptomyza* from Tristan da Cunha, and, as already suggested, this is probably a case of simple isomorphism **(Figs. 61 - 64).** The internal reproductive organs are known for only 3 of the 13 *Lordiphosa* species: *D. (L.) andalusiaca* Strobl (Basden 1961), *D. (L.) collini* Lastovka and Maca (= *Scaptomyza apicalis,* sensu Okada 1956, **Fig. 39** , misidentification) and D. (L.) *fenestrarum* Fallen. The spermatheca are of the same type as in several *Scaptomyza* species **(Figs. 68—74),** whereas the testes and vasa deferentia (in *D. andalusiaca* and *D. fenestrarum)* are not of the same shape as in the few *Scaptomyza* species for which these organs are figured in the literature *(Parascaptomyza pallida, Scaptomyza (s.* str.) *consimilis* Hackman and *S. (s. str.) consimilis* Fallen given by Okada 1956; *Bunostoma* species, schematic figures given by Throckmorton (1966; cf. **Figs. 82—85** in this paper). Testes and paragonia of the same

type as in *D. fenestrarum* and *D. andalusiaca* occur in species of both *Hirtodrosophila* and *Sophophora* and *Chyrnomyza japonica* Okada; the testes are strongly coiled and the vas deferens thin. It is interesting to note in this connection that in the comparatively small genus *Chymomyza* (derived from the *Sophophora* branch by Throckmorton, 1962) one species, *C. caudetula* (Zetterstedt), is shown in the figure by Okada (1956) with almost elliptic testes and a strongly enlarged vas deferens. When trying to derive the continental *Scaptomyza* species from the Hawaiian Scaptomyzoids Throckmorton (1966) was faced with the problem of the North American *Scaptomyza (s.* str.) *montana,* whose elliptical testes (cf. Wheeler, 1952) are of a more primitive type than those in any of the Hawaiian Scaptomyzas. In the few other non-Hawaiian *Scaptomyza* species so far investigated, the testes are loosely coiled, being most elliptical in S. (s. str.) *graminum,* and the vas deferens is short and enlarged.

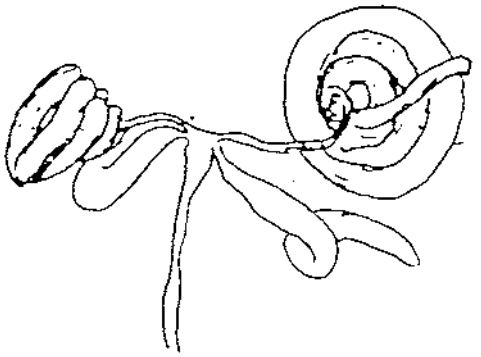
As far as can be judged from the rather incomplete data available, *Lordiphosa* is distinctly separated from *Scaptomyza.*



Figs. 61-67: Male genitalia of *Scaptomyza* and *Drosophila* species. Side view, ventral parts omitted. **61.** *Scaptomyza (Rosenwaldia) mitchelli* Hackman. **62.** *S. (Elmomyza) recava* Hardy. **63.** *S. (Troglоscaptomyza) brevilamellata* Frey. **64.** *Drosophila (Lordiphosa) nigricola* Strobl. **65.** *Scaptomyza (Bunostoma) bryanti* Hackman. **66.** *Drosophila (Sophophora) kikawai* Burla. **67.** *Scaptomyza (Parascaptomyza) frustulifera* Frey. Redrawn figures: 61 and 65 from Hackman, 1959; 62 from Hardy, 1965; 63 and 67 from Fery, 1954; 66 from Olroyd, 1958 (Hachman, 1982).



Figs. 68-81: Spermatheca of *Scaptomyza* and *Drosophila* species. **68**. *D. collini* **69**. *S. anomala* **70**. *S. pallida* **71**. *S. taiwanica* **72**. *S. (s. str.) consimilis* **73**. *S. (s. str.) sinica* **74**. *S. (s. str.) graminum* **75**. *D. nasalis* **76**. *S. hsui* **77**. *S. chylizosoma* **78**. *S. (E.) kilemba* **79**. *S. (E.) deemingi* **80**. *S. horaeoptera* **81**. *S. mauiensis*. All redrawn: 68, 72 and 74 after Okada, 1956; 69, 70, 75, 76 and 81 after Throckmorton, 1962 and 1966; 71 and 73 after Lin and Ting, 1971; 77-79 after Tsacas, 1972; 80 after Cogan, 1979 (Hachman, 1982).



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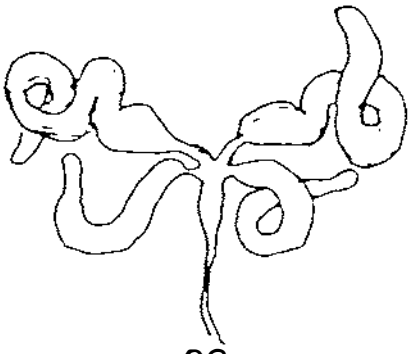

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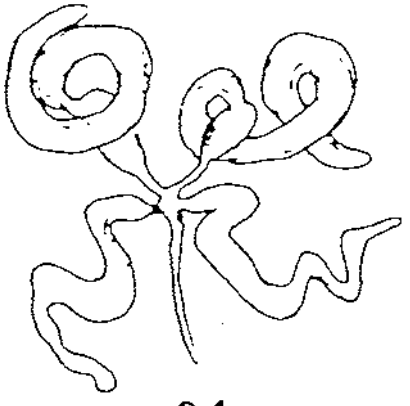

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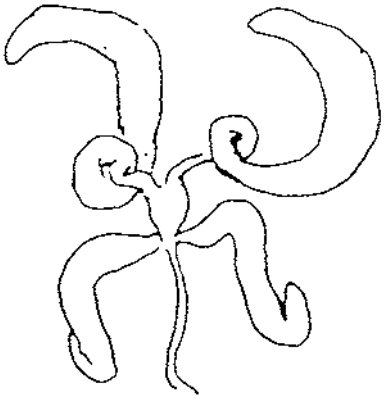

85

Figs. 82-85: Testes and paragonia of *Drosophila fenestrarum* and *Scaptomyza* species. **82.** *Drosophila (Lordiphosa) fenestrarum* Fallen. **83.** *Scaptomyza (Parascaptomyza) pallida* Zetterstedt. **84.** *S. (s. str.) consimilis* Hackman. **85.** *S. (s. str.) graminum* Fallen. Fig. 82 drawn after a sketch by Saura, 83-85 after Okada, 1956 (Hachman, 1982).

Table 1: Comparison of characters of *Drosophila subg. Lordiphosa, Scaptomyza subg. Bunostoma* and two unplaced *Scaptomyza* species from New Zealand (Hachman, 1982).

	Lordiphosa	*Bunostoma*	*S. flavella, S. fuscitarsis*
Head	not flattened	not flattened	not flattened
Eye	± oblique	± oblique	
Facial carina	low and restricted to dorsal half of face	usually distinct in dorsal half of face (in the type species nose-like below)	prominent and nose - like below
Rays of arista	proximal to end fork:2-3 ventral	2 - 3 ventral	1 - 2 ventral
Mesonotum	shiny without pattern brownish yellow or blackish	shiny, brownish black (1 species: yellow)	yellowish brown or purplish black
Humeral bristles	2	1 prominent	1 prominent
Acrostichal rows of hairs	4 - 6	2 - 4	2
Dorsocentrals	1 + 3	0 + 2 (1+ 3 in one species)	two enlarged hairs anterior dorsocentral
Sternopleurals	3 (posterior one longest)	2 (anterior one longer) 1 + 3 in one species	2 prominent
Male genitalia	no secondary clasper, clasper (surstylus) stout, dentate (usually as in **Fig. 64**)	no secondary clasper, clasper rather smaller, usually dentate (cf. **Fig. 65**)	no secondary clasper,claspemod erately stout (*S.flavella)* or small (*S.fuscitarsis*), dentate
Egg-guides	heavily sclerotized, dentate	weakly sclerotized	not mentioned in description
Distribution	9 Palaearctic 2 Oriental 1 (2 ?) Nearctic species	Hawaii: 8 species Other Pacific Islands: 4 sp. Australia: 1 sp	New Zealand

SCAPTOMYZA DIVERSITY

Hardy (1974) Given the large number of species and world-wide distribution of *Scaptomyza*, the extreme paucity of the Australia and New Zealand fauna seems remarkable on first consideration; the world distribution of *Scaptomyza* species is, however, highly uneven. The Hawaiian islands contain a large proportion of the world total of species, most of them in the single subgenus *Trogloscaptomyza* 86 of 87 known species occur only in Hawaii; there has thus been as substantial a proliferation of *Scaptomyza* species in Hawaii as of *Drosophila* species. A good case can, in fact, be made for considering Hawaii the place of origin of the genus *Scaptomyza* (Throckmorton, 1975), with subsequent radiations into other parts of the world. Wheeler and Takada (1966) listed 55 species from the Nearctic and Neotropical zone; smaller numbers of species have been recorded from various Pacific Islands. Fewer species occur in other parts of the world. Okada (1956) listed six species from Japan; a few more were subsequently added (Okada, 1973a, 1973b); several species occur in neighbouring mainland Asia. Burla (1954) noted a total of four species from the Ethiopian zone; another three were added by Tsacas (1972). Harrison (1959) found three species in New Zealand, the cosmopolitan *pallida* and two endemic; New Zealand thus has a richer *Scaptomyza* fauna than Australia. Few species occur in Europe. In particular there appears to have been no radiation in south-east Asia, and area notable for several major bursts of Drosophilid speciation from which, ultimately, Australia appears to have derived its *Drosophila* fauna and that of most if not all of its other Drosophilid genera.

Only one species of *Scaptomyza, S. pallida,* is cosmopolitan; most of the remaining species have quite limited distributions. *S. australis* has been collected as far north as Thursday I.; whether or not it occurs further north than this (*i.e.* in New Guinea) remains to be determined. Although, as mentioned above, *australis* has been found to be common in an orchard, the species is not generally attracted to *Drosophila* fruit baits and is collected by sweeping, The widespread occurrence of this species in Australia and the fact that it can be cultured in the laboratory suggest that it may be a candidate for polytene chromosomal investigations (Maca, 19782).

Appendix 2

SOME IMPORTANT LEAF MINER (AGROMYZIDAE) PESTS (Hill, 1987)

Agromyza ambigua Fall. - (cereal leaf miner) Europe and N. America.

Agromyza oryzae (Mun.) - (rice leaf miner) Japan, Java and E. Siberia.

Agromyza maculosa (Mall.) - (lettuce leaf miner) USA, Hawaii and S. America.

Cerodontha spp. - (cereal leaf miner) only Gramineae; worldwide.

Liriomyza brassicae (Riley) - (cabbage leaf miner) Cruciferae mostly; cosmopolitan.

Liriomyza bryoniae (Kalt.) - (tomato leaf miner) polyphagous; Europe, W. Asia.

Liriomyza cepae (Hering) - (onion leaf miner) Europe (not UK).

Liriomyza chinensis (Kato) - (onion leaf miner) Japan, China and Malaysis.

Liriomyza sativa Blanch. - polyphagous: Cucurbitaceae, Solanaceae, Leguminosae; USA, C. and S. America.

Liriomyza trifolii (Burgess) - (American) serpentine leaf miner)) polyphagous; N. and S. America and introduced to UK.

Melanagromyza obtusa Mall. - (bean pod fly) India and S. E. Asia.

Melanagromyza sojae (Zehn.) - (bean fly) Africa and S. E. Asia.

Ophiomyia phaseoli (Tryon) - (bean fly) Africa, Asia and Australia (CIE map A.130).

Napomyza carotae Sp. - (carrot root miner) Europe (not UK).

Appendix 3

ABILITY OF ADULT *SCAPTOMYZA FLAVA* TO SURVIVE AT LOW TEMPERATURE

INTRODUCTION

IT is well known that temperature has a pervasive effect on insects. Nearly every aspect of an insect's life is influenced by temperature, from direct effects on the kinetics of enzymatic reactions, to defining the limits of physiological function and behaviour, and ultimately to shaping of evolutionary pathways. As a group, insects, more than any other eukaryotic taxon, have evolved not only to survive but to flourish in a wide variety of thermal environments (Lee, and Denlinger, 1991).

Low temperature is not precisely defined since it covers a wide variety of topics and temperature ranges, and includes the maintenance of normal activity at low temperature, tolerance of chilling during the summer versus survival of prolonged exposure to cold during the winter, and applied aspects including the cryopreservation of insects (Beck, 1983a).

Insects are ectothermic organisms, and as such their physiological, metabolic, and developmental processes are highly responsive to ambient temperatures. Environmental temperatures undergo daily cycles (thermoperiods) in which the daytime temperature (thermophase) tends to be higher than the night-time temperature (cryophase). The daily alternation of thermophase and cryophase is, of course, approximately coincidental with the alternation of the photophase and scotophase, respectively, of the daily photoperiod.

Temperature is a key environmental factor determining the duration of survival and life stage of insects (Adler, 1987; McCreadie and Colbo, 1990). The time that an organism can survive at a temperature can be related to such factors as duration of exposure, and state of "acclimation" or "hardening" (Baust, 1982).

The purpose of this study was to describe the influence of three low temperatures

on survival of adult *Scaptomyza flava.*

MATERIALS AND METHODS

The ability of adult *Scaptomyza flava* to survive at 0°, 5° and 12°C without food or water was determined by placing groups of 10 newly emerged adults (5 ♀ and 5 ♂) in stoppered glass vials at these temperatures in darkness. The same procedure was followed with flies caged with plant material, at 0 and 5°C (all with a variance of ± 2°C). Five Chinese cabbage seedlings ca. 24 cm tall (plants growing in 300 ml plastic pots) were placed in small ventilated cages (in darkness) with cohorts of 100 *Scaptomyza flava* adults (3 days after emergence, mixed sexes). Experiments were unreplicated.

Humidity was maintained at or near 35 ± 2% RH for the experiment without plant material and at or near 40% RH for the experiment where flies were confined with Chinese cabbage plants. The number of insects alive and dead at 5 and 12°C were counted daily until all insects had died. Insects were counted twice daily at 0°C. Longevity (in days) of an individual fly was taken as the mid point between two successive counts. In this way mean survival time could be calculated over all individuals for each group.

RESULTS

Results are presented in **Table 2.**

The results indicate that adult *S. flava* is somewhat tolerant of low temperatures as there was high survival up to three days at 0°C even for insects without access to food or water. This is in accordance with the fact that *S. flava* is active throughout the year (in the Manawatu region at least) and shows no evidence of winter diapause from field observations (see Chapter 4).

Table 2: Survival in days of adult *S. flava* at low temperatures

Day	Number of insects alive				
	Without plant material			With plant material	
	0°C	5°C	12°C	0°C	5°C
0	100	100	100	100	100
1	100	71	69	100	97
2	100	69	50	100	87
3	100	55	36	89	80
4	65	49	29	67	62
5	17	43	15	42	23
6	0	31	0	10	20
7		27		0	20
8		15			19
9		8			14
10		6			9
11		3			8
12		3			6
13		2			3
14		1			0
15		0			
Mean lifespan (days)	9.45	4.84	2.99	11	16.95

The availability of live plant material at 0°C did not increase survival. At this temperature insects with access to a live plant did not feed or oviposit (no punctures were detected on leaves).

Mean lifespan was reduced at 5°C compared to 0°C in the absence of a plant even though a few individuals survived for 13-14 days. This is probably because the insects were more active than at 0°C (*i.e.*, adult *Scaptomyza flava* insects were immobilized and entered a state of chill coma at 0°C [personal observation]).

The availability of plant material at 5°C markedly prolonged lifespan. At this temperature feeding punctures on leaves were produced and a few eggs were laid but none of the eggs hatched. At 12°C (in the absence of plant material) survival was further reduced compared to 5° and 0°C. An increase in temperature causes survival of adult Diptera to be reduced up to about 20°C (Ballou, 1986).

Lockwood and Story (1986) demonstrated that low relative humidity (25-50%) was detrimental to survival of some insects (*e.g.*, *Heteroptera*). In my experiment, mean RH was 35% - 45%. Low relative humidity may therefore have been a factor in survival of the flies.

From the results of this experiment it is likely that *Scaptomyza flava* can survive short periods at temperatures below 10°C with no effect other than an extended development time.

Appendix 4

OVIPOSITION IN SUN AND SHADE

INTRODUCTION

UNEQUAL shading of host-plants undoubtedly contributes to variation in the suitability of hosts for herbivorous insects (Schultz, 1983) but has received little attention as it relates to herbivory. Shading invariably reduces net photosynthetic rate and levels of foliar sugar, starch and protein, reduces leaf thickness, increases leaf area (Young and Smith, 1980; Schultz, 1983), and apparently reduces levels of some noxious secondary compounds in leaves (Lincoln, 1987). Changes in leaf chemistry with shading, if widespread, suggest phytophagous insects might prefer shade plants owing to the reduction of secondary compounds, or avoid them because of low levels of sugars and proteins compared to unshaded leaves. Similarly, physical changes in foliage that accompany variation in solar radiation also offer no general predictions concerning herbivore preference. Rather, it appears changes in leaves that accompany changes in sunlight intensity present conflicting selection pressures for herbivore insects. Over evolutionary time, insect preference for sun or shade leaves should be influenced by the balance between these opposing pressures as well as other factors like variation in predation and parasitism in sun and shade (Bultman, 1988).

Collings and Louda (1988) demonstrated that total insect herbivore load on bittercress (*Cardamine cordifolia*) is greater on plants in the sun than on plants in the shade and that there were increases in the water associated soluble (nitrate) nitrogen concentrations in leaves (Louda, 1986); reduced plant vertical growth, leaf development, and seed reproductive success (Louda, 1984); and increases on experimentally water-stressed plants in the shade (Louda, 1986) or on experimentally shaded plants in the sun (Collings, 1987).

Collings (1988) tested the hypothesis that light intensity was the direct, proximal mechanism causing significantly higher vulnerability of bittercress clones in the sun to herbivory by a leaf-mining fly (*Scaptomyza nigrita* Wheeler). Adult densities and leaf-

mining damage were consistently and significantly higher on plants in sun than on those in the shade. Shading sun plants shifted their growth pattern toward that of naturally-shaded plants. However, no information was available on the response of the leaf miner either to environmental variation or to differences in host plant quality.

MATERIALS AND METHODS

To study the effect of sun and shade on *Scaptomyza flava* an experiment was conducted under laboratory conditions during summer of 1990 at Massey University, Palmerston North.

10 two months old potted Chinese cabbage plants were selected and one pair of insects was released in gauze cages onto each of them. 5 plants were placed in a position in the laboratory so that they were directly exposed to any natural sunlight and another 5 were kept in the shade. Relative oviposition and larval survival was assessed based on the number of emerging adults of the next generation.

RESULTS AND DISCUSSION

Results are summarized in **Table 3**.

From each pair of insects on Chinese cabbage kept in the sun, a mean of 125 new adults emerged after 28 days, but from each pair of insects held in the shade, a mean of only 5 adult insects emerged **(Table 3)**.

Adult flies were observed to be more active on plants in sun than on those in shade (unrecorded data). Plants in the shade were taller and had a longer fifth leaf than those growing in the sunny area.

Table 3: Number of new emerged adult insects from 1 pair of *Scaptomyza flava* from Chinese cabbage plants in sun and shade.

Days	Mean number of adults	
	Plants in sun	**Plants in shade**
1[1]	8	1
2	15	1
3	40	1
4	30	2
5	10	0
6	10	0
7	7	0
8	2	0
9	2	0
10	1	0
11	0	0
12	1	0
Total adults	125	5

[1] First day of adult emergence.

The results show a clear pattern of greater leaf-miner success in sun compared to shade. The amount of leaf area damaged was also greater in sun (approximately 75% of leaf area) than in shade (approximately 25%).

This result is consistent with those obtained for several other species of leaf miners. For example, Faeth *et al.,* (1981), working with lepidopteran and coleopteran leaf miners on oak trees, observed higher densities on sun-exposed leaves than on shaded leaves. This same pattern also occurred with a dipteran leaf miner on bracken fern (MacGarvin *et al.*, 1986). However, other leaf-mining species are more abundant in shaded habitat (MacGarvin *et al.*, 1986).

Appendix 5

LABORATORY INSECTICIDE EXPERIMENTS WITH *SCAPTOMYZA FLAVA*

INTRODUCTION

IN order to determine the susceptibility of *Scaptomyza* leaf miner to a range of insecticides, several experiments were conducted in the laboratory with adults and larvae.

MATERIALS AND METHODS

To determine the susceptibility of adult *S. flava* flies to insecticides, two experiments were carried out . In the first experiment, there were six treatments as follows, each replicated 3 times:

1. Control, water only applied.
2. Carbaryl applied at full label rate (100 g Sevin 80 EC /100 l water).
3. Permethrin applied at full label rate (100 ml Ambush 50 EC/ 500 l water).
4. Pirimicarb applied at full label rate (125 g Pirimor 50 EC/100 l water).
5. Diazinon applied at full label rate (60 ml Diazinon 80 EC/ 100 l water).
6. Acephate applied at full label rate (100 g Orthene 75 EC/ 100 l water).

The first experiment was conducted in a greenhouse commencing 31 October 1991. One-month old potted Chinese cabbage plants were sprayed with a hand mist sprayer, allowed to dry, then placed individually into cages containing 10 adult flies obtained from a colony reared on Chinese cabbage. Plants were watered as needed. After 48 hr, the number of insects remaining alive in each cage was recorded.

In a second experiment, the procedure of the first experiment was followed but the plants were placed in a controlled environment (Incubator Room) at 20 ± 1°C under a 12 L:12 D photoperiod. RH was not controlled. The treatments were as follows:

1. Control, water only applied.
2. Pirimicarb applied at 1/2 standard rate recommended (60.25 g Pirimor 50 EC / 100 l water).
3. Diazinon applied at 1/2 label rate (30 ml Diazinon 80 EC / 100 l water).
4. Acephate applied at 1/2 label rate (50 g Orthene 75 EC / 100 l water).

RESULTS

The results are summarised in **Tables 4** and **5**.

Table 4: Mean number of live adult *Scaptomyza flava* in experiment one after 48 h.

Treatment	Mean number of live insects per cage
1- Untreated control	8.3 a
2- Carbaryl	7.3 a
3- Permethrin	3.3 b
4- Pirimicarb	0.0 c
5- Diazinon	0.0 c
6- Acephate	0.0 c

Treatments accompanied by the same letter are not significantly different at $P \geq 0.05$ (ANOVA followed by LSD test for separation of means).

Table 5: Mean number of live adult *Scaptomyza flava* in experiment two after 48 h.

Treatment	Mean number of live insects per cage
1- Untreated control	9
2- Pirimicarb (1/2 rate)	0
3- Diazinon (1/2 rate)	0
4- Acephate (1/2 rate)	0

EVALUATION OF CONTROL

From **Tables 4** and **5** it can be seen that pirimicarb, diazinon and acephate gave complete mortality of adult *Scaptomyza flava.* Carbaryl had practically no effect and permethrin was intermediate.

Appendix 6

THE ABILITY OF SCAPTOMYZA ELMOI TO DEVELOP ON CHINESE CABBAGE

INTRODUCTION

IN order to determine whether another species of *Scaptomyza* collected from the field study area is able to leaf mine on Chinese cabbage, adults of *Scaptomyza elmoi* were released onto plants in an experiment.

MATERIALS AND METHODS

Four one-month old Chinese cabbage plants at the 3 to 4 leaf stage were caged with 5 pairs of *Scaptomyza elmoi* obtained from the field by sweep netting. The insects were not provided with water or honey solution. Plants were grown under natural lighting in a greenhouse in plastic pots (6.3 cm square) containing a soilless growing medium (horticultural sphagnum peat moss, vermiculite and perlite). Temperature in the experimental chamber was maintained at 10 ± 2°C (night) and 18 ± 2°C by day and natural daylength (10h light:14h dark cycle).

RESULTS

After 2-3 days all insects were dead. No feeding punctures were found on the plants and no eggs had been laid. The plants were kept for more than 3 weeks with no evidence of larval development.

The results confirm that *Scaptomyza elmoi* cannot leaf mine and develop on Chinese cabbage.

Appendix 7

SEASONAL LIFE CYCLE OF *S. FLAVA*

Table 6: Numbers of *Scaptomyza flava* recovered by three different sampling methods from Chinese cabbage over a two-year period

Date	Week	Number of adult insects captured by sweep netting	Number of adult insects recovered from water trap	Number of larvae recovered from ten leaves
15.11.1990	1	4	8	10
22.11.1990	2	5	16	20
29.11.1990	3	20	15	70
6.12.1990	4	35	10	20
13.12.1990	5	20	3	30
20.12.1990	6	30	19	120
27.12.1990	7	27	20	65
3. 1.1991	8	30	15	46
10. 1.1991	9	35	4	30
17. 1.1991	10	10	1	3
24. 1.1991	11	60	40	4
31. 1.1991	12	25	3	2
7. 2.1991	13	24	12	3
14. 2.1991	14	15	0	1
21. 2.1991	15	18	19	0

28. 2.1991	16	18	18	8
7. 3.1991	17	14	4	15
15. 3.1991	18	17	0	2
22. 3.1991	19	10	0	0
29. 3.1991	20	9	2	10
5. 4.1991	21	0	5	40
12. 4.1991	22	3	5	12
18. 4.1991	23	60	10	18
26. 4.1991	24	17	6	28
3. 5.1991	25	25	2	60
10. 5.1991	26	26	1	50
17. 5.1991	27	120	0	5
24. 5.1991	28	35	2	5
31. 5.1991	29	10	1	25
6. 6.1991	30	30	3	4
13. 6.1991	31	50	6	0
20. 6.1991	32	24	10	6
27. 6.1991	33	15	15	8
4. 7.1991	34	25	8	32
11. 7.1991	35	20	1	25
18. 7.1991	36	10	0	20
25. 7.1991	37	30	1	10

1. 8.1991	38	35	1	10
8. 8.1991	39	100	1	2
15. 8.1991	40	78	4	9
22. 8.1991	41	54	7	0
30. 8.1991	42	25	10	10
6. 9.1991	43	24	8	20
13. 9.1991	44	4	3	25
20. 9.1991	45	25	3	35
27. 9.1991	46	50	2	60
4.10.1991	47	60	5	60
11.10.1991	48	56	15	30
18.10.1991	49	65	24	103
25.10.1991	50	75	38	83
1.11.1991	51	45	20	20
8.11.1991	52	130		120
15.11.1991	53	100		110
22.11.1991	54	20		24
29.11.1991	55	160		
5.12.1991	56	160		
12.12.1991	57	35		
19.12.1991	58	40		
26.12.1991	59	20		

2. 1.1992	60	80		
9. 1.1992	61	55		
16. 1.1992	62	112		
23. 1.1992	63	120		
30. 1.1992	64	45		
6. 2.1992	65	30		
13. 2.1992	66	45		
20. 2.1992	67	5		
27. 2.1992	68	5		
5. 3.1992	69	20		
12. 3.1992	70	1		
19. 3.1992	71	5		
26. 3.1992	72	8		
2. 4.1992	73	10		
9. 4.1992	74	8		
17. 4.1992	75	15		
24. 4.1992	76	25		
30. 4.1992	77	32		
8. 5.1992	78	48		
15. 5.1992	79	120		
22. 5.1992	80	72		
29. 5.1992	81	95		

5. 6.1992	82	68		
12. 6.1992	83	300		
19. 6.1992	84	120		
26. 6.1992	85	49		
3. 7.1992	86	30		
10. 7.1992	87	25		
17. 7.1992	88	14		
24. 7.1992	89	4		
31. 7.1992	90	7		
7. 8.1992	91	7		
15. 8.1992	92	29		
22. 8.1992	93	90		
29. 8.1992	94	50		
7. 9.1992	95	10		

Table 7:Numbers of *Scaptomyza flava* recovered by three different sampling methods from turnip over a one year period

Date	**Week**	**Number of adult insects captured by sweep netting**	**Number of adult insects recovered from water trap**	**Number of larvae recovered from ten leaves**
15.11.1990	1	3	16	10
22.11.1990	2	9	8	5
29.11.1990	3	26	25	12
6.12.1990	4	37	30	1
13.12.1990	5	10	2	13
20.12.1990	6	18	16	30
27.12.19	7	60	30	0
3. 1.1991	8	55	12	0
10. 1.1991	9	30	3	0
17. 1.1991	10	20	2	0
24. 1.1991	11	30	4	2
31. 1.1991	12	6	1	3
7. 2.1991	13	6	2	4
14. 2.1991	14	10	0	9
21. 2.1991	15	12	18	9

28. 2.1991	16	18	18	10
7. 3.1991	17	14	4	4
15. 3.1991	18	20	1	26
21. 3.1991	19	7	0	48
28. 3.1991	20	10	2	60
5. 4.1991	21	21	8	50
12. 4.1991	22	100	5	42
18. 4.1991	23	25	10	38
26. 4.1991	24	11	6	33
3. 5.1991	25	60	2	30
10. 5.1991	26	80	1	40
17. 5.1991	27	60	0	37
24. 5.1991	28	110	2	30
31. 5.1991	29	70	1	30
6. 6.1991	30	80	3	20
13. 6.1991	31	90	6	4
20. 6.1991	32	104	4	5
27. 6.1991	33	30	15	4
4. 7.1991	34	70	5	5
11. 7.1991	35	70	2	15
18. 7.1991	36	75	0	10
25. 7.1991	37	60	1	6

1. 8.1991	38	55	1	0
8. 8.1991	39	100	1	4
15. 8.1991	40	72	4	0
22. 8.1991	41	40	4	15
30. 8.1991	42	9	10	20
6. 9.1991	43	45	8	25
13. 9.1991	44	9	3	20
20. 9.1991	45	39	2	16
27. 9.1991	46	40	2	16
4.10.1991	47	60	5	16
11.11.1991	48	65	15	14
18.11.1991	49	75	24	11
25.11.1991	50	75	35	10
1.11.1991	51	60	15	13
8.11.1991	52	40		12
15.11.1991	53	150		4
22.11.1991	54	99		
29.11.1991	55	39		

Table 8:Number of *Scaptomyza elmoi* & *Scaptomyza fuscitarsis* captured by 10 sweep net samples from Chinese cabbage over a one year period

Week	Date	Number of adult *S.elmoi*	Number of adult *S. fuscitarsis*
1	31.10.1991	0	1
2	08.11.1991	0	0
3	15.11.1991	2	0
4	22.11.1991	0	0
5	29.11.1991	1	0
6	05.12.1991	7	3
7	12.12.1991	5	0
8	19.12.1991	0	0
9	26.12.1991	3	2
10	02.01.1992	0	0
11	09.01.1992	2	0
12	16.01.1992	30	25
13	23.01.1992	13	20
14	30.01.1992	2	2
15	06.02.1992	0	0
16	13.02.1992	4	2

17	20.02.1992	7	2
18	27.02.1992	0	0
19	05.03.1992	2	0
20	12.03.1992	0	0
21	19.03.1992	4	0
22	26.03.1992	2	0
23	02.04.1992	4	0
24	09.04.1992	1	0
25	17.04.1992	0	0
26	24.04.1992	0	0
27	30.04.1992	2	0
28	08.05.1992	0	0
29	15.05.1992	0	0
30	22.05.1992	0	0
31	29.05.1992	0	0
32	05.06.1992	0	0
33	12.06.1992	0	0
34	19.06.1992	0	0
35	26.06.1992	3	0
36	03.07.1992	13	0
37	10.07.1992	6	0
38	17.07.1992	2	0

39	24.07.1992	1	0
40	31.07.1992	1	0
41	07.08.1992	1	0
42	15.08.1992	1	0
43	22.08.1992	0	0
44	30.08.1992	0	0
45	07.09.1992	0	0
46	15.09.1992	0	0
47	22.09.1992	0	0
48	29.09.1992	0	1
49	08.10.1992	0	1
50	15.10.1992	0	1
51	22.10.1992	0	1

Table 9:Plant measurements and numbers of larvae from samples of five Chinese cabbage plants.

No. of sample	Date	No. of leaves / plant	Leaf area/ plant (cm^2)	Leaf area mined (%)	Height of plant (cm)	No. of larvae/ plant
1	15.11.91	5	350	3	18	2
2	30.11.91	3.4	47	2.6	13	2.2
3	12.12.91	6.3	177	0.05	20	0.6
4	26.12.91	3.2	37	3	11	2
5	10.1.92	4	244	3.2	26	3
6	24.1.92	6.4	1560	5.5	22	5.6
7	6.2.92	9	973	4.4	67	1.6
8	20.2.92	12.4	2226	0.5	39	2
9	5.3.92	9	905	7.4	30.5	8.4
10	19.3.92	7	520	18.5	30	4.2
11	2.4.92	7.6	645	6.2	31	3
12	16.4.92	7	796	11	30	3.8
13	1.5.92	6.2	290	5	23	3
14	15.5.92	7	358	8.4	26	5.4
15	21.5.92	8	362	9	26	6.6
16	12.6.92	9	767	4	32	5
17	26.6.92	11	1077	12	35	5

18	10.7.92	10	999	2.2	25	4
19	25.7.92	5	400	10	14	6
20	10.8.92	5	546	0	15	0
21	24.8.92	7	968	5	17	4
22	10.9.92	5	1100	0	22	0
23	26.9.92	5	1050	12	26	10
24	15.10.92	6	1170	20	29	12
25	1.11.92	5	310	3.1	14	1
26	15.11.92	5	200	15	20	6
27	30.11.92	7	600	18.1	22	7.4
28	12.12.92	9	1000	16.7	26	5.6
29	26.12.92	5	51	12	15	3
30	10.1.93	6	304	15	18	5

Appendix 8

CULTURAL NOTES ON HOST PLANTS OF *SCAPTOMYZA FLAVA*

INTRODUCTION

SCAPTOMYZA flava is an oligophagous insect, with a range of host plants (cabbage, turnip, radish, cauliflower, hedge mustard, and other species) in the plant family *Brassicaceae*. A blotch leaf miner, *Scaptomyza flava* has been reared from a number of host plants and is considered a pest of several vegetable crops. However, some hosts appear to be more attacked than others especially Chinese cabbage and turnip (personal observations and see Chapter 3, section "Comparison of plant species as hosts for *Scaptomyza flava*").

CHINESE CABBAGE

This vegetable sometimes called lettuce-cabbage could be grown more widely in New Zealand. Chinese cabbage is considered the most difficult brassica to consistently grow well. Being semi-tropical, it is very fast growing and capable of producing a 0.75 kg head, six weeks from planting. It is extremely sensitive to bolting at low temperatures and is susceptible to a large number of pests, diseases and physiological disorders (Anon, 1984).

There are now well over 200 varieties in commercial use. Chinese cabbage has evolved in a warm climate where days are short. They are sensitive to excessively high temperatures (over 30°C); some varieties have considerable cold tolerance and may withstand minus 5°C in New Zealand, in good growing conditions. February-sown plants mature before winter; alternatively plants can be sown in spring for early summer harvest.

The following are the main pests and diseases of Chinese cabbage:

PESTS

Slugs, cutworms, leather jackets (*Tipula* spp.), cabbage root fly (*Delia brassicae*)[1], aphids (grey cabbage aphid *Brevicoryne brassicae* and peach-potato aphid *Myzus persicae*), Caterpillars (cabbage moth *Mamestra brassicae*[2], and white butterfly *Artogeia spp*), insects with tunnelling larvae (leaf miners such as *Phytomyza rufipes* and *Scaptomyza flava)* may tunnel into leaves and stems. The cabbage stem weevil *Ceuthorhynchus quadridens*[3] tunnels in stems, and thrips (*Thrips tabaci*).

DISEASES

Club root (*Plasmodiophora brassicae*), wirestem (*Rhizoctonia solani*), dark leaf spot (*Alternaria brassicicola* and *brassicae*), downy mildew (*Peronospora parasitica*) and soft rot (*Erwinia carotovora*).

VIRUS DISEASES: Cauliflower mosaic virus and turnip mosaic virus

PHYSIOLOGICAL DISORDERS: Tipburn / heart rot, boron deficiency, glassiness, nitrogen excesses and black leaf speck.

TURNIP

Turnips have a distinct flattened taproot, little or no neck, and hairy, coarse, yellow green leaves. There are both white - and yellow - fleshed varieties.
Turnips are cool-season vegetables. Turnips can be sown over a longer period than Chinese cabbage through the spring until autumn. They mature in 30 - 80 days.

[1,2,3] Not in New Zealand

PESTS Aphids, caterpillars, grass grub (*Costelytra zealandica*) and wireworms.

DISEASES Leaf spot, rust, downy mildew and clubroot.

CAULIFLOWER

In most part of New Zealand, cauliflowers can be grown all year round, although some areas have a preferred season. In the past, certain winter-grown varieties were called broccoli.

The various stages of cauliflower development are in many ways similar to those of the cabbage crops. They are difficult to grown in very hot, dry conditions, and their quality suffers equally under severe winter conditions. Except in mild climates, plants for setting out in early spring should be raised in very sheltered situations.

RADISH

Radishes are one of the quickest vegetables to raise. They grow best at moderate temperatures (10°C - 18°C). Under favourable conditions, only 23 - 30 days are required from sowing to maturity.

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