EFFECTS OF THE OAT CROP ENVIRONMENT ON COLONIZATION BY *OSCINELLA FRIT* L. (DIPTERA: CHLOROPIDAE)

by

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ABSTRACT

Investigations were conducted in the field and in the laboratory on the effects of the age of oat plants on attraction, oviposition and survival of *Oscinella frit* L., on the effects of weedy and weed-free backgrounds on attraction of adult flies and on oviposition, and on the effects of the density and row spacing of oats on colonization and development of *O. frit* in the crop.

More adult flies landed and laid more eggs on taller, older plants than on younger, shorter plants; however, penetration into the main shoot by emergent larvae became less successful with increasing plant age.

In the field, similar numbers of flies were caught in water traps over oat crops with weedy or weed-free background. In the laboratory, clover plants as undercover among oat plants interfered with oviposition when present at appropriate density and height.

The numbers of flies that were seemingly attracted and trapped over oat crops and the numbers of eggs laid on oat plants increased with increasing plant density. The arrangement of oat plants in space also influenced the numbers of adults trapped, the numbers of eggs laid and the survival of the other stages.

Adults trapped in the field and adults from field collected pupae both indicated that the sex ratio of adults colonizing an oat crop at the beginning of the season is approximately 5 females to 1 male compared with 1:1 at emergence.

The manipulation of the above factors is discussed in relation to plant resistance to insects induced by crop environment and also in terms of the population system of the insect, starting with the invasion of the crop at the beginning of the season.

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INTRODUCTION

The frit fly, Oscinella frit L. is a denizen of grassland and a pest of oats (Southwood, 1961) and other cereals. It is also a highly migratory insect (Southwood, Jepson and van Emden, 1961; Johnson, Taylor and Southwood, 1962). The outcome is that cultivated spring cereals are usually infested by flies originating from grasslands or winter cereals in the vicinity of the crop or perhaps from considerable distance.

Studies on crop pests have indicated that insects at the end of migratory movement and those engaged in trivial flight can respond to various stimuli, mostly visual, by settling. The conventional cultivation practice is to set cereal seeds in drills and eliminate weeds from the crop by the use of herbicides. This practice, particularly where the seed drills are widely spaced, often gives a picture of green plants silhouetted against weed-free soil, which has been observed in some crops e.g. brassicas (Smith, 1969; 1976), field beans (Way, 1971) to favour pest attack. Perrin (1977) has given more examples. The manipulation of visual stimuli by altering the crop density, or the colour of the background and the amount of ground cover has been used with some success in reducing aphid colonization on groundnuts (A'Brook, 1968; Farrell, 1976), brassicas (Smith, l.c.) etc. No such work on plant density of the crop and of intervening non-crop plants has been done in relation to the frit fly and its host plants.

Plant age of oats is known to affect oviposition and larval survival. This factor must also be taken into account as interacting with the effects of plant density of oats and other species. This investigation was therefore made to assess the effects of manipulating crop density, crop background and the age of oat plants on both the initial attraction of adult flies to young oat plants and on establishment and development and success of the immature stages in the plants. Data on the subsequent generations developing within the crop and on the effects of competition between the larvae and between ovipositing adults are presented and an attempt made to assess the importance of the differing oviposition and of mortalities as affected by plant density and age.

An examination was also made of the sex ratios of the overwintering generation of the fly invading the crop and of the flies of the next generation.

SECTION I

INVASION AND ESTABLISHMENT OF O. FRIT IN CULTIVATED CEREAL CROPS:

A REVIEW

Attraction to the plant and crop

When insects are below their 'boundary layer' (Taylor, 1958), that is, in virtually complete control of their displacement, they are able to respond to various stimuli that lead to landing. The series of properties that may serve as stimuli in the selection of habitat, host plant, prey and oviposition site by most insects have been tabulated by Southwood and Way (1970). Thus, the stimuli are initially visual (colour of and colour contrasts within the stand, size and shape of plant stand, density of stand), or more rarely olfactory which usually become important either immediately before or after landing. Certain aphids are particularly attracted to yellow (Moericke, 1950; Kennedy and Stroyan, 1959) or to leaves reflecting a greater proportion of long-wave energy, with little or no regard for the botanical host status of the plants (Kennedy et al, 1961), citrus thrips to white (Beavers et al, 1971), apple maggot flies to yellow, red and black in contrast to green, grey, white and blue (Moericke et al, 1975), greenhouse white fly to yellow (Vaishampayan et al, 1975) and cabbage butterflies to green and blue-green (Ilse, 1937; Radcliffe and Chapman, 1966). Using models of various sizes and shapes, Moericke et al (l.c.) have recently demonstrated that these two factors (size and shape) could be important in the attraction of apple maggot flies, *Rhagoletis pomonella*.

Studies on some insects, particularly aphids have confirmed that growing plants strikingly silhouetted against the bare soil attracts more insects to the plants than to plants grown against different backgrounds e.g. weeds or artificial backgrounds (Smith, 1969), or dense legume cover (Wood, 1968). The density of the plant stand has also often been reported as an important factor in attracting insects to the crop, e.g. (A' Brook, 1968). Infestation level of pest per unit area of land is often higher in dense plantings than sparse ones, e.g. [*Aphis fabae* (Way and Heathcote, 1966), *Cephus species* (Luginbill and McNeal, 1958), *Erioischia brassicae* (Finch and Skinner, 1976), and cabbage pests (Pimentel, 1961a)]. There are fewer examples of a significant role of olfactory stimuli for plant feeders even over short distances (Southwood and Way l.c.). Notable exceptions include some bark beetles (Scotylidae) which can be attracted from a considerable distance by plant exudates and the Cabbage Root flies which are attracted by the odour of their host plants (Hawkes, 1971) and therefore lay their eggs near them.

The frit fly, *Oscinella frit* L. does not feed as adults on the larval host plant, but only uses it for oviposition. Some of the factors enumerated above are therefore pertinent to the adult female frit in relation to its function in finding suitable hosts for its larvae which feed exclusively on graminaceous plants. Since the role of pheromones in attracting opposite sexes in frit flies has not been ascertained, perhaps males also seek larval food plant to mate females.

Sanders (1960), in laboratory trials, and Mayer (1961) in the laboratory and in the field demonstrated that landing frit fly adults respond to different shapes, colour and size (height). They did not specify the sexes involved in their studies. Vertically arranged stripes (wooden skewers) were shown to attract similar numbers of flies as oat plants (Sanders, l.c.). These studies tend to emphasize the importance of visual response to shape, with olfactory stimulus playing no role, at any rate in the initial stages of landing. Mayer (l.c.) trapped more adults in water-filled blue dishes placed in fields of oat or barley than in water-filled yellow ones; and also found blue stakes about 14 inches high set up in an oat crop when the plants were just appearing above the soil more attractive to the flies than those that were only three inches high. The importance of light intensity has been demonstrated both in the laboratory and in the field by Zhukovskii (1961) when he showed that brightly illuminated vegetation attracted more frit flies than shaded vegetation. The role of density of the host plant and the presence of weeds or other plants within the host crop on attraction of flies in the field has not been determined.

Role of host plant in oviposition

Several authors have suggested that a biochemical stimulus is necessary for egg-laying, even though the site at which eggs are subsequently deposited is selected in response to tactile stimuli. Sanders (l.c.) observed that female frit flies attracted to green wooden skewers executed the initial phases of oviposition behaviour, but with no chemical token stimulus to follow, the insects soon wandered from the dummies. He then described ovipositon behaviour as occuring in 3 stages - 'orientation', 'testing' and 'decision'. During the 'testing' phase, the ovipositor tip was kept in contact with the plant surface as the fly ran up and down the plant; when a crack or crevice was found the fly stopped and attempted to insert the ovipositor with a backward movement of the body. If the insertion was successful, the 'decision' phase supervened and eggs are extruded by contractions of the abdomen. Ibbotson (1960) also emphasized the importance of a chemical stimulus from the host plant before oviposition can take place, although Le Berre (1959) has demonstrated that females screened from contact with host from emergence will oviposit after an initial delay, but fecundity was very low. The presence of the host plant is as important for copulation as it is for actual oviposition. Hillyer (1965) found that in the absence of the host plant, copulation did not occur before flies were at least 5 days old. Even after 10 days only one third of the females had copulated. In the presence of the host plant, however, copulation occurred in some 2-day-old flies and over two thirds of the females had been fertilized after only 4 days. Jones (1969) observed in potted plants in the laboratory that the number of eggs laid per pot increased with increasing plant density, but the rate of increase decreased after a certain plant density. Idowu (1975) observed also in the laboratory that the time spent on the plants by the flies increased with increasing plant height and plant density. The species or variety of cereal is also known to affect the rate of ovary maturation (Hillyer, l.c.) and the number of eggs laid (Idowu, l.c.). The evidence on oviposition therefore, tends to indicate that in the absence of any stimulus from the host plant oviposition can only occur after a considerable delay. It will be readily induced by a combination of stimuli from the host plant. These may include the density or age of the host plant.

Oviposition sites on the host plant

There are several oviposition sites on the plant or in the soil and their presence and importance depend on factors such as the age of the plant, its rate of growth, the variety of the plant, cultural practices and climatic conditions. Zhukovskii (1931) showed that there was a change in oviposition site as the plants grew. He also observed that as the percentage of plants with loose coleoptiles increased, the percentage of eggs laid between them and the stems increased, subsequently falling off again when the coleoptiles began to wither. The total number of eggs laid on the plants was greatest when all the plants had loose coleoptiles. Cunliffe and Hodges (1946) loosened the tight coleoptiles of some young oat plants, while those on others were left tight. Not only did they observe differences in the sites at which the eggs were laid because there was a crevice between the coleoptile and the stem, but they also observed a significant difference in the total number of eggs laid between the treated and the untreated plants. Thus, the coleoptile appears to be the preferred oviposition site on a cereal plant, at least during certain growth stages.

However, the soil very close to the plant can be an important oviposition site before the coleoptile becomes suitable, and the leaf sheath and tillers after the coleoptile has withered. The moisture content of the soil (Cunliffe and Hodges, l.c.) and the soil particle size (Vickerman, 1975) are both important in soil oviposition. Wet soils tend to reduce soil oviposition by consolidating the soil round the stem, so closing the gaps which would normally act as oviposition sites. Cultural practices such as depth of sowing can affect oviposition through its influence on the number and quality of oviposition sites exposed above the ground for oviposition (Zhukovskii, 1931). Climatic factors such as rainfall, temperature and wind can affect the site chosen for oviposition, and also the displacement of eggs from some oviposition sites (Shapiro and Vilkova, 1963).

Fate of the eggs

An important factor affecting the fate of the eggs is the growth of the plant and the position of the eggs on the plant. Shapiro and Vilkova (l.c.) observed that eggs put on the leaves of maize moved a long way from the vegetative cone as the leaves grew, while those put on the coleoptile did not move throughout their experiment. The eggs laid on the exposed parts of the plants such as the leaves are also more likely to be displaced from the plant by rain or wind. Rigert (1935) found that the eggs are fairly vulnerable to sustained low humidity, and that the emergence of larvae is only possible at high humidity. Nye (1959) stated that there is no evidence for biochemical attraction of the larvae to the host plant, unlike Stokes' (1957) evidence with the wheat bulb fly, so larvae originating in sites away from the host plant or displaced from the host plant must seemingly search at random for a suitable host. Dry soil often favours oviposition in the absence of suitable oviposition site on the host plant, but egg eclosion and larval survival is better under moist soil condition. Shapiro (1961) showed that the primary position of the larva developing within the host plant is just above the growing point where it obtains nutriment by extra-cellular digestion. From the circumstances enumerated above, it is perhaps readily explicable that ovipositing flies are usually very selective in their choice of oviposition sites, laying most eggs on sections of plant tissue which are protected and have either finished growing or are growing slowly.

Role of the host plant on the survival of frit fly larvae

Van Emden and Way (1972) cited many examples of the role of host plants in the population dynamics of insects and Bardner and Fletcher (1974) have reviewed the role of insect infestations and their effects on the growth and yeild of field crops. In the frit fly, Southwood and Jepson (1962) indicated that the successive estimates of frit fly population suggested a key mortality factor between the laying of the eggs and the entry of the young larvae into the oat plant. On the dynamics of the frit fly on regional basis however, van Emden and Way (1972) concluded that in such a highly mobile insect it is the amount of grass as well as the proportion of suitable shoots that annually stabilizes the size of the population in spring. Hence, survival in grasses is the key factor in the dynamics of the species.

The entry of the young larva into the plant may be influenced by the structure of the plant and its growth rate (Shapiro, 1961); the position of the egg on the plant relative to the growing point of the plant at the time of eclosion (Shapiro and Vilkova, l.c.); the size of the plant cells and thickness and hardness of the epidermis (Belyaev et al, 1936) and the age of the plant (Dorfschmidt, 1952). Shapiro (l.c.) found that resistance in maize depended on the difficulty experienced by the larvae in reaching the growing point. Susceptible varieties of maize had thin stems with a smaller number of such layers, thus making it more difficult for the larva to reach the correct position in the stem. Shapiro and Vilkova (l.c.) observed that most of the eggs which had been moved well away from the vegetative cone perished, but some still presented a threat to the plant. The larvae would mine through the leaves and struggle along them towards the cone, some of them being expelled from the plant by the continuous growth of the plant.

The study of the anatomical structure of the leaf-sheaths by Belyaev et al (l.c.) showed that the cells in resistant varieties are comparatively small, the external membrane of the epidermal cells is thick and the sclerenchyma is vigorously developed. Cunliffe and Hodges (l.c.) were not able to correlate resistance of the oat plant to frit fly with either carbohydrate or silica content. Dorfschmidt (l.c.) found that the resistance of young oat seedlings increased with the age of the plants. He attributed this to the deposition of cellulose pectin in the epidermal cells of the leaf bases forming the outer layers of the 'stem' in older plants. The age at which this deposition will occur varies in different varieties. The Narrator (Adesiyun) has observed in some of his trials that very young larvae were initially unable to penetrate older stems but were able to do so after feeding for some time on the tillers, which consisted mainly of 'soft' tissues.

Once fully established within the plant, a larva will complete its development and pupate within the plant provided there is adequate food of the right quality within the plant. Both Collin (1918) and Meyer (1924) have suggested that there is little migration of larvae from plant to plant, but Jones (1969) and the Narrator in the present study have recorded migration of larvae from a central plant with many eggs to surrounding plants. Jepson and Southwood (1958) found as many as ten to fifteen almost fully grown larvae in single shoots from small plots and concluded that an oat shoot contained ample food for many more larvae than commonly occur. However, Jones (l.c.) reported that when more than one larva penetrates the shoot, there is competition for food and some fail to survive to pupation.

Shapiro and Vilkova (l.c.) observed that 80 per cent of the plants were damaged when eggs were placed 0.5cm away from the plant, no damage at all to plants 10 cm away from the eggs and only a few individual plants were attacked by larvae from eggs 2cm away. Their observation tends to suggest that young larvae can attack plants that are only a few centimetres away. Jones (1969) showed in the laboratory however, that larvae migrated from a central plant with many eggs to surrounding plants, and concluded that it made little difference to survival whether plants were 1cm or 5cm away. The Narrator has also found in some of his trials that older larvae leaving a plant due to competition infested some plants that were 8cm away. The age and size of the larvae probably has some effect on the distance that can be travelled by them. Larvae migrating out of plants are also likely to succeed in infesting other plants in a dense planting than in a sparse one and also in moist soil condition than in a dry one.

SECTION II

GENERAL METHODS

2.1. FIELD PLOT EXPERIMENTS

2.1.1. Experimental site

Field experiments were laid out in Silwood Bottom at Imperial College Field Station, Silwood Park, Sunninghill, Berkshire in the springs and summers of 1975 and 1976.

The sites of the experiments were the same in both years. They were bounded on three sides by grassland and on the fourth side by a field of potatoes in 1975 and field beans in 1976. Grasslands were sampled with a sweep net in May 1977.

2.1.2. Cultural operations

Oat seeds, variety Maris oberon were used in all laboratory and field experiments. The variety was provisionally recommended for general use by the Ministry of Agriculture in 1975; it is a high yielding variety with very stiff straw.

Sowing was delayed until April 23 in 1975 and May 4 in 1976 to ensure a heavy infestation of the plants by the flies. The seeds were sown with a hand drill in 1975. This released a uniform number of seeds in each drill. In 1976 however, when it was considered necessary to vary the seed rate in the drills and also alter the distance between the drills, the hand drill used the previous year proved unsuitable and sowing was done by hand in furrows made with a hand hoe. The soil was dry at the time of sowing in 1976 as a result of the exceptionally dry preceding months, and water had to be applied to the furrows at the time of planting to ensure uniform germination.

In 1975, New Zealand (NZ) white clover and white mustard seeds were broadcast in the relevant plots. The seeds were then covered with a thin layer of soil.

The predominant weeds were Charlock (Sinapis arvensis L.) and fat hen (Chenopodium album L.). These were controlled in 1975 by a herbicide treatment of 2, 4-D and MPCA applied to the plots on 19th May, when the oat plants were at the 3 to 4-leaf stage. In the plots not treated with herbicide, the population of weeds was so high and their growth so vigorous that they swamped the white clover. Weeds were removed by hand in 1976 because the closeness of some rows to each other made the use of a hoe impracticable. Herbicide was also not used for fear of trampling on the plants during application.

The seed rate and plant populations in the different treatments and the calendar of operations on the plots were tabulated in Appendices I and II, respectively.

Rabbits and birds are sometimes a menace to experimental plots at Silwood Bottom, and both had to be kept off the experiments. Rabbits were excluded from the experimental site by a fence of wire netting in both years. Birds were scared off by explosives in 1975, but this method did not prove very efficient, so in 1976 they were excluded by a net suspended about 2m over the plots.

2.1.3. Experimental lay-out

(a) Bare and Weedy backgrounds

An experiment using a 4 X 4 Latin Square Design was laid out in 1975 with the following 4 treatments:

A. Oats with bare background

B. Oats plus white clover and weeds

C. Oats plus white mustard and weeds

D. Oats plus weeds

Plate 1. Oat plants with bare background in the foreground and with a background of weeds (June 11, 1975).

Plate 2. Oat plants with a background of white mustard and weeds in the foreground and with a bare background (June 11, 1975).

Plate 3. Oat plants with bare background (July 11, 1975).

Plate 4. Oat plants with a weedy 'overgrowth' (July 11, 1975).

Plot size was 5m by 4m and the oat plants were in rows 15cm apart. Weeds gave almost a blanket cover over bare soil and completely subdued the growth of white clover which gave the initial soil cover in treatment B. Treatments B, C and D therefore appeared similar visually, after some time, but looked quite distinct from treatment A (Plates 1 and 2). By the time oat plants reached the reproductive phase, both the charlock and the cultivated white mustard were more of an 'overgrowth' to oats than an undercover (Plates 3 and 4).

(b) Different densities of oats

1975

A randomized block design experiment was laid out to investigate the effects of different plant densities and row spacing on attractiveness to colonizing adult flies and on oviposition. There were three treatments:

A. Oat plants in rows spaced 7.5cm apart (8.6m plants/ha)
B. Oat plants in rows spaced 15.0cm apart (4.3m " ")
C. Oat plants in rows spaced 45.0cm apart (1.4m " ")

Each treatment had four replicates. The plant population within the row was the same in all three treatments (66 plants per metre), but plant population per unit area differed in relation to row spacing (Appendix I).

1976

The experimental design here was also a randomized block as in experiment (b) in the previous year, but there were five treatments with four replicates each (Appendix IV). This made it possible to compare not only the effects of different plant densitites and row spacing, but also that of seeding density

Plates 5a to 5e. Oat plants of different densities and row spacings (May 23, 1976).

Plate 5a. 14.4m plants/ha in rows spaced 5cm apart
" 5b. 13.7m " " " " 15cm apart
" 5c. 5.1m " " " " 15cm apart
" 5d. 1.4m " " " " 15cm apart
" 5e. 1.4m " " " " 45cm apart

Plate 5a

Plate 5b

Plate 5c

Plate 5d

Plate 5e

within the row on attractiveness to colonizing adult flies and on oviposition. Additional data on larval and pupal populations were also collected. The treatments were as follows:

A. 22 plants/30cm length in rows spaced 5cm apart (Plate 5a)
B. 64 " " " " " " 15cm " (Plate 5b)
C. 24 " " " " " " 15cm " (Plate 5c)
D. 7 " " " " " " 15cm " (Plate 5d)
E. 19 " " " " " " 45cm " (Plate 5e)

Germination counts and estimates of plant population were made on May 21 (i.e. 17 days after sowing) (Appendices I and III). Photographs of the plots were taken on May 23 (Plates 5a to 5e).

2.1.4. Sampling of flying insects using water traps

Relative estimates of the abundance of adult flies in the crop were made with transparent water traps. It was essential in the experiments to cause as little disturbance as possible to the habitat (oat crop), so as not to dislodge the eggs laid on the plants, hence the choice of water trap in preference to sweep net or vacuum sampler. Although Mayer (1961) had observed that frit flies are attracted to blue, no colour factor was introduced in the traps because of the nature of the experiments. Catches from coloured water traps might be influenced not only by the colour of or colour contrast between the plants and their background, but also by the colour of the traps. This invariably would render interpretation of trap catches more difficult. In view of this, transparent pyrex dishes were used.

The dishes 12.5cm in diameter and 6.5cm deep were placed on metal lids from paint cans screwed to the top of wooden pegs. Narrow holes up to 45cm deep were dug in the centre of each plot to accept the trap stand. This enabled various lengths of the stand to be withdrawn from the soil from time to time to bring the trap height to approximately the same level as the tops of the plants. The stands were replaced by longer ones when the plants attained considerable heights. There was a trap at the centre of each plot (Plates 5a to 5e).

Each trap was two-thirds filled with an aqueous solution made from 20ml of 'Sqeezy' - formalin in 4.5 litres of water. The 'Sqeezy' was to reduce the surface tension and formalin to act as preservative for the insects. The same concentration of the solution was used throughout the study period, as it was shown by Mayer (1961) that different concentration of detergent affects the number of flies caught. The traps were emptied weekly and identification and sexing were carried out under a binocular microscope in the laboratory.

2.1.5. Sampling of immature stages on oat plants

The eggs of the tiller generation are laid on the shoots of the growing oat plant or possibly in the soil adjacent to it. Plants with adjacent soil from four 7.5cm row lengths chosen with the aid of a table of random numbers were carefully dug out from each plot with a trowel and bulked in a polythene bag to make a 30cm sample per plot. These were taken to the laboratory for examination with a hand lens. Only full eggs were counted.

The eggs of the panicle generation are laid in the spikelets. These were sampled by placing a polythene bag over individual panicles and detaching each from the rest of the plant with a pair of scissors with serrated edges. Care was taken during this process because Jepson and Southwood (1958) found that up to three-quarters of the eggs may be dislodged during cutting. The Narrator in this study however, observed that less than 1% of the eggs sampled were found loose and detached from the spikelets inside the polythene bags. Only two panicles per plot were sampled on each sampling occasion because of the time needed to dissect the individual spikelets to obtain egg counts. Some panicles contained as many as 85 spikelets. Both full and empty eggs were counted. Smith (1962) did not find eggs other than those of *O. frit* on the spikelets of oats during sampling.

Southwood and Jepson (1962) pointed out that the identification of the Chloropid species of grasslands is extremely difficult and to some extent impossible, but in the oat field they rarely found anything but 'typical' *O. frit* larvae and adults. Identification on oats was therefore much easier. Larvae and pupae of the tiller generation were sampled by dissecting shoots from random samples of four 7.5cm rows already referred to above. Plant samples were stored in some cases for up to three weeks at 5°C before dissection. Larvae and pupae subjected to such cold storage were found to be unaffected as they resumed development at a faster rate to pupae and adults when brought to 20°C after dissection. The pupae dissected out of the plants were weighed on a Cahn Gram Electrobalance (Plate 6) and kept separately in 5cm by 1cm specimen tubes at 20°C until either parasites or adult frit flies emerged. The emergent flies were anaesthetized with Carbon Dioxide (CO_2) gas from a 'Corkmaster' to make sex determination easier.

A 'Corkmaster' is a small equipment containing CO_2 capsule and is normally used for opening wine bottles (Fig. 1). Female and male flies anaesthetized with CO_2 were observed to stick out their ovipositor and aedeagus, respectively.

Plate 6. Cahn Gram Electrobalance

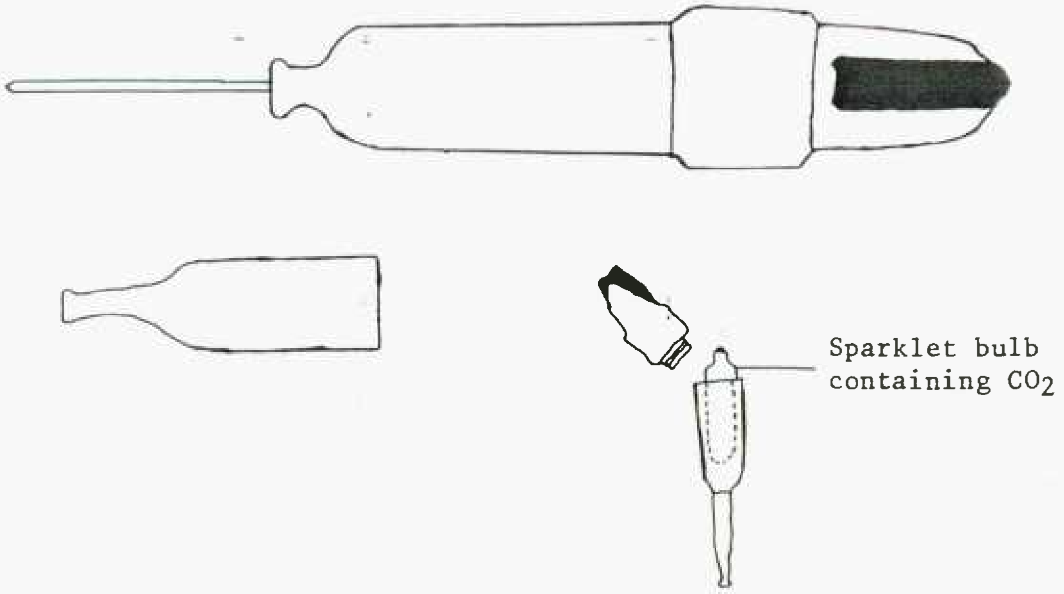

Fig. 1. Corkmaster used for anaethetizing adult flies.

2.2. FIELD EXPERIMENTS WITH OAT PLANTS IN POTS AND SEED TRAYS

These experiments were conducted in most cases to supplement the data from field plot experiments and were planned to coincide with the emergence of either tiller or panicle generation adults when maximum prevalence of frit fly adults was assured in the field.

2.2.1. Pre-field preparation

Oats seeded in plastic pots 14cm in diameter and 8.5cm deep or in seed trays of different sizes depending on the experiment were kept in wooden frames placed outside the greenhouse complex. The frames rested on soil, the sides were of wood, while the top was covered with white terylene net. The frames were thus insect-proof, but allowed adequate ventilation and light for normal growth and development of the plants.

2.2.2. Oviposition in the field

The potted plants or those growing in seed trays were transferred to the field once they attained the stage of growth desired. They were laid out either in a completely randomized design or a randomized block design next to an oat crop from which adults were emerging. The pots were partly buried in the soil to reduce evaporation. The plants were left in the field for seven to ten days depending on the activity of frit flies in the field, and were then taken to the laboratory where egg counts were made.

2.2.3. Post-infestation preconditions and examinations

Where data on larval penetration into the plant and on survival and development were required, plants infested with eggs in the field were taken back to the insect-proof frames until shoot dissection was required. The plants were then dissected in the laboratory and counts of larvae and pupae made.

2.3. LABORATORY EXPERIMENTS

2.3.1. Insect culture and rearing techniques

The initial culture was established from samples of infested rye grass collected from the field in December, 1974. That culture was used throughout the winter and spring of 1975. A fresh culture was established from samples taken from oat plants in the field during the summer of 1975 and this was replaced with a sample taken from oat plants in the field during the summer of 1976.

Rearing was carried out in a 20°C illuminated constant temperature room. A constant 16-hour photo-period was maintained by overhead fluorescent bulbs. The relative humidity was not controlled. These conditions provided a suitable environment for the development of the insect and the normal growth of the host plant.

Oat plants (variety *Maris Oberon*) were used as host for the insect. The plants were seeded in 14cm diameter plastic pots at the rate of 50 to 60 plants/pot. The pots were kept in the greenhouse where the temperature fluctuated between 10° and 18°C. The potted plants were introduced into the culture of the ovipositing adult flies at the 3-leaf stage, when the coleoptiles were most suitable for oviposition.

The oviposition cage was a cube of sides 45cm with a cellulose acetate top, fine muslin sides and back, a sliding door made of perspex at the front and a wooden base. Holes were made in the roof of the cage, but these were later plugged with white dental rolls attached to the roof with 'Durofix'. Food was supplied to the breeding flies in the cage, through the holes on to the dental rolls. Once the dental rolls were soaked with the food, the holes were sealed with masking tape to reduce the rate of evaporation from the rolls.

The food comprised 50gms A.R. Grade sucrose dissolved in 1 litre of distilled water. An earlier attempt to feed the insects on a solution made from 20gms of glucose plus 20gms of marmite (yeast extract) dissolved in a litre of distilled water did not meet with much success. The glucose-marmite solution encouraged rapid fungal growth on the dental rolls and these often trapped the flies.

Two pots, each containing 50 to 60 oat plants at the 3-leaf stage were placed in the cage in which a population of about 200 ovipositing flies was maintained. Oviposition on the plants was allowed to take place for about 48 hours. The pots were removed from the cage and kept under light for the next 18 days and away from light for the next seven days. The 7-day period during which the potted plants containing pupae or fully developed larvae were removed from light was to ensure that the surviving plants died. It was easier to collect emerging adults from pots in which all the plants were dead than from those containing both dead and live plants. Finally, the pots which now contained dead plants were placed in another cage, similar to the oviposition cage into which the next generation adults emerged about 4 to 5 weeks after oviposition.

It was observed that about 80 per cent mortality occured between the egg stage and adult emergence, judging from the initial number of eggs laid on the plants at the 3-leaf stage in the oviposition cage and the subsequent number of adults that emerged from them. Occasionally therefore, eggs laid on the plants in the oviposition cage were carefully removed and used to infest younger plants at the 1-leaf stage. This was found to enhance survival and led to a higher proportion of adult emergence.

2.3.2. Pot and seed tray experiments

Oats were seeded in 8.75cm or 14cm diameter pots or in seed trays. Thinning was done to required densities during the first week of germination. The plants were kept in the greenhouse until they reached the required growth stage, when they were transferred to the laboratory, where they were offered to ovipositing adults in cages or were artificially infested with eggs. Plants kept at 20°C were usually dissected 25 days after oviposition, that is, when pupation was complete.

In some experiments, 'artificial plants' were used instead of oat plants. These were wire-reinforced dark green cardboards commonly called 'twist-ems ties' and normally used by gardeners for tying plants to supports (Plate 7). The standard size was 15cm long by 0.65cm wide, but this was modified in the different experiments.

Plant protection banding grease manufactured by J. Gibbs Ltd., Agricultural Engineers, Bedfont, was applied generously to the surfaces of the 'plants' to make them sticky. The sticky 'plants' in pots or trays were then placed in cages containing 50, 100 or 150 adult flies for 48 hours. Counts were made of the numbers of flies trapped in the different treatments at the end of the period.

Plate 7. Potted 'Artificial Plants'

2.4. ANALYSIS OF DATA ON THE DISPERSION OF THE IMMATURE STAGES OF O. FRIT.

A computer programme, TOPFIT was used to analyze the dispersion of eggs, larvae and puparia among oat shoots and of eggs among spikelets. TOPFIT calculates the indices of dispersion and fits optionally up to 10 theoretical distributions to an observed frequency table. The programme has been described in some detail by Robles (1969).

The results of the tests of goodness of fit reported later in the text were those produced by the 'standard' chi-squared test. This takes a value of 5 as the minimum calculated expected frequency. The grouping of classes to obtain values above a certain limit reduces the degrees of freedom for the test and sometimes the most significant differences may be obscured by grouping the frequencies at the tail of the distribution. To overcome this, the 'alternative' chi-squared test devised by Fisher (1950) was included in the programme. The only requirement in Fisher's 'alternative' chi-squared is the presence in every class interval, of at least one observed frequency (i.e. a frequency greater than zero).

Where a distribution fitted the negative binomial, the parameter k was also calculated.

$$k = \frac{\bar{x}^2}{s^2 - \bar{x}}$$

SECTION III

EFFECTS OF THE AGE OF OAT PLANTS ON ATTRACTION, OVIPOSITION AND LARVAL SURVIVAL OF *O. FRIT*.

3.1. FIELD EXPERIMENTS

3.1.1. Distribution of eggs at alternative oviposition sites

The effect of the age of oat plants on the site selected for oviposition was investigated in this experiment on oat plants in plots in the field and on those seeded in seed trays. The seed trays were kept in insect-proof frames until the plants attained the required growth stage-1, 2, 3, 4, or 5-leaf stage. For the purpose of this experiment, a plant at the 3-leaf stage was one in which the youngest (third) leaf was about one-third the length of the previous leaf (2nd leaf). This criterion was used for the other growth stages also.

For the sampling of each growth stage, twenty 30cm row samples were taken from the plots in the field. These were bulked together and carefully examined for eggs in the laboratory, ensuring that the eggs were not dislodged from the original sites where they were laid. Full eggs only were counted in the samples taken from the plots to ensure that eggs laid while the plants were at an earlier stage of growth were not included in counts recorded for later stages. Seed trays taken to the field for infestation with eggs were left there for 3 or 5 days depending on the abundance of adult frit flies in the field at the time. All the plants and adjacent soil in the seed trays were carefully examined for eggs at the end of oviposition in the field.

The distribution of eggs among the different oviposition sites on the plants and adjacent soil at the different growth stages of oats was very similar in the tray and field plots. For this reason, both results were pooled and presented in table 1 and fig.2. The crevice between the plant and soil was clearly the most preferred oviposition site at the 1-leaf and 2-leaf stages, 76.7 and 75.0 per cent of the eggs being laid there, respectively. However, at the

3-leaf stage when the coleoptile has started separating from the stem thereby creating a crevice, 85.6 per cent of the eggs were laid in the crevice, while no more eggs were laid in the soil. The role of the coleoptile as an oviposition site declined at the 4-leaf stage with the production of tillers. At the 5-leaf stage, the coleoptile has withered and because suitable tillers were available, 96.9 per cent of the eggs were laid on the tillers. At no stage in this experiment did the leaves (leaf blades, leaf sheaths) constitute important oviposition sites. Differences in the total number of eggs recorded for the different growth stages in table 1 are partly a reflection of the prevalence of adult flies in the field at the time the samples were taken from the plots on seed trays taken to the field, and do not necessarily indicate preference for a particular growth stage.

It is evident from this experiment that the preferred oviposition site changed as the plant grew and that the coleoptile is the most important oviposition site on the plant. The soil was very dry in the plots and in the trays when the experiment was conducted, hence the high proportion of soil oviposition at the 1-leaf and 2-leaf stages.

Table 1 Distribution of eggs on oat plants and adjacent soil in the field in relation to the age of the plants.

Stage of growth of oat plants	No. of eggs laid at the different oviposition sites 1	2	3	4	5	6	Tillers
1 - leaf stage	161	18	0.0	0.0	0.0	31	0.0
2 - leaf stage	369	88	34	0.0	1	0.0	0.0
3 - leaf stage	0.0	4	119	0.0	2	0.0	14
4 - leaf stage	0.0	4	22	2	3	0.0	30
5 - leaf stage	0.0	0.0	1	0.0	0.0	0.0	31

Oviposition sites

1 = Between plant and soil or in the soil very close to the plant

2 = Outside the coleoptile

3 = Inside the coleoptile

4 = On the stem between the tip of the coleoptile and the 1st leaf blade

5 = Inside the leaf sheath

6 = On the leaf blade

Tillers = Between tillers and primary shoot or on tillers themselves

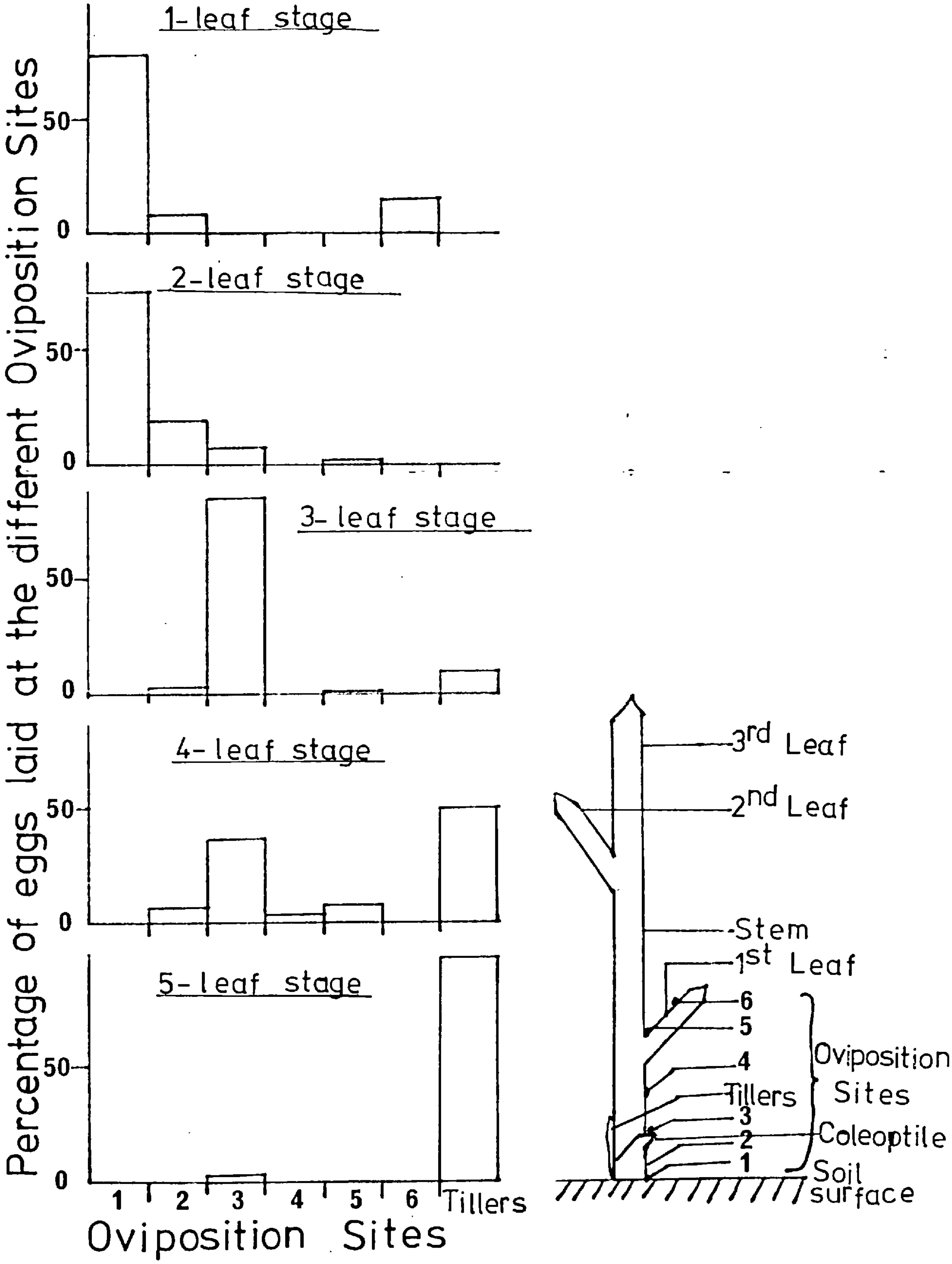

Fig.2 The distribution of eggs at different oviposition sites in relation to the stage of growth of oats in the field.

3.1.2. Effects of the age of oat plants on oviposition, entry of larvae into the plants and larval survival in the plants.

The experiment described above showed that the preferred oviposition site changed as the plant grew, but did not provide information on the preference shown (if any) by ovipositing females for oat plants of different growth stages when available simultaneously, and on the fate of eggs and larvae hatching from them. This was therefore the purpose of the following experiment.

At weekly intervals, oat plants were seeded at the rate of 10 per pot in 14cm-diameter pots. Ten pots were sown every week and they were all placed in insect-proof frames after sowing. The plants were thinned to 8 per pot three days after germination. In all, there were five weekly plantings, starting on 29.5.76. and ending on 25.6.76.

Eight pots from each weekly planting in which the plants exhibited fairly uniform growth were taken to the field 5 days after the last sowing on 30.6.76. The age classes of the plants were 5, 12, 19, 26 and 33 days after sowing corresponding approximately to 1, 2, 3, 4 and 5-leaf stages, respectively. Height measurements of the plants were taken from the soil surface to the tip of the longest leaf. The pots were partly buried in the soil in a randomized block design as shown in Appendix V. Each growth stage was replicated 8 times, making 40 pots in all. Because of the unusual summer of 1976, the evapotranspiration rate from the pots was high and the plants had to be watered at least twice daily throughout the 1-week exposure period to adult flies in the field. At the end of the 1-week exposure, 20 of the pots from blocks II, IV, VI and VIII were taken to the laboratory. The remaining 20 pots from blocks I, III, V and VII were transferred to the insect-proof frame.

Pots taken to the laboratory were kept there for a further 3 days by which time it was expected that all the fertile eggs laid on the plants should have hatched and the larvae either entered the plants or died if unable to penetrate the plants. The mean daily laboratory temperature during this period was 28°C, and 20 newly laid frit fly eggs left in a damp petri dish hatched between 48 and 60 hours at that temperature. The plants were examined for eggs and dissected for larvae. Over 90 per cent of the eggs were empty and it was concluded that unhatched ones were infertile. The 20 pots kept in the insect-proof frame outdoors were taken to the laboratory on 21.7.76, 14 days after exclusion from further oviposition. The mean daily temperature in the field for 14 days was 18.1°C. The plants were dissected for larvae and pupae as before. It was not possible to make egg counts on these plants because most of the egg shells were no longer visible. Egg counts obtained from the previous sets of pots taken direct to the laboratory were therefore used in computing the data plotted in fig.5. There was no reason to suppose that oviposition on plants from the second set of pots would differ from those of the others since the 2 lots were replicates of the same experiment and were excluded from further oviposition simultaneously.

For the purpose of this experiment, the phrase 'oat plant' means primary shoots plus tillers. The primary shoot alone where tiller production has not started, e.g., in oat plants at the 1-leaf stage. Also, since the plants were exposed for oviposition in the field for one week all of them had produced at least one more leaf at the end of the exposure period, but the growth stages used in the text were those at the time the plants were taken to the field. The results are presented and discussed below in sub-sections 3.1.2 (a) to 3.1.2. (c).

3.1.2. (a) Egg deposition on oat plants at different growth stages

The mean number of eggs laid per plant, per primary shoot and per tiller initially increased with the age of the plants up to the 3-leaf stage (table 2, fig. 3 (i)). This increase reached a plateau between the 3-leaf and 4-leaf stages with a decrease at the 5-leaf stage, though this decrease was not statistically significantly different ($P > 0.05$) from those of the former (table 2, fig.3 (i)). Like in the previous experiment (fig.2), all the eggs were laid on the primary shoots or the crevice between them and the adjacent soil at the 1-leaf stage, most of the eggs laid inside the coleoptiles at the 2-leaf stage (3-leaf stage at the end of the exposure period in the field) and the tillers subsequently became relatively important at the later growth stages (fig.3 (ii)). However, unlike the previous experiment, many eggs were laid on the leaves of the primary shoots at the 4-leaf and 5-leaf stages after the coleoptile had withered (fig.3 (ii)). Most of these eggs were laid on the dry leaf blades and sheaths of the older leaves which had fallen over to the surface of the soil in the pots, but still attached to the stems. In the previous experiment, plants at similar growth stages in field plots still had their older leaves upright and several centimetres from the surface of the soil, hence an insignificant proportion of eggs were laid on the leaves. Le Berre (1959) and Sanders (1960) observed that most searching for oviposition sites after the flies have landed on the plants was concentrated at the base of the plant while Allen and Pienkowski (1974) observed in the laboratory that frit fly adults preferred dead leaf sheaths attached to newly emerging tillers as oviposition sites. It seems reasonable therefore, to suggest that the flies concentrating their search at the base of the plants in this experiment laid most of their eggs on the dead leaves at the base of the plants at the 4-leaf and 5-leaf growth stages.

Table 2 Effects of the stage of growth of oat plants on the number of eggs laid

Age of oat plants (days after sowing)	Stage of growth of plants	Mean height of plants (cm)	Mean no of tillers per plant	Mean no. of eggs laid per		
				plant	primary shoot	tiller
5	1 - leaf	3.5a	——	5.1a	5.1a	——
12	2 - leaf	7.3b	2.0a	11.6b	10.2b	0.7a
19	3 - leaf	15.1c	2.8b	23.9c	14.6b	3.3b
26	4 - leaf	27.0d	2.8b	24.3c	15.1b	3.2b
33	5 - leaf	34.3e	2.6b	20.3c	14.7b	2.2b

Figures not followed by the same letters in the same column are significantly different at P=0.05

—— indicates no tillers or eggs on tillers

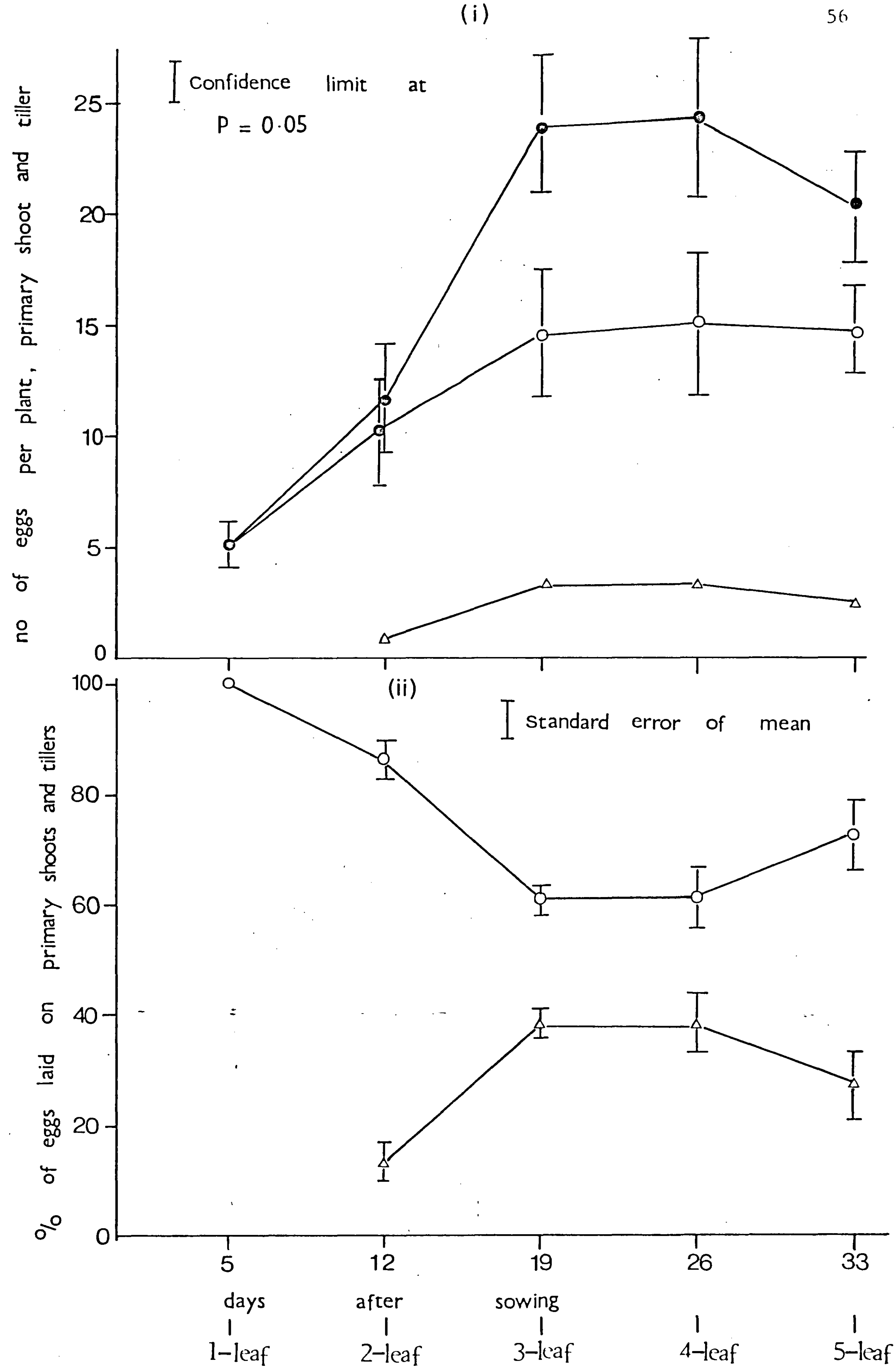

Fig. 3 Effects of age of oat plants on oviposition

3.1.2. (b) Entry of larvae into oat plants

The entry of young 1st instar larvae into oat plants and primary shoots became increasingly difficult with ageing of the plants (table 3, fig.4). At the 1-leaf stage, as many as 88.2 per cent of the young larvae which survived the egg stage penetrated either the plants or primary shoots. This was significantly different from 75.0 and 46.5 per cent obtained for plants and primary shoots at the 2-leaf stage. At the 3-leaf stage, the corresponding figures for penetration into the plants was 47.7 per cent, which was significantly ($P < 0.05$) less than that at the 2-leaf stage, but significantly ($P < 0.05$) more than 28.8 and 25.2 per cent obtained at the 4-leaf and 5-leaf stages, respectively. The primary shoots were totally immune to penetration by the young 1st instar larvae at the 4-leaf and 5-leaf stages, while only 8.2 per cent of those which survived the egg stage penetrated at the 3-leaf stage. The tillers remained susceptible at all stages of growth. There was a good negative correlation between the percentage penetration of the larvae into the plants ($r = -0.98$) and primary shoots ($r = -0.92$) and the age of the plants (fig.4).

3.1.2. (c) Survival of the larvae in the plant

The results presented below (table 4 and fig.5) were obtained from the dissection of the plants in the second lot of pots mentioned above (page 53).

Most larvae and pupae were found in the plants at the 3-leaf stage (10.7 per plant), followed by 2-leaf stage (7.8 per plant) and 4-leaf stage (4.2 per plant). It was lowest at the 1-leaf and 5-leaf stages which had 1.2 and 1.1 per plant, respectively. However, the largest proportion of larvae penetrating and surviving to the late larval and pupal stages from the initial numbers of eggs occurred at the 2-leaf

Table 3 Effects of the stage of growth of oat plants on the entry of the larvae

Age of oat plants (days after sowing)	Stage of growth of the plants	Mean no of tillers per plants	Larvae found in					
			PLANTS		PRIMARY SHOOTS		TILLERS	
			Mean no/ plant	% of total eggs	Mean no/ shoot	% of total eggs	Mean no/ tiller	% of total eggs
5	1 - leaf	——	4.5a	88.2d	4.5b	88.2c	——	——
12	2 - leaf	2.0a	8.7a	75.0c	5.4b	46.5b	1.65a	28.5a
19	3 - leaf	2.8b	11.4a	47.7b	1.9a	8.2a	3.39b	39.5b
26	4 - leaf	2.9b	7.0a	28.8a	0.0a	0.0a	2.41a	28.8a
33	5 - leaf	2.6b	5.1a	25.2a	0.0a	0.0a	1.96a	25.2a

Figures not followed by the same letters in the same column are significantly different at P=0.05

—— indicates no tillers or larvae in tillers

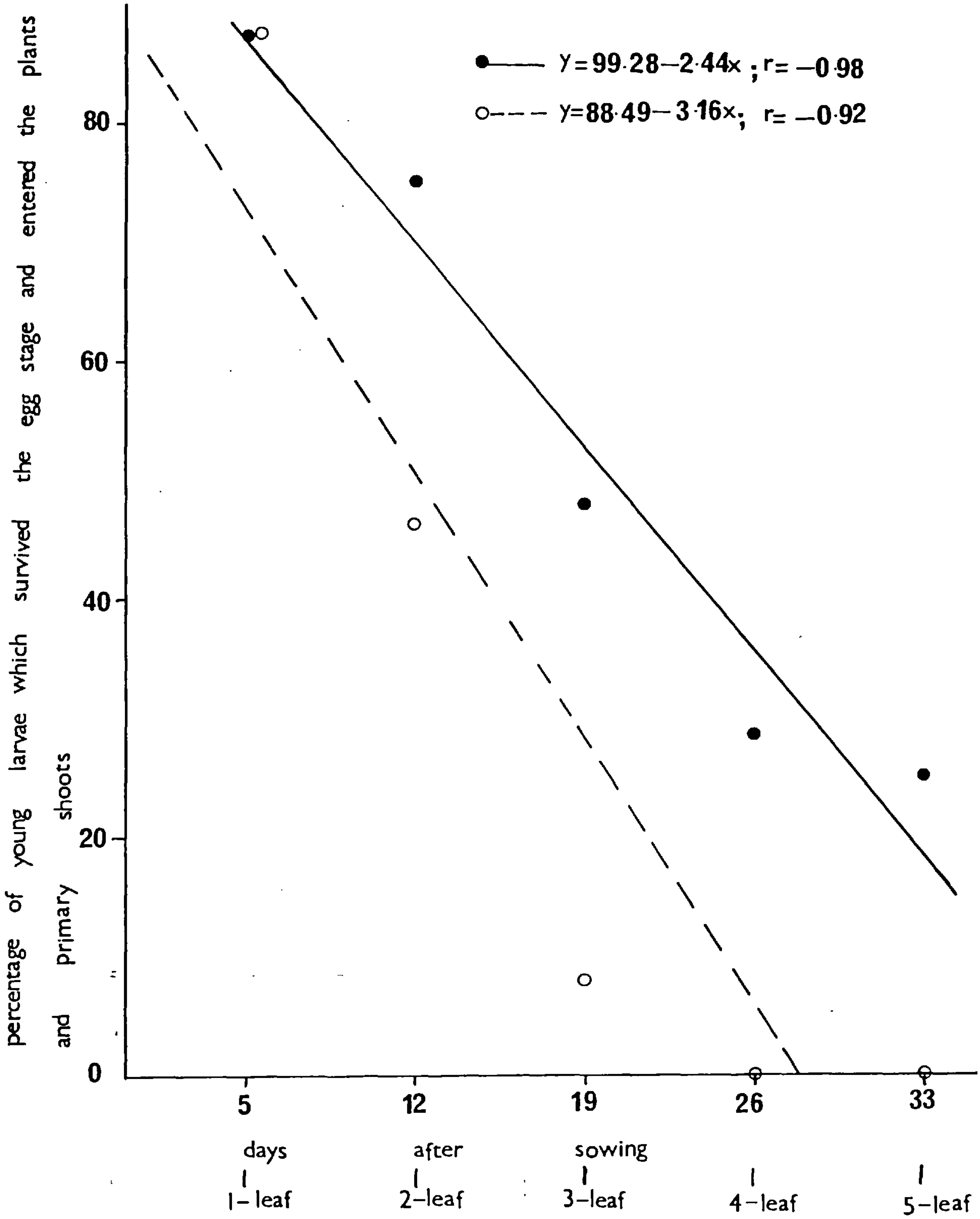

Fig.4 Effects of age of oat plants on larval penetration.

●—— Oat plants (primary shoots plus tillers)

○--- Primary shoots

stage (3-leaf stage at the end of oviposition period in the field) (69.0 per cent), followed by the 3-leaf stage (45.8 per cent), 1-leaf stage (23.5 per cent), 4-leaf stage (17.3 per cent) and the smallest proportion at the 5-leaf stage with only 5.5 per cent (table 4, fig.5 (ii)). Survival inside the plants, that is, apparent survival between young 1st instar larval stage inside the plants and late larval and pupal stages was highest at the 2-leaf and 3-leaf stages (92.0 and 93.9 per cent, respectively) and lowest at the 1-leaf and 5-leaf stages (26.7 and 21.6 per cent, respectively) (table 4, fig.5 (i)). Plants at the 4-leaf stage had intermediate figures for survival (60.0 per cent) because some larvae were able to penetrate and develop in the primary shoots after feeding for some time in the tillers. In all the growth stages of the plants, the tillers contained more late larvae and pupae than the primary shoots, even at the 1-leaf stage in which 2 weeks earlier no tillers were formed (table 4).

Inferences from the results just presented above however, have to be drawn with caution for the following reasons: (i) different numbers of eggs were laid initially on the plants at the different growth stages, (ii) oviposition intensity was higher than normally occur in agricultural fields of oats, (iii) penetration of the young 1st instar larvae decreased with increasing age of the plants and this would have some effects on the actual numbers of late larvae and pupae found in the plants, and (iv) the effects of all these on competition between the larvae at the different growth stages of the plants. Some inferences could still, however, be drawn within the limitations of the experiment. Plants at the 2-leaf stage offered the most suitable condition for survival from eggs to pupae (fig.5 (ii)). Although penetration was greatest in plants at the 1-leaf stage (fig.4), the

Table 4 Effects of the stage of growth of oat plants on the development of larvae

Age of oat plants (days after sowing)	Stage of growth of the plants	Mean no of tillers per plant	Late larvae and pupae found in				
			PRIMARY SHOOTS	TILLERS	PLANTS		
			Mean no/ shoot	Mean no/ tiller	Mean no/ plant	% surviving from eggs	% surviving from young larvae inside plants
5	1-leaf	0.6a	0.5a	1.0a	1.2a	23.5	26.7
12	2-leaf	3.2b	1.5b	1.9b	7.8c	69.0	92.0
19	3-leaf	6.5d	2.8c	1.2ab	10.7d	45.8	93.9
26	4-leaf	4.0c	0.8ab	0.9a	4.2b	17.3	60.0
33	5-leaf	2.7b	0.0a	0.4a	1.1a	5.5	21.6

Figures not followed by the same letters in the same column are significantly different at P = 0.05

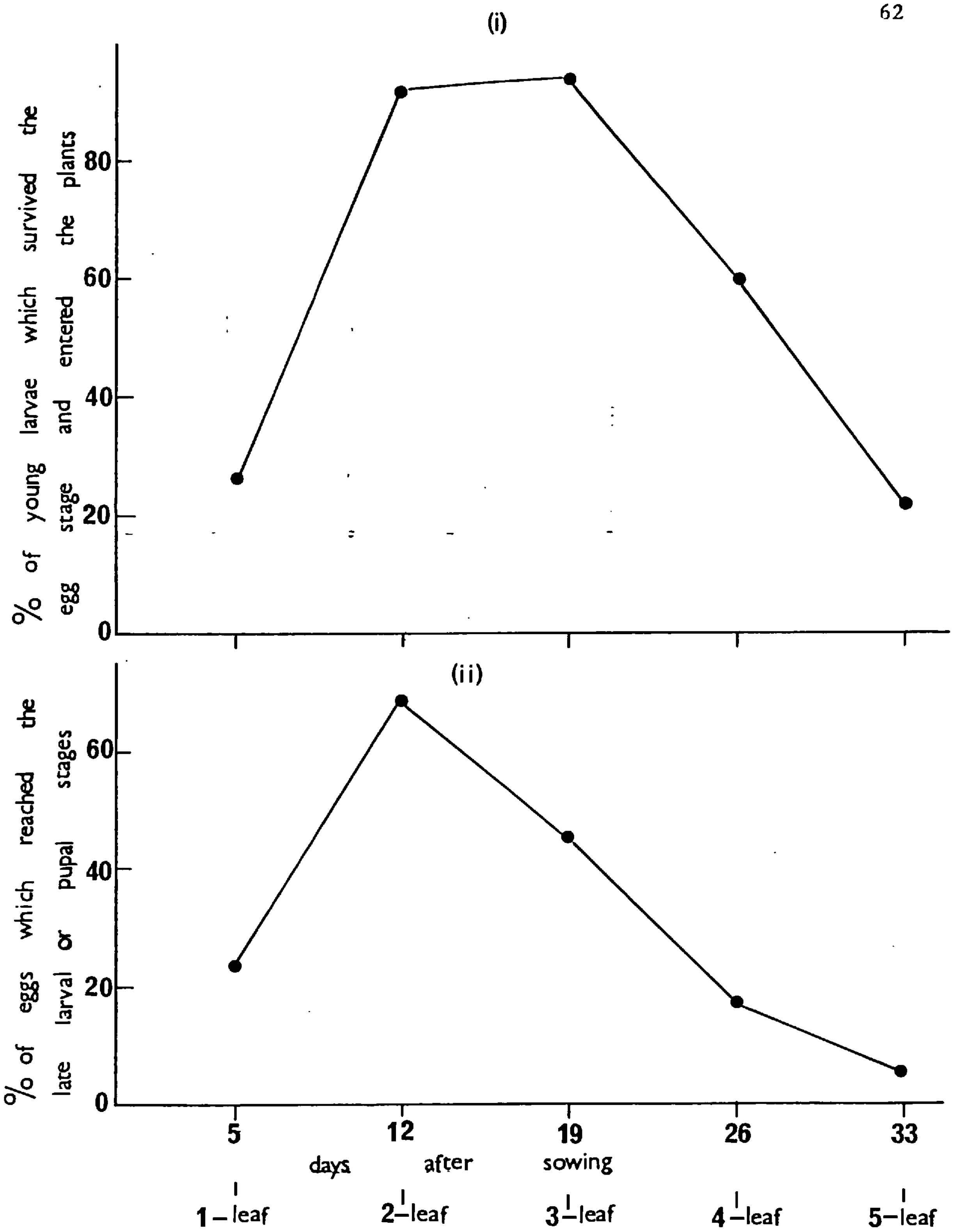

Fig.5 Effects of age of oat plants on survival from young larvae (top) and from eggs (bottom) to late larval or pupal stages.

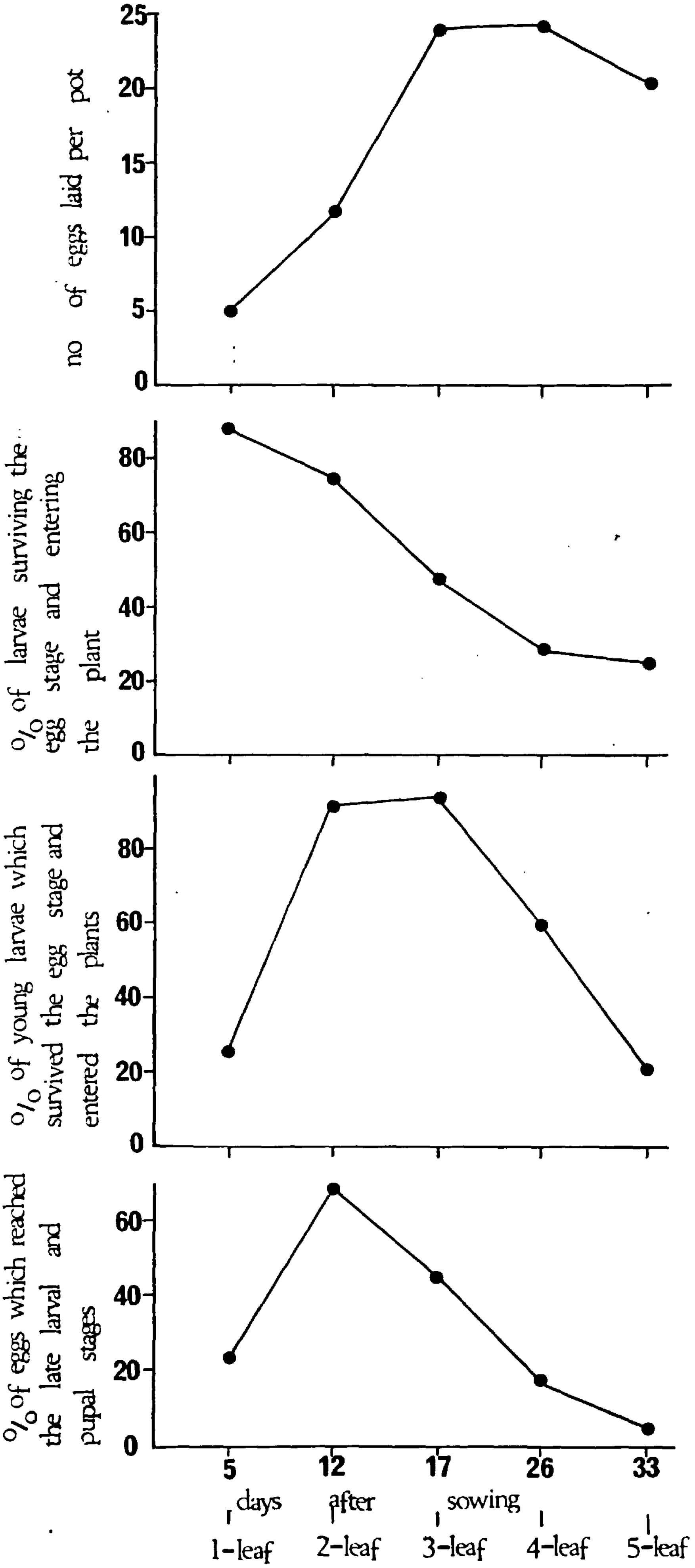

Fig.6 Diagramatic relationships between the stage of growth of oats and oviposition, penetration of larvae into the plants and survival to late larval or pupal stages.

primary shoots of the plants were not big enough to support a large number of larvae, neither were the plants old enough to produce enough tillers. On the other hand, the tissues of the plants at the 4-leaf and 5-leaf stages were so hard that penetration into the primary shoots by the young 1st instar larvae was impossible. The tillers were still not big enough to support large numbers of larvae and it was evident that some older larvae that had fed and survived initially on tillers were able to penetrate the primary shoots of plants at the 4-leaf stage which earlier were impenetrable to younger larvae. No larva was found in the primary shoots of plants at the 5-leaf stage.

In conclusion, this experiment has revealed that the stage of growth of oat plants most suitable for oviposition is not necessarily that most suitable for larval penetration and subsequent survival to pupae and adults. Under high oviposition intensity as in this experiment, the 3-leaf stage was most suitable for oviposition, the 1-leaf stage was most suitable for penetration and the 2-leaf stage for survival from eggs to pupae (fig.6). The highest mortality occurred amongst larvae colonizing plants at the 4-leaf and 5-leaf stages.

3.2. LABORATORY EXPERIMENTS

3.2.1. Landing, resting and oviposition behaviour of adult frit flies in response to the height of oat plants or of 'artificial' plants.

The experiments described in sub-section 3.1.1. above showed that coleoptile suitability for egg deposition varied with the age of the plant and in 3.1.2.(a), it was shown that the numbers of eggs laid on oat plants increased with the age (stage of growth) of oat plants. Two factors, the height of the plant and coleoptile suitability for egg deposition are linked with the age of oat plants. It is as yet not clear how the height of the plants influences the initial numbers of colonizing adults and how this later affects the numbers of eggs laid. The series of experiments described below in 3.2.1. (a and b) were designed to throw some light on this problem.

3.2.1. (a) Effects of size (height) of 'artificial' oat plants on the numbers of adult flies landing.

Sticky 'artificial' plants described in sub-section 2.3.2. were used in these experiments. The two heights employed were 6.5cm and 13.0cm corresponding approximately to the heights of oat plants between the 1-leaf and 2-leaf stages (6.5cm), and 2-leaf stage to 3-leaf stage (13.0cm) described in sub-section 3.1.2.(a) and table 2. Oat plants taken to the field in the previous experiment at the 1-leaf stage (3.5cm) were at the 2-leaf stage (7.3cm) at the end of the 1-week exposure period in the field.

In the first experiment, 2 pots, one containing 8 'plants' each 6.5cm high by 0.65cm wide and the other containing the same number of 'plants' with the same width, but 13.0cm in height were placed in a 45cm cube cage containing 100 adult flies. At the end of a 24-hour period, the numbers of flies that had landed and trapped on the 'plants' in each pot were counted. The trial was replicated 4 times, with more adult flies introduced into the cage at the start of each trial to maintain the number within a cage at 100. The position occupied by each pot was also alternated from replicate to replicate. Results are presented in table 5.

The second experiment was similar to the first one in essential details. The only difference was that the width of the taller 'plants' was halved to 0.325cm in this experiment, so that the surface area available for trapping and the amount of 'greenness' exposed in the 2 pots were the same (plate 8).

Plate 8. 'Artificial plants' of different heights (left: 6.5cm; right: 13.0cm) but the same area (4.23cm^2).

In both experiments significantly more flies landed on the taller 'plants' (13cm high) than on the shorter ones (6.5cm high) (table 5). Reducing the width of the taller 'plants' in the second experiment did not reduce the ratio of the flies that landed. It is concluded that the height of the 'plants' rather than the width is important in influencing the numbers of flies that landed in each pot.

Table 5. Effects of the size of 'artificial plants' on the numbers of adult flies landing.

Size of 'artificial plants'		No of flies trapped per pot	
Area (cm^2)	Height(cm)	$\bar{X}$	$S_{\bar{X}}$
		1st experiment	
4.23	6.5	3.5	1.33
8.45	13.0	11.3	3.20
		2nd experiment	
4.23	6.5	2.5	0.87
4.23	13.0	10.8	3.45

3.2.1.(b) Effects of height of oat plants on the numbers of adult flies resting, performing oviposition movement and on the numbers of eggs laid.

Oat plants at the 3 - leaf stage with loose coleoptiles suitable for oviposition were trimmed as shown in fig.7a. There were 8 plants per 14cm-diameter pot. The 1st leaf blade was cut short to approximately 1cm in both pots and the 2nd and 3rd leaf blades were cut to give plant heights of 10cm and 20cm from the soil surface, respectively. These heights corresponded to those of plants at the 2-leaf to 3-leaf stage and 3-leaf to 4-leaf stage described in sub-section 3.1.2.(a). The leaves were cut about 16 hours before the experiment commenced to ensure that exudates produced from the wounds did not interfere with the experiment. The pots were then placed in a cage (45cm cube) containing 100 mating adults and left for 24 hours (9 a.m. to 9 a.m. the following day). Counts were made of the numbers of flies resting or performing oviposition movements in each pot at 3-hourly intervals until 9 p.m. and of the number of eggs laid per pot at the end of a 24-hour period. The experiment was replicated 4 times.

Only 2 flies (1 per pot) were observed to be performing oviposition movements throughout the 3-hourly observations. There was no significant difference ($P > 0.05$) in the numbers of flies resting or performing oviposition movements (table 6A) or in the numbers of eggs laid (table 7A) between the pots containing plants that were either 10cm or 20cm high.

In a second experiment, oat plants were trimmed as shown in fig.7b. Unlike in the previous experiment, a third pot containing oat plants cut to 5cm high, corresponding approximately to the plant growth stage 1-leaf to 2-leaf described in 3.1.2.(a) was included, also unlike in the previous experiment, the second leaf blade was further cut down to 1cm as was the 1st leaf blade. Otherwise, similar methods were employed as before.

Only 2, 3, and 4 flies were observed to be performing oviposition movement in pots containing plants that were 5, 10 and 20cm, respectively throughout the sixteen 3-hourly observations. Twice as many flies rested or performed oviposition movements on plants that were 10cm high than on those that were 5cm high (table 6B). Similarly, twice as many eggs were laid on the former than on the latter (table 7B). Over 98 per cent of the eggs were laid at oviposition site 3, that is, inside the colcoptiles in both cases. Like the previous experiment, there was no significant difference between the numbers resting or performing oviposition movements on plants that were 10cm or 20cm high (table 6). However, unlike it, twice as many eggs were laid on the latter than on the former (table 7). Again, virtually all the eggs were laid inside the coleoptiles.

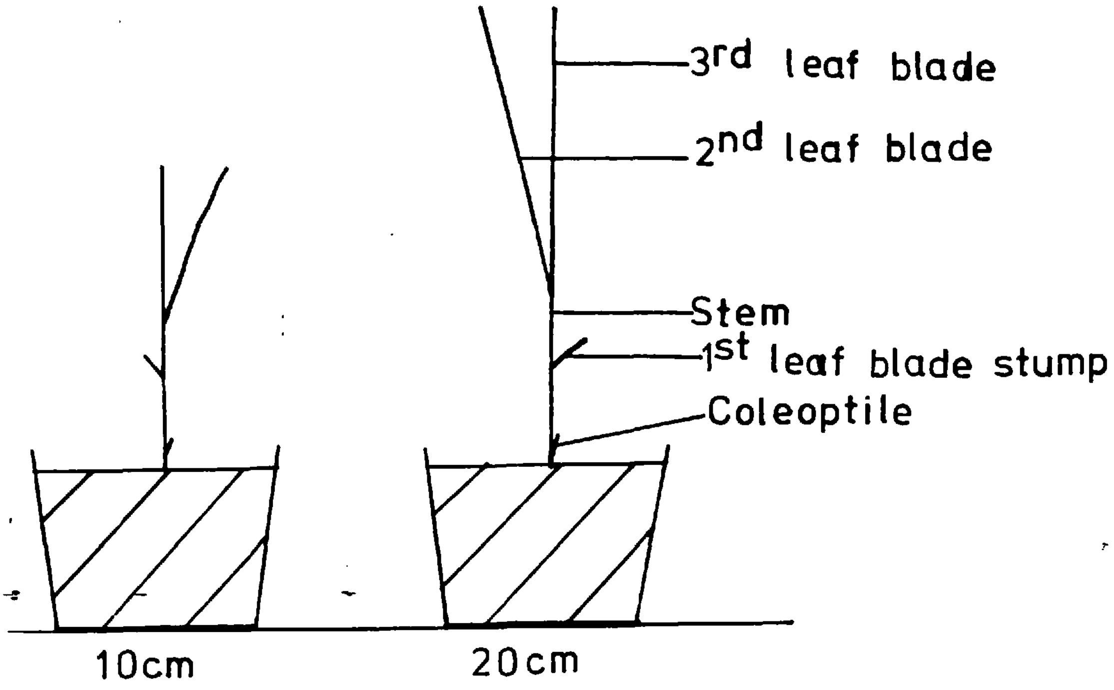

Fig.7a Diagram of oat plants at the 3-leaf stage cut to different heights.

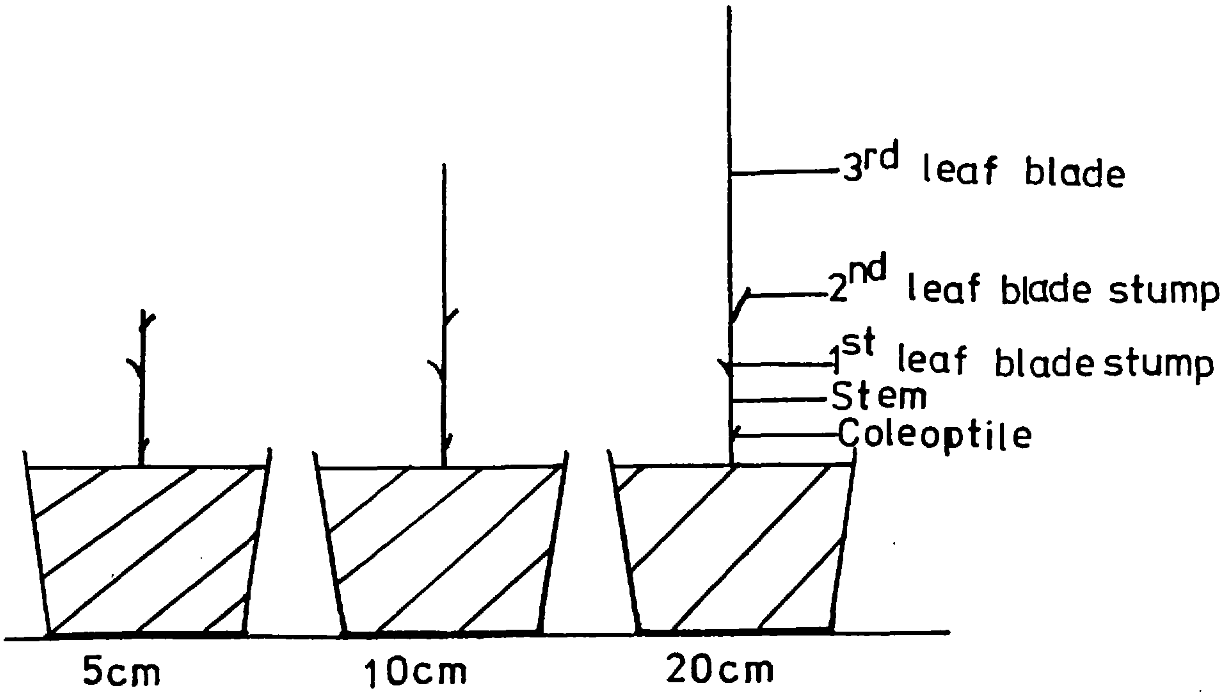

Fig.7b Diagram of oat plants at the 3-leaf stage cut to different heights.

Table 6 Effects of height of oat plants on the numbers of flies resting or performing oviposition movements.

	A		B	
	No. of flies/pot/observation		No. of flies/pot/observation	
Height of plants (cm)	$\bar{X}$	$S_{\bar{X}}$	$\bar{X}$	$S_{\bar{X}}$
5.0	—	—	1.3	0.25
10.0	5.0	0.93	2.4	0.31
20.0	7.5	1.48	2.8	0.31

Table 7 Effects of height of oat plants on the numbers of eggs laid

	A		B	
	No.of eggs/pot		No.of eggs/pot	
Height of plants (cm)	$\bar{X}$	$S_{\bar{X}}$	$\bar{X}$	$S_{\bar{X}}$
5.0	—	—	6.8	0.63
10.0	40.3	5.11	11.5	1.19
20.0	45.5	2.90	24.0	2.44

The oat plants in the second experiment (fig.7b) provided good height contrasts to each other because of the reduction in the length of the 2nd leaf blade to only 1cm. Perhaps in the first experiment the 2nd leaf blade masked to some extent the actual differences in the heights of the plants (fig.7a). The response of the flies to the different heights was therefore likely to be bigger in the second experiment than in the first. Idowu (1975) observed in the laboratory that the time spent on the plants by the flies increased with increasing plant height. Such a behaviour coupled with that of higher numbers of flies landing on taller plants will inevitably result in more eggs being laid on taller plants, provided there are suitable oviposition sites.

It is inferred from the results (tables 6 and 7) that the height of oat plants is important in influencing the numbers of adult flies that land, rest and oviposit on the plants up to a critical height, which probably lies between 10cm and 20cm. If this is so, it coincides with the plant growth stage when the coleoptile is most suitable for oviposition. Young plants (less than 5cm high) are not only visually less attractive, but they also offer fewer and less suitable oviposition sites. Older plants (more than 20cm high) are less suitable for larval penetration. Under natural conditions in the field the greater spreading of the leaves as the plants grow older may render height differences less important to colonizing adults, but the latter may be important before the critical height is reached.

3.2.2. Effects of oviposition site on the fate of the eggs

Reference was made in the literature review to the preference of the basal parts of oats for oviposition (Cunliffe and Hodges, 1946) and to the trophic association in the larval stage of *O. frit* with the embryonal and poorly differentiated tissues of a number of species of grain grasses (Shapiro, 1961; Shapiro and Vilkova, 1963). This experiment is an attempt to obtain information on the fate of eggs placed at different oviposition sites on oat plants.

Oats were seeded in thirty 8.75cm-diameter pots in the greenhouse and thinned to 5 plants per pot soon after germination. The plants were transferred to a room maintained at 20°C when at the early 2-leaf stage and each plant infested with newly-laid eggs at different oviposition sites - crevice between plant and soil or in the soil very close to the plant (site 1), outside the coleoptile (site 2), inside the coleoptile (site 3), on the plant between the tip of the coleoptile and the 1st leaf blade (site 4), inside the leaf sheath (site 5) and on the leaf blade (site 6). Oat plants at the 2-leaf stage were used in this experiment because younger plants did not have all the oviposition sites e.g. site 5, and larval penetration usually became less successful with increasing plant age (fig.4). Since the coleoptile was still tightly attached to the plant at the early 2-leaf stage, the shoot was artificially separated from the coleoptile to create a crevice between the stem and the coleoptile (oviposition site 3). All 5 plants in a pot were each infested with 1 egg at the particular oviposition site (treatment) and there were 5 pots, that is, 25 infested plants per treatment. The distance between the soil surface and the position of the eggs on the plants was measured at the time of infestation with eggs and 4 days later when egg hatch was complete. The numbers of plants showing symptoms of deadheart were recorded and all the plants dissected 10 days after infestation with eggs to ascertain the numbers of eggs that have resulted in larvae inside the plants.

Eggs placed at oviposition sites 1 to 3 did not move throughout the experiment, those placed at sites 4 and 5 had moved 1cm further from the soil surface while those placed on the leaf blade (site 6) had moved the farthest distance, 2.5cm further from the soil surface (table 8). Most eggs from site 1 resulted in larvae inside the plant, less from sites 2 and 3 and least from sites 4, 5 and 6 where the eggs were exposed (except probably those at site 5) and larvae had to travel fairly long distances to get to the growing point, which is situated just below the soil surface (table 8). There is no direct evidence in the literature as to the point of entry of the larvae into the plant, but Shapiro's (1961) findings that the primary position of the larva developing within the host plant is just above the growing point where it obtains nutriment by extracellular digestion and that susceptible varieties of maize had relatively thin stems with a small number of layers of leaves around the growing point suggests that the larvae probably penetrate the plant in the areas around the growing point which often have embryonal and poorly differentiated tissues, at least in the early stages plant growth. The growing point of cereals is just below the soil surface initially and most penetration from site 1 might have been as a result of this. Penetration from site 3 was relatively low in this experiment probably because some of the eggs placed at that site were damaged either when they were being placed there or by the growth of the plant, since the crevice had to be artificially created. The result of this experiment suggests that the oviposition habit of female flies in laying most eggs on sections of plant tissue which are protected and have either finished growing or are growing slowly is related to the survival of the other stages of the insect.

Table 8 Fate of eggs from different oviposition sites on oats

Oviposition sites	Distance of egg from the soil surface (cm) at infestation	at hatching	difference	% of eggs resulting in larvae inside plants
1	0.0	0.0	0.0	56.0
2	1.0	1.0	0.0	32.0
3	1.5	1.5	0.0	24.0
4	2.5	3.5	1.0	8.0
5	3.0	4.0	1.0	0.0
6	5.0	7.5	2.5	4.0

3.2.3. Carrying capacity of young oat plants infested with different numbers of eggs soon after germination.

The numbers of pupae that can survive from eggs when oat plants are infested with different numbers of eggs is complicated by tillering, which among other factors is also affected by frit fly attack. Thus, when the main shoot is killed tillers are produced and these act as new sources of food for the developing larvae; but attack on very young oat plants does not often result in the production of tillers, and larvae developing in such plants may have inadequate food to complete their development. The latter situation may occur in the field if sowing is delayed and the peak of overwintering generation adults coincides with the stage when oat plants are just emerging from the soil or are still too young to tiller. This experiment attempts to find out the numbers of pupae that can survive on young oat plants infested with different numbers of eggs.

Oats were seeded in twenty 8.75cm-diameter pots in the greenhouse, thinned to 5 plants per pot soon after germination and transferred to the laboratory at 20°C. The pots were divided into 4 sets of 5, and the plants in each set were infested with either 1, 2, 3 or 4 newly-laid eggs per plant at oviposition site 1, i.e., crevice between the plant and the soil. All the plants were dissected 25 days after infestation when pupation was complete. The top 1cm of the soil in the pots were also examined to ascertain whether any pupation took place in the soil or if any pupae dropped to the soil from the plants. The pupae were weighed and kept in glass vials until adults emerged in order to determine the sexes.

A significantly higher proportion of late larvae and pupae survived from eggs on plants infested with 1 egg/plant than on those infested with 2, 3 or 4 eggs per plant (table 9). Only 1 plant out of 25 contained 4 late larvae or pupae in the set infested with

4 eggs/plant, 2 out of 25 contained 3 late larvae or pupae in the set infested with 3 eggs/plant, 3 out of 25 contained 2 late larvae or pupae in the set infested with 2 eggs/plant, and as many as 21 out of 25 contained 1 late larva or pupa in the set infested with 1 egg/ plant. All the plants in the 4 eggs/plant set were killed. No pupae were found in the soil. Both male and female pupae were heaviest in the sets with 1 or 2 eggs/plant and lightest in the set with 4 eggs/ plant, with 3 eggs/plant having intermediate values (table 9). It is concluded from this experiment like Jones (1969) and unlike Jepson and Southwood (1958) that when more than one larva penetrates an oat shoot there is competition between them and many of them fail to survive to pupation, although the latter authors might have drawn their inference from results with plants of different ages.

Table 9 Effects of egg density on survival to pupation and pupal size

	Weight of pupae (mg)						Per cent of late larvae or pupae surviving from eggs
	Males			Females			
No of eggs/plant	N	$\bar{X}$	$S_{\bar{X}}$	N	$\bar{X}$	$S_{\bar{X}}$	
1	8	0.56	0.03	10	0.93	0.04	84.0
2	2	0.59	0.03	4	0.90	0.03	40.0
3	3	0.54	0.02	3	0.63	0.06	44.0
4	2	0.31	0.03	2	0.36	0.10	32.0

3.2.4. Effects of egg aggregation on larval penetration into 'old' oat plants without tillers.

It was shown in sub-section 3.1.2b that larval penetration into the main shoot usually becomes less successful with increasing plant age and observations in the field indicated that eggs occur in clumps on suitable plants (Section VI). Ghent (1960) observed that mortality of the Jack pine sawfly (Neodiprion pratti banksianae Roh.) was extremely high when larvae were reared singly on pine needles but survival increased in aggregated young larvae - apparently due to 'weaker' larvae in the aggregates making use of feeding cuts of other individuals. No such similar information is available with the frit-fly, even though it is not uncommon to observe frit fly eggs in clumps on suitable oat plants in the field, hence this experiment.

Oats were seeded in eight 8.75cm-diameter pots in the greenhouse and thinned to 5 plants per pot soon after germination. The pots were transferred to the laboratory at 20°C when the plants were at the 3-leaf stage with loose coleoptiles. The pots were divided into 4 sets of 2 pots and the pots in each set were infested with either 1, 2, 4 or 6 newly-laid eggs per plant inside the coleoptiles - the site preferred for oviposition at the 3-leaf stage. The plants used had no tillers at the time of infestation. The numbers of plants showing symptoms of deadheart were recorded, counts of the egg shells made and all the plants dissected 10 days after infestation with eggs to ascertain the numbers of eggs that have resulted in larvae inside the plants.

No eggs were missing and all of them were empty 10 days after infestation when stem dissection was carried out, indicating that all the eggs had hatched and that the larvae did not feed on the eggs. The proportions of larvae that entered the main shoots from the different egg aggregates were similar in all cases, except in the treatment with 2 eggs/plant (table 10). It can be inferred from this experiment that survival of larvae in terms of overcoming the plant resistance mechanism (hardness of tissue with ageing) is probably not enhanced by hatching from clumped eggs compared with hatching from eggs laid singly.

Table 10 Effects of egg aggregation on larval penetration

No of eggs per plant	Total no of plants infested with eggs	Total no of eggs	Total no of plants with deadhearts	Total no of larvae that entered plants	Per cent larval penetration
1	10	10	1	1	10.0
2	10	20	0	0	0.0
4	10	40	3	4	10.0
6	10	60	5	6	10.0

SECTION IV

EFFECTS OF OAT CROP BACKGROUND ON ATTRACTION OF O. FRIT ADULTS AND ON OVIPOSITION

4.1. FIELD EXPERIMENTS

4.1.1. Water trap catches

Many fewer adult flies of the overwintering generation were caught in water traps in the oat crop (table 11) than were adults of the tiller generation (table 12). The numbers of both generations caught over weedy and weed-free backgrounds were not significantly different from each other (tables 11 and 12).

Water traps give a relative estimate of a population, and their efficiency depends on many factors, e.g.: the activity of the insect which may in turn be dependent on climatic conditions. The low figures recorded for the overwintering generation in all the treatments (table 11) might be due to one or a combination of such factors, as well as to low absolute numbers of invaders in 1975. It is difficult to draw any firm conclusions on the possible effects of the background of the crop from such low figures.

Flies caught in the traps between 26.6.75. and 8.8.75. (table 12) were those of the tiller (second) generation. These could have arisen from within the crop or could have come from other cereal fields or grasslands, or from both sources; since the frit fly is a migratory insect at all seasons and so the individual composition of the population in an oatfield is continually changing (Southwood, 1964). The figures therefore provide only an indication of the relative abundance of the flies of that generation active over plots of the various treatments and do not necessarily reflect the numbers of flies of that generation colonizing the crop in response to the different backgrounds.

Table 11 Adult frit flies of the overwintering generation caught in water traps in weedy or weed-free background (8.5. to 26.6.75)

Type of background	No per trap
Oat plants with bare background	7.5
Oat plants plus natural weeds	5.3
Oat plants plus natural weeds and mustard	5.5
Oat plants plus natural weeds and clover	5.5
	$P > 0.05$

Table 12 Adult frit flies of the tiller generation caught in water traps in weedy and weed-free background (26.6. to 8.8.75)

Type of background	No per trap
Oat plants with bare background	134.5
Oat plants plus natural weeds	137.3
Oat plants plus natural weeds and mustard	131.3
Oat plants plus natural weeds and clover	94.3
	$P > 0.05$

4.1.2. Oviposition in primary shoots and tillers

More eggs were laid on oat plants with a background of natural weeds plus white mustard and on those with a background of natural weeds plus white clover on samples taken 35 days after sowing, when oat plants were at the 4-leaf stage, than on those with a bare background or a background of only natural weeds (table 13, fig.8). These differences were however not statistically significant at $P = 0.05$. Similar numbers of eggs were laid in all treatments at 42 days after sowing, but by the 57th day, statistically significantly more eggs were laid on oat plants with weed-free background than on

Table 13. Numbers of O.frit eggs laid on oat plants in weedy or weed-free background

Type of background	No of eggs laid per 30cm row of oats age of plants (days after sowing)				
	35	42	49	57	64
Oat plants with bare background	6.0a	4.3a	17.0a	12.0b	4.0a
Oat plants plus natural weeds	5.8a	7.0a	4.8a	2.0a	0.0a
Oat plants plus natural weeds and mustard	12.3a	8.3a	6.0a	1.8a	0.8a
Oat plants plus natural weeds and clover	17.0a	6.3a	10.5a	5.3a	0.0a

Figures not followed by the same letters in the same column are significantly different at P = 0.05

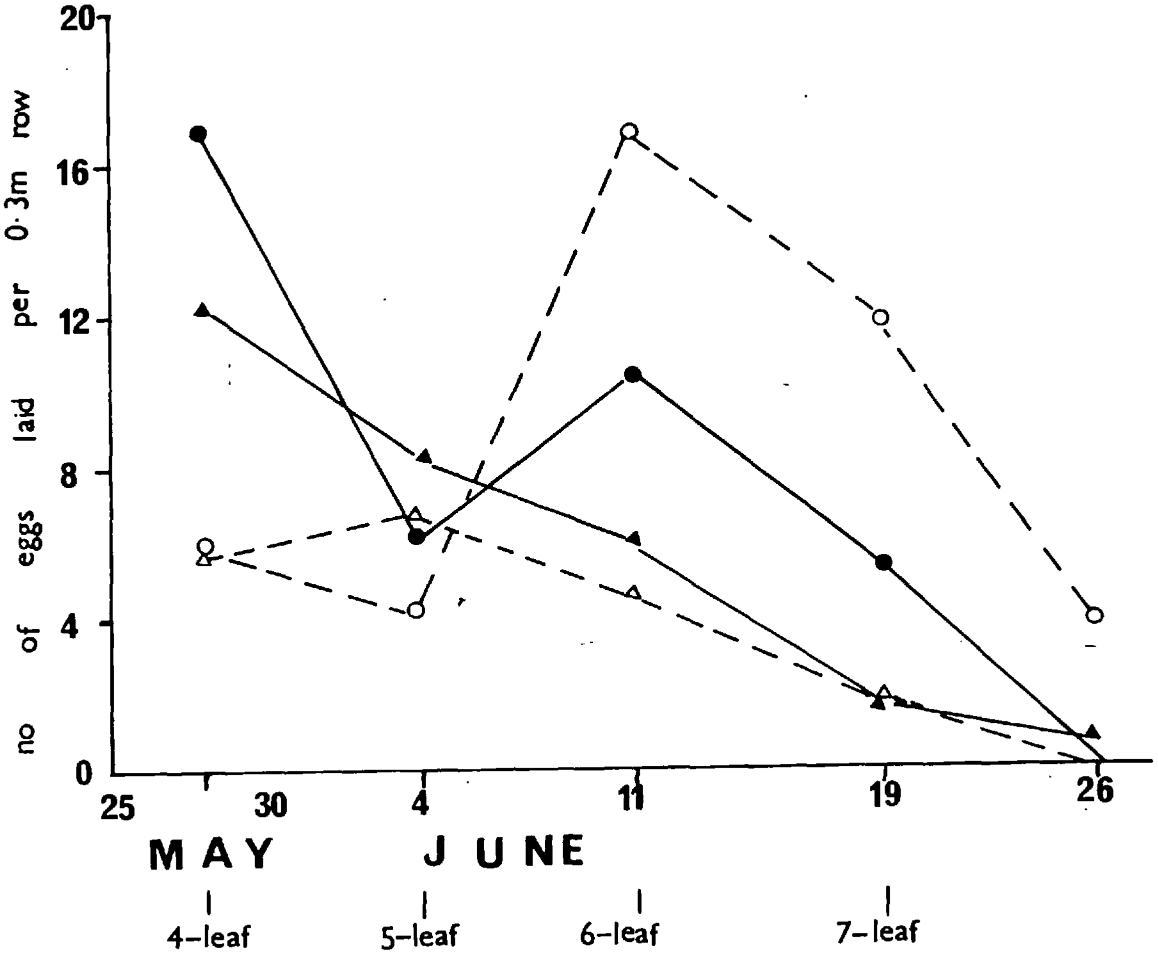

Fig.8 Numbers of O. frit eggs laid on oats with bare background or with a background of weeds, weeds plus mustard, or weeds plus clover.

○– – –○ Oats with bare background

△– – –△ Oats with a background of weeds

▲——▲ Oats with a background of weeds and mustard

●——● Oats with a background of weeds and white clover those with weedy background. Weedy background means one with only natural weeds or natural weeds plus mustard or natural weeds plus clover.

Plots in which clover or mustard seeds were sown broadcast gave a quick, initial soil cover due to early germination of those seeds, in contrast to the plots whose soil cover depended only on natural weeds. Thus, for the first few weeks the plots with a background of only natural weeds looked bare like those with a weed-free background and unlike those with either clover or mustard. This probably accounted for the observed differences in the numbers of eggs laid. Southwood (1962) stated that temporary habitats, for example annual plants are in the early stages in biological succession and are in one locality for a relatively short time. By inference, such temporary habitats would in the main, contain open stands of green plants silhouetted against brown or black soil; denizens of such habitats, e.g. _Brevicoryne brassicae_ are therefore often attracted more to such open stands. On the other hand, however, the frit fly is a denizen of grassland (permanent habitat) where plants occur in dense stands with very little or no bare soil exposed. _O. frit_ is therefore more likely to respond to cultivated annual crops in dense stands or at least to be neutral in its response to background or colour contrast.

Significantly more eggs were found on oat plants with weed-free background than on those with weedy background later in the season, probably because the dense canopy of weeds rendered the oat tillers less suitable for oviposition. The tillers at this stage were etiolated in the presence of weeds.

4.1.3. Comparative levels of damage to primary shoots and tillers

The number of deadhearts, i.e., killed shoots with visible symptoms is a cumulative measure of the total initial larval invasion, and where multiple infection is small, the peak number of deadhearts can be taken as representing slightly less than the initial number of invading larvae (Jepson and Southwood, 1958). No shoot dissections were carried out in 1975 to ascertain the extent of multiple infections, hence the figures presented in table 14 cannot be taken as representing the initial number of invading larvae. It however, represents the extent of damage in each treatment. Again, as was the case with eggs, more damage (but not significantly at $P < 0.05$) occurred in the treatments with natural weeds plus clover or mustard than in those with a bare background or a background of only natural weeds. The eggs laid later during the season on oat plants with bare background (table 13) had not resulted in visible damage symptoms on the tillers by the last sampling date because of the time interval which often occurs between oviposition, entry of larva into the plant and the actual sign of damage to the main shoot or tiller becoming visible. At any rate, larvae emerging from such 'late' eggs are unlikely to be of any consequence to the growth and development of the primary shoots which are by now immune to larval penetration; they may damage the tillers whose contribution to yield often become important only when the main shoot is either damaged or killed or at low oat plant densities (Wiggans and Frey, 1957).

4.1.4. Panicle growth of the plants

Counts of the panicles present in the different plots were made at the end of the season (28.8.75.) to ascertain whether the presence of weeds interfered with panicle growth.

Table 14. Number of primary shoots and tillers with 'deadhearts' per 30cm row of Oat plants in a weedy and weed-free background

Type of background	Nos of primary shoots and tillers with 'deadhearts'				
	age of plants (days after sowing)				
	35	42	49	57	64
Oat plants with bare background	0.0	1.8	3.8	14.8	22.3
Oat plants plus natural weeds	0.5	1.3	5.3	12.8	25.8
Oat plants plus natural weeds and mustard	0.3	2.0	5.8	20.5	33.0
Oat plants plus natural weeds and clover	0.0	1.3	9.3	20.8	26.5

$P > 0.05$

Significantly more panicles were found in the weed-free crop than in the weedy crop (table 15), and many of the panicles found in the latter were hidden under the 'overgrowth' formed by charlock and the cultivated mustard (sub-section 2.1.3.(a), plates 3 and 4). Clearly, as expected the weeds had interfered with the growth of the panicles.

Table 15 Numbers of panicles in weedy and weed-free oat crops

Type of background	No of Panicles per metre row
Oat plants with bare background	53.0b
Oat plants plus natural weeds	35.3a
Oat plants plus natural weeds and mustard	24.3a
Oat plants plus natural weeds and clover	31.0a

Figures not followed by the same letters are significantly different at P = 0.05.

4.1.5. Oviposition in panicles

More eggs per panicle and per spikelet were laid in the weed-free than in the weedy oat crop (table 16, fig.9). This was hardly surprising because most of the panicles in the weedy crop were obscured by the 'overgrowth' formed by the weeds and the insects probably had difficulty in detecting them.

Table 16 Oviposition in the panicles in weedy and weed-free oat crop

Type of background	No of eggs per	
	panicle	spikelet
Oat plants with bare background	69.9	1.41
Oat plants plus natural weeds	33.3	0.78
Oat plants plus natural weeds and mustard	32.5	0.72
Oat plants plus natural weeds and clover	42.6	0.85

$P > 0.05$

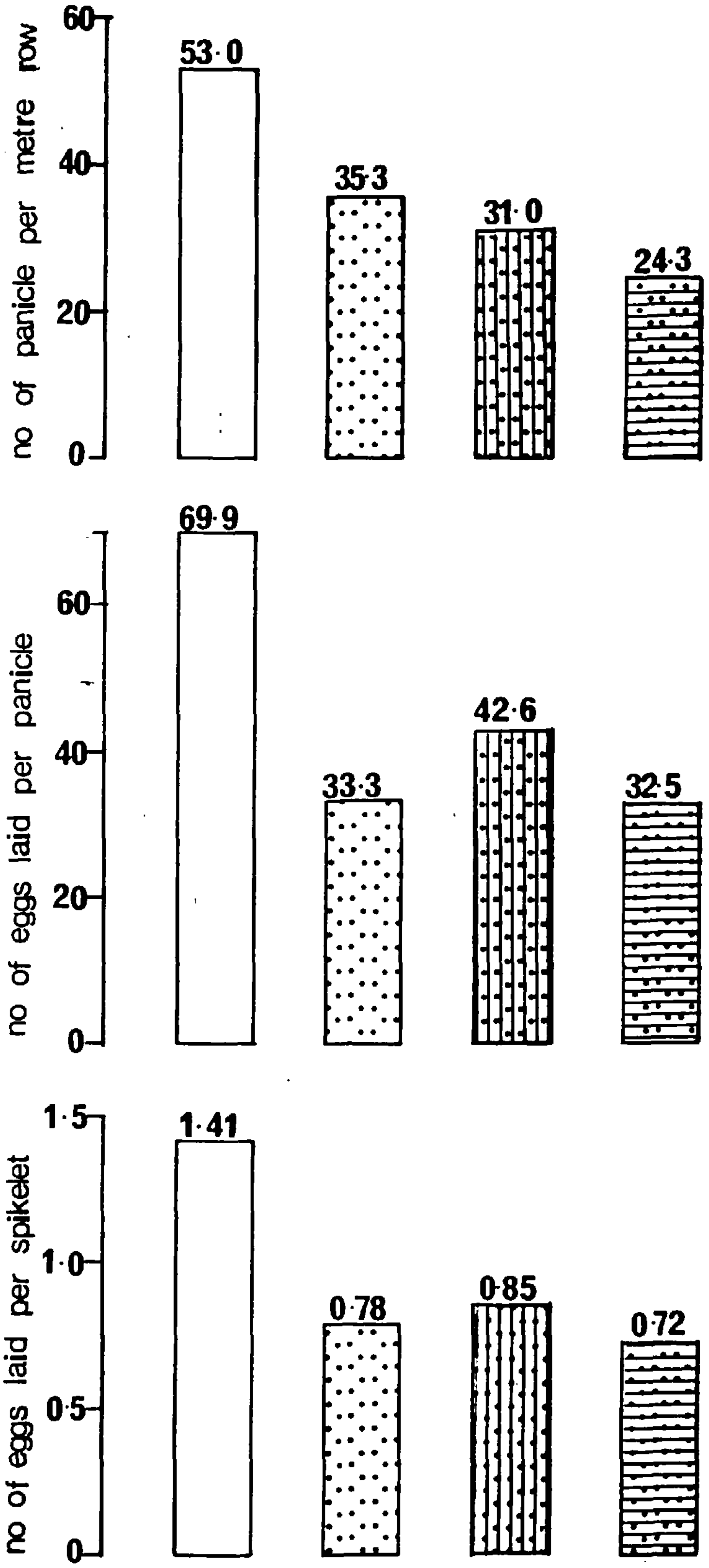

Fig. 9 Oviposition in panicles by adults of the tiller generation

□ Oats alone

░ Oats + natural weeds

▥ Oats + natural weeds + white clover broadcast at 22.5kg/ha

▤ Oats + natural weeds + white mustard broadcast at 13.5kg/ha

4.2. LABORATORY EXPERIMENTS

4.2.1. Attractiveness of 'artificial plants' in a weedy and weed-free background

Sticky 'artificial plants' (page 45) were inserted in four sets of two trays, one containing soil only and the other containing white clover seeded at 36gm/sq m (1250 seeds approx). Preliminary trials on clover density indicated that seeding densities lower than this did not give adequate soil cover soon after germination. The seed trays were placed in a cage containing 100 adult flies when the average height of the clover plants was 1.5cm giving a soil cover of approximately 70 per cent. The 'artificial plants' were 13cm high. After 24 hours, the trays were removed from the cage and the number of trapped flies counted.

More flies were trapped in the tray containing clover in 3 out of the 4 replicates, but the mean values were not significantly different at $P < 0.05$ (table 17).

Table 17 Effects of the type of background on the numbers of flies landing.

Type of background	Replicates I	II	III	IV	Mean no of trapped flies per tray	't' test at P = 0.05
'Plants' with bare soil	5	3	27	6	10.3	ns
'Plants' with undercover of clover	8	6	21	16	12.8	

4.2.2. Effects of the density of plant undercover on oviposition

Oats were seeded in 12 seed trays and the plants thinned to 24 per tray soon after germination. Two of the trays had only oats while 2 each of the remaining had oats plus white clover seeded at

4.5, 18.0, 22.5, 36.0 and 40.5gm/sq m, corresponding to 156, 625, 780, 1250 and 1405 seeds/sq m, respectively. The trays were removed from the greenhouse to the laboratory when oat plants were at the late 2-leaf stage and the clover plants at the 3-leaf stage. The average height of the clover plants was then 2.2cm, that of the oat plant coleoptile 1.9cm and of the oat plant to the tip of the longest leaf 21cm. Thus, the coleoptiles of the oat plants were partly under the clover plants, and this was most apparent at the highest clover density. Clover seeded at 4.5, 18.0, 22.5, 36.0 and 40.5gm/sq m gave soil cover of approximately 15, 60, 70, 80 and 90 per cent, respectively. The trays were placed at random in a cage (82.5 X 82.5 X 67.5cm high) containing a group of ovipositing adult flies for 72 hours, at the end of which egg counts were made.

Most eggs were laid in the tray seeded with clover at the rate of 4.5gm/sq m, followed by 18.0, 36.0 and 22.5gm/sq m; then, that containing no clover at all, i.e., oat plants with bare soil. It was least in the tray seeded at 40.5gm/sq m (table 18).

Despite the lack of significant ($P > 0.05$) differences it can be tentatively inferred from the results of this experiment (table 18) that the presence of clover among oat plants may have a 2-fold effect on oviposition. Firstly, their presence makes the crop visually more attractive to the flies compared with the crop with bare background, and increasing their (clover) density probably increases this visual attractiveness because of the corresponding increase in soil cover. However, above a certain density, the presence of clover may be acting counter to oviposition.

Table 18 Effects of the density of plant undercover of clover on oviposition.

	No of eggs laid		
	Seed tray		
Density of undercover	I	II	Total
Oat plants with bare soil	4	6	10
Oat plants plus clover at 4.5gm/sq m	11	23	34
" " " " " 18.0 "	13	10	23
" " " " " 22.5 "	10	3	13
" " " " " 36.0 "	16	1	17
" " " " " 40.5 "	6	0	6

$P > 0.05$

The preferred oviposition site on an oat plant with loose coleoptile is inside the coleoptile and only rarely are eggs laid on the leaves at this growth stage (table 1, fig. 2). It is also known that the female fly undergoes certain oviposition procedures, such as moving up and down the host plant before actually ovipositing (Sanders, 1960). Le Berre (1959) observed that most searching for oviposition sites was concentrated on the bottom 5cm of the host plant. Weeds, other non-host plants or clover in this experiment, which contact the oat plant, particularly the basal parts are therefore likely to interfere with the oviposition behaviour and egg deposition. This interference is likely to be most intense at very high clover density and increasing clover height. In this experiment, the clover height and coleoptile height were not very different, but oviposition was seemingly sufficiently interfered with at the high clover density of 40·5gm/sq metre. Experiments described below were attempts to test the hypothesis that the presence of other non-host plants, namely, clover in sufficient density and height constitutes a physical barrier to ovipositing females and therefore causes a reduction in the number of eggs laid.

4.2.3. Effects of the density and height of plant undercover on oviposition

Oats in trays were thinned as in the previous experiment. There were four sets of four trays, one set containing oats with bare soil and the others containing oats plus white clover seeded at 4.5, 9.0 and 18.0 gm/sq m, respectively. Four trays, one from each set were placed at random in a cage containing a group of ovipositing adult flies for 48 hours, at the end of which egg counts were made. The experiment was replicated four times. The average height of clover, oat plant coleoptile and oat plant were 4.5cm, 1.8cm and 29cm, respectively at the time the plants were offered for oviposition. The coleoptiles of the plants were at least 2cm below the top stratum of the clover, and the latter formed a fairly dense cover around, and in most cases were actually making contact with the basal parts of the former. The number of leaves on clover ranged from 6 to 8 and the soil cover was approximately 25, 50 and 90 per cent for trays previously seeded with clover at 4.5, 9.0 and 18.0gm/sq m, respectively.

There was a linear decrease, $r = -0.99$, in the numbers of eggs laid on oat plants as the seeding density of white clover increased at the clover height of 4.5cm maintained in this experiment (fig.10). Significantly ($P < 0.05$) fewer eggs were laid in the tray containing clover at 18.0gm/sq m than on those with clover at 9.0gm/sq m or 4.5gm/sq m or those without clover at all, i.e., bare soil (table 19).

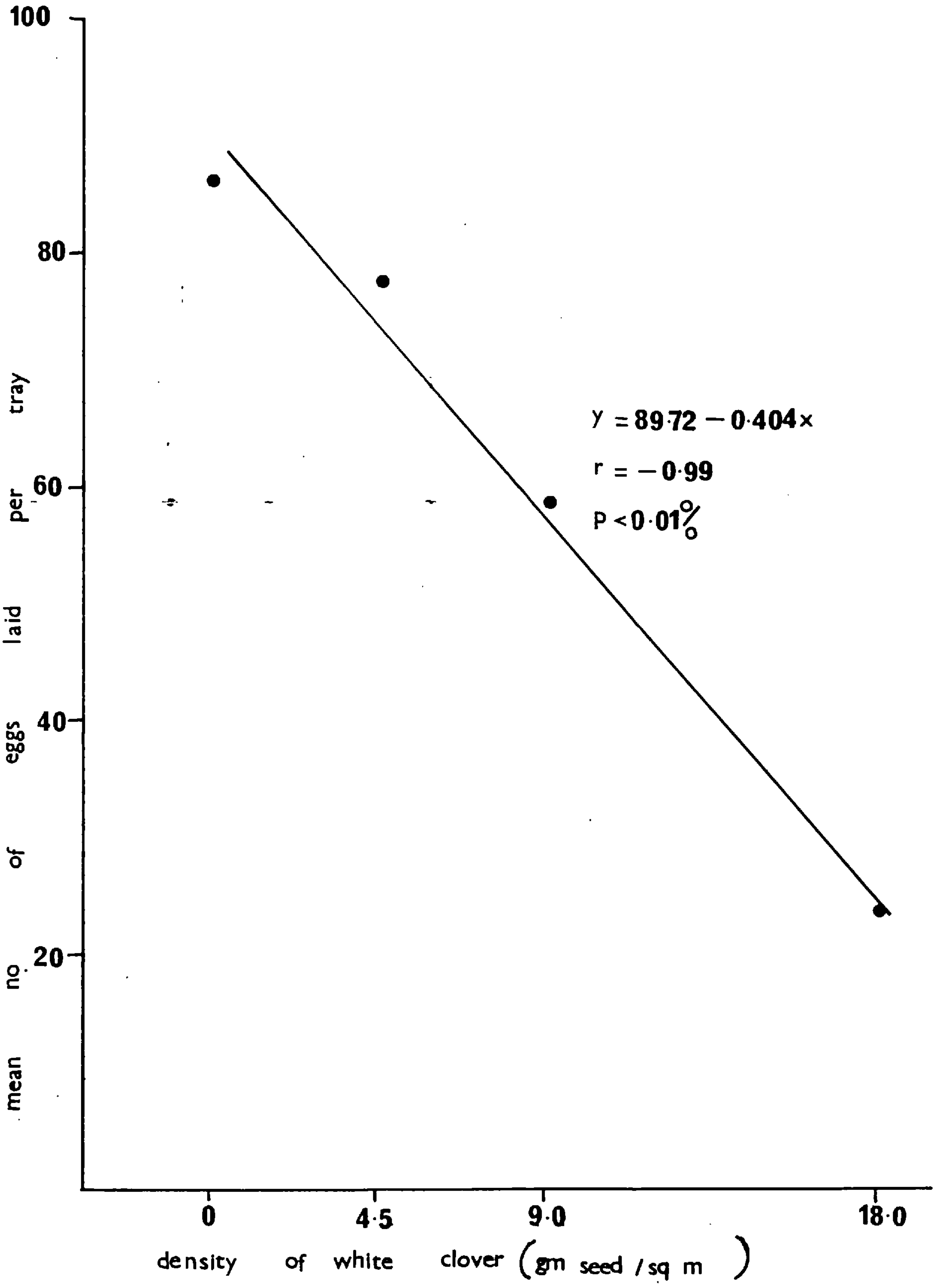

Fig.10 The relationship between the density of white clover acting as an undercover among oat plants and the number of eggs laid on oats.

Table 19 Effects of the density and height of plant undercover on oviposition.

Density of clover	Mean no of eggs laid per tray
Oat plants with bare soil	86.0b
Oat plants plus clover at 4.5gm/sq m	77.8b
" " " " " 9.0 "	58.5b
" " " " "18.0 "	23.5a

Figures not followed by the same letters are significantly different at P = 0.05

4.2.4. Effects of height of plant undercover on oviposition

This was investigated in 3 stages (series). A seeding density of 18gm/sq m was chosen for the following 3 series because this clover density gave almost complete blanket undercover in the seed trays when oat plants were at the early 3-leaf stage with loose coleoptiles— the stage the plants were offered for oviposition.

Series 1: Oats and oats plus clover were seeded in trays as in previous experiments. The clover plants were cut back from 4.5cm to 0.5cm when the oat plants were at the early 3-leaf stage and with loose coleoptiles. The cutting was done to ensure that the basal parts of the oat plants were exposed, even in the presence of clover plants, which in this case were giving a soil cover of approximately 90 per cent. Two trays, one with cut clover and the other without, i.e., bare soil, were placed in a cage and oviposition allowed to take place as before. The experiment was replicated four times.

Series 2: The plants were seeded as in series 1 above, but the clover plants were not cut back. So, the average height of clover plants remained at 4.5cm with a soil cover of approximately 90 per cent at the time the plants were offered for oviposition. Also, as in series 1, there were 4 replicates.

Series 3: Here, rather than using 2 separate seed trays as before, only one tray containing both oat and clover plants was employed. Clover plants were removed from the immediate vicinity of some of the oat plants (0.5cm on either side of the oat plants) to expose the basal parts of the plants, while leaving the others unexposed (fig.11). Like in the two previous series, the tray was offered for oviposition and the trial replicated four times.

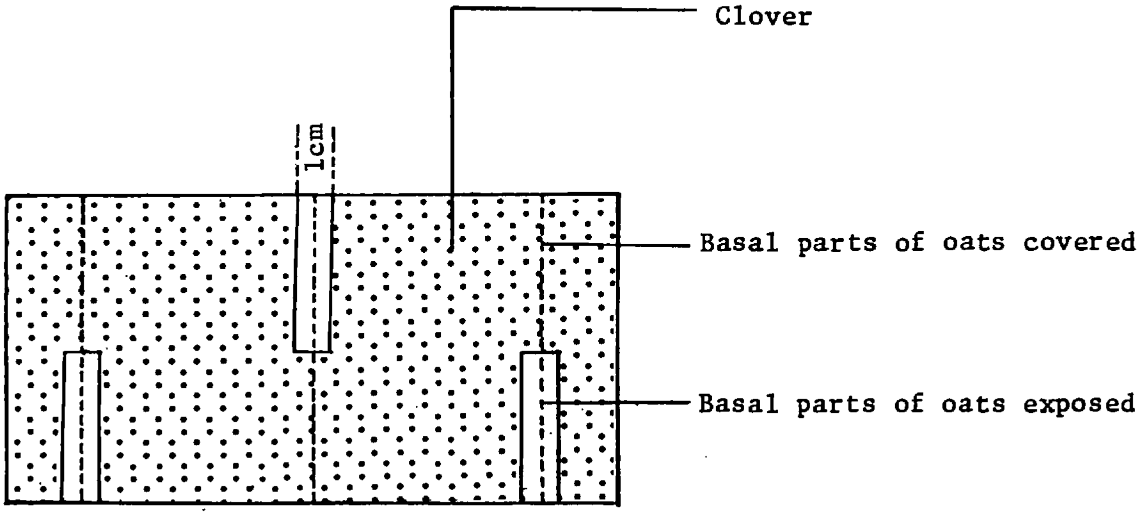

Fig.11. Seed tray containing oat plants with exposed and covered basal parts.

Table 20 Effects of height of plant undercover on oviposition

Series 1

Treatment	Mean no. of eggs/tray	't' test at P=0.05
Oat plants with bare soil	36.0	ns
Oat plants plus cut undercover of clover (0.5cm high)	42.0	

Series 2

Treatment	Mean no. of eggs/tray	't' test at P=0.05
Oat plants with bare soil	44.0	*
Oat plants plus uncut undercover of clover (4.5cm high)	11.0	

Series 3

Treatment	Mean no. of eggs laid	't' test at P=0.01
Oat plants with exposed basal parts	14.3	**
Oat plants with covered basal parts	1.7	

More eggs were laid on oats in the tray with cut clover than on those with bare background in Series 1, but this difference was not statistically significant at $P < 0.05$ (table 20). In Series 2 however, significantly ($P < 0.05$) more eggs were laid on oat plants with bare background than on those with a background of uncut clover (table 20)— the reverse of what was obtained in Series 1. In

Series 3, significantly ($P < 0.01$) more eggs were laid on oat plants with exposed basal parts than on those whose basal parts were covered by clover. Careful observations made on the state of the coleoptiles in the presence or absence of clover plants did not indicate that the presence of clover plants had interfered with the coleoptiles in any way - the coleoptile is the preferred oviposition site at the growth stage used in the three series of experiments. It can be concluded that the clover plants probably present a purely physical barrier to oviposition, as Dempster and Coaker (1974) observed with the cabbage root fly, and that the height of clover plants in relation to those of oat plants plays an important part in the process.

4.2.5. Strip-cropping compared with blanket cover of clover

It has been shown above (sub-section 4.2.4.) that the presence of clover among oat plants at a seeding density of 18.0gm/sq metre and a height of 4.5cm reduced oviposition on oats. This seeding density is very high - about 8 times the recommended rate - and would certainly not be a practicable proposition for reducing field infestation of the fly. It has been shown that complete soil cover with clover can in some circumstances enhance invasion by adult flies rather than suppress it (table 17). The oviposition habit of the fly is rather specific - the basal parts of the host plant being the most preferred for oviposition. This experiment was therefore designed to investigate the possibility of reducing the population of clover in an oat crop without necessarily removing its 'beneficial' effect in reducing oviposition.

Plate 9a. Oat plants with bare soil

Plate 9b. Oat plants strip-sown with clover

Plate 9c. Oat plants with blanket cover of clover

Plate 9a

Plate 9b

Plate 9c

Oats and oats plus white clover at 18.0gm/sq metre were seeded in trays as in previous experiments in 12 seed trays. In one set of 4 trays with clover, the area in the tray was divided into eight equal strips and clover plants removed before the experiment started from six strips, leaving only two strips within the rows of oats (Plate 9b). In this way, the basal parts of oat plants were still covered, although clover plants were now present in only one-quarter of the tray. The actual density of clover plants per unit area of occupied soil in this set (Plate 9b) and another set of 4 trays in which the clover plants were left intact (Plate 9c) remained essentially the same. The last set of 4 trays contained only oat plants, i.e. bare soil (Plate 9a). One tray from each set were placed simultaneously in a cage containing a group of ovipositing adults for 48 hours, when oat plants were at the early 3-leaf stage and the soil cover by clover in plate 9c was approximately 90 per cent. The experiment was replicated 4 times allocating the position occupied in the cage at random to the trays at beginning of each replicate. Egg counts were made at the end of each replicate.

Significantly more eggs were laid on oat plants with bare soil than on those strip-sown or had a blanket cover of clover (table 21). There was however, no significant difference between those laid on the strip-sown plants and those with a blanket cover of clover. Statistically significantly ($P < 0.05$) higher proportions of the eggs laid on oat plants strip-sown with clover (10.5 per cent) and blanket cover (21.6 per cent) were found on the leaves (oviposition sites 5 and 6 in table 1) compared with only 2.7 per cent found on the leaves of oat plants with bare soil (table 22).

It is concluded from results in table 21 that it is not necessary to cover the entire soil surface with clover to achieve a reduction in frit oviposition on oats. What is important is the presence of clover at appropriate density and height in the immediate vicinity of oat plants. The results in table 22 further strengthens the conclusion drawn from earlier experiments that the reduction in oviposition in the presence of clover was due to clover plants creating a physical barrier, which either rendered the basal parts of oat plants (most preferred for oviposition) inaccessible, or interfered with oviposition behaviour. In this case, the physical barrier at the basal parts of oat plants probably resulted in a higher proportion of the eggs being laid on the leaves (usually less preferred for oviposition) than would otherwise have been laid.

Table 21. Effects of the distribution of plant undercover on oviposition

Type of background	Mean no of eggs per tray
Oat plants with bare soil	199.7b
Oat plants strip-sown with clover	84.3a
Oat plants with blanket cover of clover	62.0a

Figures not followed by the same letters are significantly different at $P = 0.05$

Table 22 Effects of plant undercover on the site selected for oviposition on oat plants

Type of background	Percentage of eggs laid on the leaves of oat plants
Oat plants with bare soil	2.7a
Oat plants strip-sown with clover	10.5b
Oat plants with blanket cover of clover	21.6b

Figures not followed by the same letters are significantly different at P = 0.05

SECTION V

EFFECTS OF THE DENSITY OF OAT PLANTS ON COLONIZATION AND ON DEVELOPMENT OF *O. FRIT* IN THE OAT CROP

5.1. FIELD EXPERIMENTS

5.1.1. Water trap catches

In 1976, many more adults of the overwintering generation (May - early June) were caught in the water traps than in 1975 (fig.12). The immature stages of the tiller generation in the oat cropdeveloped much faster and adults emerged much earlier in 1976 than in 1975. This was evident from the sharp increase in the numbers of adults caught in water traps between June 17 and 24 in 1976, compared with July 1 to 8 in 1975 (fig.12).

There were no significant differences ($P > 0.05$) between the trap catches in plots sown at the three oat densities and row spacings tested in 1975, for both the overwintering generation adults at the beginning of the season (table 23) and the total numbers caught for the season (table 24).

In 1976 slightly different plant densities and row spacings were tested (Appendix I). Consistently more adults were caught in the dense plantings than in the sparse and disperse plantings (fig.13). Treatments which had most plants per unit area of oats probably attracted more adult flies of the overwintering generation as indicated by significantly more flies caught in water traps placed in these treatments than in those placed in treatments with fewer plants (fig.14(i) and table 25). Significantly more overwintering generation adults were caught in traps placed in the dense planting with closely-spaced rows (rows spaced 5cm apart, plate 5a) than in those of equivalent density per unit area of oats with intermediate row spacing (rows spaced 15cm apart, plate 5b) (fig.14(i) and table 25). The total numbers of flies caught throughout the sampling period showed similar trends in all the treatments as those of the trapped overwintering generation adults (fig.14(ii) and table 26).

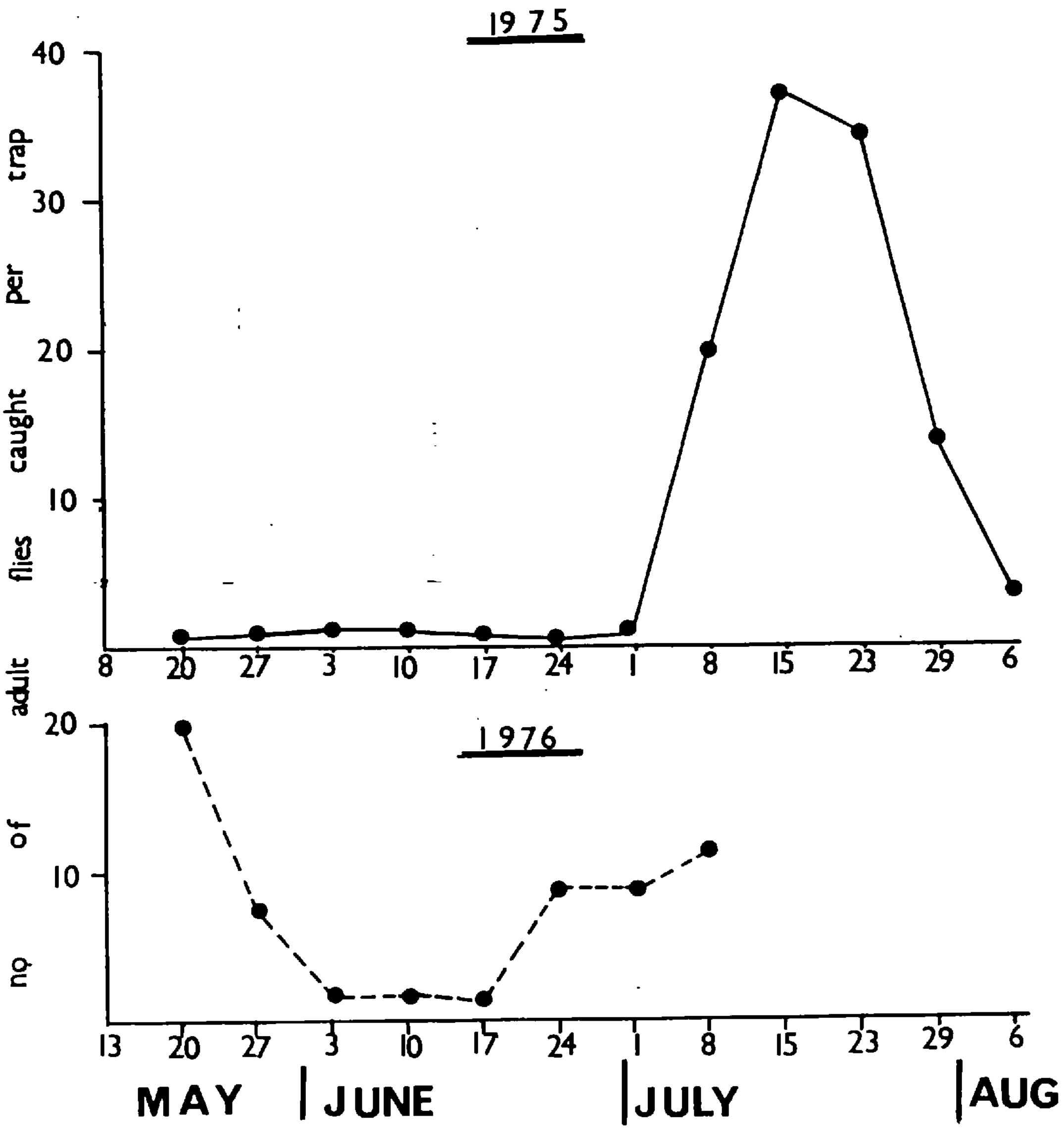

Fig.12 Weekly catches of adult frit flies in water traps in 1975 and 1976.

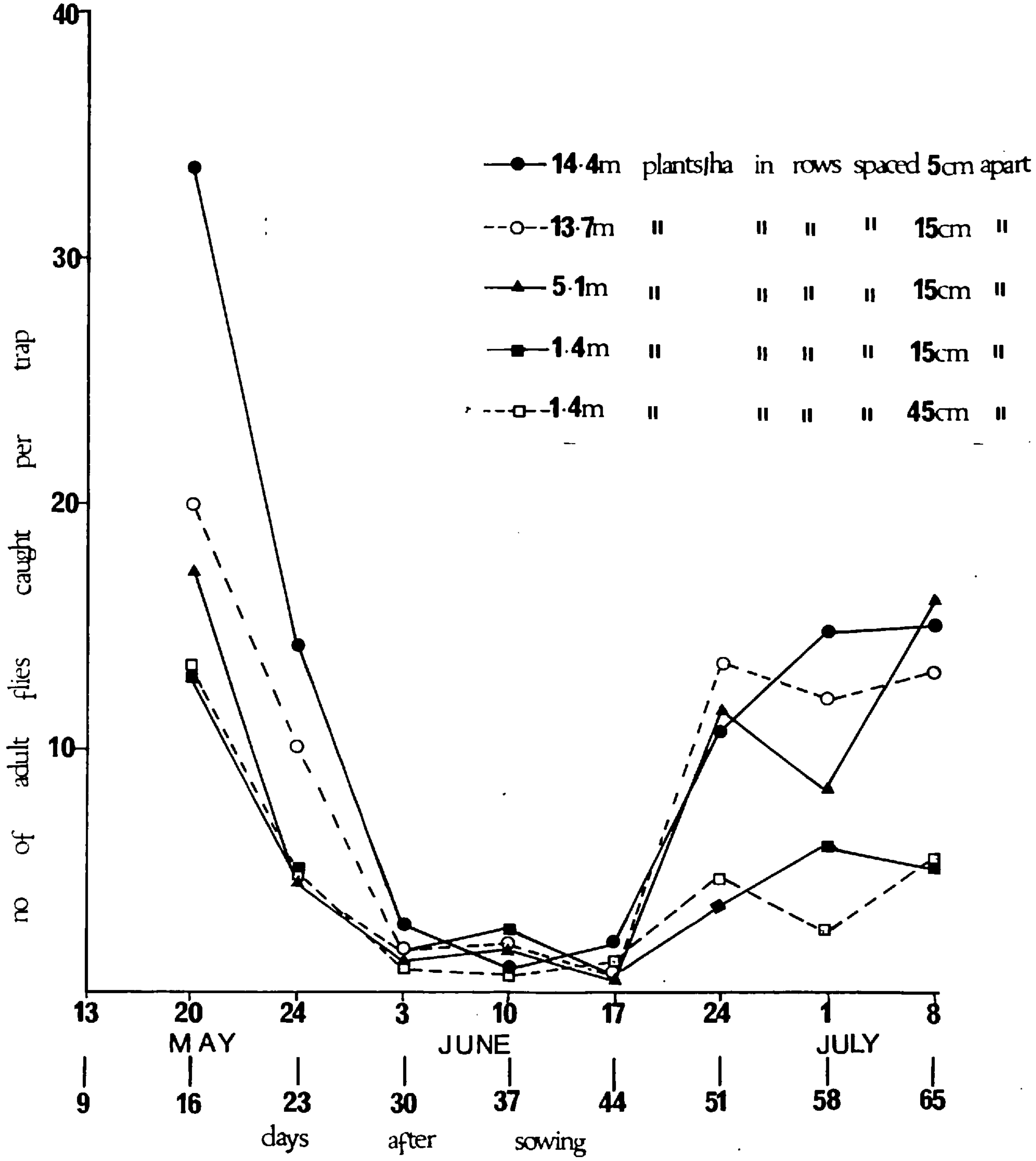

Fig.13 Weekly catches of adult frit flies in water traps over oat crops of different densities and row spacings (13.5. - 8.7.76.).

Table 23 Adult frit flies of the overwintering generation caught in water traps (8.5. to 1.7.75)

Oat densities and row spacings	No. per trap
8.6m plants/ha in rows spaced 7.5cm apart	5.3
4.3m " " " " 15cm "	8.0
1.4m " " " " 45cm "	5.0
	$P > 0.05$

Table 24. Adult frit flies caught in water traps throughout the whole season (8.5. to 6.8.75)

Oat densities and row spacings	No. per trap
8.6m plants/ha in rows spaced 7.5cm apart	104.8
4.3m " " " " 15cm "	131.5
1.4m " " " " 45cm "	113.5
	$P > 0.05$

Table 25 Adult flies of the overwintering generation caught in water traps (13.5. to 10.6.76.)

Oat densities and row spacings	No. per trap
14.4m plants/ha in rows spaced 5cm apart	51.8c
13.7m " " " " 15cm "	35.8b
5.1m " " " " 15cm "	24.8ab
1.4m " " " " 15cm "	21.5a
1.4m " " " " 45cm "	19.8a

Figures not followed by the same letters are significantly different at $P = 0.05$

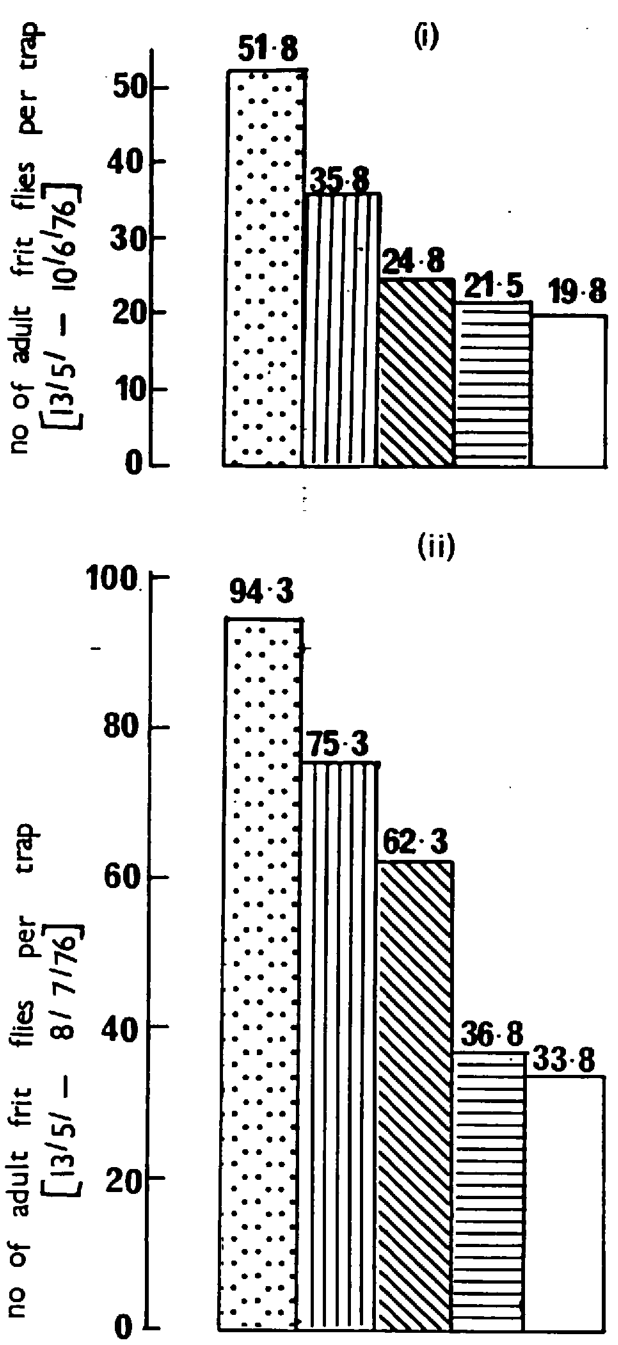

Fig.14 (i) Adult frit flies of the overwintering generation invading the oat crop.

(ii) Total numbers of adult frit flies (adults of the overwintering generation and tiller generation) caught in water traps.

KEY

⁙ 14.4m plants/ha in rows spaced 5cm apart

▥ 13.7m " " " " 15cm "

▨ 5.1m " " " " " "

▤ 1.4m " " " " " "

☐ 1.4m " " " " 45cm "

Table 26 Adult flies caught in water traps throughout the sampling period (13.5. to 8.7.76)

Oat densities and row spacings	No. per trap
14.4m plants/ha. in rows spaced 5cm apart	94.3c
13.7m " " " " 15cm "	75.3bc
5.1m " " " " 15cm "	62.3b
1.4m " " " " 15cm "	36.8a
1.4m " " " " 45cm "	33.8a

Figures not followed by the same letters are significantly different at P = 0.05

The results of the trap catches show that both the density of the oat plants and the arrangement of the plants in space have significant influence on the numbers of adult flies that are seemingly attracted to the crop. It has already been suggested in sub-section 4.1.2. that, because the natural habitat of the frit fly is wild grasses, which often occur in dense stands with solid green appearance, they are therefore likely to be attracted to oat crop in dense stands with minimum spacing between the rows than to those with intermediate or wide spacing where a considerable amount of bare soil is exposed.

The first general emergence of flies usually occurs between 7 - 13 May (Jepson and Southwood, 1958) or 7 - 16 May (Rigert, 1935), after 1 or 2 days warm weather with mean temperatures of 14.4° - 15.6°C. The peak of the overwintering generation is attained about 2 weeks after the first general emergence, 20 - 31 May, but this period is often characterised by wide fluctuations in temperature, so that an upward population trend may be masked by decreased activity on cold days (Jepson and Southwood, 1958).

That the peak of the active overwintering generation adults occurred before 20 May in 1976 (fig.12) can be attributed to the drier, warmer spring, compared with 1975, when wet and fluctuating, mostly lower temperatures kept the population available to be trapped at a lower level without a well-defined peak (fig.12, table 27).

Table 27 Temperature and Rainfall data in May 1975 and 1976

	Temperature				Rainfall			
	1975		1976		1975		1976	
Period of the month	mean max.	mean daily	mean max.	mean daily	total (ml)	duration (hr)	total (ml)	duration (hr)
1-5 May	14.1	9.6	15.7	10.6	4.5	4.0	1.4	1.6
6-10 "	15.3	11.1	23.7	16.3	7.2	4.3	0	0
11-15 "	13.7	9.6	15.9	10.3	8.3	11.3	0.6	1.5
16-20 "	14.5	9.3	16.8	11.5	39.3	33.9	5.2	7.8
21-25 "	13.8	8.8	19.3	13.3	1.5	1.1	0.7	0.5
26-30 "	15.8	11.4	17.8	12.5	0	0	0	0

5.1.2. Oviposition in primary shoots and tillers

In 1975, the plant samples examined for eggs were taken weekly, but samples taken in 1976 were according to the developmental time of eggs at the prevailing field temperature. The average number of eggs found during each of these periods was calculated and then summed. The data collected in 1976 were also analyzed graphically, where the mean egg population per 30cm row on each sampling date was plotted against time with one square equivalent to one egg and one day. All the points were joined up and the total area, in squares, below the line counted. This was divided by the development time in days at the mean temperature prevailing over the period, which is the number of days a given egg is present in the field. The resultant value represents the total egg population per 30cm row.

In 1975, most eggs were laid per plant by the overwintering generation adults in the most dispersed planting (rows spaced 45cm apart), followed by the less sparse planting (rows spaced 15cm apart), with least laid in the dense planting (rows spaced 7.5cm apart) (top part of fig.15). However, most eggs per unit area of oat crop were laid in the dense planting and least in the most disperse planting in the early part of the season with the reverse trend later in the season, when the main shoot no longer provided suitable oviposition sites and most eggs were laid on the tillers (bottom part of fig.15). In other words, the most disperse planting which produced most tillers received most eggs later in the season. This is in general agreement with Wiggans and Frey's (1957) finding that the main factor responsible for tillering in oats was the spacing of the plants - the most widely spaced plants producing most tillers.

Similar trends were also observed in 1976, where most eggs per plant were laid in the most dispersed plantings and least per plant in the dense plantings (table 28) and the reverse in the early season per unit area of oat crop (table 29). Also, in conformity with the water trap catches (table 25), significantly more eggs were laid per unit area of oat crop in the dense planting with closely-spaced rows (rows spaced 5cm apart) than in those of equivalent density with intermediate row spacing (rows spaced 15cm apart) (table 29, fig.16). However, unlike the water trap catches (table 25), more eggs per plant and per unit area of oat

Table 28 Total numbers of eggs laid per plant by overwintering generation adults on oat plants of different densities and row spacings in 1976

Oat densities and row spacings	Summation of means method No. per plant
13.7m plants/ha in rows spaced 15cm apart	0.44a
14.4m " " " " 5cm "	0.76ab
5.1m " " " " 15cm "	1.62bc
1.4m " " " " 45cm "	2.21c
1.4m " " " " 15cm "	3.81d

Figures not followed by the same letters are significantly different at P = 0.05

Table 29 Estimates of the total egg population per 1sq metre area of oats of different densities and row spacings in 1976

	No. per sq. metre	
Oat densities and row spacings	Summation of means method	Graphical method
1.4m plants/ha in rows spaced 45cm apart	307a	262
1.4m " " " " 15cm "	546ab	528
13.7m " " " " 15cm "	610ab	506
5.1m " " " " 15cm "	830bc	679
14.4m " " " " 5cm "	1097c	908

Figures not followed by the same letters are significantly different at P = 0.05

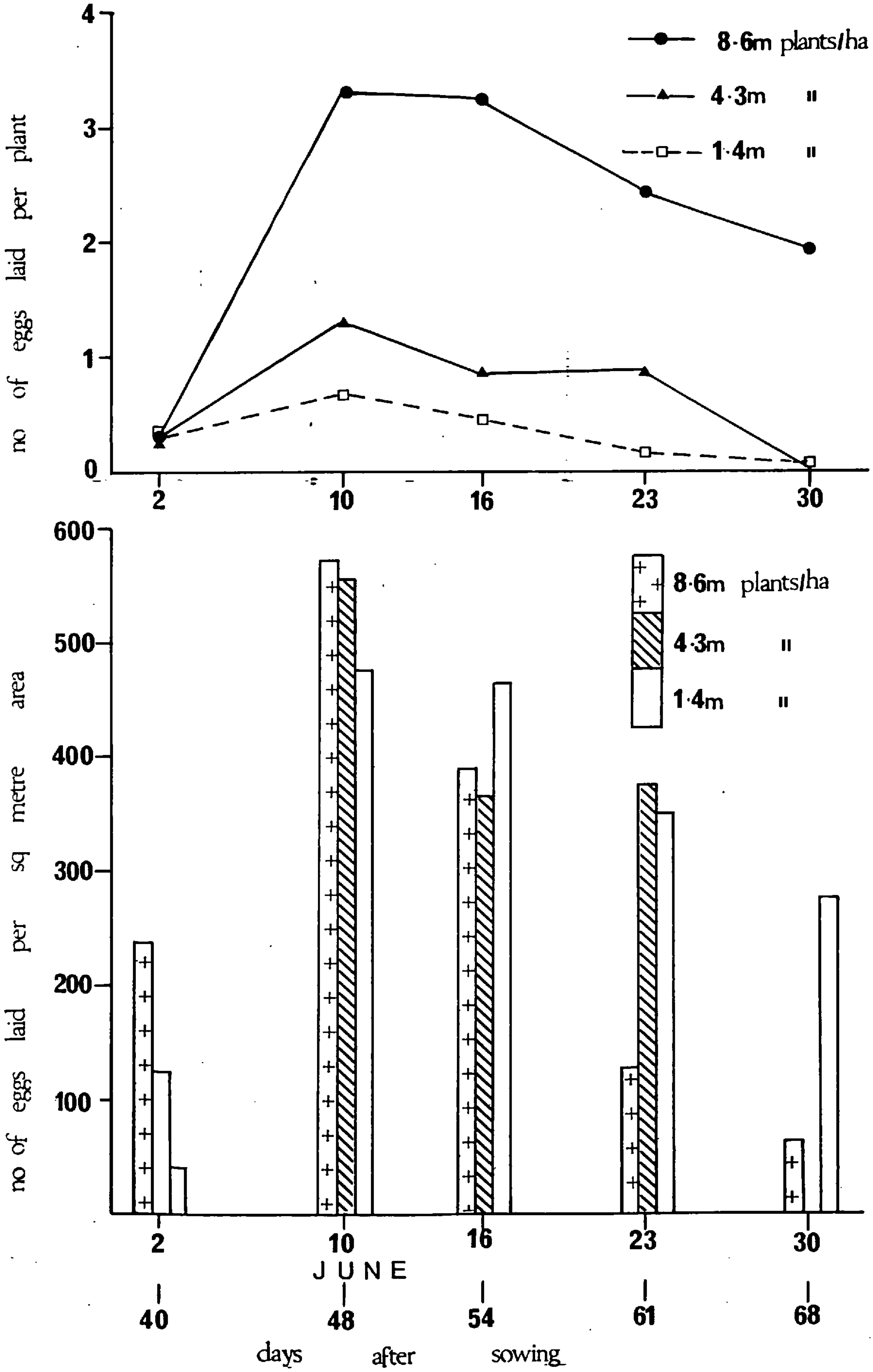

Fig.15 Numbers of eggs laid per plant and per square metre area of oats of different densities in 1975.

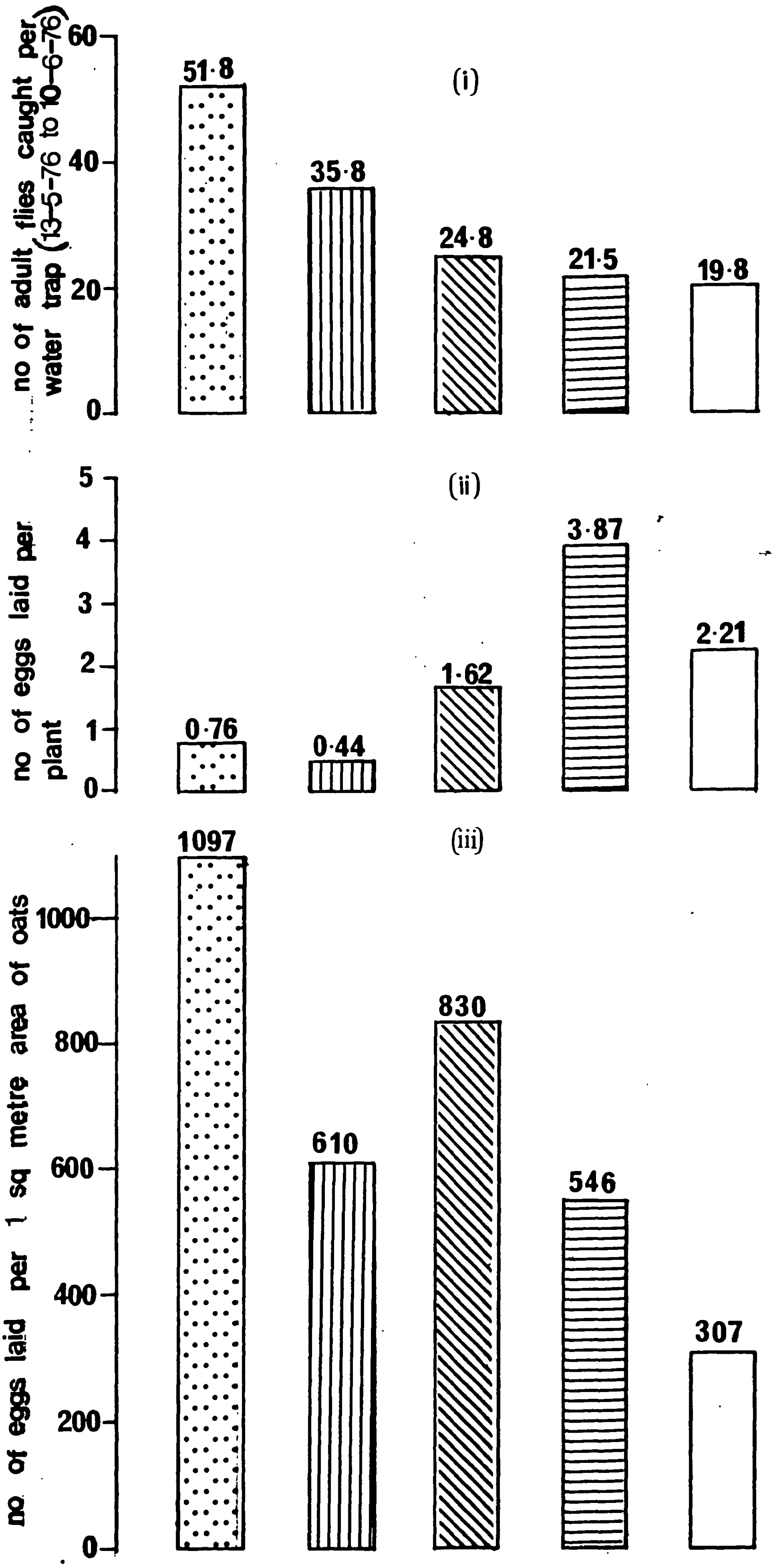

Fig.16 (i) Adult frit flies of the overwintering generation invading the oat crop.

(ii) Mean numbers of all the eggs laid by the overwintering generation adults per plant.

(iii) Total numbers of eggs laid by the overwintering generation adults per 1 sq metre area of oats crop were laid in the less sparse planting (plate 5c) than in the densest planting with densely-sown intermediate row spacing (plate 5b) (fig.16). The density of the oat plants within the row in the latter may have rendered the plants less suitable for oviposition than the former, even though more adult flies were trapped in the latter. The importance of the spatial distribution of oat plants on oviposition is also apparent in the two very dispersed plantings (plates 5d and 5e) as it was in the two dense plantings (plates 5a and 5b). Here also, more eggs per plant and per unit area of oat crop were laid in the treatment with intermediate row spacing (plate 5d) than in the widely-spaced rows (plate 5e) (tables 28 and 29, fig.16).

The peak of invasion of overwintering generation adults in the oat crop coincided with the stage of plant growth too young to be very suitable for plant oviposition. The crop was sown on May 4, 1976 and most plants were at the 1-leaf stage on May 13 (fig.13, table 1 and fig.2). Oviposition in soil was therefore inevitable and total egg population must have been underestimated in all treatments because of the sampling method employed.

5.1.3. Comparative abundance of larvae and pupae of the tiller generation.

The populations of larvae, puparia and empty puparia of the tiller generation on various sampling days in 1976 are shown in Appendix VI. No shoot dissections were made in 1975. The peak of the total larval and pupal numbers dissected from primary shoots and tillers was on June 10, 1976 (fig.17). This total may be taken as giving a picture of the complete population of these stages present in the oat field, because oviposition by the overwintering generation adults has ceased and the majority of the viable eggs had hatched by this time; also, an insignificant proportion of empty puparia was found on this date (Appendix VI).

Table 30 Estimates of the populations of larvae and pupae of the tiller generation

Densities and row spacing of oats	No. of larvae and pupae per plant	No. of larvae and pupae per sq m
14.4m plants/ha in rows spaced 5cm apart	1.4a	2,031d
13.7m " " " " 15cm "	2.0b	2,799e
5.1m " " " " 15cm "	3.6c	1,854c
1.4m " " " " 15cm "	5.3d	764b
1.4m " " " " 45cm "	3.6c	498a

Figures not followed by the same letters in the same column are significantly different at P = 0.05

Significantly more (table 30) and consistently higher numbers (fig.17) of larvae and pupae per plant and per sq metre were found in the dense planting with intermediate row spacing than in those with closely-spaced rows, and more per sq metre than in the sparse and very disperse plantings (table 20). This contrasted sharply with the water trap catches (table 25) and with oviposition (tables 28 and 29, fig.16), where more adults of the overwintering generation and more eggs per plant and per sq metre were found in the dense planting with closely-spaced rows than in those with intermediate row spacing and similarly, more eggs per plant and per sq metre were found in the sparse planting than in the latter. It seems that a mortality factor acting differentially according to the density and row spacing of oat plants within the rows must have acted before the O. frit larvae entered the shoots. This could be egg predation,

K E Y

—●—	░	14.4m plants/ha in rows spaced 5cm apart
- - ○ - -	▥	13.7m " " " " 15cm "
—▲—	▧	5.1m " " " " 15cm "
—■—	▤	1.4m " " " " 15cm "
- - □ - -	□	1.4m " " " " 45cm "

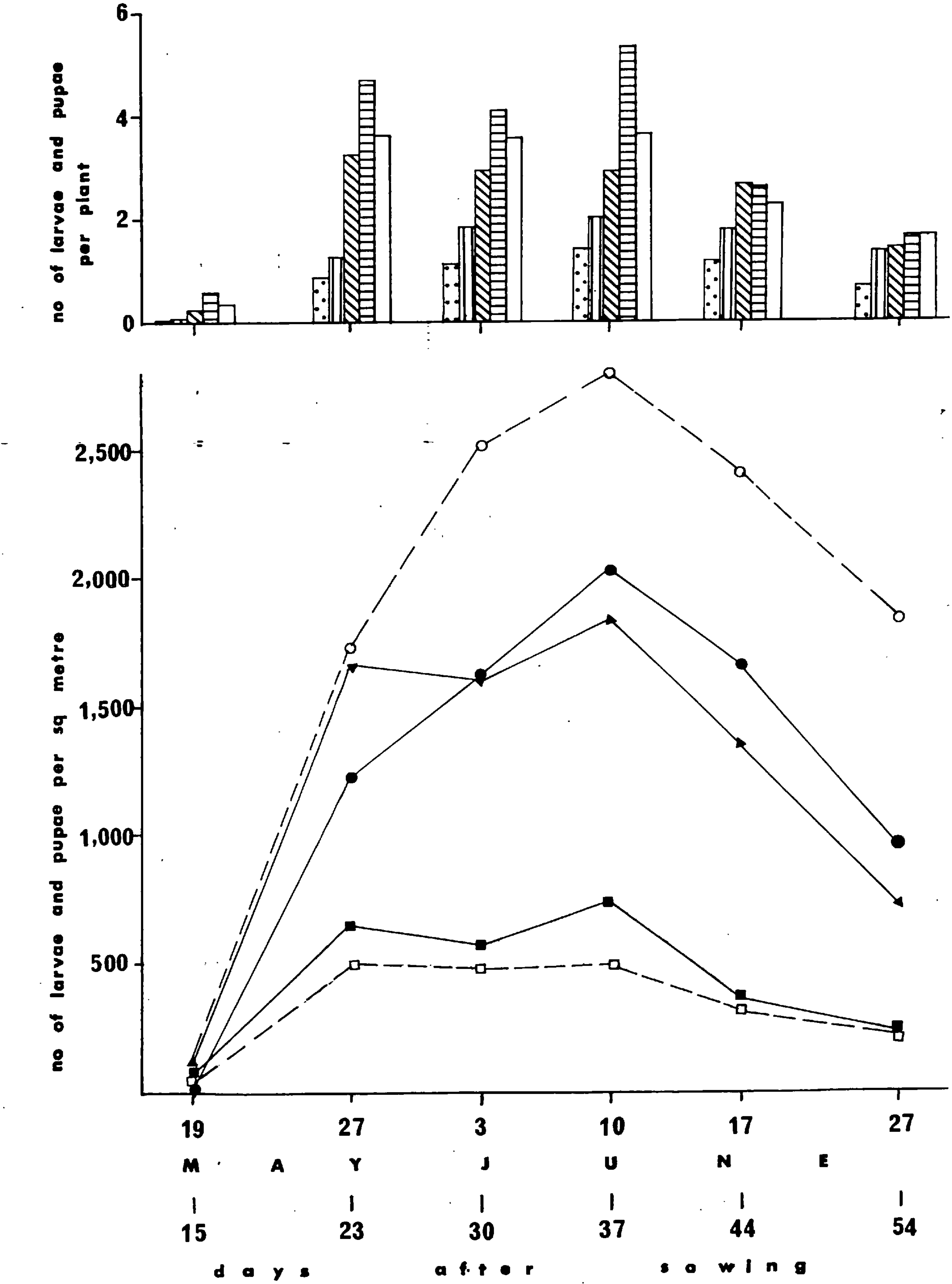

Fig.17 Estimates of the populations of larvae and pupae of the tiller generation on various sampling dates.

non-viable eggs or failure to invade oat plants. Southwood and Jepson (1962) found only very small numbers of possible predators that eat frit eggs and Jones(1969) found that an estimated 500 eggs laid on oat shoots produced 480 larvae. It seems unlikely therefore, that egg predation or non-viability of eggs could account for the differences. By elimination, one is left with failure of larvae to invade the shoots. There is at least one piece of evidence to indicate that this is the most likely cause of the observed differences. The preceding autumn, winter and spring months were extremely dry compared with the corresponding months in 1974/75 (table 31) and it has already been mentioned in sub-section 2.1.2. that water had to be applied to the seed furrows at the time of planting to ensure uniform germination. There were 3 times as many plants within the row in the dense planting with intermediate row spacing than in the dense planting with closely spaced rows or in the sparse planting or in the disperse planting with widely spaced rows; and 9 times as many than in the other disperse planting. Moisture stress was therefore more likely to be more severe in the dense planting with intermediate row spacing than in all the other treatments. It is suggested therefore, and has been demonstrated in the laboratory (sub-section 5.2.6.) that it is the more severe effect of inadequate soil moisture at the higher within-row density that rendered the plants more susceptible to larval invasion. Thus, although more adults invaded and laid more eggs in some of the treatments only a few of those eggs resulted in larvae inside the shoots, while many more of the relatively fewer eggs laid in the dense planting with intermediate row spacing resulted in larvae inside the shoots.

Table 31 Rainfall Data

	Total Monthly Rainfall (ml)	
	1974/75	1975/76
October	67.0	15.1
November	166.5	62.1
December	41.7	29.6
January	92.1	18.6
February	28.2	27.3
March	90.5	15.3
April	53.5	7.1
May	60.8	13.1
Total	599.8	188.2

5.1.4. Influence of tillering on intensity of attack

Plant samples taken from the field in 1976 (table 32) confirm some of the previous findings, e.g., of Wiggans and Frey (1957) that density and row spacing are important in tiller production. Although it was not possible to separate the effects of plant density, row spacing and infestation by O. frit on tillering in the field experiment, it could still be concluded that significantly more tillers per plant were formed in the disperse plantings than in the dense plantings (table 32). However, the numbers of larvae and puparia (full and empty) found in the disperse and sparse planting were more than the numbers of tillers on all sampling dates and about the same numbers in the dense plantings (table 32). Competition is therefore likely to be more intense in the former than in the latter.

Table 32 Numbers of tillers formed and the level of infestation

Densities and row spacings of oats	TILLERING		INFESTATION	
	No. of tillers		No.of larvae and puparia	
	per plant	per sq.m	per plant	per sq.m
27.5.76. (23 days after sowing)				
14.4m plants/ha in rows spaced 5cm apart	0.7a	1041a	0.9a	1240b
13.7m " " " " 15cm "	0.9a	1201b	1.3a	1730c
5.1m " " " " 15cm "	2.0b	1027b	3.3b	1669c
1.4m " " " " 15cm "	2.7c	384a	4.7c	663a
1.4m " " " " 45cm "	1.7b	241a	3.6b	498a
3.6.76. (30 days after sowing)				
14.4m plants/ha in rows spaced 5cm apart	1.2a	1719b	1.1a	1637b
13.7m " " " " 15cm "	1.8a	2542c	1.8a	2516c
5.1m " " " " 15cm "	3.0b	1517b	3.1b	1596b
1.4m " " " " 15cm "	3.3b	470a	4.1c	573a
1.4m " " " " 45cm "	2.8b	390a	3.5bc	488a
10.6.76. (37 days after sowing)				
14.4m plants/ha in rows spaced 5cm apart	1.6a	2283b	1.3a	1937b
13.7m " " " " 15cm "	2.1a	2947c	2.0a	2083c
5.1m " " " " 15cm "	3.7b	1881b	3.6b	1861b
1.4m " " " " 15cm "	4.7c	666a	5.4c	755a
1.4m " " " " 45cm "	3.1b	424a	3.6b	502a
17.6.76. (44 days after sowing)				
14.4m plants/ha in rows spaced 5cm apart	1.6a	2369c	1.5a	2211b
13.7m " " " " 15cm "	2.4ab	3311d	2.5a	3447c
5.1m " " " " 15cm "	3.5bc	1772b	4.0b	2068b
1.4m " " " " 15cm "	4.4c	624a	4.8b	675a
1.4m " " " " 45cm "	3.5bc	483a	4.2b	579a

Figures not followed by the same letters are significantly different at P=0.05

5.1.5. Mortalities occurring during the larval and pupal stages of the tiller generation.

It was not possible to estimate accurately the mortality which occurred between the larval and pupal stages because these two stages overlapped,mainly due to the prolonged oviposition period. The interval of one week between the sampling periods also made this difficult. However, a crude estimate of the mortality occurring between the two stages was made by using the peak population figures of the stages (table 33).

Most larvae died in the most disperse planting with wide row spacing and in the sparse planting, least mortality occurred in the dense plantings and intermediate figures were obtained in the disperse planting with intermediate row spacing (table 33). This result can be explained in terms of the numbers of tillers avaiable in each treatment for larvae to complete their development as already suggested in sub-section 5.1.4. above.

More accurate estimates of pupal mortality and that due to parasitism were made as described below. Plant samples were taken, dissected and pupae kept in glass vials in the laboratory until parasites or adult _O. frit_ emerged as already described in sub-section 2.1.5. The first pupae were dissected from plant samples on June 3 (Appendix VI). These and those collected on June 10 were bulked to construct table 34. The samples taken on June 17 and June 27 contained many empty puparia (Appendix VI) and because it was not possible to ascertain which of the empty puparia were previously parasitized, they were not used in estimating pupal mortality.

Most pupae per sq metre of oats were found in the dense planting with intermediate row spacing, less in the dense planting with closely-spaced rows and in the sparse planting and least in the

Table 33 Larval mortality in oat crop of different densities and row spacings

	Larvae (no/sq m)		Pupae (no/sq m)
1,440 oat plants/sq metre in 5cm rows			
Peak population	1,622		1,393
Nos dying in interval		229	
% Mortality		14.1	
1,370 oat plants/sq metre in 15cm rows			
Peak population	2,415		1,976
Nos dying in interval		439	
% Mortality		18.2	
510 oat plants/sq metre in 15cm rows			
Peak population	1,671		1,082
Nos dying in interval		589	
% Mortality		35.2	
140 oat plants/sq metre in 15cm rows			
Peak population	663		493
Nos dying in interval		170	
% Mortality		25.6	
140 oat plants/sq metre in 45cm rows			
Peak population	498		320
Nos dying in interval		178	
% Mortality		35.7	

very disperse plantings (table 34, col.1). The percentage of pupae killed, i.e., failed to produce adult _O. frit_ were remarkably similar in all the treatments and ranged from 27.5 to 34.0 (table 34, col.2). In absolute terms, most pupae were killed in the dense plantings, less in the sparse planting and least in the disperse plantings. It is however, the percentage mortality that has more ecological significance since it gives an indication of the proportion of pupal populations that produce adults.

Three species of hymenopterous parasites were reared from the puparia. Although detailed identification was not made, the result confirmed Imms' (1930, 1932) and Bhattacharya's (1957) findings that there are three hymenopterous parasites of the pupal stage of the tiller generation. There was no significant difference between the treatments in the percentages of pupae from which parasites emerged (table 34, col.3). This remained very low and ranged from 9.2 to 17.9 per cent in all the treatments. The disparity between total mortality (table 34, col.2) and the proportion of pupae from which parasites actually emerged (table 34, col.3) is however unexpectedly high - more than 20 per cent in the disperse and sparse plantings and between 10 and 17 per cent in the dense plantings. This indicates that parasitism is not the only important factor causing pupal mortality in the frit fly. Perhaps adverse weather conditions such as dry and persistent high temperatures as was the case during the pupation period in the field in late May, June and July, 1976 killed many of the pupae, e.g. through desiccation, since there is no record of primary pathogens of frit fly pupae.

A pattern emerges when parasitism is expressed as percentages of total pupae killed. Here, a significantly higher percentage of the pupae killed produced adult parasites in the dense plantings

Table 34 Pupal mortality in oat crop of different densities and row spacings

	Column 1	Column 2	Column 3	Column 4
Densities and row spacing of oats	Total no of pupae per sq metre	% of total pupae killed	% of total pupae from which parasites emerged	% of total pupae killed from which parasited emerged
14.4m plants/ha in rows spaced 5cm apart	857b	27.5a	17.9a	61.9b
13.7m " " " " " "	1,256c	34.0a	16.9a	46.6b
5.1m " " " " " "	876b	32.6a	11.8a	37.2a
1.4m " " " " " "	553ab	34.0a	9.2a	27.5a
1.4m " " " " " "	357a	33.0a	13.1a	38.1a

Figures not followed by the same letters are significantly different at P = 0.05

than in the sparse and disperse plantings (table 34, col.4). Since there were no significant differences in the percentage of total pupae killed in all the treatments (table 34, col.2), it seems likely many of the pupae killed by parasites in the sparse and disperse plantings were those destined to be killed through other causes, and therefore, when parasitized both frit and parasites were killed. Other factors of lesser importance in the present circumstance are intraspecific competition during the larval stage in the sparse and disperse plantings resulting in the production of lighter pupae and superparasitism. Intra-specific competition and the resultant smaller pupae (table 54, fig.26) can in turn have two effects: adult frit may fail to emerge from puparia because of inadequate food reserve or parasites may die in the puparia also because of inadequate food. Because pupae as light as 0.263mg and 0.277mg produced under intense competition during the larval stage in the laboratory have hatched into adult female and male frit, respectively, the former suggestion appears less likely than the latter. Parasites may die inside puparia if the puparia are too small and contain inadequate food for their development. If there is superparasitism they may also die irrespective of the size of the puparia. Superparasitism is however unlikely under the present situation because of the low overall percentage pupal mortality. It can be concluded in the light of the foregoing discussion that weather probably plays an important role in determining the number of pupae that survive to become adults.

5.1.6. Panicle and spikelet production

In 1975, the numbers of panicles produced in the different treatments were estimated in the field on August 28 by counting all the panicles in 1 metre row lengths chosen at random in each plot. Two panicles were also chosen at random from each plot and the spikelets counted to give an estimate of the number of spikelets per panicle in the different treatments. In 1976 however, a slightly different sampling method was employed because of the variation in the numbers of plants within the rows in the different treatments. Photographs of the plots were taken on July 13, 1976 (plates 10a to 10e), and counts of the panicles were made on July 29. In the dense planting with intermediate row spacing, panicles in four randomly chosen 0.33 metre rows per plot were counted. In the dense planting with closely-spaced rows, in the sparse planting and in the disperse planting with wide row spacing counts were made in four randomly chosen 1 metre rows per plot because these had fewer plants within the rows; and in the disperse planting with intermediate row spacing with still fewer plants within the rows counts were made in four randomly chosen 3 metre rows per plot. No counts were made of the spikelets on the panicles in 1976. The results of the 1975 counts are presented in table 35 and fig.18; and those of 1976 in table 35 and fig.19.

In 1975, most panicles were produced per row in the disperse planting and least in the dense planting, but the reverse trend was obtained per unit area of oats (table 35). Fewer panicles than in the initial number of plants (primary shoots) were produced in the dense and sparse plantings, but in the disperse planting slightly more panicles than the initial number of primary shoots were produced (fig.18 (i)). Clearly, some of the unattacked tillers in the disperse planting produced panicles. Tillers were also produced in the dense and sparse plantings, and indeed, many of them were also not attacked, but they did not develop into secondary shoots of the kind that produced panicles in the disperse planting. The density of the plants must have had some effect on panicle production by tillers. There were relatively few spikelets per panicle in the dense planting and relatively many in the disperse planting (fig.18 (ii)).

Table 35 Number of panicles produced per metre row and estimates of the number per sq metre area of oats in 1975 and 1976.

	Mean no. of panicles per metre row	Mean no. of panicles per sq metre
1975		
8.6m plants/ha in 7.5cm rows	47.5a	570b
4.3m " " 15cm "	54.5ab	327ab
1.4m " " 45cm "	76.8b	154a
1976		
14.4m plants/ha in 5cm rows	21.9b	434d
13.7m " " 15cm "	11.9ab	79c
5.1m " " 15cm "	5.6ab	37b
1.4m " " 15cm "	0.02a	0.15a
1.4m " " 45cm "	0.14a	0.30a

Figures not followed by the same letters are significantly different at $P = 0.05$.

In 1976, more overwintering generation adults invaded the oat crop than in 1975 (fig.12) and this inevitably resulted in more severe damage to the oat crop than in 1975. The type and extent of damage caused in 1976 is illustrated in plates 10a to

Plates 10a to 10e. Oat plants of different densities and row spacings after infestation (July 13, 1976).

Plate 10a. 14.4m plants/ha in rows spaced 5cm apart
" 10b. 13.7m " " " " 15cm "
" 10c. 5.1m " " " " 15cm "
" 10d. 1.4m " " " " 15cm "
" 10e. 1.4m " " " " 45cm "

Plate 10a

Plate 10b

Plate 10c

Plate 10d

Plate 10e

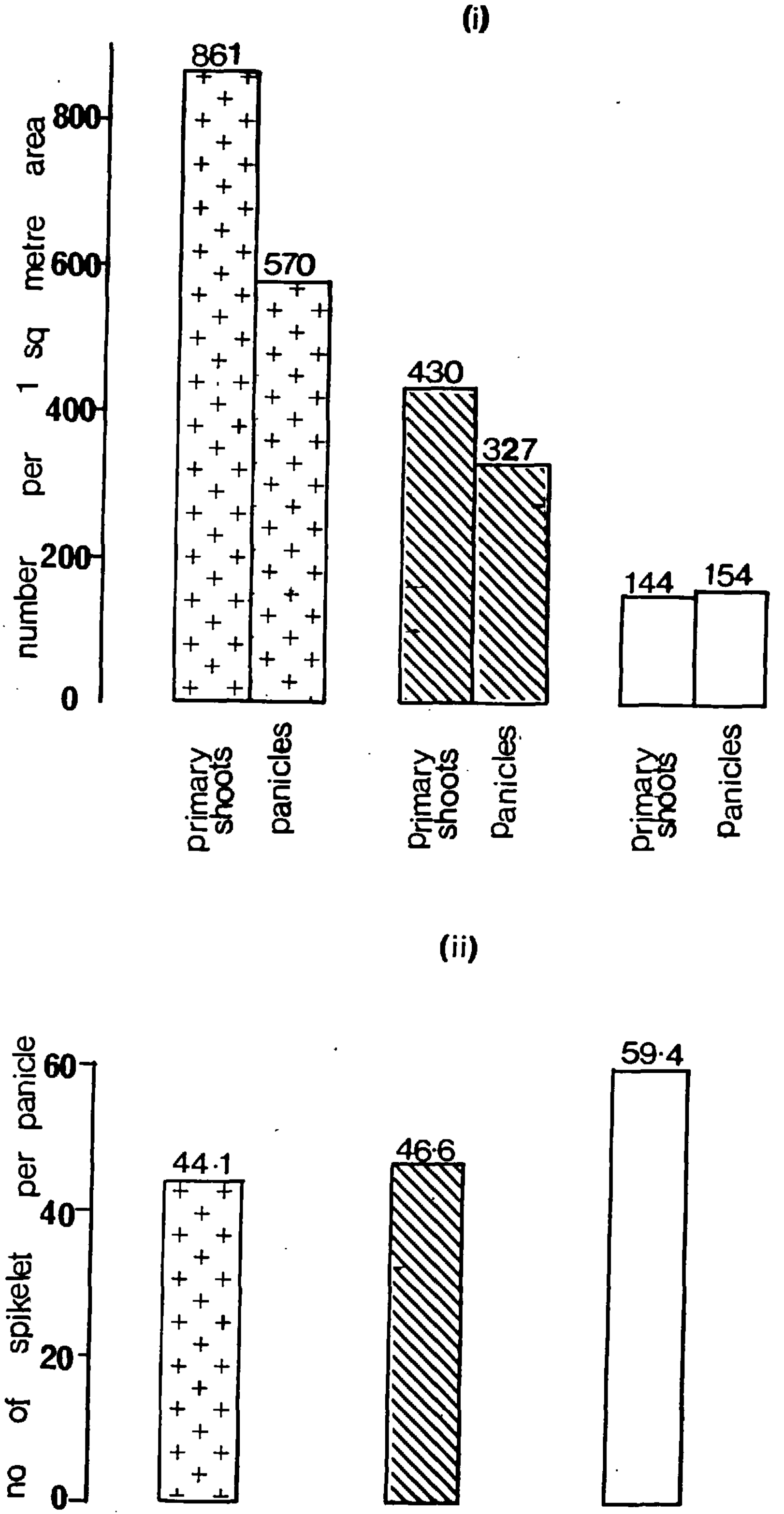

Fig.18 Numbers of panicles produced per sq metre area of oats and of spikelets per panicle in oat plants of different densities (1975).

⊞ 8.6m plants per hectare in 7.5cm rows

▨ 4.3m " " " " 15cm "

☐ 1.4m " " " " 45cm "

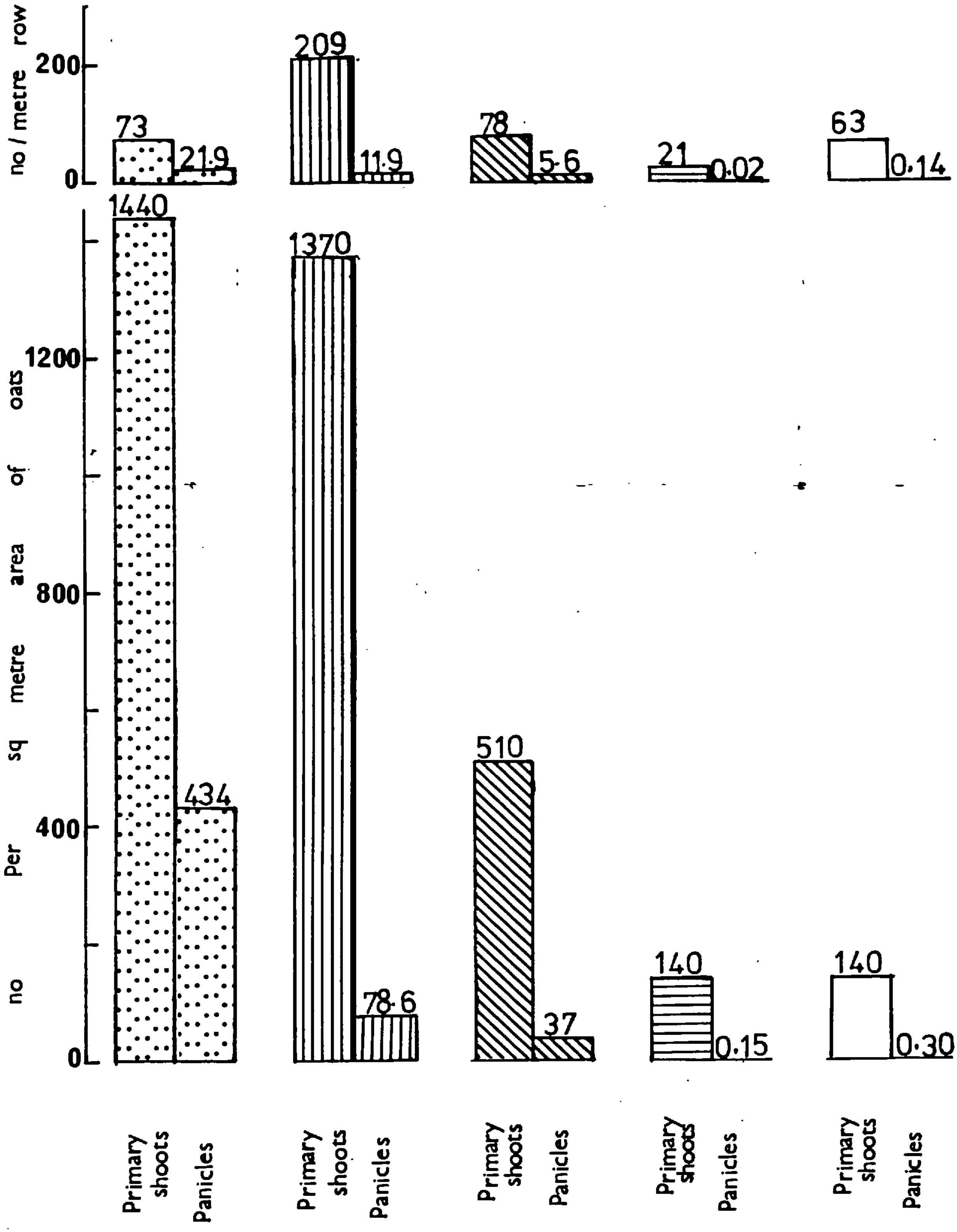

Fig.19 Numbers of panicles produced per metre row and per sq metre of oats in relation to the initial plant populations (1976).

10e where it can be seen that in the disperse plantings (plates 10d and 10e) hardly any panicles were produced. Most panicles per metre row and per unit area of oats were produced in the dense plantings, less in the sparse planting and least in the disperse plantings (table 35). It was more in the dense planting with closely-spaced rows than in the dense planting with intermediate row spacing. Unlike 1975 (fig.18 (i)), the disparity between the initial numbers of plants and the panicles produced were magnified several fold at all densities in 1976 (fig.19). It is clear from this that the extent to which primary shoots and tillers contribute to panicle production in the oat crop depends not only on the density of the plants and the spacing between the rows, but also on the severity of frit attack.

5.1.7. Oviposition in oat panicles

The eggs of the panicle generation were sampled as described in sub-section 2.1.5. The samples were taken on July 24, about one week after the peak of the tiller generation adult production as indicated by trap catches (fig.12).

Most eggs per spikelet and per panicle were laid in the disperse planting and least in the dense planting, but the reverse was true for numbers of eggs per unit area of oat plants (table 36, fig.20).

Table 36 Number of eggs laid per spikelet and per panicle and estimates of the numbers laid per sq metre area of oats in 1975.

	Mean no of eggs laid per		
	spikelet	panicle	sq metre
8.6m plants/ha in 7.5cm rows	1.6a	70a	39,900b
4.3m " " 15cm "	1.8a	76a	24,850a
1.4m " " 45cm "	2.4b	148b	22,720a

Figures not followed by the same letters are significantly different at P = 0.05.

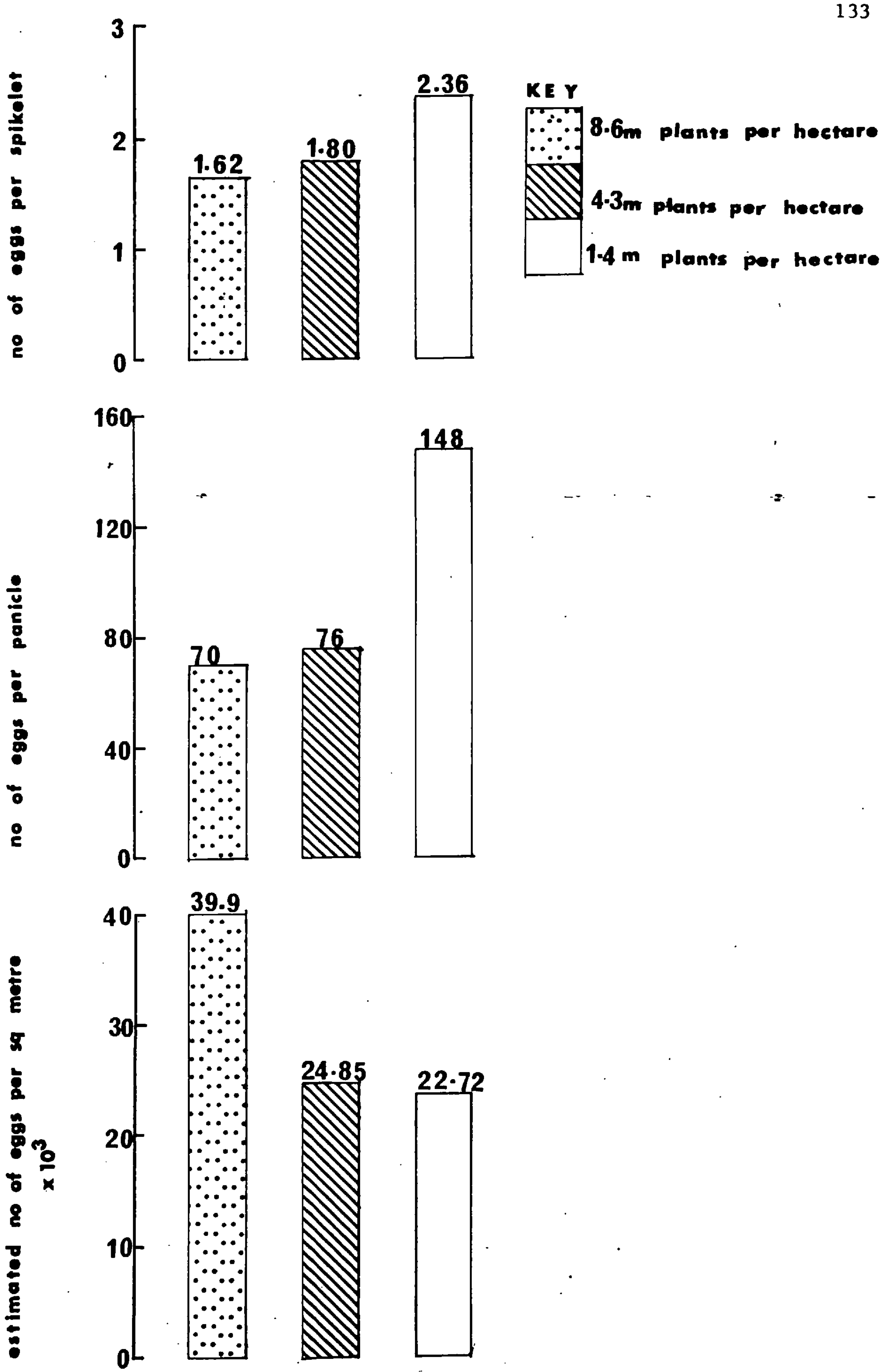

Fig.20. Oviposition in oat panicles of different densities (1975).

5.2. LABORATORY EXPERIMENTS

The results of the field experiments have highlighted certain aspects of the effects of the density and row spacing of oat plants on colonization by O. frit which were considered to need further laboratory experimentation to arrive at definite conclusions. The laboratory experiments described below in sub-sections 5.2.1. to 5.2.6. have this as their aim.

5.2.1. Effects of the density of 'artificial plants' on the numbers of adult flies landing.

Water trap catches showed in sub-section 5.1.1. that the density and row spacing of oat plants influence the number of adult flies seemingly attracted to and trapped in the different treatments. An attempt was made in this experiment to find out whether captive flies in a cage respond to different densities of oats and also whether males and females respond differently.

Four, eight, sixteen and thirty-two (4, 8, 16 and 32) sticky 'artificial plants' were placed in 14cm-diameter pots containing sand (sub-section 2.3.2., plate 7). Each 'plant' was 13cm high and 3.25mm wide. The pots were placed in a cage containing 150 adult flies of approximately 50:50 sex ratio. (The sex ratio of adult flies collected from a laboratory culture is approximately 50:50 (Section VIII)). The numbers of flies that landed and so were trapped in the different pots were counted after 24 hours and their sex determined. The experiment was replicated 4 times allocating the position occupied in the cage at random to the various pots at the start of each replicate. New adults from the laboratory culture were introduced into the cage at the end of each trial to maintain the number of flies in the cage at 150.

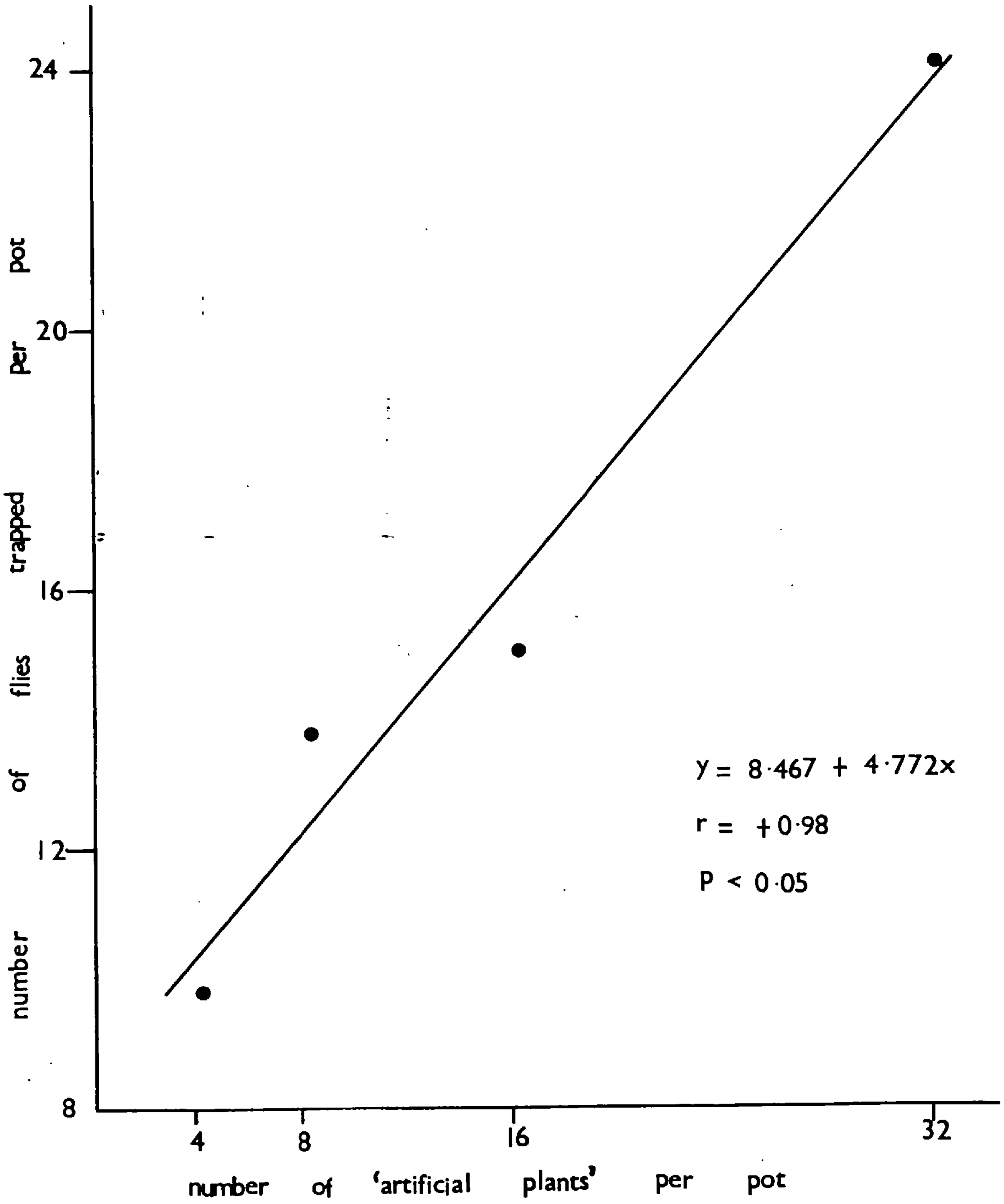

Fig.21 The relationship between the density of 'artificial plants' and the number of flies trapped.

Table 37 Numbers of flies trapped and proportion of females in trials with different numbers of 'artificial plants' per pot.

No of 'artificial plants' per pot	Mean no of trapped flies/pot	Percentage of females in the trapped flies
4	9.8	61.5
8	13.8	47.3
16	15.0	43.3
32	24.0	55.2

$P > 0.05$

Like the water trap catches in the field, the numbers of flies trapped in the different pots increased with increasing 'artificial plant' density ($r = +0.98$) (fig.21). However, an analysis of variance carried out on the data did not reveal any significant differences between the treatments (table 37) because of the variation between the replicates. Almost completely different groups of flies were used in each replicate and these differed greatly in their readiness to land; the proportion in which they landed in the different pots also differed. The proportion of females in the flies that landed in the pots containing 'plants' of different densities did not differ significantly from each other (table 37).

5.2.2. Effects of the density of potted oat plants on the numbers of eggs laid.

Oats were seeded in 14cm-diameter pots and the plants were thinned to 4, 8, 16 and 32 per pot soon after germination. The pots were kept in the greenhouse until the plants attained the early 3-leaf stage—the stage most preferred by the female flies for egg deposition inside the coleoptiles (table 1). Four pots containing each of the densities were placed in a cage containing a group of young ovipositing adults for 24 hours, at the end of which the number of eggs laid in the different pots were counted. The experiment was replicated 4 times, using the same group of flies. Hillyer (1965) observed that the number of egg rudiments aborted during an ovariole cycle is very small during the first 18 days of oviposition and Vickerman (1975) found that a large proportion of the eggs were laid during the first 7 days of egg deposition. It was therefore thought that by using the same group of young ovipositing adults in the 4 replicates, the variation over four days in the numbers of eggs laid from replicate to replicate would be minimal, unlike in the previous experiment.

It was observed that although all the plants were of the same age, the state of their coleoptiles differed and the differences between the plants were greatest in the densest stand (32 plants/pot) at the time they were offered for oviposition in the cage. Over 95 per cent of the eggs laid on the plants at all densities were laid inside the coleoptiles. The number of eggs laid per pot increased with increasing plant density (r = + 0.98) (fig.22), and the differences were statistically significant, except between those at 8 and 16 plants per pot (table 38, col.(i)). Most eggs per plant were laid in the pot with 8 plants which had 5.5 compared with 4, 16, and 32 plants per pot which had 4.6, 3.6 and 3.0 eggs/plant, respectively (table 38, col.(ii)). Eggs were laid on all the plants in the pot with only 4 plants, i.e., all the plants had at least 1 egg while eggs were laid on only 76.2 per cent of plants in the pot with 32 plants, even though there were more eggs than shoots. Pots with 8 and 16 plants per pot had intermediate figures (table 38, col.(iii)).

In the dense stands, the plants grew vertically and the coleoptiles were more tightly attached to the main stem than in the sparse stands; so there were fewer suitable coleoptiles than the number of plants in the former. This no doubt accounted for the relatively lower percentage of plants oviposited on in the densest planting (32 per pot). The sparsest stand (4 per pot) was probably visually less attractive to the flies than the denser stand (8 per pot), hence fewer eggs per plant. There is no evidence that the presence of eggs inside the coleoptile interferes with further oviposition at that site. The Narrator has observed that as many as 47 eggs were laid by a group of flies inside one coleoptile in the laboratory.

Table 38 Numbers of eggs laid and per cent of plants with eggs in trials with different numbers of oat plants per pot.

	col.(i)	col.(ii)	col.(iii)
	Mean no of eggs laid		Percent of
No of plants per pot	per pot	per plant	plants with eggs
4	18.5a	4.6a	100.0a
8	43.8b	5.5a	93.8ab
16	58.3b	3.6a	90.6b
32	96.3c	3.0a	76.2c

Figures not followed by the same letters are significantly different at P = 0.05

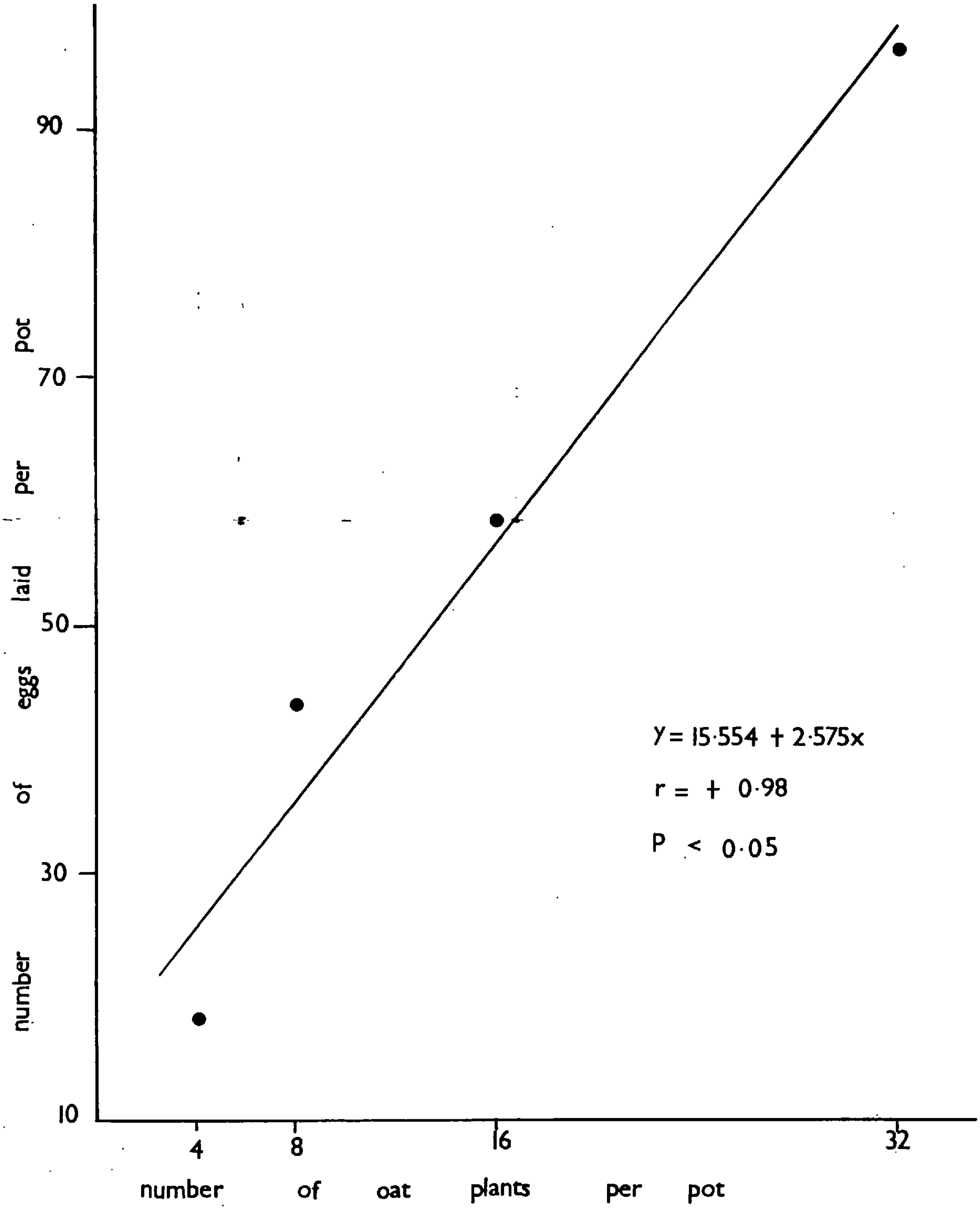

Fig.22 The relationship between the density of potted oat plants and the number of eggs laid.

5.2.3. Effects of density of oat plants on the survival of larvae

Oats were seeded in pots and thinned to 4, 8, 16 and 32 plants per pot as before. One central plant per pot was infested with 8 freshly laid eggs at oviposition site 1, i.e., between the plant and the soil, when at the 1-leaf stage. The plants were watered by pouring water into the saucers in which the pots were placed and not directly on the surface of the soil, in order not to interfere with the movement of the larvae between the plants. The distance between the central plant and the surrounding plants was measured and larvae and pupae dissected out of the plants 20 days after infestation. The results are presented in table 39 below.

In all the trials the infested central plants were killed without producing tillers. Only in one case was as many as 3 larvae or pupae found in the central plant; in most cases, either 1 or no larva or pupa was found in the infested central plant. There was migration from the infested central plant to the surrounding plants and whether the plants were 1cm or 8cm away made little difference to survival. Similarly, survival in pots with only 4 plants, where the distance between the central plant and the nearest plant was 7.5cm did not differ from those with more plants per pot with corresponding decrease in distance between the central plant and the surrounding plants.

The result, like those of Jones (1969) suggests that _O. frit_ can be actively migratory in the larval stage. Jones (1969) placed plants at distances up to 5cm away from infested central plants and observed that plants placed only 1cm away and those placed as far away as 5cm did not differ in enhancing survival of the larvae. Many of the migrating larvae did not enter new plants in this experiment, probably because the plants were too hard for the migrating larvae to penetrate. The duration of the egg stage at the laboratory temperature of 20°C is about 4 days and it probably took another two days before the larvae started having food shortage due to competition which resulted in their leaving the central plant. By this time, the surrounding plants were at the 2 to 3-leaf stage. It has already been shown in another part of this study (fig.4) that the chances of entry of larvae into the plant decreases with increasing plant age. In this experiment therefore, it seems likely that although increased plant density increased the chances of migrating larvae in finding new plants many of them failed to invade the new plants, which were now older.

A different situation is envisaged under field conditions. Oats and indeed most cereals are seeded in drills (rows) and the resulting plants within the rows are often close to each other, and in some cases, particularly at high within-row density, plants actually make contact with each other. Migrating larvae under field conditions therefore can have relatively less distance to cover. Secondly, temperature and frit attack are some of the factors that influence tillering in oats. It was observed in this study that unattacked spring sown oats tiller more readily in the field than in pots in the laboratory at 20°C. So, apart from the fact that the larvae travel shorter distances within rows in the field, they also have many young tillers to invade at the end of 'migration'. Movement of larvae between plants within rows in the field is therefore, more likely to result in successful invasion of new tillers. Movement between the rows however, entails travelling

Table 39 Numbers of frit fly larvae that survived competition or migrated from a central plant with many eggs to other plants in pots containing 4, 8, 16 or 32 plants per pot.

No of plants per pot	No of eggs on central plants	No of larvae/ pupae on central plants	No of surrounding plants attacked	No of larvae/ pupae in surrounding plants	Total no of larvae/ pupae	% survival	% surviving larvae/ pupae that migrated	Distance between central plant and surrounding plants attacked (cm). (No of plants in parenthesis)	
								miminum	maximum
4	24	3	2/9	2	5	20.8	40.0	7.5(0)	8.0(2)
8	24	2	1/21	1	3	12.5	33.0	2.5(1)	-
16	16	3	2/30	1	4	25.0	25.0	2.0(2)	-
32	32	5	7/124	3	8	25.0	37.5	1.0(1)	6.0(1)

longer distances in exposed conditions. When predators are active in the field such movements may be hazardous (Jones, 1969), and besides, the larvae also stand a greater chance of dying through desiccation. Movement of larvae between rows are therefore likely to be less successful.

5.2.4. Effects of the spatial distribution of 'artificial plants' of equal density on the numbers of adult flies landing.

Sticky 'artificial plants' were arranged in 2 seed trays as shown in plate 11. The trays (325cm^2) had sixty-four 'plants' in 6 rows spaced 5cm apart and in 2 rows spaced 15cm apart. These density and row spacings corresponded to those of the 2 dense plantings in the field in 1976 (plates 5a and 5b). The trays were placed in a cage containing 100 adult frit flies and counts were made of the numbers of flies that landed and were trapped in the trays after 24 hours. The experiment was replicated 4 times, alternating the position occupied in the cage by the trays and introducing more flies into the cage to maintain the number at 100, at the start of each replicate.

As in the field experiment (table 25 and fig.13), consistently higher and significantly more flies were trapped in the trays containing sticky 'artificial plants' with closely spaced rows than in those of equal density per tray but with more widely spaced rows (table 39). It is concluded that 'real' and 'artificial' oat plants in closely spaced rows are more attractive to adult frit flies than those in widely spaced rows and this accounts for greater initial colonization by adult flies of the former than the latter in the field and in the laboratory.

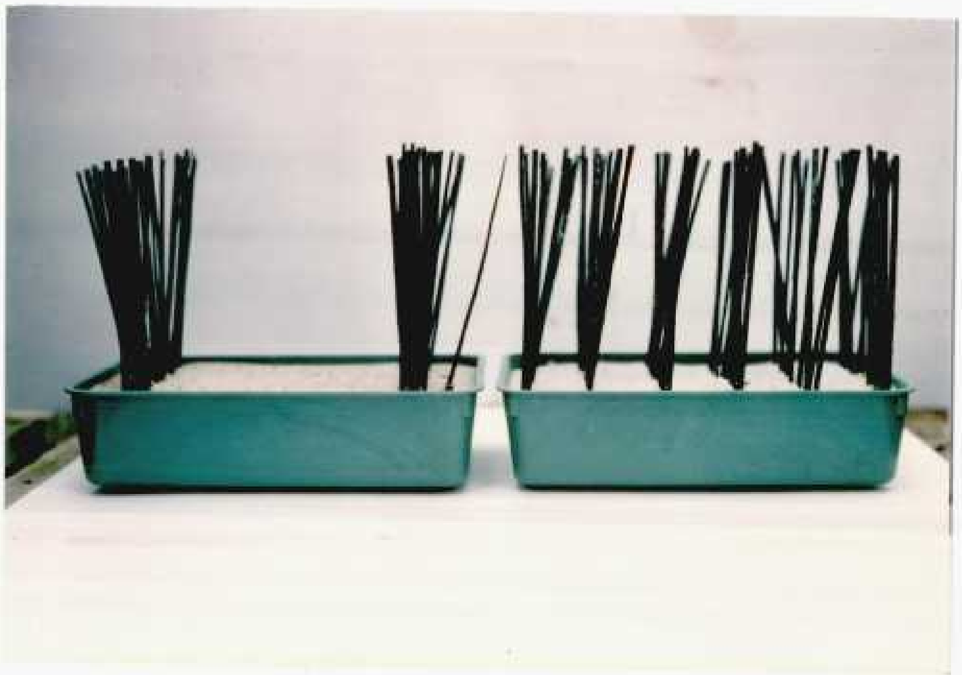

Plate 11. 'Artificial plants' in rows spaced 15cm apart (left) and in rows spaced 5cm apart (right). Sixty-four 'artificial plants' per tray.

Table 40 Effects of spatial distribution of 'artificial plants' of the same density on the numbers of flies trapped.

Spatial distribution of 'artificial plants' in trays	No of flies trapped/tray	
	$\bar{X}$	$S_{\bar{X}}$
'Artificial plants' in rows spaced 5cm apart	17.5	3.8
" " " " " 15cm "	10.5	1.5

5.2.5. Effects of the spatial distribution of oat plants of equal density on the numbers of eggs laid.

Oats were seeded in trays to have the same density per tray and different spatial distributions as with 'artificial plants' in the previous experiment (plate 12). These also corresponded with the density and row spacings of the 2 dense plantings in the field in 1976 (plates 5a and 5b). Two trays, one from each treatment were offered for oviposition for 48 hours in a cage containing a group of 100 ovipositing flies when the oat plants were at the late 2-leaf stage to early 3-leaf stage. Egg counts were made in the 2 trays at the end of the period. The experiment was replicated 5 times alternating the position occupied in the cage by the trays at the start of each replicate.

Consistently higher and significantly more eggs were laid on plants in the tray with closely spaced rows than in those of equal density per tray, but with more widely spaced rows (table 40). Again, this result is consistent with those obtained in the field (table 29). Results presented earlier (fig.13; tables 25 and 39) showed that consistently higher numbers and significantly more adult flies colonized an oat crop with closely-spaced rows than those with widely-spaced rows. It can therefore be concluded that more adult flies colonized and laid more eggs on the former than on the latter in the field and in the laboratory. Individual plants in the former were more isolated from each other and their coleoptiles less tightly attached to the stem than in the latter; plants in the former were therefore also relatively more suitable for egg deposition than those in the latter.

Plate 12. Oat plants in rows spaced 15cm apart (left) and in rows spaced 5cm apart (right). Sixty-four plants per tray in both trays.

Table 41 Effects of the spatial distribution of oat plants on the numbers of eggs laid.

	No of eggs laid per tray	
Spatial distribution of oat plants in trays	$\overline{X}$	$S_{\overline{X}}$
Oat plants in rows spaced 5cm apart	23.6	2.71
Oat plants in rows spaced 15cm apart	10.0	3.36

5.2.6. Effects of the spatial distribution of oat plants on the utilization of soil moisture and the relationship between these and the entry of larvae into the plant.

It was suggested in sub-section 5.1.3. that where soil moisture is limiting, as indeed was the case in the spring and summer of 1976, a high within-row density aggravates the water deficit in the plant which could explain the greater penetration and survival of the larvae in oat plants. The experiment described here was conducted to test this assertion.

Oats were seeded in 6 sets of 2 trays as shown in plate 12; each tray contained sixty-four plant. The trays were kept in a greenhouse where the temperature fluctuated between 10° and 18°C. All the trays received a generous supply of water daily until 10 days after sowing when all the plants had at least one fully opened leaf. Three sets of trays were watered for the last time on the tenth day while the remaining 3 sets still received a generous supply of water daily. All the trays were transferred to a 20°C room where ten plants selected at random in each tray were each infested with one 3-day old eggs on the 20th day after sowing and 10 days since 3 sets of trays were last watered. The plants had not started to wilt at the time they were infested with eggs, but the growth of plants in the unwatered trays had been set back (plates 13a and 13b). Three-day old eggs were used in this experiment to ensure that the eggs hatched within 24 hours of infestation and that emergent larvae penetrated unwilted plants. The duration of the egg stage in this study was found to be 84 to 96 hours. The plants infested with eggs were examined for symptoms of deadhearts and dissected 5 days after infestation with eggs.

Rather unexpectedly, the plants in the unwatered trays had not started to show any apparent signs of wilting up to the time they were dissected 25 days after sowing and 15 days since 3 sets of trays were last watered. However, it was apparent (plates 13a and 13b) that inadequate supply of water from the soil in the unwatered trays had set back the growth of the plants. This was more apparent in the trays with widely spaced, densely-sown rows (plate 13a) than in the closely spaced, sparsely-sown rows (plate 13b). Consistently higher and significantly more larvae penetrated the plants in the unwatered trays with widely spaced densely-sown rows than did those of the other 3 treatments (table 41). Clearly, inadequate soil moisture had enhanced the entry of larvae into the plant as suggested in sub-section 5.1.3. Slavik (1966) stated that hydration levels in plants may influence physiological processes in cereals in various ways and that water, apart from acting as a universal solvent is also a direct structural material and also an agent of plant turgor. The works of other authors, e.g; Ordin (1960) have indicated a direct effect of the turgor potential on cellulose synthesis. But cellulose is a major component of most plant cell walls. Perhaps, a water deficit occuring in the plant due to inadequate supply of water from the soil and resulting in loss of plant turgor and reduced cellulose synthesis reduces the ability of oat plants to resist penetration by O. frit larvae. Oat plants in closely spaced sparsely-sown rows have their roots more uniformly distributed in the soil and this no doubt resulted in more efficient use of the inadequate soil moisture.

Plate 13a. Sixty-four oat plants in rows spaced 15cm apart at the time of infestation with eggs.

left: plants watered throughout the experiment

right: plants watered for part of the experiment

Plate 13b. Sixty-four oat plants in rows spaced 5cm apart at the time of infestation with eggs.

left: plants watered throughout the experiment

right: plants watered for part of the experiment

Table 42 Relationship between spatial distribution of oat plants, soil moisture and entry of larvae into the plant.

Treatments	No of larvae that penetrated plants				
	Replicates			X	$S_{\bar{X}}$
	I	II	III		
Watered oat plants in rows spaced 5cm apart	1	1	1	1.0	0.0
Unwatered " " " " " " "	0	1	1	0.7	0.3
Watered " " " " " 15cm "	1	1	0	0.7	0.3
Unwatered " " " " " " "	6	7	6	6.3	0.3

SECTION VI

DISPERSION OF THE IMMATURE STAGES OF O. FRIT AMONG OAT PLANTS WITH DIFFERENT BACKGROUNDS AND AT DIFFERENT DENSITIES AND ROW SPACINGS.

6.1. Introduction

The dispersion of a population, the description of the pattern of the distribution of animals in space, can be of considerable ecological significance. In its own right, it is a way of describing the condition of a population (Southwood, 1966). Changes in the dispersion pattern of a population over time can also have some practical applications. Thus, Southwood (1966) stated that if a mortality factor reduces the clumping of a sessile organism it is an indication that it acts most severely on the highest densities, or if the dispersion of a population becomes more regular then intensification of competition should be suspected. Bardner and Lofty (1971) studied the distribution of the eggs and larvae of the wheat bulb fly, Leptohylemyia coarcata (Fall.) and of the wheat plants within attacked crops with a view to facilitating the estimation of the amount of compensatory growth and loss of yield in attacked crops. It was therefore thought that information on the dispersion of frit fly eggs in the field and in the laboratory will throw some light on the ovipositing habit of the insect and that information on the dispersion of the larvae and pupae among oat plants of different densities and row spacings could be used in detecting competition among the larvae and so influence survival of the insect.

6.2. Methods

The sampling methods employed for the immature stages in the plants in the vegetative phase and in the panicles and spikelets have been described in sub-section 2.1.5. The data were analyzed with the aid of a computer programme described in sub-section 2.4. Five distributions were tested for to each set of data. These were the Binomial, Poisson, Negative Binomial, Double Poisson (Thomas, 1949) and Neyman Type A (Neyman, 1939). The last three are contagious types of distributions. Although the negative binomial has been fitted to many contagious insect populations and appears to have a wide application, there is always a possibility that another model fits a sample better than the negative binomial, hence the inclusions of the 2 other contagious distributions, double poisson and Neyman type A. The last two are very similar and may be fitted to the same sample and both assume that clumps of individuals are distributed at random and the numbers of individuals in the clumps are also distributed at random. The most useful property of these two models is their capacity to describe both polymodal and unimodal frequency distributions, whereas the negative binomial is always unimodal (Elliott, 1973).

6.3. Dispersion of eggs in the field

The distribution of eggs among oat plants in the vegetative phase of different densities and row spacings (table 43 and 44), among oat plants in the vegegative phase with bare or weedy background (table 45), among oat spikelets in a crop with bare or weedy background (table 46) and among oat spikelets of different densities (table 47) were best described in almost all instances by the negative binomial. There was no indication that the presence of weeds in an oat crop affected the distribution of the eggs (table 45) or that the weeds as 'overgrowths' during the reproductive phase of oats affected the distribution of eggs among the spikelets (table 46). Also, neither the densities and row spacings of oats (tables 43 and 44) nor the densities of the spikelets (table 47) appeared to affect the distribution of the eggs among the spikelets.

Clumping of frit fly eggs in field conditions is no doubt due to a combination of the behaviour of the female flies and the heterogeneity of the oat plants. Although, all the plants were planted at the same time and therefore of the same age, there were subtle differences such as the degree of detachment of the coleoptile from the shoot, the presence or absence of tillers etc. These differences are important to the frit fly because it lays most eggs in crevices on the plant or between the main shoot and tillers or on tillers. It is able to detect such differences with its ovipositor (Ibbotson, 1960) and will therefore lay more readily on some plants than others. It is unlikely that an individual female will lay all her ripe eggs in any one place in the field without being disturbed, perhaps by active carabids running through the oat crop (Jones, 1968), or by wind moving plants against each other. Other flies finding the same 'suitable' plant will also choose it, thus giving an overall picture of a clumped egg distribution. The clumped egg distribution also observed among the spikelets probably occurred for the same reason - heterogeneity among the spikelets. Many eggs (up to 12) per spikelet recorded in table 47 suggest that competition between the larvae must play an important part in determining the size of the populations of pupae and adults from this generation, since it is unlikely that 12 larvae can develop fully in a spikelet. The maximum numbers of empty puparia found per spikelet by previous workers was four (Southwood and Jepson, 1962) or six (Empson, 1958).

Table 43 Distribution of eggs among oat plants of different densities and row spacings (1975)

Date	Mean no. per plant $\bar{X}$	Variance s^2	Type of distribution best fitted at P = 0.05	K in the negative binomial
8.6m PLANTS/HECTARE IN ROWS SPACED 7.5cm APART				
2.6.75.	0.25	0.34	Poisson	—
10.6.75.	0.65	1.13	Negative binomial	0.84
16.6.75.	0.46	0.86	" "	0.50
23.6.75.	0.13	0.14	Poisson	—
30.6.75.	0.07	0.10	Poisson	—
4.3m PLANTS/HECTARE IN ROWS SPACED 15cm APART				
2.6.75.	0.30	0.42	Negative binomial	0.80
10.6.75.	1.37	4.06	" "	0.73
16.6.75.	0.84	1.18	" "	1.64
23.6.75.	0.89	1.57	" "	1.03
30.6.75.	0.0	—	—	—
1.4m PLANTS/HECTARE IN ROWS SPACED 45cm APART				
2.6.75.	0.27	0.42	Negative binomial	0.32
10.6.75.	3.57	17.53	" "	0.84
16.6.75.	3.02	7.77	" "	1.38
23.6.75.	2.31	8.92	" "	0.75
30.6.75.	1.86	6.10	" "	0.69

m = million

Table 44 Distribution of eggs among oat plants of different densities and row spacings (27.5.76)

Densities and row spacings of oats	$\bar{X}$	S^2	Type of distribution best fitted at $P = 0.05$	K in the Negative binomial
14.4million plants/ha in 5cm rows	0.24	0.55	Negative binomial	0.22
13.7million " " 15cm rows	0.13	0.17	" "	0.46
5.1million " " 15cm rows	0.31	0.51	" "	0.32
1.4million " " 15cm rows	0.68	1.49	" "	0.41
1.4million " " 45cm rows	0.38	0.73	" "	0.32

Table 45 Distribution of eggs among oat plants with bare or weedy background.

Date	Mean/plant $\bar{X}$	Variance s^2	Type of distribution best fitted at P=0.05	K in the Negative binomial
		OAT PLANTS WITH BARE BACKGROUND		
28.5.75.	0.29	0.46	Double Poisson	——
4.6.75.	0.27	0.30	Poisson	——
11.6.75.	1.01	2.65	Negative binomial	0.68
19.6.75.	0.73	1.19	" "	0.76
26.6.75.	0.25	0.39	" "	0.38
		OAT PLANTS WITH A BACKGROUND OF WEEDS		
28.5.75.	0.29	0.54	Negative binomial	0.26
4.6.75.	0.44	0.88	Double Poisson	——
11.6.75.	0.33	0.47	Negative binomial	0.58
19.6.75.	0.14	0.26	" "	0.12
		OAT PLANTS WITH A BACKGROUND OF WEEDS + MUSTARD		
28.5.75.	0.54	0.98	Negative binomial	0.67
4.6.75.	0.51	0.66	" "	1.31
11.6.75.	0.48	1.76	" "	0.16
19.6.75.	0.10	0.16	" "	0.14
26.6.75.	0.05	——	——	——
		OAT PLANTS WITH A BACKGROUND OF WEEDS + CLOVER		
28.5.75.	0.91	2.44	Negative binomial	0.58
4.6.75.	0.36	0.52	" "	0.63
11.6.75.	0.74	1.45	" "	0.77
19.6.75.	0.30	0.45	" "	0.59

Table 46 Distribution of eggs among spikelets of oat plants with bare background or with an 'overgrowth' of weeds, weeds + mustard or weeds + clover (11.7.75).

Treatments	Mean/spikelet $\overline{X}$	Variance S^2	Type of distribution best fitted at $P = 0.05$	K in the Negative binomial
Oat plants with bare background	1.43	3.07	Negative binomial	1.34
Oat plants with an 'overgrowth' of weeds	0.77	1.11	" "	1.68
Oat plants with an 'overgrowth' of weeds + mustard	0.73	1.30	" "	0.90
Oat plants with an 'overgrowth' of weeds + clover	0.86	1.62	" "	1.04

Table 47 Distribution of eggs among oat spikelets of different densities (1975)

Spikelet density (x10^6)	No of eggs per spikelet													$\bar{X}$	s^2	Type of distribution best fitted at $P = 0.05$	K in the negative binomial
	0	1	2	3	4	5	6	7	8	9	10	11	12				
251.4 spikelets per hectare	92	102	69	38	25	11	3	1	3	-	-	-	-	1.62	2.45	Negative binomial	3.20
152.4 spikelets per hectare	84	96	73	37	25	16	4	3	-	3	1	-	-	1.80	3.08	"	2.69
91.5 spikelets per hectare	94	98	114	75	53	27	10	15	6	2	-	2	2	2.36	4.33	"	2.87

6.4. Dispersion of eggs among potted oat plants by individual females in the laboratory.

It was stated above (sub-section 6.3.) that clumping of frit fly eggs in field conditions was probably due to a combination of the behaviour of the female flies and the heterogeneity of the oat plants. This implies that if the plants were equally suitable or at least, very nearly so and eggs are laid singly by individual females the dispersion of the egg population should be random or very nearly so. This experiment was designed to test this hypothesis.

Oats were seeded in sixteen 8.75cm-diameter pots and thinned to 8 per pot soon after germination. The pots were divided into 2 sets of 8 and taken to the laboratory from the green-house when the plants were at the late 2-leaf stage and some of them had loose coleoptiles, that is, coleoptiles had separated from the stem to create a crevice. In one set of pots the coleoptiles that had not provided a crevice were artificially separated from the stems so that all the plants in the pots in this set had suitable coleoptiles for oviposition. The plants in the other set of pots were not interfered with, so each pot in this set contained a mixture of plants with loose and tight coleoptiles, i.e. suitable and less suitable coleoptiles for oviposition. The soil in every pot was kept wet to reduce soil oviposition. Cunliffe and Hodges (1946) found fewer eggs in wet than in dry soils. Cylindrical cellulose acetate cages were placed over the pots and 1 ovipositing female and 2 males introduced into each cage. The numbers and the distribution of the eggs laid after 48 hours were checked and the results presented in tables 48 and 49 below.

In the first set of pots (table 48) many more plants were oviposited and most of the eggs occurred singly or in twos, rarely in

Table 48 Distribution of eggs among 8 oat plants with loose coleoptiles by individual female flies during a 48-hour period.

Insect No.	No. of eggs/plant								$\overline{X}$	s^2	Type of distribution best fitted at P = 0.05
	1	2	3	4	5	6	7	8			
1	0	0	0	0	1	1	1	2	0.63	0.55	Poisson
2	0	0	0	0	0	1	2	2	0.63	0.84	"
3	0	0	0	1	1	1	1	2	0.75	0.50	"
4	0	0	0	0	1	1	2	2	0.75	0.79	"
5	0	0	0	1	1	1	2	2	0.88	0.70	"
6	0	0	1	1	1	1	2	2	1.0	0.57	"
7	0	0	0	0	2	2	2	3	1.13	1.55	"
8	0	0	0	2	2	2	3	3	1.5	1.71	"

Table 49 Distribution of eggs among 8 oat plants with tight and loose coleoptiles by individual female flies during a 48-hour period.

Insect No.	No. of eggs/plant								$\overline{X}$	s^2	Type of distribution best fitted at P = 0.05
	1	2	3	4	5	6	7	8			
1	0	0	0	0	0	0	2	4	0.75	2.21	———
2	0	0	0	0	0	0	2	4	0.75	2.21	———
3	0	0	0	0	1	1	2	4	1.0	2.0	Negative binomial
4	0	0	0	0	1	1	2	4	1.0	2.0	" "
5	0	0	0	0	1	2	2	4	1.13	2.13	" "
6	0	0	0	0	0	1	1	9	1.37	9.69	" "
7	0	0	0	0	1	2	3	8	1.75	7.64	" "
8	0	0	1	1	1	4	4	4	1.87	3.27	" "

——— means insufficient data to fit the computer programme threes and the distribution was best described by the poisson model. In the second set of pots however, (table 49) fewer plants were oviposited and therefore, the eggs occurred in clumps and the distribution best fitted the negative binomial model. The hypothesis is therefore upheld. It can be inferred from this experiment that the distribution of eggs by individual females in a homogeneous, suitable oat crop is random and the clumped dispersion of eggs often found in the field is due to the heterogeneity of the habitat acting in conjunction with the behaviour of the female flies in seeking and laying mostly on suitable plants among many seemingly less suitable plants.

6.5. Dispersion of larvae and puparia among oat plants of different densities and row spacings in the field.

Unlike the distribution of eggs among oat plants in the vegetative phase (tables 43 and 44) which was best described by the negative binomial model at all plant densities and row spacings tested and at almost all egg densites observed, the distribution of larvae and puparia of the tiller generation tended to vary according to the density of these immature stages in the plants; for example, in table 50, early in the season (May 19 and May 27) when entry into the plant was less successful because of the presence of relatively few tillers, except in the disperse plantings (table 32), the distribution was best described by the poisson model. This was the case in the dense planting with closely-spaced rows on all sampling dates and on the first 3 sampling dates in the dense planting with intermediate row spacing and in the sparse planting. Then, as _O. frit_ densities increased to an intermediate level, it could no longer be described by the poisson model, but by the negative binomial. This was the case on the remaining 3 sampling dates in the dense planting with intermediate row spacing and in the sparse planting on May 27, June 3, June 10 and June 17 in the disperse planting with widely-spaced rows. Finally, at very high O. frit densities, which occurred mainly in the disperse plantings where oviposition intensity was highest (table 28) the distribution returned to random and could once more be described by the poisson model. Although, tiller production was also highest in the disperse plantings (table 32) tillers are usually too small to support larvae to pupation (sub-section 3.1.2c.).

Southwood (1966) stated that if the dispersion of a population becomes more regular then intensification of competition should be suspected. Perhaps, framed in another way, it can be stated that if the dispersion of a population changes from clumpness to randomness then intensification of competition should be suspected. It was observed by Jones (1969) in all her tests in the laboratory that larvae migrated from a plant with many eggs to surrounding plants and this made her to conclude that it made little difference to survival whether the plants were 1cm or 5cm away. The Narrator has also observed in potted oat plants in the laboratory (sub-section 5.2.3., table 39) that larvae can travel up to 8cm to attack other shoots, although surprisingly,that same experiment failed to show that increasing the number of plants per pot, thereby decreasing the actual distance that has to be travelled by the 'migrating' larvae enhances survival. There is at any rate evidence, at least in the laboratory, that larvae can move from plant to plant. It is suggested, therefore, that the change from clumped distribution to randomness observed at high O. frit densities was a result of intensification of competition, and that the larvae responded by emigrating from the crowded shoots.

If the emigration succeeds and another less crowded shoot is found and colonized, the overall effect will be a tendency towards evenness in the population in all the plants. On the other hand, if emigrating larvae fail to find and invade new shoots, i.e., they die, the overall effect on the dispersion of the population can still be the same, but the population in all the plants will now be at a lower level.

Table 50 Distribution of larvae and puparia of the tiller generation among oat plants of different densities and row spacings (1976).

Densities and row spacings	Date	Mean/plant $\overline{X}$	Variance S^2	Type of distribution best fitted at P=0.05
14.4million plants/ hectare in 5cm rows	May 19	0.0	——	——
	" 27	0.80	0.68	Poisson
	June 3	1.16	0.88	"
	" 10	1.40	0.10	"
	" 17	1.55	2.11	"
	" 27	1.86	2.00	"
13.7million plants/ hectare in 15cm rows	May 19	0.09	0.10	Poisson
	" 27	1.25	1.38	"
	June 3	1.88	1.99	"
	" 10	2.01	2.52	Negative binomial
	" 17	2.36	3.83	" "
	" 27	2.70	3.65	" "
5.1million plants/ hectare in 15cm rows	May 19	0.27	0.25	Poisson
	" 27	3.26	3.96	"
	June 3	3.06	3.46	"
	" 10	3.58	4.86	Negative binomial
	" 17	4.05	4.42	" "
	" 27	3.79	6.57	" "
1.4million plants/ hectare in 15cm rows	May 19	0.84	1.25	Negative binomial
	" 27	4.60	5.85	Poisson
	June 3	4.03	4.03	"
	" 10	5.30	6.31	"
	" 17	4.70	7.26	"
	" 27	5.00	5.86	"
1.4million plants/ hectare in 45cm rows	May 19	0.34	0.54	Poisson
	" 27	3.57	5.07	Negative binomial
	June 3	3.51	5.16	" "
	" 10	3.67	5.66	" "
	" 17	4.04	7.30	" "
	" 27	4.44	6.19	Poisson

SECTION VII

EFFECTS OF THE DENSITIES OF ADULT FRIT FLIES AND OAT PLANTS ON OVIPOSITION AND ON THE DENSITY OF EGGS ON THE 'QUALITY' OF THE OFFSPRING.

7.1. Oviposition by individual females in relation to different densities of potted oat plants.

It was shown in the field (table 25) and in the laboratory (table 37) that the numbers of adult flies trapped increased with increasing 'real' and 'artificial' oat plant densities and that the numbers of eggs laid by a group of flies also increased with increasing oat plant densities (tables 29 and 38). This experiment attempts to provide information on the ways in which different densities of oats affect the oviposition of individual females kept captive throughout their life times in the presence of males.

Oats were seeded in 8.75cm-diameter pots and thinned to 1, 5 and 10 plants per pot soon after germination. Cylindrical cellulose acetate cages were placed over the plants when at the 3-leaf stage with suitable coleoptiles for oviposition, and 1 newly-emerged adult female fly of known pupal weight and 2 newly-emerged males introduced into each cage. Hillyer (1964) observed that the minimum pre-oviposition period was increased by about 3 days in small flies (produced by crowding the larvae) compared with larger flies. The effects of variation due to the size of the females was therefore eliminated from this experiment by using large female flies (with pupal weights of 0.80 to 0.90mg) in all the treatments. Newly-emerged males were used in this experiment since Hillyer (1965) found that a male fly is often ready to copulate a few hours after emergence. A female fly will however not copulate until the ovary is mature. The plants were replaced with new ones every 2, 3 or 4 days while the previous ones were examined for eggs. The trials were terminated when the females died. In cases where males died before the females the former were replaced. The trials were replicated twice.

The total numbers of eggs laid in the 3 treatments were similar (table 51), but the females caged continuously over 1 oat plant/pot had longer pre-oviposition periods than those caged over 5 or 10 plants/pot (fig.23). Once oviposition started, the density of oat plants did not seem to affect the oviposition rate significantly. Hillyer (1964) stated that the host plant stimulates ovary maturation; it seems probable therefore that the strength of the host plant stimulus, which is likely to increase with increasing plant density in the cage, accelerated ovary maturation at higher plant densities with the resultant shortening of the length of the pre-oviposition period.

Table 51 Fecundity of individual females caged over oat plants of different densities.

	Numbers of eggs laid		
No. of plants/pot	I	II	Mean
1	25	37	31
5	29	39	34
10	26	30	28

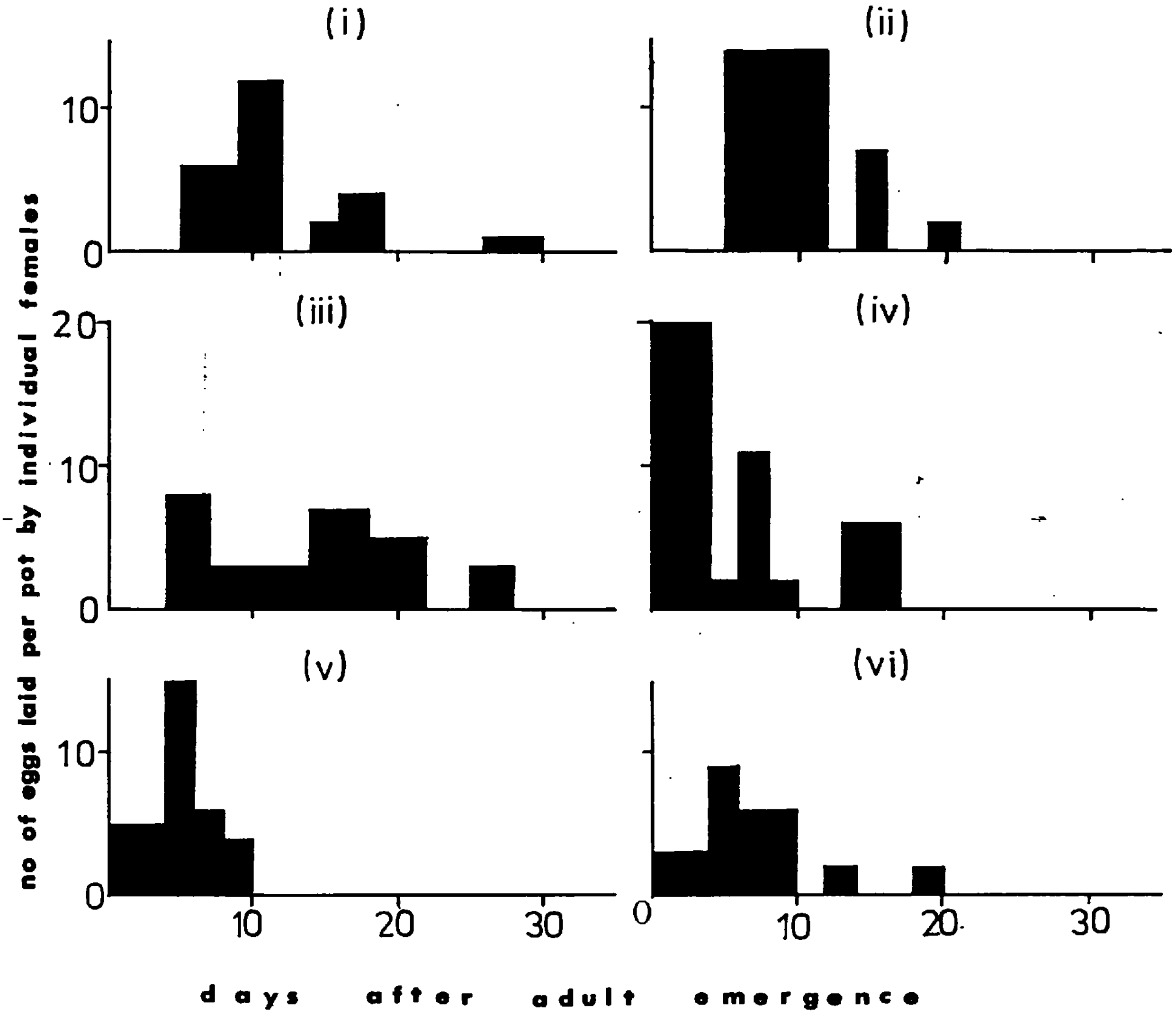

Fig. 23 Oviposition by individual females in relation to different densities of oat plants.

(i) and (ii) 1 plant per pot

(iii) and (iv) 5 plants per pot

(v) and (vi) 10 plants per pot

7.2. Oviposition by a group of adult flies in relation to different densities of oats.

This experiment was investigated in 3 stages (series). Series 1: Oats were seeded in 14cm-diameter pots and the plants thinned to 1, 5 and 20 per pot soon after germination. They were offered for oviposition when they attained the 3-leaf stage with loose coleoptiles. Three groups of newly-emerged adult flies (15 males and 15 females) of unknown pupal weights were collected from the breeding cage and confined over oat plants of different densities in cylindrical cellulose acetate cages placed over the pots. The plants were replaced by new ones every 48 hours and the numbers of eggs laid in the different pots counted. The three groups of flies were initially caged over pots containing 20 plants/pot until oviposition started, as it was thought that the strength of the host plant stimulus accelerates ovary maturation (sub-section 7.1). Subsequently, two of the groups of flies were offered 1, 5 or 20 plants/pot every 48 hours while the third group was offered 20 plants/pot every 48 hours throughout the experimental period. The results are presented in fig.24 below.

There was an initial increase in the numbers of eggs laid by the 3 groups of flies when offered 20 plants/pot due mainly to the different pre-oviposition periods of the individuals in the groups (figs. 24 (i) to 24 (iii)). The increase soon reached a plateau in the group continuously offered 20 plants/pot, i.e., when all the flies had started ovipositing (fig.24 (i)). However, in the other 2 groups of flies offered 1, 5 or 20 plants/pot there was a decrease in the numbers of eggs laid in pots containing 1 or 5 plants when the preceding pot contained 20 plants and vice versa

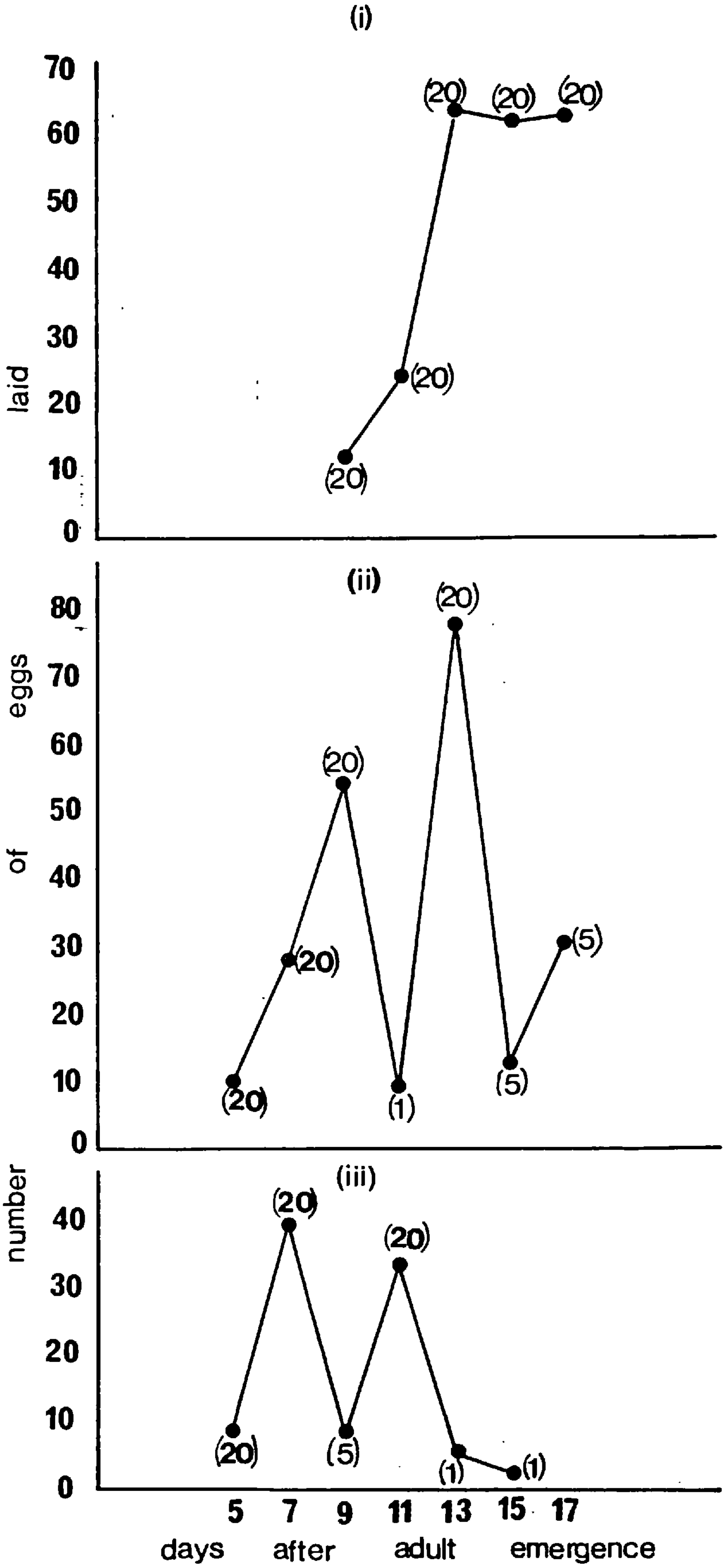

Fig.24 Oviposition by groups of adult flies (15 males and 15 females) alternately offered 1, 5 or 20 oat plants per pot.

(i) Flies continuously offered 20 plants/pot

(ii) and (iii) Flies offered 1, 5 or 20 plants/pot.

(figs. 24 (ii) and 24 (iii)). This experiment shows that a group of ovipositing captive flies can withhold some of their eggs for at least 48 hours when confronted with less than optimum conditions for oviposition, e.g., inadequate number of caged plants in this experiment. Perhaps there was interference between the ovipositing flies when fewer plants were present in the cage. The next two series of experiments were designed to investigate whether the holding back of the eggs is permanent (series 2) and also whether there is interference between groups of ovipositing flies when offered 1 plant/pot (series 3).

Series 2: Pupae dissected from infested plants in the laboratory were weighed and reared to adults. When adults emerged they were sexed and females which weighed between 0.6 to 0.7mg as pupae were collected and divided into 4 groups of 7. These were smaller females when compared with those used in the experiment described earlier in sub-section 7.1. Cylindrical cellulose acetate cages were placed over two 8.75cm-diameter pots each containing 1 oat plant at the 3-leaf stage and over another 2 pots each containing 5 oat plants also at the 3-leaf stage. The four groups of females were introduced into each of the 2 sets of pots and 8 newly-emerged males added to each cage. The plants were replaced with new ones of the same densities (1 or 5 plants/pot) after 2, 3 or 4 days while the old plants were examined for eggs. The trials were terminated when all the females died. In all instances where males died before the females, the former were replaced. The results are presented in table 52 and fig.25. Each treatment was replicated only twice because there was little variation between the replicates.

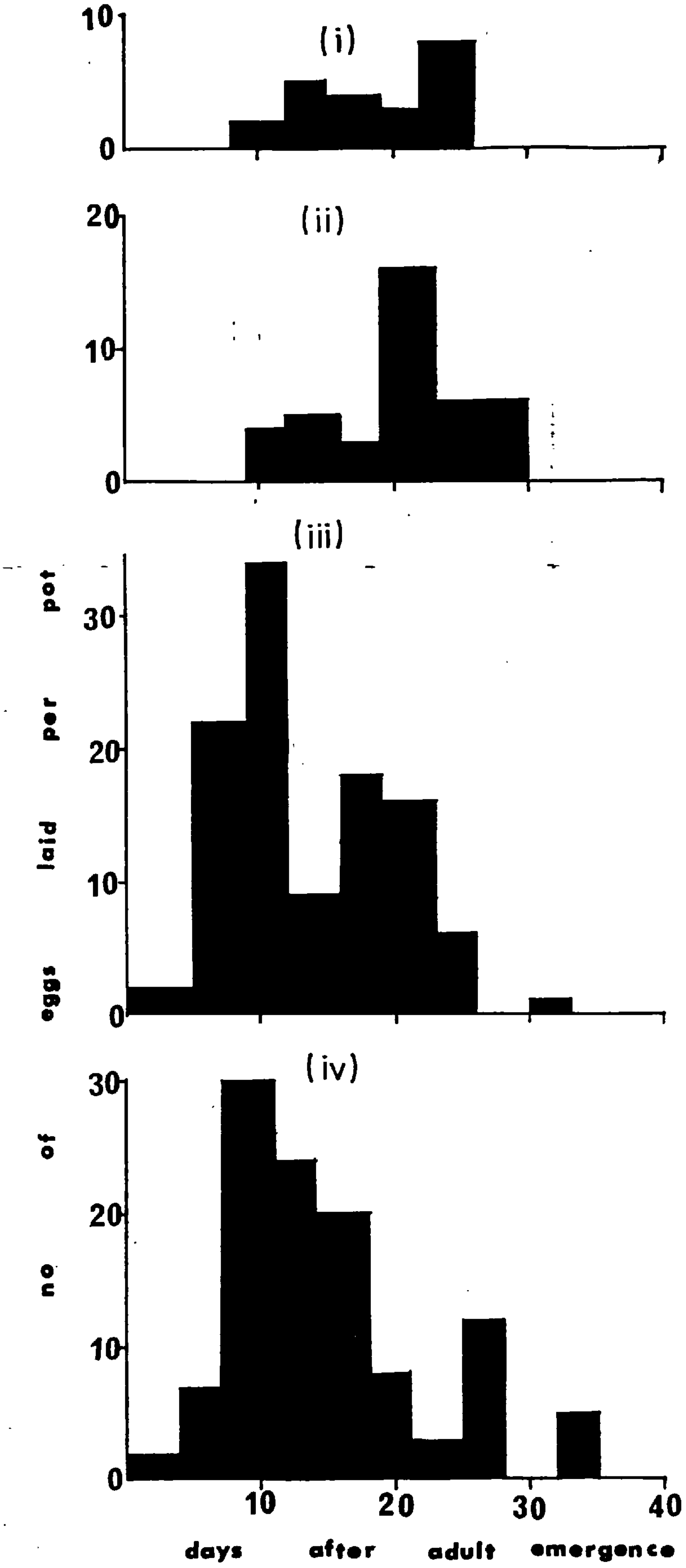

Fig. 25 Oviposition by groups of 7 small females and 8 males in relation to different densities of oat plants.

(i) and (ii) 1 oat plant per pot

(iii) and (iv) 5 oat plants per pot

Flies caged over 1 plant/pot had significantly longer pre-oviposition period (fig.25) and laid significantly fewer eggs (table 52) than those caged over 5 plants/pot. Also, most of the eggs were laid within the first 15 days in the groups of flies caged over 5 plants/pot. It is concluded from this experiment that the number of plants offered continuously in a cage to a group of ovipositing flies as distinct from a single fly (table 51) can permanently affect the total numbers of eggs laid.

Table 52 Oviposition by groups of flies caged over oat plants of different densities.

	Numbers of eggs laid by groups of 7 small females and 8 males			
No of plants/pot	I	II	Mean	$S_{\bar{X}}$
1	22	40	31.0	9.0
5	108	111	109.5	1.5

Series 3: Pupae were dissected from infested plants and weighed as in series 2, but unlike series 2 bigger females (with pupal weights of between 0.8 and 0.9mg) were used in this experiment because most of the pupae dissected from the plants fell into this weight category at the time the experiment was conducted. Pots (8.75cm-diameter) containing 3 sets of plants - 1 oat plant/pot, 1 oat plant + 9 'artificial' plants per pot and 10 oat plants/pot were employed. The 'artificial' plants have been described in sub-section 2.3.2. As before, cylindrical cellulose acetate cages were placed over the pots and 7 big female flies and 8 males introduced into each. The plants were replaced with new ones, egg counts made on old plants

and males replaced when they died as in previous experiments. Each treatment was replicated 3 times. Two hours of continuous observation on the oviposition behaviour of the flies was made on one group of flies in each treatment ten days after adult emergence, when the pre-oviposition period has ended and most females had started to lay eggs. This was to obtain information on whether there was any interference to oviposition by having different densities of plants in cages containing the same numbers of flies.

Ibbotson (1960) has described in detail the oviposition behaviour of individual female flies kept captive in the absence of other ovipositing flies. The observations made in this study in the groups of flies offered 10 oat plants/pot were similar to those of Ibbotson (1960). Basically, the oviposition behaviour is as follows - the fly crawls to the basal part of the plant after landing, makes several movements up and down the basal parts of the plant with the tip of the ovipositor in close contact with the plant surface until a crevice is detected, then the ovipositor is inserted in the crevice, extended and 1 or 2 eggs extruded. The whole process takes between 3 and 15 minutes but can be longer if a crevice is not found in time. Usually, a fly takes a short rest after laying 1 or 2 eggs and in most cases leaves for another plant if available; otherwise it rests on the plant on which it has oviposited or flies to the side or top of the cage. It was observed that when a fly has started going through to oviposition process at the base of a plant and another fly arrived, one of them left the plant and on no occasion were 2 female flies observed to be performing oviposition movement simultaneously at the base of the same plant. Whichever fly remained behind, the oviposition process often started afresh. Such interference was more frequent in the pot containing only 1 oat plant, less frequent in the pot containing 1 oat plant + 9 'artificial' plants and was not observed at all in the pot containing 10 oat plants. A fly that leaves an oat plant in a pot containing 1 oat plant plus 9 'artificial' plants because another fly was performing oviposition movement there often stayed on an 'artificial' plant close to the 'real' oat plant until the other fly had extruded her eggs, when it then returned to the 'real' oat plant to lay her own eggs. On the other hand, a fly leaving an oat plant in a pot containing only 1 oat plant was observed on one occasion to jump to the side of the cage, and then moved to the top of the cage and remained there throughout the observation period. Perhaps, such a fly will never lay her full complement of eggs again.

Most eggs were laid by the groups of flies offered 10 oat plants/pot, least by the groups offered 1 oat plant/pot and those offered 1 oat plant plus 9 'artificial' plants/pot laid intermediate numbers of eggs (table 53). These differences are probably the result of interference during the oviposition process already mentioned above leading to the flies not laying their full complements of eggs. Although, no eggs were laid on the 'artificial' plants because they did not contain host plant stimulus necessary for the release of oviposition behaviour, they however reduced the frequency of contact between the flies and also acted as 'waiting room' close to the real oat plants on which a fly can stay and wait until the 'real' oat plant becomes vacant.

Table 53 Oviposition by groups of flies caged over 'real' and 'artificial' oat plants of different densities.

	No of eggs laid by groups of 7 big females and 8 males				
Treatments	I	II	III	Main	$S_{\bar{X}}$
1 oat plant	87	94	104	95.0	4.93
1 oat plant plus 9 'artificial' plants	134	160	179	155.7	13.04
10 oat plants	202	221	266	229.7	18.98

7.3. Effects of larval and pupal densities in the field on the sizes of pupae

The larval and pupal numbers per plant and per sq metre area of oats were related to the densities and row spacings of oats as shown in sub-section 5.1.3. and table 30. There, it was apparent that larvae and pupae were most crowded in the most disperse plantings, less crowded in the sparse planting and least crowded in the dense plantings. In this sub-section, an attempt is made to find out whether pupae produced under these different larval and pupal densities differ in weight, that is, whether competition during the larval stage affects the sizes of the pupae produced.

Pupae collected by dissecting the plant samples taken from the field on June 10, 1976 were weighed and reared singly in glass vials in the laboratory until adult frit fly or parasites emerged. The weights of hatched females and males are presented in table 54 and fig.26.

Females were bigger than the males at all observed larval and pupal densities (table 54). The general trend observed was a decrease in the sizes of pupae (males and females) with increasing larval and pupal densities (table 54), except in the most disperse planting with intermediate row spacing which had most larvae and pupae per plant, but also had most tillers/plant (table 32), therefore, relatively more food was available for the developing larvae. Similarly, the observed distribution of the pupae according to weight classes (fig.26) showed that there was a higher proportion of bigger pupae (males and females) in the least crowded conditions (figs. 26 (i) to 26 (iv) than in the most crowded conditions (figs. 26 (vii) to 26 (x)). It is concluded from the above that larvae produced under crowded conditions in the field develop into smaller pupae as a result of competition.

Table 54 Weights of pupae produced under different larval densities in the field.

Densities and row spacings of oats	No of larvae and pupae/plant from table 30	Weight of pupae (mg)					
		Males			Females		
		N	$\bar{X}$	$S_{\bar{X}}$	N	$\bar{X}$	$S_{\bar{X}}$
14.4m plants/ha in 5cm rows	1.4a	29	0.57	0.01	28	0.88	0.03
13.7m " " 15cm "	2.0b	88	0.54	0.01	69	0.86	0.01
5.1m " " 15cm "	3.6c	71	0.52	0.01	69	0.85	0.02
1.4m " " 15cm "	5.3d	32	0.52	0.07	30	0.83	0.03
1.4m " " 45cm "	3.6c	71	0.50	0.08	71	0.80	0.02

Fig.26

(i) and (ii)	14.4	million	plants/ha	in	5cm	rows
(iii) and (iv)	13.7	"	"	"	15cm	"
(v) and (vi)	5.1	"	"	"	15cm	"
(vii) and (viii)	1.4	"	"	"	15cm	"
(ix) and (x)	1.4	"	"	"	45cm	"

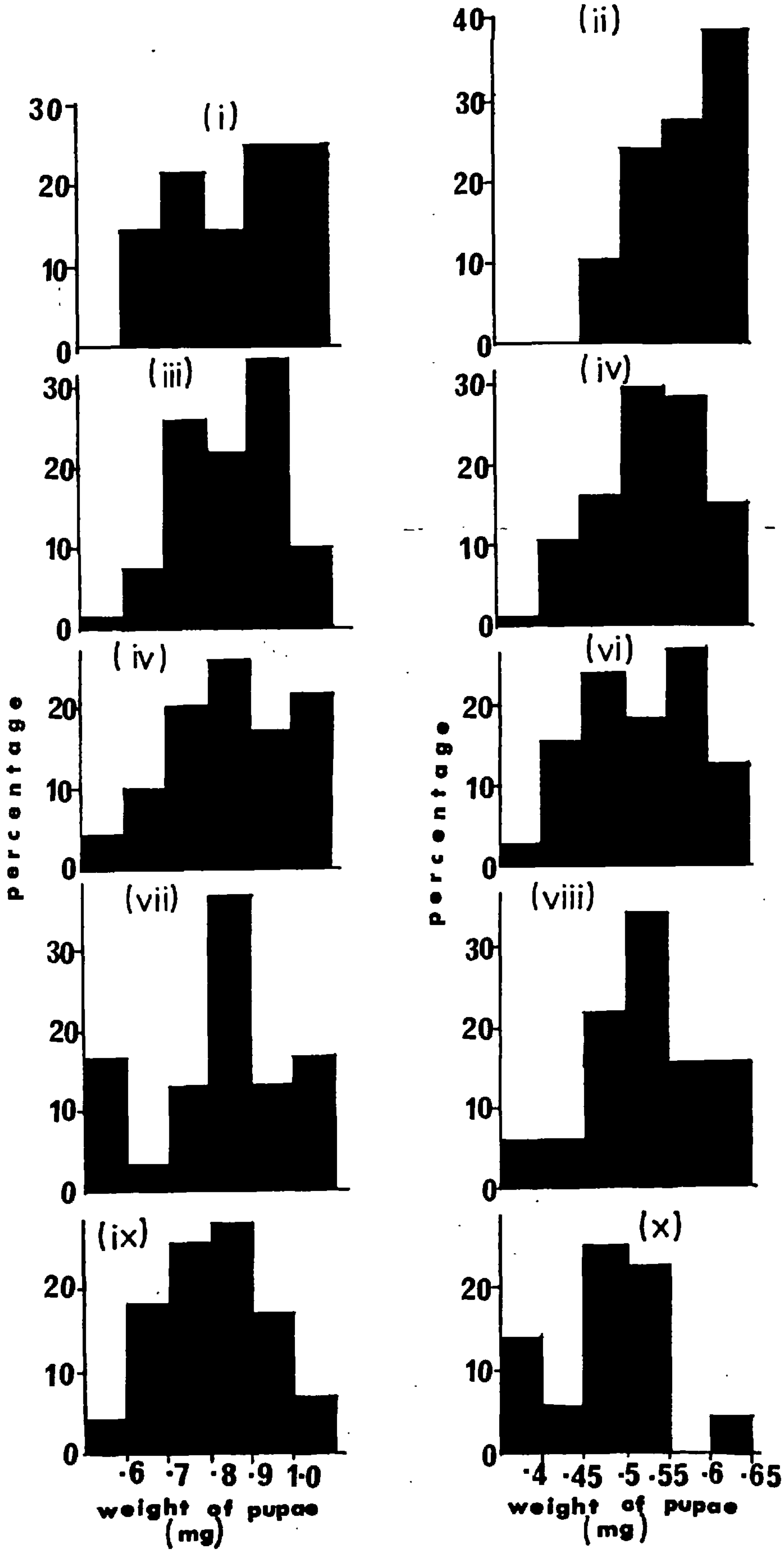

Fig.26 Observed distribution of the weights of hatched pupae from field sample taken on 10.6.76. left part - females; right part - males.

7.4. Effects of larval and pupal densities in the field on the length of the pre-oviposition period, fecundity and the sizes of eggs produced by emergent adults.

Random samples of females in the weight classes illustrated in fig.26 were caged individually with 2 males over 5 potted oat plants at the 3-leaf stage and oviposition followed as already described in sub-section 7.1, except that plants were changed daily until egg laying started in order to obtain accurate information on the lengths of the pre-oviposition period. The eggs laid were measured on a binocular microscope with a graduated eye piece which was calibrated with a stage micrometre. Some of the females either escaped or were sterile and therefore did not lay eggs, hence the differences in the numbers of females in the different classes presented in table 55 below.

There were large variations between individuals in the weight classes seemingly due to genotypic differences. These resulted in large standard errors of treatment means (table 55), however, certain trends could still be picked out. Thus, the largest females had the shortest pre-oviposition periods and laid most eggs, in contrast to the smallest females which had the longest pre-oviposition periods and laid fewest eggs (table 55, figs. 27 (i) and 27 (ii)). The effects on sizes of eggs laid was less clear cut because some females that laid fewer eggs 'compensated' by laying bigger eggs, also the age of the females was found to affect the sizes of eggs laid (table 56). Thus, the eggs laid intially were significantly bigger than those laid towards the end of the oviposition period (table 56).

Table 55. Pre-oviposition period, fecundity and the sizes of eggs produced by emergent adults from pupae of different sizes

	Pre-oviposition (days)			Fecundity			Egg length (mm)		
Wt of female pupae (mg)	N	$\bar{X}$	$S_{\bar{X}}$	N	$\bar{X}$	$S_{\bar{X}}$	N	$\bar{X}$	$S_{\bar{X}}$
0.5 to 0.59	2	15.5	1.5	2	9.5	1.5	15	0.66	.008
0.6 to 0.69	2	18.0	6.0	2	19.0	3.0	32	0.61	.010
0.7 to 0.79	6	12.2	3.9	6	24.0	6.0	88	0.67	.004
0.8 to 0.89	7	12.3	3.5	5	28.4	7.9	85	0.67	.005
0.9 to 0.99	7	10.4	1.9	5	43.0	5.4	51	0.68	.006
> 1.0	4	5.0	1.4	4	46.0	13.2	98	0.67	.003

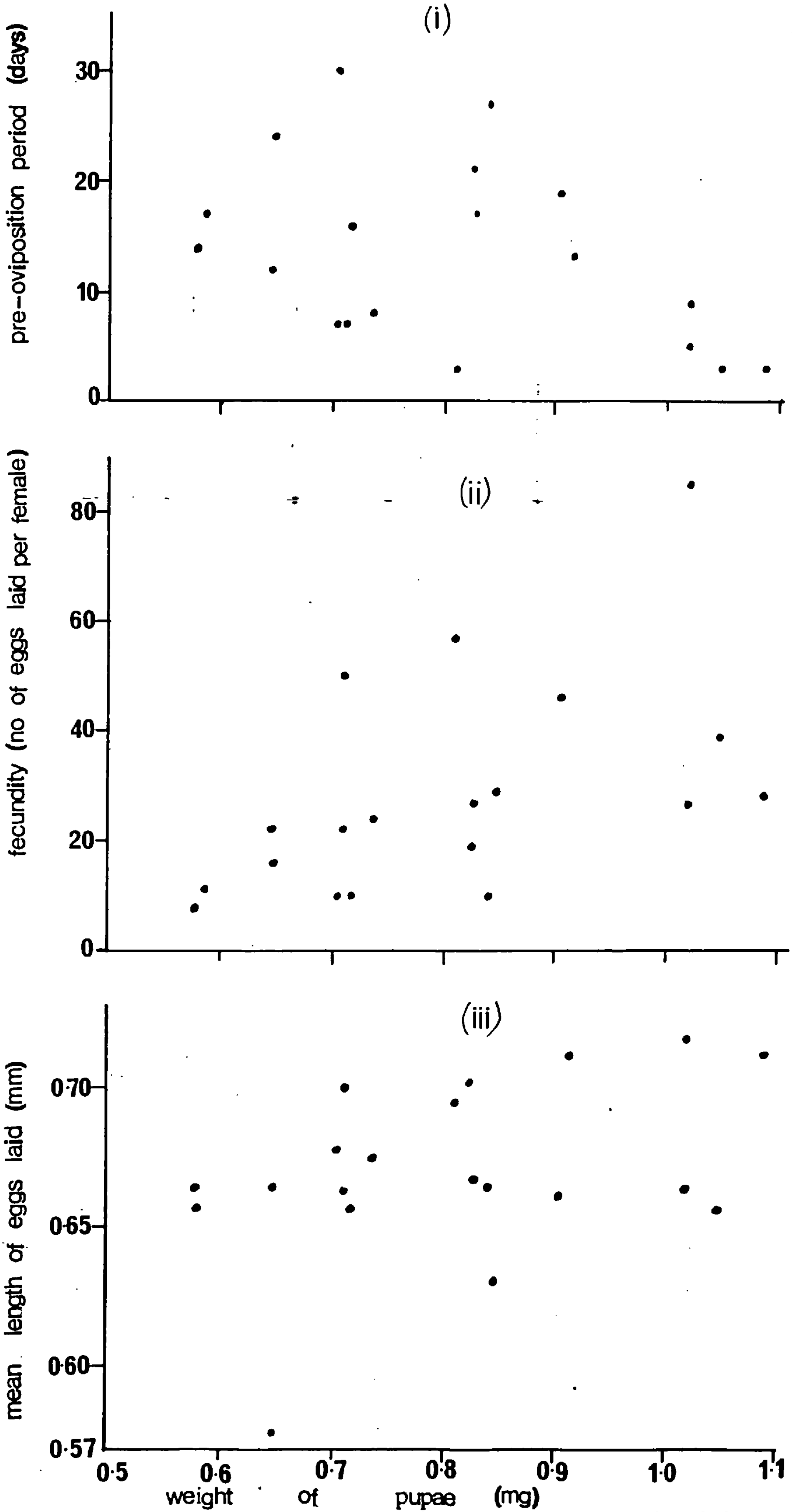

Fig. 27 Relationships between pupal weights and the pre-oviposition periods, fecundity and the sizes of eggs produced by emergent adults.

Table 56. Mean length of eggs laid at different ages by females of different sizes.

Mean wt of pupae from which the adults used emerged (mg)	Mean length of eggs (mm) Age from commencement of oviposition (days)			
	1 - 4	9 - 12	17 - 20	25 - 28
0.59	0.69a	0.62b	—	—
0.71	0.68a	0.65b	0.61c	—
0.91	0.69a	0.61b	0.62b	—
1.02	0.70a	0.69a	0.63b	0.63b

Figures not followed by the same letters in the same row are significantly different at P = 0.05.

The following points have emerged from this section, namely, that pupae collected in the disperse plantings were smaller than those from the dense plantings where there was little or no competition during the larval stage; smaller females were less fecund and had longer pre-oviposition periods than bigger females; and ovipositing females were able to hold back their eggs and thus reduced the total numbers of eggs laid when confined in a cage and in the absence of many plants.

SECTION VIII

SEX RATIOS OF ADULT O. FRIT

8.1. Introduction

The sex ratio of an insect may be a useful indicator of the size and stability of a population (Solomon, 1976). Thus, differential mortality of male and female insects would appear to be an important factor in the population dynamics of the gypsy moth (Campbell, 1963) and spruce budworm (Morris and Miller, 1954). Yet, several workers (e.g; Steinhaus, 1954; Watt, 1961) have overlooked the importance of sex ratio, while many others have opted for the very convenient assumption of an 50:50 sex ratio. But all insects do not comply with the 50:50 norm, and furthermore, different sexes may have different migratory tendencies, which may vary from generation to generation and from habitat to habitat. Cook (1945), working on migrations of Circulifer tenellus suggested that females must be leaving the hosts about as rapidly as they become adult because he found a rapidly diminishing population of nymphs, a low adult population and an excess of males (the sex ratio at emergence is 1:1) on plants where these insects were breeding. Very little information is available on the sex ratio of the frit fly in grassland; none on the sex ratio of the different generations in an oat crop or of the possible consequences of the cropping pattern on it. This aspect of the work attempts to provide information on the sex ratio of the different generations in an oat crop, on any possible effects of the cropping pattern on colonization by the sexes, and on the possible effects of competition during the larval stage on the ratio of the emergent adults.

8.2. Methods

Adult flies were trapped in the field in 1976 and sexed as described in sub-section 2.1.4. Pupae of the tiller generation were dissected from oat shoots and the sex determined when adults emerged. This gave the sex ratio of the tiller generation at emergence. The sex ratio of adults in the culture was determined by collecting adults emerging from potted oat plants initially infested with eggs by placing the pots in the oviposition cage. Also in the laboratory oat plants at the early 1-leaf stage were artificially infested with 1, 2, 3 or 4 newly-laid eggs and the sex of the emerging adults determined to obtain information on whether the sex ratio of emergent adults is altered by competition during the larval stage. Some of Southwood's unpublished data collected in oat crop at Silwood Park in 1961 are also presented to explain some of my field results. Southwood collected his data by placing pyramidal tents (plate 14) covering 0.84 sq metre (1 sq yd) on oats at dusk and collected the emerged flies in the morning at about 10.00 hours, as well as collecting adults by sweep net. The tent method gave the actual population of adults present in the field in the morning, and included both the overnight and the emerging adults up to the time of collection in the morning. However, for the period May to mid-June in oat crop, it represented only the overnight population of adults from the overwintering generation which invaded and passed the night in the crop, because no adults are emerging from spring sown oats at this time. In May and the 1st of June, 1977, adults were collected by sweep net from grasslands to obtain information on the sex ratio of the overwintering generation adults in grasslands.

Plate 14. Pyramidal tent.

8.3. Results

The proportion of females of the overwintering generation caught in water traps over oat crops was consistently higher than 80 per cent and this dropped to about 60 per cent in the tiller generation (fig.28). The total proportions of females caught in the water traps for the whole season were 84.3 and 62.9 per cent for the overwintering and tiller generations, respectively (fig.29 (i)). The former represented a significant departure from a 50:50 sex ratio at 0.001 probability level and the latter only at 0.05 level (table 57). Southwood's

(1961) unpublished results from tents and sweeps in oat crops for the overwintering generation were 80.4 and 82.4 per cent females, respectively and corresponding figures for the tiller generation were 56.8 and 47.4 per cent, respectively (fig. 29 (ii)). The former set of figures differed significantly from 50:50 sex ratio at 0.001 probability level, while the latter set of figures did not differ significantly (P>0.05) (table 57). In contrast to the above, consistently more males of the overwintering generation adults were caught with sweep net in grasslands in May and June 1, 1977 and these represented significant departures from 50:50 ratio, except on May 25 and May 26 (table 58).

An analysis of variance carried out on the proportions of females in trap catches of the overwintering and tiller generations over oat crops of different densities and row spacings did not show significant differences (P>0.05) between the treatments; however, the ratio of males to females in the trapped overwintering generation adults differed significantly (P<0.001) from a 50:50 ratio in all the treatments. The sex ratio of adults in the laboratory culture was approximately 50:50 (table 60); and competition between larvae did not alter the sex ratio of emergent adults (table 61), even though, higher mortalities and reduction in pupal sizes often occurred at high egg densities (table 9).

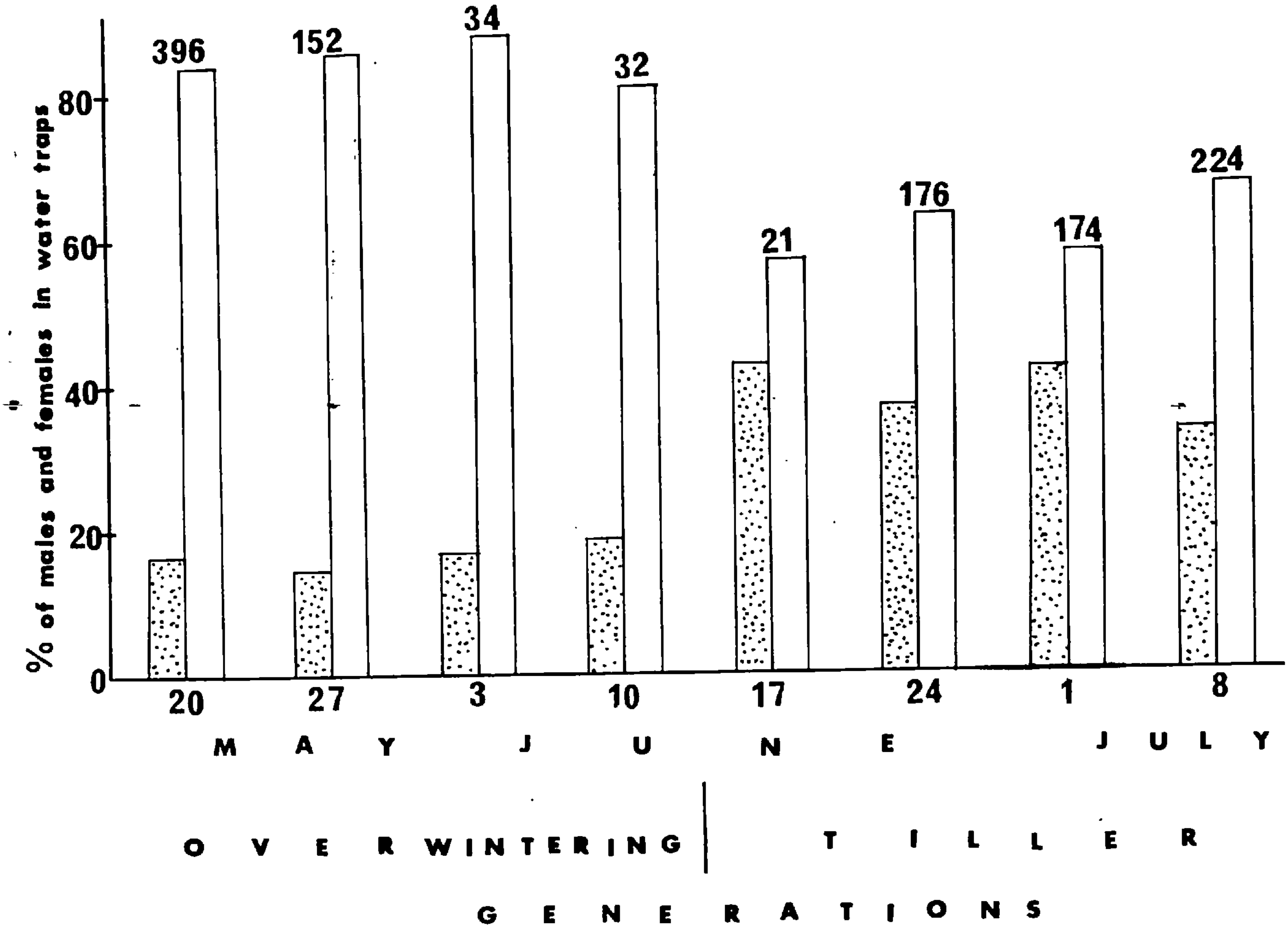

Fig.28 Sex ratio of adult frit flies caught in water traps over oat crop (1976).

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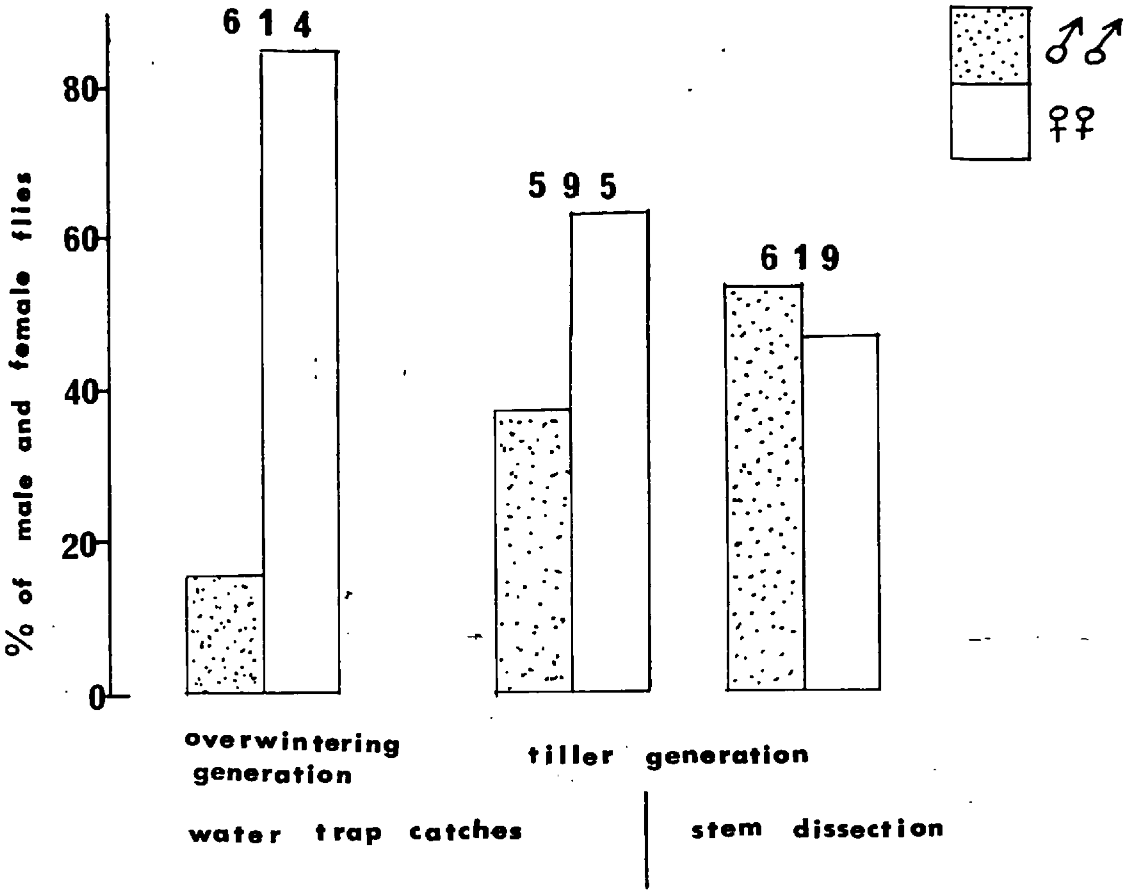


Fig.29 (i) The sex ratio of adult frit flies caught in water traps and those obtained from pupae collected by dissecting oat plants (1976).

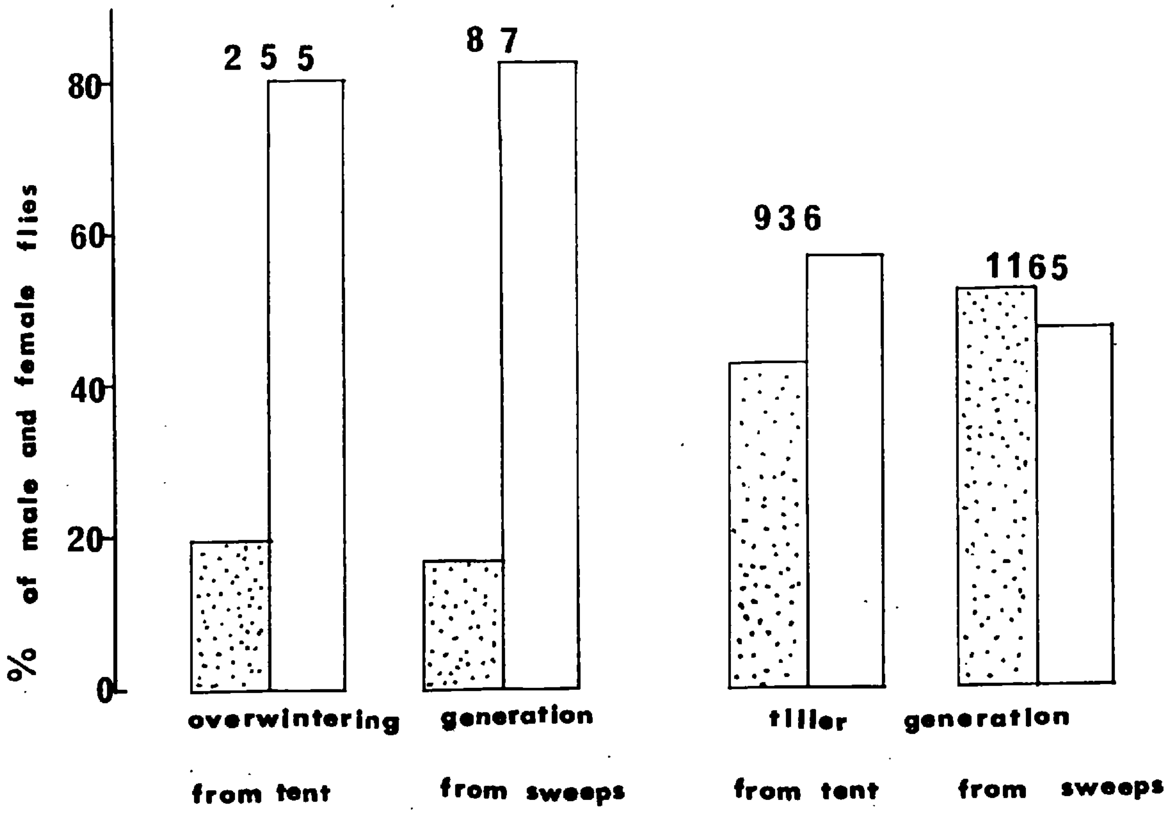


Fig.29 (ii) The sex ratio of adult frit flies caught in tents and in sweep nets (FROM SOUTHWOOD'S UNPUBLISHED DATA,1961).

Table 57 Sex ratios of adults of the overwintering and tiller generations in oat crop.

	Percentage ♂♂	♀♀	X^2 to test significant departure from 50:50 sex ratio
Overwintering generation (water traps)	15.7	84.3	***
Tiller generation (" ")	37.1	62.9	*
Tiller generation (stem dissection)	53.3	46.7	ns
Southwood's (1961) unpublished data			
Overwintering generation (tents)	19.6	80.4	***
" " (sweeps)	17.2	82.8	***
Tiller generation (tents)	43.2	56.8	ns
" " (sweeps)	52.6	47.4	ns

Table 58 Sex ratios of adults of the overwintering generation collected by sweep net from grasslands.

Date	No of adults	Sex ratio M : F	X^2 to test significant departure from 50:50 sex ratio
May 20 1977	33	72.7 : 27.3	* * *
" 23 "	66	63.6 : 36.4	* *
" 24 "	32	62.5 : 37.5	*
" 25 "	51	52.9 : 47.1	ns
" 26 "	50	54.0 : 46.0	ns
June 1 "	56	60.7 : 39.3	*
Total	288	60.4 : 39.6	*

Table 59 Sex ratios of adult frit flies of the overwintering the tiller generations caught in water traps in oat crops of different densities and row spacings and of those of the tiller generation at emergence (1976).

	Water trap catches				Stem dissection		X^2 to test significant departure from 50:50 sex ratio		
	OVERWINTERING (i)		TILLER (ii)		TILLER (iii)				
	GENERATIONS								
Densities and row spacings	No of adults	Sex ratio M : F	No of adults	Sex ratio M : F	No of adults	Sex ratio M : F	(i)	(ii)	(iii)
14.4m plants/ha in 5cm rows	207	15.5:8 .5	170	30.6:69.4	57	50.9:49.1	***	***	ns
13.7m " " 15cm "	143	17.5:82.5	158	32.9:67.1	170	57.7:42.3	***	***	ns
5.1m " " 15cm "	99	16.2:83.8	150	45.3:54.7	153	51.0:49.0	***	ns	ns
1.4m " " 15cm "	86	14.0:86.0	61	37.7:62.3	71	52.0:47.9	***	*	ns
1.4m " " 45cm "	79	13.9:86.1	56	46.4:53.6	168	52.4:47.6	***	ns	ns

Table 60 Sex ratios of adults from laboratory culture

Replicates	No of adults	Sex ratio M : F	X^2 to test significant departure from 50:50 sex ratio
I	20	45 : 55	ns
II	11	54.6 : 45.4	ns
III	18	55.6 : 44.6	ns
IV	61	49.2 : 50.8	ns

Table 61 Competition between larvae and sex ratios of emergent adults.

No of eggs/plant	No of adults	Sex ratio M : F	X^2 to test significant departure from 50:50 sex ratio
1	26	53.8 : 46.2	ns
2	20	55 : 45	ns
3	6	50 : 50	ns
4	4	50 : 50	ns

8.4. Discussion

The predominance of females (84.3%) in overwintering generation adults caught in water traps over oat crops (table 57) can be explained by two alternative hypothesis:

(i) significantly more females than males invaded the oat crop from the overwintering sites, grasslands or winter cereals, or

(ii) approximately equal numbers of males and females invaded the oat crop, but females were more readily caught in water traps.

Southwood (table 57, fig.29 (ii)) however, used tents and sweep net to collect his data and obtained remarkably similar results to those collected in this study with water traps (table 57, fig.29 (i)). In view of this, the alternative (second) hypothesis is rejected. It was found in this study that the sex ratio of adults in the laboratory culture (table 60) and of the tiller generation in oat crop at emergence (table 57; fig.29 (i)) was approximately 1:1. Southwood's unpublished results indicate that the sex ratio of the panicle generation adults at emergence from oat crop was approximately 1:1. It seems likely therefore, that the sex ratio of all generations at emergence is approximately 1:1. Yet, the sex ratio of the overwintering generation adults colonizing oat crop at the beginning of the season and responsible for the tiller generation eggs on oats is not 1:1, but approximately 1 male:5 females. This is probably explicable by the sweep net catches of the overwintering generation adults collected from grasslands (table 58). Here (table 58) consistently more males were collected in sweep net than females. It seems logical therefore, to suggest that significantly more females than males were leaving the overwintering sites (grasslands) for a new, more suitable, but temporary habitat (oat crop) at the beginning of the season.

Rygg (1966) examined females caught in suction traps and found that most females had fully developed eggs in traps from altitudes up to 31.5m over grass and the proportion of females in the total increased with height. It can be inferred from this that the majority of the female invaders probably had fully developed ovaries. The males are polygamous, so that the disproportionately few males among the invaders probably has no direct effect on the future of the population except, perhaps, at extremely low numbers. The key mortality factor occurs before the insect enters the plant (Southwood and Jepson, 1962) and it has also been shown in other parts of this study that this is further magnified when eggs are laid on older plants. This makes it mandatory that many eggs by many females must be laid if the species is to utilize the new habitat fully. The success of the frit fly as a pest of oats therefore, probably lies in the ability of mature females to colonize new habitats rather than males and this in itself may have an evolutionary base which enables the species to exploit new habitats so effectively.

Water trap, tent and sweep net catches of the tiller generation in oats are more difficult to interpret than those of the overwintering generation for reasons already given in sub-section 4.1.1.

SECTION IX

GENERAL DISCUSSION.

9.1. Population development of frit fly in oat plants at different growth stages.

The frit fly, unlike the wheat bulb fly which lays eggs during late summer, in fallow or in bare soil among root crops (Bardner et al, 1972), lays when the host plant is present, with most eggs (>95%) laid on the basal parts of the plant. Several workers, e.g. Ibbotson (1960) and Sanders (1960) have emphasized the host plant as being important for the release of oviposition behaviour in frit fly, while others, e.g. Cunliffe and Hodges (1946) have demonstrated the importance of the host plant coleoptile as an oviposition site.

A summary of the results obtained in sub-section 3.1.2. on the role of the host plant age on the population of frit fly is presented in table 62. It is apparent from the table that, although the coleoptile is important for oviposition, particularly at the 3-leaf stage when a crevice exists between it and the shoot, other plant structures at the basal parts of the plant, e.g. tillers, dry leaves, and even the soil may be important for oviposition at other times when the coleoptile is either not yet suitable for oviposition because it is attached tightly to the shoot and therefore the fly cannot insert its ovipositor, or because it has withered. The height of the plants could also be important initially in attracting different numbers of adults to the plant (tables 5 and 6) and in oviposition (table 7). Once a fly has landed on a plant with coleoptile suitable for oviposition, the fly tends to lay most (>95%) eggs inside the coleoptile of the suitable plant unless other plants with suitable coleoptiles are nearby (tables 48 and 49). Probably eggs laid inside the coleoptiles, when suitable for oviposition, are relatively protected from adverse weather conditions and predators; the ovipositing flies are also less likely to be eaten by ground predators than when laying in the soil.

Like the wheat bulb fly (Raw, 1967; Bardner, 1968) young larvae may have considerable difficulty in invading the main shoot and this tendency increases with ageing of the plants. Oat plants at the 1-leaf stage are relatively easy to penetrate, but they seem too young to produce tillers when the main shoot is destroyed and so are too small to support many larvae; older plants may be adequate for the development of many larvae if the larvae can penetrate them; but the main shoots of the plants at the 4 and 5-leaf stages are mostly immune to penetration by the young 1st instar larvae (table 3). Hence, many larvae from eggs laid on the plants at the 4 and 5-leaf stages have to depend on small tillers for food to complete their development. It is therefore hardly surprising that very few survived from eggs to pupae in plants colonized at the 4 and 5-leaf stages, as at the 1-leaf stage (table 62). The 2 to 3-leaf stage when the coleoptile is present and suitable for oviposition looks like the compromise stage when survival from eggs to pupae and hence to adults was greatest (table 62). Frit attack on the main shoot at the 3-leaf stage led to the production of most tillers (table 4), hence much food for the larvae to complete their development. Perhaps the oat plant coleoptile acts as a pointer to the ovipositing female which probes the basal part of the plant several times with her ovipositor before depositing her eggs. If this is so, it is suggested that preference by the frit fly of the insides of live coleoptiles for oviposition is associated with the best chance of survival from eggs to adults, i.e. the open coleoptile is not only a good egg laying niche, but it is an indicator of plant age best suited for larval survival and development.

9.2. Population development of frit fly in oat crops of different densities and row spacings.

Variations in the populations of insects in crops may be due to differences in the initial numbers of arrivals or to different rates of multiplication or mortalities in the crop. Pimentel (1961a) found that widely spaced plants initially attracted more insects and tended to be more damaged than dense stands of the same species, similarly, Way and Heathcote (1966) have cited examples of less damage per plant in densely planted stands due partly to slower multiplication rates of the insects in the dense crop.

In this study, field and laboratory experiments showed that higher oat and 'artificial' plant densities (tables 25 and 37) and narrow row spacings (tables 25 and 40) seemingly attracted more insects and this resulted in higher trap catches, than in lower densities and in wider row spacings. This is in contrast to some other insects, e.g. Aphis craccivora (A'Brook, 1968; Farrell, 1976) whose colonization on groundnuts is reduced by increasing plant densities and reducing row spacing. The reason for this probably lies in the suggestion that the frit fly is a denizen of grassland (Southwood, 1961) where grasses often occur in dense stands with solid green appearance. The frit fly is therefore likely to be attracted more to oat plants in dense stands with narrow row spacing than to those with fewer plants and wider row spacing, where much bare soil is exposed. The latter conditions would tend to attract other kinds of exploiting species e.g. aphids which in nature colonize early stages in plant succession on bare soil. Field data on frit fly oviposition (table 29) was less accurate than laboratory data because of the sampling method employed, but the more accurate results on oviposition in the laboratory (tables 38 and 41) showed that the numbers of eggs laid on oat plants increased with increasing plant densities and decreasing row spacings. Field and laboratory experiments showed a relationship between high within-rowdensity of oats causing soil moisture stress, and susceptibility of the plants to larval invasion (tables 30 and 42). Slavik (1966) stated that hydration levels in plants may influence physiological processes in cereals while Ordin (1960) had earlier indicated a direct effect of turgor potential on cellulose synthesis. It seems that the loss of turgor in water deficient plants at high within-row densities reduced the ability of oat plants to resist penetration by <u>O. frit</u> larvae. Survival of the larvae in the plants was high in the dense plantings and relatively low in the sparse and disperse plantings with wide row spacing because of greater competition in the latter (table 33). Intermediate levels of survival was obtained in the disperse planting with intermediate row spacing no doubt because the individual plants were relatively more isolated from each other, thus creating optimum conditions for tillering (Wiggans and Frey, 1957); there was therefore relatively more food available for the larvae to complete their development. Survival of the pupae was similar in all treatments seemingly because a density independent mortality factor, perhaps adverse hot dry weather was the main cause of death of pupae. The competition during the larval stage resulted in different sized pupae in the different treatments (table 54, fig.26). Smaller pupae were found to produce smaller adults; smaller females had longer pre-oviposition periods and laid fewer eggs than bigger females which had shorter pre-oviposition periods and laid most eggs (table 55, fig.27). It seems likely that in field conditions a longer pre-oviposition may be a disadvantage if there are many agents that kill the adults.

In table 63, all the above components in the population are scored for the different densities and row spacings. It seems clear from the table that the dense planting with narrow row spacing, akin to the natural habitat of the insect (grassland) had the highest score of 22 and was therefore the best for the species. The disperse plantings had the lowest scores, but even here, the species did better in the disperse planting with intermediate row spacing with a score of 10 than in the disperse planting with wide row spacing which had a score of only 8 .

9.3. Oat crop environment and plant resistance to frit fly attack

Since Painter (1951) first defined resistance as the relative amount of heritable qualities possessed by the plant which influences the ultimate degree of damage done by the insect, several workers have modified the term to include not only the intrinsic characteristics of the host plant, but also extrinsic (ecological) factors. Thus, plant resistance may be based on both intrinsic and extrinsic factors, and the interaction of both (Pimentel, 1961b), or altered by the environment such as water, nutrients, growth regulants, etc (Harris, 1960; van Emden, 1966) or by cultural practices, such as crop arrangement in time and space. Insects often succeed in attacking crops because of the synchronization between their arrival in the crop and the susceptible stage of the plant - the plant 'window'.

However, where other considerations make it mandatory to grow crops to synchronize the plant 'window' with the arrival of the insect in the crop, a knowledge of the often complex relationship between the requirements of the different stages of the insect and their behaviour and the ways in which these are affected by the crop environment could be used for devising methods of minimising the effects of insect infestation on the crop.

Figure 30 summarises the factors in the oat crop environment investigated in this study that influence the population of O. frit. Thus, the numbers of insects arriving in the crop can either be increased (figs. 30 - 1a, 30 - 2a, 30 - 3a) or decreased (fig.30 - 4a) depending on the cropping pattern employed.

Oviposition can either be increased (fig.30 - 1b, 30 - 3b) or decreased (fig.30 - 2b, 30 4b). In fig.30 - 2b, constructed from information obtained from tables 19, 20, 21 and 22, not only was there a decrease in the numbers of eggs laid once an appropriate height and density of clover has been attained, the site on which the eggs were laid was also changed, that is, the females were left with no choice other than lay their eggs at higher oviposition sites from where larval penetration is often less successful (fig.8). The experiments conducted in this study did not indicate that clover has a repellant effect like that caused by tomato intercropped with cotton which repels cotton flea beetle, Podagrica species (Usenbo, 1976) or tomato intercropped with cabbage which repels Plutella xylostella (Burandayand Raros, 1975). It seems more likely that the clover at appropriate height and density presents a purely physical barrier to oviposition, as Dempster and Coaker (1974) observed with the cabbage root fly. In fig. 30 - 1b, the site chosen for oviposition changed with ageing of the plants, but unlike fig. 30 - 2b most of the eggs were still laid at the basal parts of the plants, irrespective of the age of the host plant.

Penetration of the larvae into the plants was enhanced by increasing plant densities (fig.30 - 3c) and increasing row spacing with corresponding increase in within-row density (fig.30 - 4c) because of moisture stress at high host plant density which in turn makes the plant less able to resist larval invasion. Larval penetration decreased with increasing plant age (fig.30 - $1c_1$ and $1c_2$). The likely effect of density and height of clover undercover on larval penetration is to cause a sharp decrease in penetration like in fig. 30 - 2b once the appropriate density and height of clover is attained, because larvae from eggs laid high up on the plant, such as on the leaf blades are less likely to invade shoots (fig.8).

Survival of the larvae at low and high larval densities are presented for the different cropping patterns in figs. 30 - 5 to 30 - 8. At low larval density, larval survival was highest in young plants because the larvae can penetrate young plants more easily than they can penetrate older plants and because there is no competition, the larvae survive to pupae (fig.30 - $5d_1$). The frit fly is able to complete its development in one shoot if there is no competition, unlike the wheat bulb fly which needs several shoots to complete development (Bardner et al, 1971). However, with high larval density, although larvae penetrated young plants more easily than old plants, many that penetrated the young plants died due to competition and insufficient food to complete their development. The best stage for larval survival when many larvae have invaded the plant is when the coleoptile is present and suitable for oviposition, the critical stage (fig.30 - $5d_2$). Larval survival is likely to follow the same pattern as larval penetration at low and high larval densities when different densities and heights of undercover are considered (fig.30 - $6d_1$ and $6d_2$) because the same density of host plant is involved. At low larval densities, the numbers of larvae that survive will be similar at all plant densities because of lack of competition between developing larvae (fig.30 - $7d_1$). However, at high larval densities survival is likely to be enhanced by high plant densities because larvae moving from a crowded plant are more likely to find another less crowded plant in a dense planting than in a sparse or disperse planting (fig. 30 - $7d_2$). The effect of the row spacing of the host plant on larval survival is likely to be less dramatic because the same density of the host plant is considered (fig.30 - $8d_1$ and $8d_2$), with different numbers of tillers slightly modifying the outcome.

From the foregoing discussion it is conceivable that the oat crop environment can be manipulated to reduce frit fly attack in ways other than by early sowing. For example, the numbers of flies that invade the crop at the beginning of the season can be reduced by planting in widely-spaced rows rather than in narrow rows and subsequent oviposition in the crop can be reduced by intercropping or strip-cropping oats with suitable undercover that will give a quick, initial, tight cover around the basal parts of oat seedlings which are usually preferred for oviposition. The competing undercover could be destroyed by a herbicide once the oat crop has reached the 4-leaf non-susceptible stage.

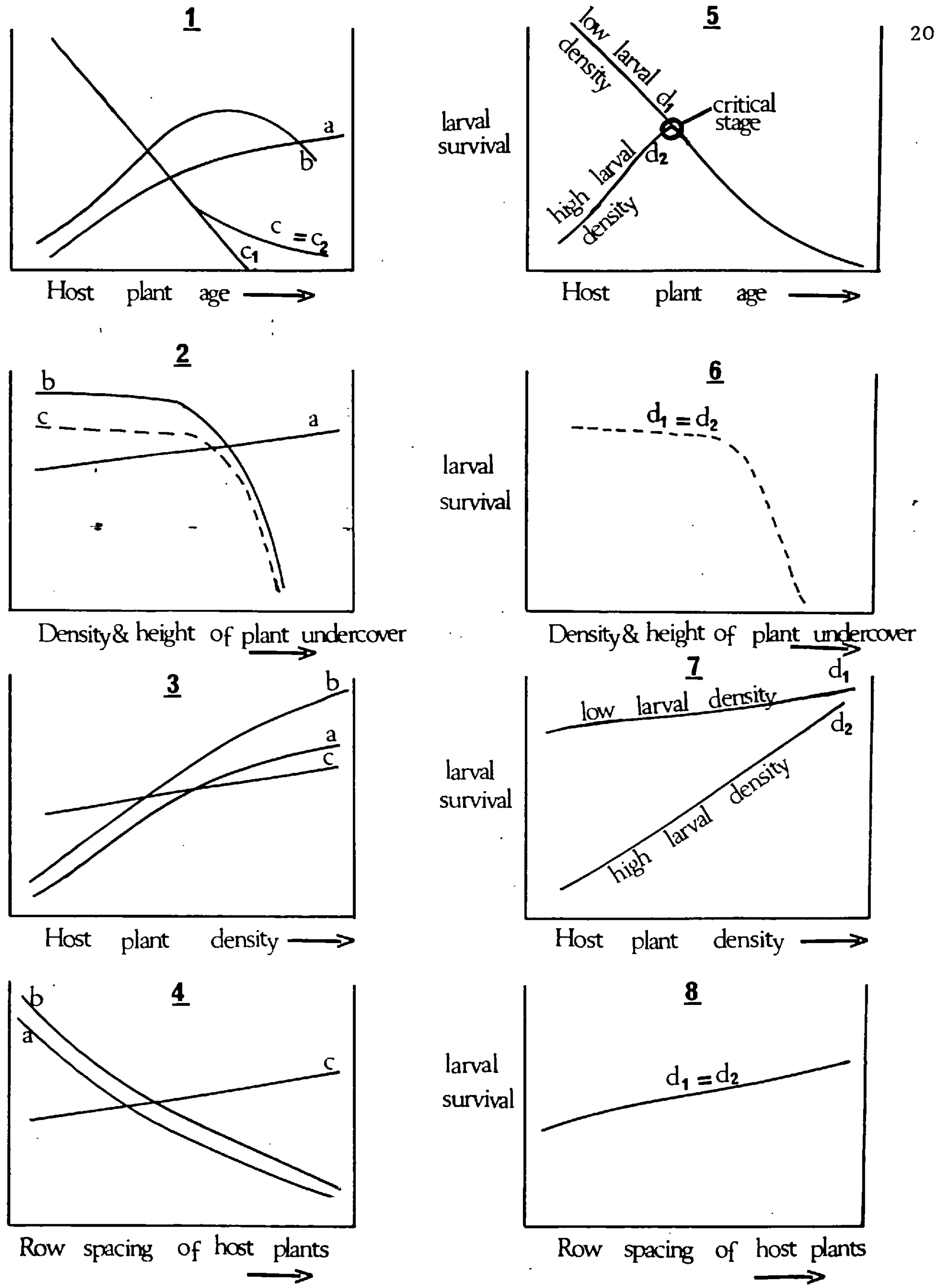
Table 62 Population development of frit fly in oat plants at different growth stages

	Eggs		Young larvae inside plants		Late larvae or pupae
1-leaf stage					
Population	5.1		4.5		1.2
No dying in interval		0.6		3.3	Sum=3.9 dead
% Mortality		11.8		64.7	Sum=76.5% mortality
Successive % mortality		11.8		73.3	
2-leaf stage					
Population	11.6		8.7		7.8
No dying in interval		2.9		0.7	Sum=3.6 dead
% Mortality		25.0		6.0	Sum=31.0% mortality
Successive % mortality		25.0		8.0	
3-leaf stage					
Population	23.9		11.4		10.7
No dying in interval		12.5		0.7	Sum=13.2 dead
% Mortality		52.3		2.9	Sum=54.2% mortality
Successive % mortality		52.3		6.1	
4-leaf stage					
Population	24.3		7.0		4.2
No dying in interval		17.3		2.8	Sum=20.1 dead
% Mortality		71.2		11.5	Sum=82.7% mortality
Successive % mortality		71.2		40.0	
5-leaf stage					
Population	20.3		5.1		1.1
No dying in interval		15.2		4.0	Sum=19.2 dead
% Mortality		74.8		19.7	Sum=94.5% mortality
Successive % mortality		74.8		78.4	

Table 63 Population development of frit fly in oat crop of different densities and row spacings

Densities and row spacings of oats	Colonization by adults (mean no/trap) (Table 25)	Subsequent oviposition (no/sq m) (Table 29)	Larval penetration (no/sq m) (Table 30)	% survival between larval and pupal stages (Table 33)	% survival between pupal and adult stages (Table 34)	Mean pupal sizes of hatched females (mg) (Table 54)	Pre-oviposition period (days) (Table 55)	Fecundity of emergent adults (by inference from Table 55 and fig.26)	Generation
14.4m plants/ha in 5cm rows	52c	1097c	2031d	85.9	72.5a	0.88	-	-	-
13.7m " " 15cm "	36b	610ab	2799e	81.8	66.0a	0.86	-	-	-
5.1m " " 15cm "	25ab	830bc	1854c	64.8	67.4a	0.85	-	-	-
1.4m " " 15cm "	22a	546ab	746b	74.4	66.0a	0.83	-	-	-
1.4m " " 45cm "	20a	307a	498a	64.3	67.0a	0.80	-	-	-
14.4m plants/ha in 5cm rows	H	H	M	H	M	La	Sh	H	-
13.7m " " 15cm "	M	M	H	H	M	La	Sh	H	-
5.1m " " 15cm "	L	M	M	L	M	M	M	M	-
1.4m " " 15cm "	L	L	L	M	M	S	Lo	L	-
1.4m " " 45cm "	L	vL	L	L	M	S	Lo	L	-
14.4m plants/ha in 5cm rows	+++	+++	++	+++	++	+++	+++	+++	22
13.7m " " 15cm "	++	++	+++	+++	++	+++	+++	+++	21
5.1m " " 15cm "	+	++	++	+	++	++	++	++	14
1.4m " " 15cm "	+	+	+	++	++	+	+	+	10
1.4m " " 45cm "	+	-	+	+	++	+	+	+	8

H = high (+++); M = medium (++); L = low (+); La = large (+++); S = small (+); Sh = short (+++); Lo=long (+)
vL = very low (-)



a = colonization by adult flies

b = oviposition

c = penetration of larvae into plant

c_1 = " " " " primary shoot

c_2 = " " " " . tillers

d_1 = larval survival at low larval density

d_2 = " " " high " "

Fig.30 Factors in oat crop environment influencing populations of *O. frit*

SUMMARY

1. A review of literature is given on the effects of crop environment, notably plant age, crop background, and crop arrangement in space on colonization by insects, with special reference to the Frit fly, *Oscinella frit* L.
2. It was shown in the field that ovipositing *O. frit* preferred the basal parts of oat plants, variety *Maris oberon* to the upper parts and that the main site selected for oviposition changed from the crevice between plant and soil at the 1-leaf stage to the inside of coleoptile at the 3-leaf stage and to the tillers or old leaves after the coleoptiles have withered.
3. In choice experiments using potted plants in the field, fewest eggs per plant, per primary shoot and on tillers were laid on plants that were at the 1-leaf stage, followed by the 2-leaf and 5-leaf stages. Most were laid on plants that were at the 3-leaf or 4-leaf stages.
4. The proportion of newly-hatched larvae that penetrated the plants was greatest in oat plants at the 1-leaf stage and decreased with increasing age of the plants; the primary shoots of plants at the 4 and 5-leaf stages were not penetrated. After feeding and developing for some time on the tillers, some young larvae were able to penetrate some primary shoots which they were initially unable to enter.
5. The coleoptile provided the preferred egg laying site on oat plants at the 2 or 3-leaf stages which were also best for survival from eggs to adults.
6. In the laboratory with oat plants at the 3-leaf stage cut to different heights, more flies landed and rested on plants that were cut to 10cm high than on those that were cut to 5cm high;

there was no significant difference ($P>0.05$) between the numbers that landed on plants that were 10cm or 20cm high. Taller greased 'artificial plants' trapped more flies than shorter ones.

7. Significantly ($P<0.05$) more eggs were laid on plants at the 3-leaf stage cut to 10cm high than on those that were cut to 5cm high; eggs laid on plants that were 10cm or 20cm high were not significantly different ($P>0.05$), except when the second leaf blades were further cut to show-up the contrasting effects of the heights of the plants.
8. Larvae that hatched from eggs placed on less preferred oviposition sites on the upper parts of the plant failed to penetrate the plant.
9. In the field, similar numbers of flies were caught in water traps over oat crops with bare background or with a background of weeds.
10. In the laboratory, 'artificial plants' placed in bare soil trapped similar numbers of flies as those placed in soil covered with clover.
11. In laboratory experiments the density of clover undercover did not affect the numbers of eggs laid on oat plants provided the basal parts of the plants were exposed. However, the height of clover of appropriate density was found to be critical: thus, when clover was at least 1.5cm higher than the tips of coleoptiles of oat plants and formed a dense cover around the basal parts of the plants, the preferred oviposition sites seemingly became less accessible to the ovipositing flies, the numbers of eggs laid there decreased, while oviposition on

the leaves not covered by the clover increased. In these conditions, fewer eggs were laid on oat plants than those on oat plants with bare soil.

12. Water trap catches in the field in oat crops of different densities and row spacings indicated that these two factors influence the numbers of colonizing adult flies that invade oat crops. Consistently more flies were caught in dense plantings than in sparse and more widely disperse plantings. Significantly more flies were caught in treatments with closely-spaced rows than in those of equivalent densities but with more widely-spaced rows. Similar results were obtained in the laboratory with 'artificial plants'.
13. Most eggs were laid per plant in the most disperse plantings, followed by the intermediate sparse planting and least per plant in the dense plantings. Most eggs per unit area of oat crop were laid in the dense plantings and least in the most disperse plantings. Plants in plots with closely-spaced rows had more eggs than those of equivalent densities in more widely-spaced rows.
14. In the field and in the laboratory, larval penetration into the plants was more successful in treatments with crowded plants within the row than where individual plants were more isolated.
15. Larval mortality was greatest in the most dispersed plantings and least in the dense plantings, probably due to competition for insufficient food in the former.
16. Eggs in the field were clumped (negative binomial) due to a combination of the behaviour of ovipositing female flies and

heterogeneity of the plant population, e.g., differences in the state of the coleoptile, but in the laboratory, the distribution of eggs by individual females among a group of homogeneous plants was not different from random.

17. Larvae and pupae were clumped (negative binomial) early in the season in the most dispersed plantings, but because of the high oviposition intensity which resulted in competition between the larvae for food, the distribution later in the season was not different from random (poisson).
18. Pupae collected from the most dispersed plantings in the field were lighter than those collected from the dense plantings, where there was little or no competition during the larval stage.
19. Smaller females from the smaller pupae had longer pre-oviposition periods and were less fecund than bigger females.
20. Laboratory experiments indicated that groups of captive ovipositing females can respond to adverse conditions, such as absence of many oviposition sites within a cage by holding back their eggs for at least 48 hours until suitable conditions of sufficient plants become available. When suitable conditions remained unavailable, fewer eggs were laid.
21. The sex ratio of adults of the overwintering generation colonizing oat crops at the beginning of the season was about 5 females to 1 male, compared with 1:1 sex ratio at emergence. Sex ratio of colonizing adults was unaffected by variations in density and row spacing of oat plants, nor was the sex ratio of emergent adults altered by competition during the larval stage.

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APPENDIX I. Field experiments: experimental area, plot size, row spacing, seed rate and plant population

Type of experiment	Year	Treatment	Total area of experiment (sq.metres)	Total area per plot (sq.metres)	Spacing between rows (cm)	OATS				WHITE CLOVER OR WHITE MUSTARD	
						Seed rate per		Plant population per		Seed rate per plot (gms)	% area of ground covered by clover + weeds, mustard + weeds, or weeds when oats was at 2 to 4-leaf stage
						row (gm)	hectare (kg)	metre	hectare (millions)		
Bare background and weedy background	1975	A	380	20	15.0	--	-	66	4.3	-	
		B		20	15.0	-	-	66	4.3	C=37.5	50 to 90
		C		20	15.0	-	-	66	4.3	m=18.8	50 to 90
		D		20	15.0	-	-	66	4.3	-	50 to 90
Different densities of oats	1975	A	285	20	7.5	-	-	66	8.6	-	-
		B		20	15.0	-	-	66	4.3	-	-
		C		20	45.0	-	-	66	1.4	-	-
	1976	A	475	20	5.0	12.0	220	73	14.4	-	-
		B		20	15.0	36.0	659	209	13.7	-	-
		C		20	15.0	12.0	220	78	5.1	-	-
		D		20	15.0	4.0	73	22	1.4	-	-
		E		20	45.0	12.0	220	63	1.4	-	-

C = white clover

m = white mustard

APPENDIX II. Field Experiments:

Calendar of Operations

Operations	Bare background and weedy background	Different densities of oats	
	1975	1975	1976
Oats, clover and mustard planted	April 23	April 23	May 4
Germination count	May 28	June 2	May 20*
Water traps operation	May 8 to August 8	May 8 to August 6	May 13 to July 8
Weeding by hand or herbicide application	May 22	May 22	June 4
Sampling of oat shoots and tillers for eggs, larvae and puparia	May 28 June 4, 11, 19, 26	June 2, 10, 16, 23, 30	May 19, 27 June 3, 10, 17, 27
Sampling of oat panicles eggs	July 11	July 24	----
Panicle count	August 28	August 28	July 29

* See Appendix III for full details

APPENDIX III. GERMINATION COUNT AND ESTIMATE OF PLANT POPULATION

(21.5.76)

A = 12gm of oat seeds/4m length in rows spaced 5cm apart

B = 36gm " " " " " " " " 15cm "

C = 12gm " " " " " " " " 15cm "

D = 4gm " " " " " " " " 15cm "

E = 12gm " " " " " " " " 45cm "

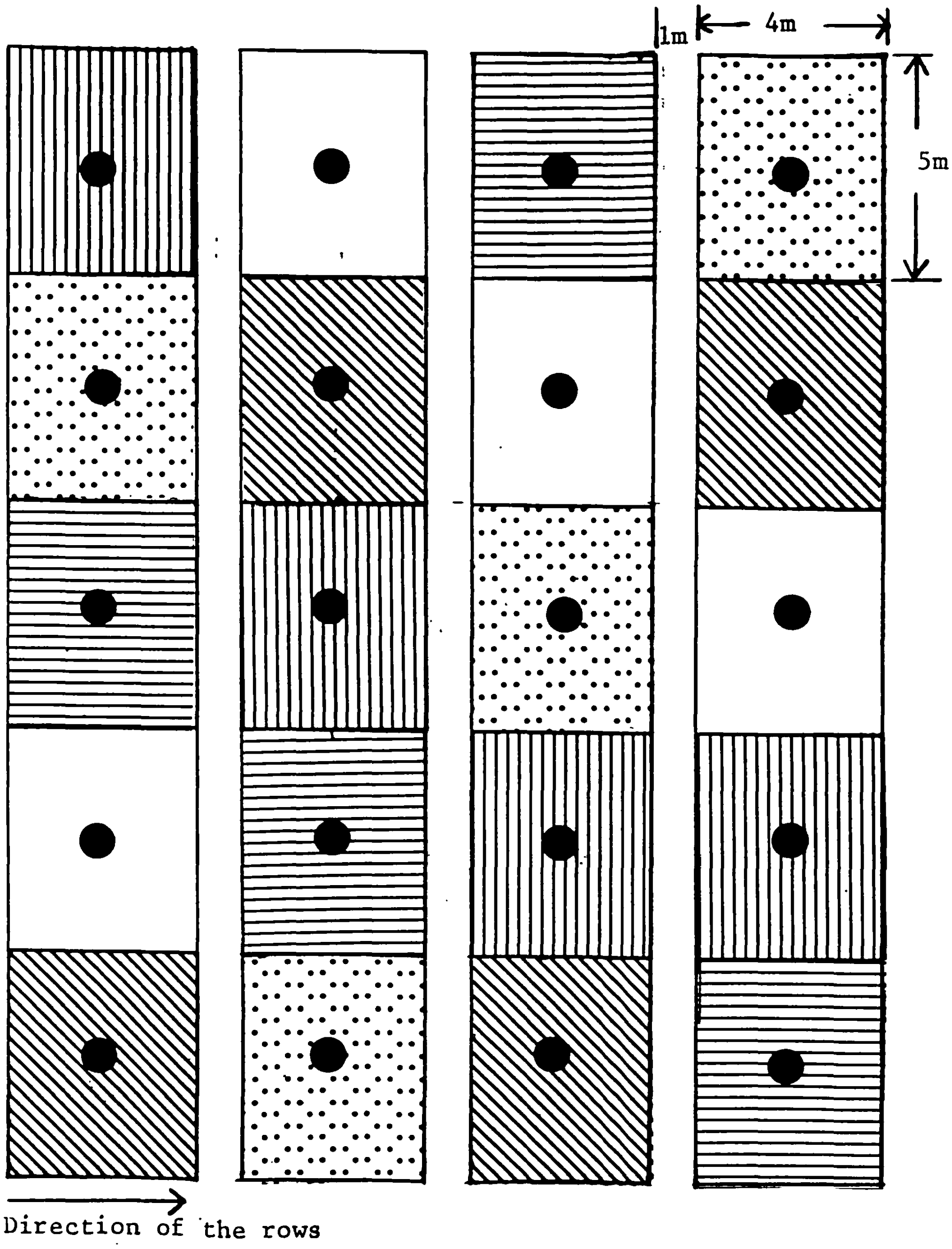
Counts were made in four .33m row lengths per plot in C

" " " " " 1m " " " " " A, B and E

" " " " " 3m " " " " " D

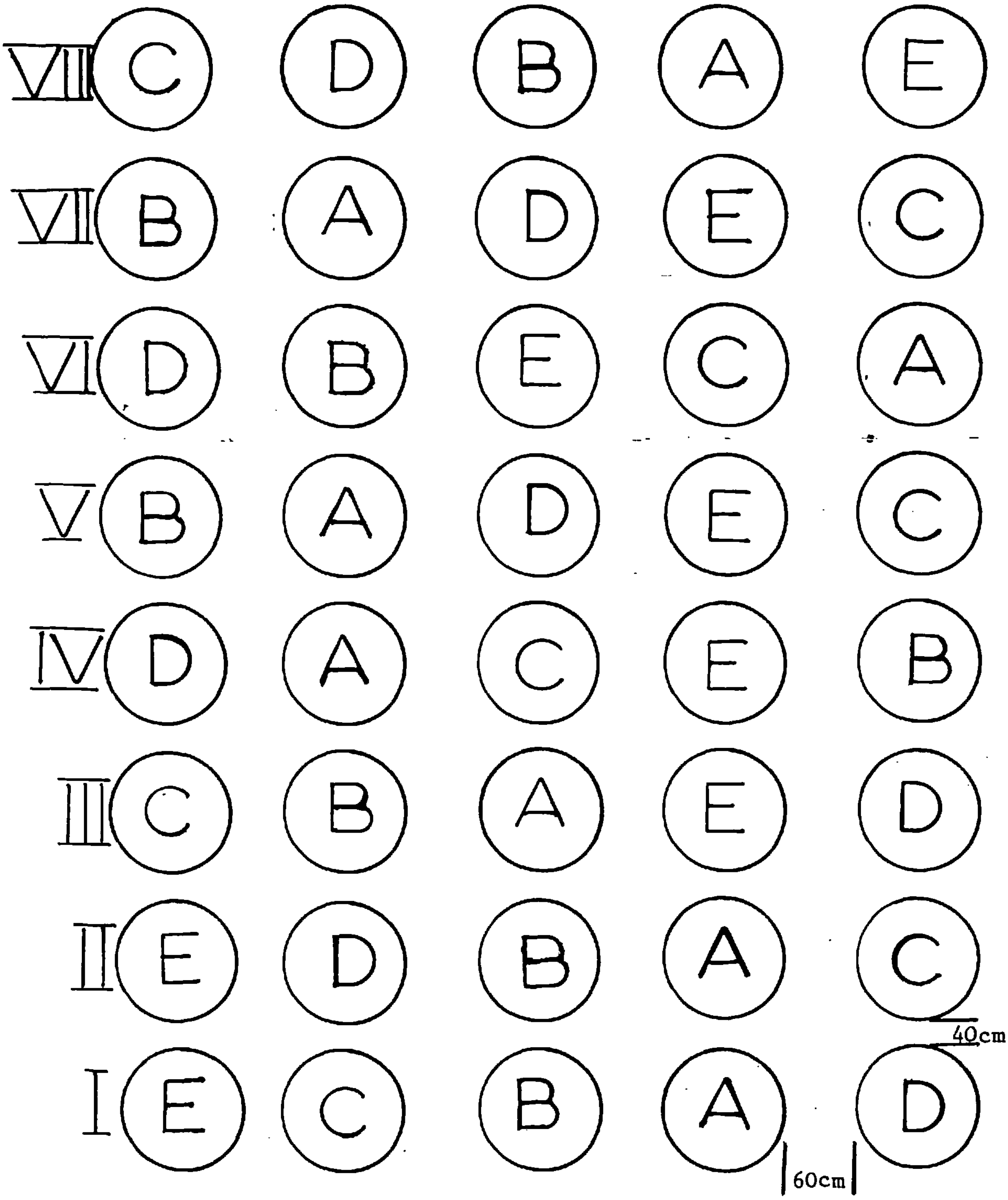
	Replicates				Sample Totals	Mean no.of plants per 30cm row	Mean no. of plants per hectare (millions)
	I	II	III	IV			
A	277	265	264	261	1,067	22	14.4
B	268	274	213	265	1,020	64	13.7
C	295	286	320	242	1,143	24	5.1
D	221	250	207	265	943	7	1.4
E	240	262	209	212	923	19	1.4

APPENDIX IV. PLAN OF 1976 FIELD EXPERIMENT



●	Water traps
░	22 plants/30cm length in rows spaced 5.0cm apart
▥	64 " " " " " " 15.0cm "
▧	24 " " " " " " 15.0cm "
▤	7 " " " " " " 15.0cm "
□	19 " " " " " " 45.0cm "

APPENDIX V. PLAN OF 1976 POT EXPERIMENT IN THE FIELD



VIII	C	D	B	A	E
VII	B	A	D	E	C
VI	D	B	E	C	A
V	B	A	D	E	C
IV	D	A	C	E	B
III	C	B	A	E	D
II	E	D	B	A	C
I	E	C	B	A	D

A = 5 days after sowing

B = 12 " " "

C = 19 " " "

D = 26 " " "

E = 33 " " "

APPENDIX VI. EGGS, LARVAE & PUPARIA OF THE TILLER GENERATION IN 1976

Density and row spacing of oats	Date	Eggs		Larvae		Puparia		Empty Puparia	
		No/plant	No/sq.m	No/plant	No/sq.m	No/plant	No/sq.m	No/plant	No/sq.m
14.4m plants/ha in rows spaced 5cm apart	10-19 May	0.37	531	0.008	10.77	-	-	-	-
	20-27 May	0.24	345	0.86	1,235	-	-	-	-
	28- 3 June	0.11	158	1.13	1,622	0.01	14	-	-
	4-10 June	0.04	57	0.82	1,177	0.60	861	-	-
	11-17 June	-	-	0.19	273	0.97	1,393	0.39	559.8
	18-27 June	-	-	0.12	172	0.55	790	1.12	1,608.3
13.7m plants/ha in rows spaced 15cm apart	10-19 May	0.23	316	0.09	124	-	-	-	-
	20-27 May	0.13	178	1.26	1,729	-	-	-	-
	28- 3 June	0.09	124	1.76	2,415	0.08	110	-	-
	4-10 June	0.003	4	1.15	1,578	0.89	1,221	0.003	4.19
	11-17 June	-	-	0.32	439	1.44	1,976	0.76	1,043.1
	18-27 June	-	-	0.25	343	1.09	1,496	1.40	1,921.6
5.1m plants/ha in rows spaced 15cm apart	10-19 May	1.0	513	0.25	128	-	-	-	-
	20-27 May	0.31	159	3.26	1,671	-	-	-	-
	28- 3 June	0.16	82	2.92	1,497	0.2	103	-	-
	4-10 June	0.16	82	1.74	892	1.88	964	0.02	10.17
	11-17 June	-	-	0.52	267	2.11	1,082	1.41	723.1
	18-27 June	-	-	0.26	133	1.16	595	2.29	1,174

APPENDIX VI. (Cont'd.)

Density and row spacing of oats	Date	Eggs		Larvae		Puparia		Empty Puparia	
		No/plant	No/sq.m	No/plant	No/sq.m	No/plant	No/sq.m	No/plant	No/sq.m
1.4m plants/ha in rows spaced 15cm apart	10-19 May	3.01	424	0.60	85	-	-	-	-
	20-27 May	0.67	94	4.7	663	-	-	-	-
	28- 3 June	0.20	28	3.69	520	0.38	54	-	-
	4-10 June	-	-	1.80	254	3.5	493	0.07	9.57
	11-17 June	-	-	0.45	63	2.15	303	2.2	310.4
	18-27 June	-	-	0.20	28	1.43	202	3.35	472.5
1.4m plants/ha in rows spaced 45cm apart	10-19 May	1.60	221	0.34	47	-	-	-	-
	20-27 May	0.39	54	3.61	498	-	-	-	-
	28- 3 June	0.11	15	3.22	444	0.32	44	-	-
	4-10 June	0.10	14	1.29	178	2.33	320	0.03	4.19
	11-17 June	-	-	0.45	62	1.82	251	1.93	266.2
	18-27 June	-	-	0.27	37	1.37	189	2.78	383.4