STUDIES ON THE BIOLOGY OF DIPTEROUS STEM-BORING LARVAE IN GRASSES

BY

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ABSTRACT

The infestation of sown grasses, especially *Lolium perenne* var. S24, by stem-boring dipterous larvae was studied in the field from the time of germination onwards. Grass growing on the farm at Rothamsted Experimental Station, Harpenden, Herts., during 1972 and 1973 was attacked by five species of stem-boring fly. These were, in decreasing order of abundance, *Oscinella vastator* (Curt.), *O. frit* L., *Geomyza tripunctata* (Fall.), *O. frit ex anthoxanthum* and *O. frit ex arrhenatherum*. Infestation built up rapidly in the field after the emergence of the adult flies in spring, larval numbers reaching a peak in late summer and autumn before falling with high winter mortality. *G. tripunctata* colonised grasses earlier in the season and was numerous during the first year of a sward's life, but was supplanted by *Oscinella* spp., especially *O. vastator*, as the sward matured.

The factors influencing attack were examined in laboratory and field experiments. Infestation was governed by oviposition and larval survival which were dictated by host plant conditions: parasitism was negligible. Plant species, age and stem density all affected infestation. In laboratory tests with ten grass species or varieties, *Poa trivialis*, *Agrostis tenuis*, *L. perenne* S24 and Reveille, *L. multiflorum*, *Avena fatua*, *Phleum pratense*, *Holcus lanatus*, *Festuca rubra*, and *Dactylis glomerata*, specific or varietal differences in oviposition rates were not necessarily followed by similar differences in ultimate larval infestation. Oviposition on any plant species or variety depended upon the number of sites available, but larval success, and hence the level of infestation achieved, depended upon the length of time during which the tillers remained suitable for larval penetration. This period is determined

by the particular growth characteristics of the species involved.

The consequences of this are that under field conditions slow-developing and freely-tillering grasses such as _Poa trivialis_ support higher larval populations than fast-growing less freely tillering species such as _Dactylis glomerata_. Also the increased rate of young tiller production of _Lolium perenne_ in response to defoliation increased the populations of stem-boring larvae in this grass. The inclusion of a proportion of a less susceptible species, such as _D. glomerata_, in a perennial ryegrass sward, reduced the number of larvae in the latter, perhaps by functioning as a trap crop for eggs and young larvae.

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IV. GENERAL DISCUSSION AND CONCLUSIONS

I. INTRODUCTION

(i) Review of Previous Work

Cyclorraphous larvae of some families of Diptera and, in particular, the families Chloropidae and Opomyzidae are known to infest many species of grasses, living within them and feeding on the stem tissues.

In the U.K., there are records of stem-borer damage to grasses as early as 1912 when Edmunds observed damage to the three grass species Lolium perenne, Avena flavescens and Arrhenatherum avenaceaum. Petherbridge (1917) recorded infestation of these grass species by dipterous larvae, and subsequent infestation of cereal crops following leys. In addition to the afore-mentioned grass species, Collin (1918), in his review of previous work on frit flies recorded the infestation of Poa annua, Poa pratense, Bromus sp., Triticum repens, Triticum cristatum, Phleum pratense, and Mulium effusum. Cunliffe (1921, 1922, and 1923) added to this list of grass hosts of the frit fly, the species Alopecurus myosuroides, Hordeum murinum, Holcus lanatus, Bromus sterilis, Dactylis glomerata and Agrostis myosuroides. Frew (1923) listed among other host plant species of frit flies the following grasses, Agrostis alba and Festuca elatius.

Nye (1959) published the results of a complementary study in which he investigated the distribution of dipterous stem-boring larvae in pure and mixed swards of grasses during winter months. He found seventeen species of larvae attacking sixteen grass species, the most susceptible of which were Agrostis tenuis, Lolium perenne, Holcus lanatus, Arrhenatherum elatius, Anthoxanthum odoratum and Dactylis glomerata, in decreasing order of magnitude.

Infestation of grasses appears to be widespread: Vasina (1929) in Russia observed that grasses always produced frit flies, especially the autumn generation. Zhukowiski (1937) and Vasina (1929) in Russia, Mayer (1926) in Germany, and Roos (1937) in Switzerland, regarded the grass species, *Agropyron repens* to be the principal host. By contrast, Aldrich (1920), and Wilbur and Sabrosky (1936) in North America, showed a wide distribution of *Oscinella frit* L. on grasses, especially in areas where Kentucky blue grass (*Poa pratensis*) was predominant. Wetzel (1967) investigated the occurrence and injuriousness of Dipterous larvae in grasses grown for seed in Germany, and found 14 spp. of larvae from four families associated with 16 spp. of grasses. Based on his rating technique, *O. frit* L. appeared to be the most important pest attacking *Poa pratensis* and *Trisetum flavescens* in particular. *O. vastator* attacked nine spp. of grasses and caused considerable damage to seven grass species including *L. perenne*, *Alopecurus pratensis*, and *Festuca pratensis*. *O. frit* L. *ex. Arrhenatherum* was confined to *Arrhenatherum elatius* and *Geomyza tripunctata* to *Arrhenatherum elatius* L. I et. C. Presl. In E. Germany, Mühler and Wetzel (1969) found that the host range of *O. frit* included 14 spp. of grasses. These larvae caused considerable losses due to 'yellow hearts' in *P. palustris*, *T. flavescens* and *A. alba*, and also caused 'total white ear' condition in *P. palustris* and *Arrhenatherum elatius*.

Factors other than host plant specificity have been shown to affect stem-borer numbers in grassland. Jepson and Southwood (1958, 1962) found populations of frit fly in grassland to be much less than they expected, considering the large population on an adjacent oat crop. Infestation of the grassland was more closely associated with the nature and condition of the sward than its distance from the oat field. They also found that short grassland contained about eight and eleven times more overwintering frit fly larvae than long grass in 1958 and 1962, respectively. Jepson and Heard (1959) found dipterous larvae, and in particular those of *Oscinella frit*, to be facultative parasites of the six common grasses, *Poa pratensis*, *Agrostis tenuis*, *Festuca arundinacea*, *F. rubra*, *L. perenne* and *D. glomerata*. Their results also showed preference for certain grass hosts in a number of species, and thus at the end of a ley, the larval population, both in number and species composition may vary considerably according to the botanical composition of the ley. Emecz (1960) carried out investigations on the agronomic importance of Diptera to various species, varieties and genotypes of grasses. He observed the significance of topographical location in the rate of infection of *L. perenne* varieties. There was severe damage to the grasses on flat land, whereas the same varieties were unaffected on the sloping part of the same field. He suggests that oviposition took place within certain time limits and also within a certain radius from the source of infection. He also found very different infection rates between varieties and genotypes. This was attributed to the variation each year in growing conditions for the flies as well as for the grasses, and also to the varying proportion of the contributing larval species, though the larvae were not identified.

Southwood and Jepson (1961) compared the populations of frit fly on grassland and on oats and suggested that among other factors, a relative shortage of suitable sites for development, which may in turn be influenced by climate, might be the main factor accounting for the more or less steady population on grassland. They added that the attack of natural enemies and interspecific competition with other dipterous stem borers may also be important factors.

Hillyer (1965) worked on some aspects of host-plant relations of *O. frit* L. and found that the host species range of the fly within the Gramineae appears to be potentially very large. He suggested that host selection under natural conditions will depend on host response thresholds of the particular female and the relative stimulating powers of available host plants. He also stated that there was no evidence that the host preference of the adult was influenced by the nature of its food during larval development and assumed that host preferences are genotypic. Kreuter (1928) in the U.S.S.R., Balachowiski and Mesnil (1936) in France, Collin (1946) and Nye (1955) in the U.K. and Nartshuk (1956) in the European part of the U.S.S.R. carried out studies on the external morphology and host relations of many species of dipterous stem borers, and produced various useful keys for identification of the larval stages. Nye's key, published in 1958, clarified most of the earlier contradictions and is the most up-to-date. Le Berre (1959) and Ibbotson (1958, 1972) have initiated studies which may allow the separation of adult stages of Oscinella spp.

Bhattacharya (1957) investigated the biology and interrelations between the parasites of Oscinella frit L. on cereals. He recorded six major larval and four pupal parasites and found that the parasitism of overwintering O. frit larvae in Lolium sp. was 11%, but that O. vastator and O. nitidissima were not parasitised. Van Emden, Southwood and Jepson (1961) estimated a value of about 17% parasitism on oats while Southwood and Jepson (1962) gave values of between 0.2% - 18% parasitism on oats depending on the generation and the year. They also estimated a natural mortality of about 50% on overwintering populations of larvae in grassland.

Estimates of the effect of larval infestation on the grass crop are fewer. Webley (1958, 1960) applied dieldrin to a direct reseeded ley on mountain pasture in S. Wales and attributed the improved survival of Lolium perenne to a reduction of the frit fly population. Improved growth of Phalaris arundinacea L. was obtained in N. America by Wolf (1966) after application of heptachlor, the effect also being attributed to control of O. frit L. Henderson and Clements (1970, 1971, 1972 and 1974) showed that treatment of swards, and especially of perennial ryegrass, with pesticides which control dipterous stem-borers and many other groups of pests could increase yield. However, it was not clear to what extent the control of stem borers alone contributed to such increases. Emecz (1960) made similar suggestions while Jepson and Heard (1959), on the basis of their observations suggested that the substitution of D. glomerata and possibly F. arundinacea for more susceptible grass species in leys, and in headlands might be of value in reducing damage by O. frit in districts in which grass leys or winter cereals frequently fail to become established.

(ii) Aim of Study

From the foregoing review, it appears that some aspects of the biology of stem-boring Diptera have been closely studied, while other aspects have been neglected. Stem-borers in cereal crops, in particular Oscinella frit L., have received much attention probably because they cause serious and economic damage, and hence the need to provide immediate control measures. In grasses, where insect damage generally is not obvious, the biology of stem-boring flies has been studied less intensively. Since sown and managed grasses are crops in their own right, it is desirable that further studies should be made on the various aspects of the biology of these insects, which may cause serious though less obvious damage.

Most of the detailed information available relates to one species, Oscinella frit L. In the U.K., this species has three generations (Southwood and Jepson, 1958, 1959 and 1962; Ibbotson, 1960) and sometimes a partial fourth generation (van Emden et al., 1961). The number of generations for any particular year depends mainly on the duration of temperatures favourable to development between spring and autumn. The first and second generations breed mainly on cereal crops during summer whereas the third breeds chiefly on various grass species in autumn and overwinters as third instar larvae on these hosts. These overwintering larvae serve as the main source of the adults of the first generation which emerge in the spring of the following year. Other species of dipterous stem-borers, e.g. Geomyza tripunctata (Fall.), O. vastator (Curt.), O. frit ex Anthoxanthum and O. frit ex Arrhenatherum, appear to live entirely on grasses. However, the number of generation of each species, produced in a year, and the extent of damage that they and O. frit L. cause on sown grasses are not well known.

How these various genera and species co-exist on grass has not yet been investigated. Various factors such as differences in breeding periods, selection of different habitats or different strata within the same habitat have been used by other authors (Waloff and Southwood, 1960; Le Quesne, 1972; Kiritani et al., 1963) to explain the mechanism of co-existence for various other species of insects which utilise a common habitat. However, it is not known yet which of these factors apply to the phenomenon of co-existence of the various dipterous stem-borer species on grasses. Relevant information needs to be provided to fill this gap in our knowledge of their ecology.

Toward these ends, the field population of all stages of stem-borers in field plots of sown perennial ryegrass and perennial ryegrass/cocksfoot mixtures were sampled regularly from the time of germination onwards. The species which constitute the complex were identified, and the relative numbers of each species present at any time of year was assessed. With this information, and knowing the number of tillers present, an estimate of the damage done by the insects was obtained right through the year. Studies were also carried out to identify the environmental and host plant factors which regulate stem-borer numbers in the ryegrass swards.

A description of the distribution of an insect population, according to Southwood (1966), apart from being of desirable ecological significance, is in its own right a description of the population. An attempt was therefore made to study the pattern of the distribution of the immature stages of the borers in swards of different ages. Although instances of 'clumping' of overwintering larvae have been noted by some authors (Nye, 1958; Jepson and Heard, 1959; Southwood and Jepson, 1962b) the basic factors underlying the pattern seem to be a neglected aspect in the study of these insects. It is known that for some insect species, the pattern of distribution may change with population sizes (Finney, 1941; Iwao, 1956; and Harcourt, 1961b). It may also vary with differences within the same habitat (Kuno, 1963) or as in the case of molluscs, it may vary with differences between habitats (Yoshihara, 1953). However, it is not known how these factors affect the distribution pattern of dipterous stem-borers on grasses. To provide information on this aspect, the pattern of insect distribution was examined by regular sampling in swards of different ages, all through the year. The behaviour of egg-laying flies and the pattern of egg distribution was also investigated and the results related to that of distribution of subsequent stages.

Studies on the behaviour of *O. frit* L. on cereals have shown that younger plants are preferred to older ones by ovipositing flies. Young plants are also more suitable to entry and successful establishment by the newly hatched larvae. In sown grassland, the mean age of the sward is dictated by the ages of the composite tillers, which for most of the year are not at the same growth stage. It was therefore necessary to clarify how tiller or sward age affects the success of the newly-hatched larvae.

Although the host range of the frit fly within the family Gramineae is wide, evidence of preference for certain grass species has been observed by various authors, as noted earlier, but the available evidence is conflicting. This may be due to the confusion in the identification of the species of insects involved. The fact that opinions still differ as to whether all the frit flies belong to different species or different biological races make the results of previous experiments by these authors difficult to interpret.

This apparent inconsistency in host preferences of the adult frit fly may also have been due to the wide variation in growth stages or growth-habits, within a given grass species, as well as among various grass species, used by various authors. Environmental factors may vary from place to place, and their effects on the various grass species may also influence the preferences of the flies. A similar situation may also affect the success of the larvae while establishing in the plant. Oviposition and larval infestation were therefore examined on plants of different species at different growth stages and in stands of different density.

The adult stage of the most common hymenopterous parasites are known to be more active in, and to remain behind in grassland as frit flies move out to cereal fields (van Emden, 1966), but the degree of control of the frit fly and allied stem borers in grassland by the hymenopterous parasites is known to be low (Bhattacharyya, 1957). While this programme did not aim at detailed work on biological control, field observations were made on the seasonal changes in the numbers of adult parasites and their hosts, in order to investigate this apparent contradiction.

Some degree of success on the control of frit fly on cereals has been achieved through the use of insecticides and cultural practices such as early sowing which enable the plants to 'escape' attack. However, in grassland, the use of chemical control measures is difficult due to the toxicity hazard to stock, while cultural methods are less effective because of the perennial nature of the crop. Since evidence existed of host preferences, the possibility of using resistant grasses to reduce attack was examined.

To summarise, in view of the incomplete knowledge of stem-borer biology in grass it was decided to try to provide information on the following topics:-

(a) the composition of the species complex of borers in perennial ryegrass

(b) its fluctuation in numbers with time from date of sowing onwards,

(c) the amount of damage caused to the sward,

(d) the factors influencing the process of invasion of sown grass,

(e) the importance of natural enemies, and

(f) the possibility of utilising the information obtained to reduce infestation by cultural control measures.

II. METHODS

(i) Experimental Site

The field site was an existing sward of pure S24 perennial ryegrass (Lolium perenne) sown in September 1970, at a seed rate of 56 kg/hectare, in rows 15 cm apart, on a moderately well drained soil of brown loam over strong mottled clay. This sward was located on Long Hoos III field at Rothamsted Experimental Station, Hertfordshire. The established sward was divided into twelve equal-sized (7m x 10m) plots arranged in four blocks of three plots.

Pure swards of perennial ryegrass

In September 1971, grass on one plot from each block was killed with a paraquat spray (2.3 mls in 2.3 litres of water per 0.001 hectare). These plots were left fallow and resown in April 1972 to S24 perennial ryegrass at the same seed rate.

In June 1972, the grass on one other plot in each block was also sprayed with paraquat. The plots were kept fallow until resown to S24 perennial ryegrass in April 1973, again at the same seed rate.

The object was to provide plots of S24 perennial ryegrass of different ages, randomised within each block, so that in any of the sampling seasons (1972 and 1973), studies could be made on young grasses sown at the beginning of that season, and simultaneously on older grasses sown at least one year earlier.

At the beginning of field sampling in June 1972, there were four plots of young ryegrass sown in April 1972 and four plots of old ryegrass sown in September 1970. Similarly, when sampling began in May 1973, there were four plots of young ryegrass sown in April 1973 and four plots of older ryegrass sown in April 1972.

Mixed swards of cocksfoot and ryegrass

In June, 1973 the grass on the remaining plots sown in September 1970 was killed and the land was prepared for sowing. Before sowing, each of these plots was subdivided into four equal-sized (3.5 x 5 m^2) subplots. The subplots were resown to either pure S24 perennial ryegrass, or mixtures of varying proportions of S24 perennial ryegrass and commercial cocksfoot (*Dactylis glomerata*). In order to obtain swards of varying composition, all the subplots were sown to a base quantity of S24 perennial ryegrass at the rate of 56 kg/hectare. In three of these subplots varying amounts of cocksfoot seed, 9 kg, 18 kg and 27 kg were mixed with the ryegrass seeds. This provided one pure sward of perennial ryegrass (0% cocksfoot) plus three mixed swards with 10.6, 16.6 and 26.9% cocksfoot respectively.

This procedure was repeated in April 1974 on another set of three plots. The subplots were then resown to either pure S24 perennial ryegrass, or ryegrass cocksfoot seed mixtures as before. This again provided one pure sward of ryegrass and mixed swards with 11.1, 14.8 and 19.6% cocksfoot, respectively.

All plots received a top dressing of 750 kg N/ha, applied as "Nitro chalk" granules, at sowing, and after each mowing. The subplots sown to pure and mixed seeds were hand-weeded shortly after germination in order to obtain a good establishment of the sown grass species.

(ii) Field sampling methods

Insect populations in the field were sampled regularly by three methods. These were: core sampling, soil washing, and suction sampling.

(a) Core sampling. A cylindrical, 10 cm diameter, manually operated soil core-sampler was used for taking samples of turf to a depth of ten centimetres. Excess soil was cut off the bottom layer with a knife so that the grass and the top 2 cm of soil were finally collected. Each sample was kept in a polythene bag and stored in a 5°C constant temperature room, until examined. The low temperature of the C.T. room prevented further development of the larvae and pupae during storage.

Because the heterogeneous nature of the crops surrounding the experimental area may have influenced the pattern of invasion by adult flies, a method was adopted to take this into account. Each plot was divided into five areas corresponding to the five different types of surface cover surrounding the plots. Core samples were taken from each aspect to see whether larval populations differed between them.

Samples were taken at weekly intervals between May and November in 1972 and 1973. Four plots of old and 4 plots of young grass were sampled. Twenty cores were taken from each grass type each week, as described above.

Analysis of the results of the 1972 sampling, showed that the division of plots into aspects was unnecessary so this was subsequently abandoned. In 1973 the number of samples was also reduced to ten cores from young grass and ten cores from old grass per week. All the other treatments and routine were as for 1972.

Each core sample was later treated in the laboratory as follows. The grass stems were carefully separated from the soil by hand. The soil was stored at 5°C until subsequently washed. The grass plants and tillers from each sample were then carefully dissected using a fine pair of forceps (No. 5) under a binocular microscope. The larvae and pupae were extracted, either identified immediately or stored at 5°C in stoppered 6-dram vials lined with moistened filter paper until identified. Larvae could thus be kept alive for several months.

For detailed examination, two or three larvae of about the same size were mounted together in distilled water on glass slides covered by a two-centimetre square cover-slip. Each larva was examined with transmitted light under a compound microscope, using magnification of up to x350. Larvae which moved too much for examination were rendered inactive by merely draining off excess distilled water under the cover slip with dry filter paper. Identification was facilitated by examining live rather than preserved specimens. These were identified to species with the aid of the key produced by Nye (1958).

Lacking a published key to the pupae, these were identified to genus under a binocular microscope, using mainly their morphological characters, such as size, shape and number of digits on anterior spiracles. The pupa of the genus Geomyza is unmistakeably different from that of Oscinella and Agromyza, and could be separated by its characteristic club-like, digitate anterior spiracles, its bigger size and depressed facial mask. The pupa of Agromyza has non-digitate anterior spiracles, which separates it from the other groups. Oscinella species were bulked together as one group. The pupae of the three major groups of dipterous stem-borers were thus quickly separated. By these methods I was able to determine the succession, the species composition and the relative abundance of each species in old and young grass throughout the season.

(b) Soil Washing. The soil portion of each sample was later washed under a jet of water using the methods of Salt and Hollick (1944) and Raw (1955, 1962). The insects extracted were later floated in a concentrated solution of commercial magnesium sulphate. Dipterous larvae and pupae obtained from the float were picked out with a camel hair brush or blunt forceps and identified. When it was found that none of these dipterous larvae and pupae were stem borers (mostly Ephydridae and Sphaeroceridae), regular soil washing was discontinued as a routine measure and restricted to two subsequent sampling dates following harvesting when some stem-borer larvae and pupae became dislodged from the bases of infested stems. These either remained on soil surface with plant litter or burrowed into the soil. Otherwise the larvae and pupae remained within the host plant tissues throughout their development, and empty pupal cases from which adults emerged were always found in the dead tissues of the host plant.

(c) Suction Sampling. In addition to regular sampling of larvae and pupae, adult stages of the borers and associated hymenopterous parasites were sampled from old grass (1972 season) and young and old grass (1973 season). A self-powered portable insect suction sampler devised and described in detail by Arnold et al. (1973) was used. The sampler consisted essentially of a petrol-motor-driven radial out-flow turbine attached to a collection chamber and sampling tube. Bags for collecting the adult insects were made from paper towels sown into bags (35 cm x 20 cm). These bags were cheap and could be used both under dry and fairly moist field conditions. Under very moist field conditions, bags of the same size, made from fine muslin cloth were used. The area of grass to be sampled was chosen at random in each plot and demarcated with a bottomless collapsible box (0.5 m^2 x 50 cm high) made from plywood. The top was sealed by two flaps of fine muslin 70 cm x 40 cm to prevent flies from escaping during sampling.

During sampling, the suction machine was kept running for a period of three minutes on each half square metre of grass sampled. Regular sampling was carried out every other day between 9.00 and 10.00 a.m. from Mondays to Fridays. A total area of one square metre or two square metres per plot was sampled on each sampling date, the total area sampled on one day depending on the size of the current adult population. Insects in the collection bags were killed with ethyl acetate vapour and tipped into a white tray for determination of species and sex. Hymenopterous parasites were also recorded.

(d) Emergence traps. The emergence of adult flies in the spring of 1973 and 1974 was estimated by 0.5 m^2 emergence traps consisting of a metal frame clad with plywood and having a cone-shaped upper portion covered with white muslin cloth. A ten-centimetre wide hole at the tip of the cone provided an outlet from the cage for emerging insects. A device for collecting the insects was fixed to the outlet of the cage. In March 1973, five emergence traps were set up on young and old plots. In April 1974 four cages were set up on old plots established in spring 1972, and mixed swards established in summer 1973. The collecting celluloid cylinder was replaced with transparent glass plates (12 x 12 cm^2) coated with a thin layer of Plant Protection "Boltac" tree-banding grease which trapped emerging insects. The plates or the collecting cylinders were changed twice weekly and the insects counted and identified. During both seasons all traps were set up in April and removed at the end of July.

Soil temperature at 10 cm depth under the sward was recorded from February 1973 to October 1974, using a thermograph.

(iii) Laboratory Culture Methods

Cultures of species of dipterous stem-borers, Geomyza tripunctata, Oscinella vastator and O. frit L., were established from identified third instar larvae collected from the field. Rearing was carried out in a glasshouse in which the temperature fluctuated in the range 15-20°C. A constant 16-hour photo-period was maintained in the glasshouse by overhead lamps. This combination of light and temperature in the glasshouse provided a suitable environment for the survival of the insects and normal growth of the host plants.

S24 perennial ryegrass (Lolium perenne L.) was used as host plant for establishing various colonies. Plants five to six weeks old growing in 10 cm diameter pots were clipped to a height of about 3 cm above soil level. Incisions were made at about 1 cm above soil level in each plant stump, with a pair of fine forceps and some internal plant tissue removed so that a small space, big enough to contain a larva was formed. Identified larvae previously stored in 5°C.T. room were transferred into a solid watch glass containing tap water and were left in the glasshouse until they became active again. Most larvae became active within five minutes in these conditions. One active larva was introduced into each incision. In this manner as many as 15 to 20 stems were innaculated in each pot. Each pot was then covered with another and left overnight, while the introduced larvae established themselves within the stumps. The cover protected the larvae from light and desiccation which otherwise caused them to leave the plants, and burrow into the soil where they failed to complete their development.

On the following day the cover was removed and was replaced with 8 cm diameter cylindrical muslin cages. Under these conditions the larvae pupated and adults emerged within two to three weeks of larval introduction. Newly emerged adults were transferred to a bigger rearing cage containing a tray of young grass plants 2-3 weeks old. Adult flies laid eggs on these plants within ten days, within which time some of the plants had already started to show symptoms of larval attack. The tray of infected plants was transferred into another rearing cage for further development of larvae to the adult stages. A new tray of young plants was again introduced to the adult flies. In this way up to three batches of plants could be infested using the adults produced by the inoculated larvae.

To begin with various food materials; honey, yeast extract, sucrose solution or combinations of these were used for feeding adult flies. However, these mixtures trapped adult flies and promated fungal growths on plants and cages. Latterly a simple saturated solution of A.R. Grade sucrose was used. White dental rolls were soaked in this solution and attached to the roof of the cages. The adults located and fed on these rolls. If the cage roofs and floors were cleaned every fortnight, the same batch of soaked rolls, replenished by pipette, could be used for two to three weeks without risk of fungal growth.

(iv) Lab./Field Experiments

These were experiments carried out with plants propagated in an insect-free glasshouse and later transferred to the field for infestation by adult dipterous stem-borers.

(a) Potted plants of different ages and densities. These were obtained by sowing medium to large-sized seeds of S24 perennial rye-grass at the same density and spacing in 15 cm diameter pots on various dates. Insecticide-free John Innes F.F. Sterile soil was used in all instances. One week before transferring the plants to the field the pots in each sowing were subdivided into batches and each batch was thinned down to the required number of plants per pot. Thinning was done either by carefully pulling out excess plants in the case of young seedlings, or with older plants, by cutting below soil level with a fine pair of scissors. Secondary tillers of the remaining plants were also cut off. For field exposure the pots were buried side by side with their rims touching one another, and the rims two centimetres above soil level. The plants were exposed to infestation in the field and then returned to the laboratory and stored at 5°C pending examination. The grass stems from each pot were dissected and the number of damaged stems, larvae and pupae of dipterous stem-borers recorded. The larvae and pupae were identified only to genus in view of the amount of work involved and time available.

(b) Potted plants of different ages and varieties. Seeds of different varieties of grasses were sown in 10 cm diameter pots at a uniform seeding rate of 20 seeds per pot and uniform spacing. Insecticide-free John Innes F.F. sterile soil was used. Each variety was sown on various dates so that plants of different varieties and at different ages were available for field tests. To remove the variation due to differences in germination rate each pot was thinned down to 15 plants per pot two weeks after germination.

(v) Laboratory Behaviour Studies

Experiments were conducted in a controlled environment room, under a 16 hour-day regime, with day and night temperatures of 20°C and 15°C respectively. The uncontrolled relative humidity fluctuated narrowly around an average value of 50% throughout the period of the experiments. An observation cage in the form of a long rectangular box

50 x 60 x 130 cm was used. The sides, back and base were wooden, and the top and front were of transparent 2 mm 'Perspex' sheet. The box was divided into two equal compartments by an internal wooden partition. All the inner walls of the cage, except the transparent panels, were painted white. Muslin-covered 5 cm-diameter ventilation holes were cut at each corner of the roof, and on the rear wall of the box. The front walls slid sideways for access, and when these were closed access was gained by arm holes sealed by muslin sleeves at each end of the box.

Whenever individual insects were being studied, small cylindrical cages made from thin "Perspex" sheet 1 mm thick were used. Each cylinder fitted over the plastic pot in which the host plant was growing and the open end was sealed with fine muslin. Insects inside the cage were fed by placing dental rolls soaked in sucrose solution on the muslin at the top of the cage. Potted plants were watered by keeping the pots in dishes of water. In some experiments, plants grown in wooden trays 30 x 15 cm^2 and 4 cm deep were used. The plants were grown from seed sown at uniform spacing and kept in the glasshouse until required. Trays of such plants were placed in the observation cage. The insects were introduced into the observation cage where they were fed on sugar-solution soaked pads attached to the cage walls. Plants in the trays were watered from a wash bottle, taking care to water the soil but not the foliage. This method of watering ensured that eggs were not dislodged from plants on which they were laid. It also ensured minimum disturbance to adult insects performing other various activities, mating, and ovipositing.

III. RESULTS

(i) Population build-up and breeding cycles of flies in the field

(a) Pupation in the field

G. tripunctata. Some third instar larvae which have completed development by early autumn of 1973 overwinter as prepupae and pupae, further development being arrested as the soil temperature (at 10 cm) falls near to 0°C. Prepupation and pupation of most larvae recommenced as early as February of the following year and as soil temperature at 10 cm depth rose above 2°C. The number of pupae gradually increased as the number of days when soil temperature was above 2°C accumulated, the peak of pupation being reached very early in April.

Oscinella spp. Unlike *G. tripunctata* these species did not overwinter as prepupae or pupae but as larvae (mainly third instar). Pupation commenced in mid-April as soil temperature rose to about 5°C. The first peak of pupation occurred in mid-May as temperature accumulated above 5°C. A second peak of pupation occurred in mid-June as soil temperature rose above 6°C in response to the mowing of the sward. Pupation in the field was completed by late June (Figure 1).

In the ploughed-up sward the pupation of *G. tripunctata* and *Oscinella* spp. during spring commenced and attained peaks two to three weeks earlier than in the unploughed swards.

These results show that the pupation of *G. tripunctata* started earlier in the season than those of the various species of *Oscinella*. This was probably because *G. tripunctata* required a lower threshold of temperature for pupation than do the *Oscinella* species. The two peaks of pupation observed in the case of the *Oscinella* group may be due to differences in the minimum temperature thresholds required by various species for pupation. It may also be due to individual variation in the rates of development of the overwintering larvae.

The results also show that the rates of development of overwintering larvae, and their pupation may depend on the rate at which temperature accumulates above the thresholds required for pupation. These rates may in turn be affected by the condition of the sward as the temperature rises in spring. For example, if the sward is ploughed up or if grass length is reduced by cutting or grazing, the soil temperature rises more quickly. This will cause overwintering larvae to pupate sooner, and bring forward the time of peak emergence of adults of all species.

(b) Adult emergence in spring

G. tripunctata. In 1974, the emergence of flies from the overwintering immature stages commenced in early April and reached its peak within two to three weeks. Samples collected at the early stages of emergence contained more females than males whereas at the later stages of emergence, the opposite was the case. It therefore seems that females generally emerge much earlier than males or the former were less negatively phototactic than the latter and climbed to the cage top much earlier than the males. In either case, peak emergence appeared to be delayed until soil temperature at 10 cm below the sward, exceeded 5°C (Fig. 1). Taking the figures for the whole emergence period, the overall sex ratio of emerging flies was about 1:1.

Oscinella spp. The emergence of these flies started much later in the season than in the case of G. tripunctata, commencing in late May, and attaining a first peak within one week. Subsequent to the mowing of the sward, a second brood of flies started to emerge from mid-June, giving rise to a second, but much higher peak in late June. Again, more females were found in the samples at the early stages of emergence in both broods, and emergence was completed by mid-July.

In the case of the first brood, emergence did not begin until the soil temperature at 10 cm within the sward exceeded 5°C. By contrast, peak emergence of the second brood of flies was not attained until the soil-temperature was over 8°C (Fig. 1). The first brood of emerging flies consisted mainly of the typical black frit, whereas the second brood consisted mainly of the lighter-coloured, yellow-legged, O. vastator.

In swards ploughed up in late autumn of the previous year, the emergence of flies of both species started much earlier in spring, and attained peaks two to three weeks ahead of peak emergence in unploughed leys. This was probably because soil temperature in spring accumulated at a faster rate in ploughed up swards than in unploughed ones.

These results indicate that G. tripunctata, with the lowest emergence temperature threshold of 4°C, appears much earlier in the season than the four Oscinella species. Within the Oscinella group each species has its own emergence threshold temperature.

O. frit L., and probably O. frit ex Arrhenatherum at 5°C required a higher temperature than G. tripunctata, and O. vastator and O. frit ex Anthoxanthum had a still higher temperature requirement, with a threshold value of 8°C.

In both genera, however, the time of emergence appears to depend mainly on how quickly the temperature of the soil within the sward accumulates above the threshold required for emergence. The rate at which this takes place depends mainly on seasonal variations but is also influenced by the management or the condition of the sward (e.g. mowing and ploughing-up).

(c) Seasonal variation in populations of adult flies in the field

G. tripunctata. The result of regular vacuum sampling of swards showed that the population of female flies in the newly-sown swards built up gradually from about $1.5/m^2$ as adults of the first generation emerged from the older sward in early April, to $3/m^2$ during the first peak in late June. Thereafter the population declined to about $1/m^2$, and remained at this level until late July. Following the mowing of the sward in late July, the emergence of adults of the second generation began and the population of female flies increased again, attaining a second peak of about 6 females/m^2 between the middle and end of August. Thereafter the population of flies gradually fell again to about $1/m^2$ by the end of September and persisted at this level throughout the winter and the following spring.

In the older sward, the trend of population build-up was similar to that in the newly-sown sward, except that there were more flies in the former sward in April and May. The number of female flies attained the first peak of $5/m^2$ in May. After the sward had been mown (early June) the number of flies fell to about one per square metre. A second peak of 5 female flies per square metre occurred in mid-September, thereafter declining to about one per unit area.

? Oscinella spp.

In the newly sown sward, the population of female flies in the field built up gradually from about $1/m^2$ in mid-May as adults emerged from overwintering immature stages, and reached the first peak of about $3/m^2$ at the end of May. Thereafter the population declined gradually to about $2/m^2$ and remained at this level till early August. Following the first mowing of the young swards at the end of July, a second brood of flies was found and the population of female flies attained a second peak of about $10/m^2$ in late August. It then declined very rapidly to about $1/m^2$ in late October. From early November onwards, adult Oscinella spp. were not found in the field until the beginning of the following summer.

The number of female flies in the old sward was smaller than that in the younger sward, particularly during the earlier part of the season. After the older sward had been mown (early June) the number of flies in both swards became very similar. In 1973 two peaks of flies occurred, the first at $2/m^2$ in June, and the second, but larger, one at $8/m^2$ in August. Thereafter, the number of flies declined to about one per square metre during autumn.

(d) Comparative abundance of flies in young and old swards

The result of regular suction sampling in both sward types showed the number of flies in a sward type differed with insect species and with the conditions of the swards.

In the case of G. tripunctata the number of flies in any sward type was influenced by the amount of vegetation cover it afforded. Thus, in the early part of the season (April-May) when the plants in the unmown older sward provided more vegetation than the recently germinated seedlings in the younger sward, the number of flies in the older sward was greater than in the younger sward. After the former had been mown, the situation was reversed and the flies became more numerous in the younger sward, remaining so until late August. From this time onwards the numbers of flies in both swards were very similar. This was probably because the older sward, having fully regrown its vegetation by late August, became as attractive as the younger sward for the flies' shelter and breeding activities.

This tendency of G. tripunctata to avoid newly mown swards was more evident during the hotter and brighter hours of the day. Towards dusk, when the environment became usually cooler and less bright, the flies were observed to move freely from one sward to the other.

With the Oscinella spp., more flies invaded the newly-sown sward earlier in the season, before the older sward was mown. After the latter had been mown the flies were more evenly dispersed between the two types of sward. This was probably because the frit flies were attracted to the bare soil surface in the older sward.

(e) Comparative abundance of flies of different generations in the field

G. tripunctata: The population of flies in the newly-sown sward attained two peaks during the year, the first in early June and the second in August. The flies of the first brood consisted mainly of immigrant first generation flies which emerged from overwintering immature stages in the adjoining old sward, though the flies may have been partly supplemented by the few individuals which had survived the winter as adults.

The second brood of flies were mainly the progeny of the first generation flies. The population size of this second brood was about twice that of the first.

The difference in the size of the two adult peak populations is related to the size of the larval population giving rise to them. The larval population producing the first brood is greatly reduced by winter mortality.

Oscinella spp.: Due to the difficulty of separating the four Oscinella spp. in the adult stage with any confidence, recognition of the appearance of the different generations was based on the interpretation of the abundance of adults in conjunction with the data on larval numbers identified to species. Suction sampling revealed two apparent population peaks of adult Oscinella spp. The first, between May and July consisted of flies of the first (overwintering) and second (tiller) generations of the four Oscinella spp., which overlapped sufficiently to give the appearance of a single peak. It was noted earlier that the time of emergence of the first generation of flies varied from one species of Oscinella to another.

The second peak of flies was noted in late August and consisted mainly of flies of the third generation of the four species.

Comparing the population abundance of flies of the three generations, the size of each of the first and second generations are similar but smaller than that of the third. This may be because the population sizes of the larvae which produced each of the first and second generations were smaller. Southwood and Jepson (1962) found a very close relationship between the population size of over-wintering larvae of <u>O. frit</u> L. in grasslands and that of the first generation of frit flies which emerged from the same area in the following spring. Here, a similar relationship probably occurred between the population of adult flies of the summer and autumn generations and those of the larvae which preceeded them.

Most of the frit flies of the first and second generations are known to be produced mainly in grassland in spring and summer (Jepson and Southwood, 1958). These flies are also known to be as migratory as those of the third generation and to account mainly for the adult population in oats during these periods (Southwood, Jepson and van Emden, 1961; Johnson, Taylor and Southwood, 1962). This may also account for the smaller number of the first and second generation flies in grassland during summer. By contrast, the greater increase in the number of flies of the third generation in sown grasses may also have been due to the influx of the immigrant frit flies of the large panicle generation from fields of oats during autumn. Southwood and Jepson (1962) found that the migration of such flies from oats to permanent grassland began as temperature fell in autumn. Of the four <u>Oscinella</u> spp. associated with perennial ryegrass only <u>O. frit</u> L. exploits both the cereal and grass habitats. It is therefore very difficult to estimate to what extent immigrant <u>O. frit</u> L. alone contributes to the higher population of the autumn (third) generation in grassland. However, if allowance is made for the movements of the frit flies between the two habitats, taking place at various times of the year, it seems that the frit fly populations of the three generations produced by sown grasses would be similar.

These results agree with those of the authors mentioned above and with those of others. Smith (1962) and Calnaido (1962), who studied the population fluctuation of O. frit L. in oats, grass leys and permanent grassland, found that in contrast to wide variation in population abundance of frit of the generations in oats, the population size of the three generations in grasslands remainsmore or less steady. Southwood and Jepson suggested that this was probably because there was a continuous availability of suitable tillers for development of the flies in grassland. The enormous variation between the populations of the different generations in oats was attributed mainly to the relatively much greater number of oviposition sites available to the flies laying eggs on the panicles, and the high degree of synchronisation between this and oats' development.

The confinement of breeding to the tillers in perennial ryegrass, and the relative stability of the tiller numbers, means that the potential size of the third generation is relatively limited vis a vis oats. The normal seasonal pattern is of a steady increase in successive generations to a peak in autumn.

(f) Sex ratio of flies in the field

In both genera, female flies were more numerous in the samples taken earlier in the season, constituting about 60% of the samples. This may have been because most of the female flies emerged a little earlier than the males. As more flies emerged later in the season the situation became reversed and more male flies occurred in the samples although there was some variation. This may have been due to the fact that the flies were made up of the overlapping first and second generation adults. Towards the end of the season the sex ratio was again in favour of females in the case of G. tripunctata. This was probably because the female flies were better adapted to survive the low temperatures in late autumn and in winter. By contrast, the samples taken at the end of the season contained more male than female flies of the Oscinella spp. Since this genus did not over-winter as adults, the smaller number of female flies in the sample may have been due to the differences between the activities or rate of dispersal of the two sexes. It may also be because most males lived longer than the females.

Within each genus, the aggregate sex-ratio during the year was about 1:1 (Figures II and III).

(g) Breeding cycles - number of generations of each species per year

The invasion of newly-sown grass by flies of various species, and the breeding of the flies started at different times in the season, that of any particular species corresponding with the time of emergence of its adults in spring or early summer.

G. tripunctata: This species was the first to emerge and invade the newly-sown sward. It bred from early May onward. Early instar larvae were found in the field from this time onward until the end of November. Three peaks of early instar larvae, probably corresponding to three breeding cycles, were detected within one season, the first in early May, the second towards mid-August and the third in November. The first two peaks were of about the same size. The third population peak was the highest, and about twice as great as the previous two.

In the old sward, the three peaks of early instar larvae also occurred, though the levels reached were lower than, and occurred slightly later than, those reached in the younger sward.

Oscinella spp.: Adults invaded the young sward as from mid-May and bred from this time onwards. The early instar larvae of O. frit L. and O. frit ex Arrhenatherum were found much earlier in the season (late May to early June) than those of O. vastator and O. frit ex Anthoxanthum, which were not found until late June.

In the young sward three peaks each of early instar larvae of O. vastator and O. frit ex Anthoxanthum were found (in early July, late August and mid-October), whereas only two distinct peaks of early instar larvae of O. frit L. and O. frit ex Arrhenatherum were detected in the same sward within a season. In the case of the latter two species, the first peak occurred between mid-June and mid-July, and the second peak occurred in late September. The peaks of early instar larvae of the former pair occurred slightly later, the first peak occurring between late July and mid-August, and the second between late September and mid-October.

In the old sward, the breeding cycles of Oscinella spp. followed trends similar to those in the younger sward, and the intensities of breeding were similar, particularly after the old sward had been mown and new young tillers produced.

These results suggest that in spring and early summer the first generation of the various stem-borer species invaded the sward at different times. The number of breeding cycles a species was able to complete in a sward depended upon the degree of synchronisation between its reproductive period and the period during which the sward remained suitable for larval establishment.

(ii) General behaviour of adults as influenced by the host plant

The experimental methods adopted in this study, the details of which are given later, were the same as those used for investigating the effects of the various host plant factors on the intensity of oviposition (section iii). A brief description of these methods is as follows.

Various grass species of the same growth stage, or single tiller plants of perennial ryegrass, variety S24, of different ages or at different densities were used. These plants were offered to small colonies of mated flies (15 couples) in observation cages, under controlled light and temperature conditions. The number of flies landing, resting, and performing oviposition movements was recorded four times daily. In this way it was possible to obtain information on how various host plant factors influenced the behaviour of G. tripunctata, O. frit L. and O. vastator. The results were as follows.

(a) Landing and resting behaviour

Effect of plant age. Immediately after being released into the observation cage, most adults of G. tripunctata flew to either the side-walls or to the floor of the cage. Landing on plants then followed, occurring much earlier in the case of G. tripunctata than in the case of the Oscinella spp.

When single-tillered shoots of five different ages were offered to the flies in a free-choice trial, more adults flew to and landed on the older (and bigger) shoots, than on the younger ones. This was the case with both groups of flies. The number of insects of each species landing and staying at rest increased with increased age of shoot (Table 1a).

More flies landed and stayed on the older shoots probably because these plants provided both stronger visual and optomotor attraction.

In order to separate the effect on fly behaviour of the age of the shoot from shoot size, artificial "stems" of five different lengths (2.5, 5.0, 7.5 cm, 10 and 15 cm) were pushed vertically into the soil in a seed tray and offered in free-choice to the flies. These "stems" were wire-reinforced paper strips normally used for binding plants to supports ("long twisters").

Again, most flies landed and remained on the tallest models. The number of flies responding in this way increased with the height of the models (Table 1b).

This suggests that the preference of flies for the older plants is based on their greater height rather than other more subtle factors associated with age.

Effect of plant density: Shoots of perennial ryegrass at the three-leaf stage but at varying densities (2,4,8,16 and 32/pot) were offered in free choice to the flies.

At first, more Oscinella spp. and G. tripunctata landed on the shoots offered at lower densities. Within half an hour this situation changed and the number of flies (of both species) which landed and stayed on the shoots was greatest at the highest densities; this was more marked in the case of G. tripunctata than in Oscinella spp. (Table 1c).

When first introduced to the plants the less-densely sown plants appeared to stand out more strikingly, and exert a greater optomotor effect on the flies. This certainly influenced the landing behaviour at first but within a short period this pattern changed, and both species of fly redistributed themselves so that more were on the denser plants. This may be because densely sown plants produced stronger visual attraction, but one may only conjecture about the reason for this change, as no critical experiments were made to elucidate the mechanisms involved.

Effect of plant species: In a free-choice of eight different grass species at the same growth stage (3-leaf stage), flies landed and stayed on plants at random. The number of flies which landed and stayed on the shootswas similar (Table 3a).

This indicates that in this situation, flies did not show any obvious preference for a particular grass species during landing or when at rest. Presumably, at this growth stage, each grass species produced a similar intensity of visual and optomotor attraction to the flies.

(b) Courtship and mating behaviour in Geomyza tripunctata

This is made up of a series of behavioural phases taking place in the following sequence.

Phase 1. Encounter: This is the meeting which takes place between any two flies, regardless of sex, as they crawl about. It occurs mostly during periods of peak activities. On meeting the two adults stop, usually with a distance of about 3-5 cm between them. Both remain still for a few seconds.

Phase II. Orientation: The two flies, still a few centimetres apart, now face each other. Either one or both flies spreads and beats its wings and simultaneously moves the body gently from side to side ("body-gliding"). This may occur between flies of the same or opposite sexes. If the flies are of the same sex, one or both crawls away, usually in the opposite direction. If they are of opposite sexes, the next phase may ensue.

Phase III. Wing flapping and body-gliding: The female at first remains still but may flap her wings gently at intervals. The male by contrast makes a short series of advances, at the same time increasing the rate of wing-flapping. When about 2 cm from the female, the male stops and recommences the body-gliding movement, while moving very slowly forward until the gap separating the two flies is closed. Before this happens the female may respond in either of two ways: (a) crawl or fly away, or (b) remain still. If the female remains, the next phase follows.

Phase IV. Antennal tapping: The male taps the female's antennae with his own, while vibrating his wings. The female remains still for most of the time. This antennal stroking continues until the female remains more or less motionless.

Phase V. Male queuing: The male alters his position until he finally comes behind the female. In this position, the male stimulates the female genitalia, again with the antennae for some seconds. The female then exhibits rhythmic movements of the abdominal tip. This presumably involves the gradual extrusion of the genitalia, but this was not observed in detail in order to avoid interference with the process

Phase VI. Mounting: Once the female exhibits rhythmic movement of the genitalia, the male suddenly mounts the female and holds her head with his labella. At the same time the male balances on the female, holding her body with his forelimbs. The final phase of balancing involves the locking of wings of both adults.

Phase VII. Mating: The male inserts the genitalia into that of the female.

During mating the male remains almost parallel on the back of the female, with the wings interlocked. The pair, when viewed from above, give the impression of a single four-winged fly.

The insects remain coupled for periods between 10 minutes to 2½ hour.

Dismounting: At the end of copulation, the male is dislodged by the female, who then crawls or flies away from the mating site. She then spends time cleaning the abdominal tip with the hind limbs.

Once the phase of antennal-stroking is successfully completed, the sequence usually leads on to successful mating.

The description above is based on observations made on nine flies in which the whole process culminated in successful copulation, and those made on many others in which courtship was terminated in various phases. Courtships which omitted any phase, and in particular the body-gliding and antenna-tapping sequence, did not lead to mating.

The approximate time spent in the different phases of courtship behaviour are given below. Suggestions are also put forward on the purposes or function of each phase.

Encounter. This was not timed because it occurred as the flies crawled or flew about during the course of normal activities.

Orientation. This happens within 2-3 seconds of encounter. The main purpose of this phase is probably to confirm the identity of the other insect or object which has been recognised visually. This suggestion is strengthened by the observation that adult Geomyza tripunctata behaved similarly towards dummies or dead insects of the same or other spp. up to this stage.

Wing beating and body-gliding. In comparison with most of the other phases (except mating) this took a considerable length of time, ranging between 60-120 secs.

This phase appears to be that of further confirmation of the identity of the other fly, and the signalling of the male's intention.

Crawling and wing vibration by males. This phase, taking some 10-40 secs, appears to be the main phase in which the male signals his intention. The movement which accompanies this phase may distinguish this approach from an aggressive encounter, and is the stage at which the female decides to participate or to leave.

Antennal tapping. This phase lasted for a mean period of 35 secs. Along with the previous phase, its main purpose appears to be that of stimulating the female.

Queuing and tapping of abdominal tip. This phase also lasted for about 30 secs. Again, the purpose of this is to stimulate the female further until the latter presents the genital plate.

Wing locking. This occurred as long as the flies remained in-copula. It ensures that the male is not dislodged until the end of copulation. In this position the couples may crawl about or make short-distance hops from plant to plant.

Mating. This was the longest phase. Adults were observed to remain in copulation for periods ranging between 10 mins and 3½ hours.

The main purpose of mating is obviously that of inseminating but it is not known whether all matings involved successful insemination.

(c) Oviposition movements and egg-laying behaviour

Detailed observations made in the laboratory on O. vastator and G. tripunctata showed that their oviposition movements and egg-laying behaviour are similar to those of O. frit L. as described by Ibbotson (1960).

Essentially, oviposition movements at the initial stages involve the active crawling of the female fly up and down the basal half of the shoot. Several runs are made in the process, differentiating these movements from normal exploratory activity, particularly in G. tripunctata. Later, the movements become jerky as the fly stops and taps the shoot surface with the proboscis or partially extended ovipositor. The ovipositor is then completely extended with the tip tapping the shoot surface at intervals or drawn along shoot surfaces for distances varying between 5-10 mm. The final stage involves active insertion of the ovipositor into plant crevices. In situations where crevices or cracks are absent, the tip of the ovipositor describes a spiral movement. This process continued until the fly was ready to lay an egg.

Immediately prior to egg-laying, the tempo of the oviposition movements slows down, the fly assumes a vertical position with the claws gripping the stem surface. The ovipositor is pushed into the crevice until an egg is laid. If there are no crevices or cracks, the eggs are laid on the bare shoot surface. Under such conditions the deposition of eggs takes a considerably longer time.

In Oscinella vastator and O. frit, more than one egg may be laid at the same oviposition site. In G. tripunctata, only one is usually laid per oviposition site, but if more than one oviposition site occurs on a single stem, then that stem may receive more than one egg. Larger egg masses per stem are laid by the Oscinella spp. than in the case of G. tripunctata where the number of eggs per stem rarely exceeds three.

The oviposition movements of *G. tripunctata* differed from those of the *Oscinella* spp. in their less violent nature and the spreading of and flapping of wings, which in the *Oscinella* spp. are usually folded.

In *G. tripunctata* one egg is laid at a time, whereas in *Oscinella* spp. eggs may be extruded in a chain of two or three.

(d) Performance of oviposition movements

Effect of plant age. Single tiller plants of perennial ryegrass at five different growth stages were presented to mated couples of *G. tripunctata*, *O. frit* L., and *O. vastator*. Instances of the performance of oviposition movements (presumably followed by oviposition) were recorded.

More ovipositional movements were noted on the older (larger) plants than on the smaller. This was the case with all the insect species (Table 2a).

This was probably because the older plants by virtue of their stranger optomotor attraction, also had a stronger arrestant effect on flies which stayed on them. This supposed arrestant effect may, however, also depend upon the higher intensity of stimulation which the insects received from various parts of the shoots, as they crawled up and down. In later experiments it was shown that apart from the increase in size the number of crevices also increased as the shoot grew. It was also shown that these crevices were the main source of tactile stimulus, which in turn greatly influenced the flies during egg-laying.

It appears that the older, and hence larger, plants attract a greater number of landings, and that tactile stimuli, probably associated with the larger number of crevices on the older plants, ensures that they remain for oviposition.

Effect of plant density. Mated couples of *G. tripunctata*, *O. frit* L. and *O. vastator* were offered perennial ryegrass plants at the three-leaf stage at densities of 2, 4, 8, 16 and 32 shoots per 10 cm diam. pot.

Performance of oviposition movements increased with increasing plant density. A maximum was reached at 8 plants/pot with *G. tripunctata* and *O. frit* L. and *O. vastator* females performed more movements at the 16 plants/pot density (Table 2b).

These results indicate that very high plant densities interfered with the oviposition movements, particularly those of *G. tripunctata*. However, during the establishment of a newly sown sward, shoot densities normally produced are below the maximum of 32/pot (78 cm^2) used in this experiment. The performance of ovipositional movements and the subsequent egg laying would therefore be unlikely to be limited by too high shoot densities under field conditions during the early stage of establishment of a sward.

Effect of plant species. When females of the three insect species were offered eight species of grass at the 3-leaf stage in free choice trials, they performed oviposition movements on all eight with similar frequencies (Table 3b).

This result differs from that obtained when actual counts of eggs laid were made, when clear preferences were expressed by all insect species (section iii).

Fly behaviour - discussion. Where plants were left intact the frequency of fly activity (landing, resting, crawling and egg laying movements) closely followed the intensity of oviposition, increasing as the plant grew older. Where secondary tillers were removed as they were produced, the intensity of oviposition did not follow that of fly activity.

It therefore appears that the plant factors influencing adult behaviour are different from those actually inducing oviposition.

Various authors have suggested plant factors which may influence insect behaviour: visual stimuli based on plant size and plant colour were considered by Moericke (1955); Kennedy et al. (1961); Dunn, (1961); Propoky (1968); and Bevers, Shaw and Hampton. (1971). Using aphids, Moericke and Kennedy et al. showed that the stimulus to alight depends on the colour of the leaf surface and the amount of reflectance produced by it. Both authors showed that aphids were attracted more to yellow than to other colours. Kennedy et al. (1961) showed that the amount of reflectance may vary with the physiological conditions of the leaves. Thus in mature leaves of sugar beet, wilted leaves produced greater reflectance than turgid leaves. In this work, although plants of different ages were used, all the leaves were green and turgid. Variation in reflectance could therefore not be due to colour or physiological differences. However, leaf size and number do increase with plant age and if the amount of reflectance does increase with leaf area, then leafier plants may be expected to be more attractive to flies. Unfortunately, reflectance of leaf surface was not measured in this work. If, however, reflectance is the dominant source of plant attraction, it would be expected that plants with secondary tillers irrespective of their age would produce greater reflectance and attract significantly more flies than single-shoot plants. This was, however, not the case. Flies landed on and performed various activities equally well on single-tiller plants. Therefore, the colour of the leaves and the amount of reflectance is unlikely to be the main component of the visual stimulus from the plant, which determine flies' landing and activities.

Kennedy et al. (1961) identified the second component of the visual stimulus of the plant as a close range optomotor stimulus with both orienting and arresting component. The optomotor stimulus is a resultant effect of the contrasting nature of the plant and its background. The same workers offered non-reflecting vertical stripes of black or white paper (4 cm wide) with a background of black paper to landing aphids. They found that more aphids landed on the white than on the black stripes. The response of the aphids was reversed when a white background was used, more aphids alighting on the black stripes. This indicates that the optomotor stimulus described above played a more prominent role in the visual attraction of insects. Propoky (1968) also showed that the size of the apple contributes to the optomotor stimulus which attracts the apple maggot, Rhagoletis pomonella. Thus, fruits 7.5 cm diameter were more attractive to flies than fruits of other sizes. Plants used in this work were not only of different ages, but they also had stems whose length and thickness increased with the age of the tillers. The optomotor stimulus originating from the 'stems' standing against a common background of soil in the tray will probably vary with the size of the stem, and increase as stem size increased. Bigger stems probably produced stronger optomotor stimulus, particularly in the case of isolated tillers, where the effect of the contrasting background will be most pronounced. More flies therefore landed on these plants and the flies were arrested for a longer period on these classes of plants for the same reason.

Also when dull green paper strips ("Long Twisters") (width 5 mm) of different lengths pushed vertically into soil in a seed tray were presented to the flies, significantly more flies landed and remained on the taller strips. This indicates that the intensity of the optomotor stimulus increased as the size (height) of the strip increased. This finding also agrees with that of Dunn (1969) who studied the colonisation of carrot plants of different sizes (heights) in the field, by the carrot aphid, Cavariella aegopodii Scop. He found that aphids appeared always attracted to the larger plants. This, according to Dunn, was probably because the larger plants were the most obvious target. Perhaps in this study too the presence of secondary tillers in the untreated plants also increased their visual attraction.

It might therefore be concluded that at close range, bigger plants produced stronger visual and optomotor stimuli which attract the flies and arrest them for a longer period. A greater number of flies therefore landed and performed various activities preceding egg-laying, with greater intensity, on the older (bigger) plants.

Plant density appeared to influence the landing, resting and oviposition behaviour of the flies through visual stimuli. Whereas less-densely sown shoots provided a stronger optomotor attraction, those shoots growing in denser stands would provide stronger overall visual attraction. This would account for the gradual increase in the number of flies performing the various activities as the density of young shoots increased. During egg-laying, the number of eggs laid per unit area increased with shoot density. However, the rate at which the intensity of oviposition increased fell as shoot density increased. This was probably because flies were unable to reach the oviposition sites under such conditions.

Although at the 3-leaf stage the various grass species could be classified into two size groups, the various activities of the flies were less influenced by the species of the grass host plant. This was probably because at this growth stage the variation in the sizes of the plants did not produce a corresponding variation in the intensity of visual and optomotor attraction which they produced. At later growth stages, when the differences in the vigor and size of the various grass species became more marked, more flies would probably land and stay on the bigger and more vigorous plants.

During egg-laying, however, the intensity of oviposition depended more on the number of oviposition sites present on a grass species. As indicated in later experiments, the fast-growing, more vigorous species received more eggs than the slow-growing ones. (Section (iii) b).

(iii) Oviposition

(a) The distribution of oviposition sites

Experiment 1. To determine the distribution of oviposition sites on host plants at different stages of growth. (No choice offered).

Method. Small colonies of newly-emerged flies (10 females and 15 males) were transferred from the rearing cage into the observation cage which contained trays of *L. perenne* var. S24. Plants of one of three ages, 1-2 weeks old, 3-4 weeks old, and 8-12 weeks old, were presented to *Oscinella frit* L., *O. vastator*, or *Geomyza tripunctata* on separate occasions. An exposure period of ten days, at a glass-house temperature fluctuating between 15° and 20°C, was adopted. This period embraced one mating-to-oviposition cycle. (Average longevity of adult females was of the order of 2-3 months under these conditions, but for all oviposition trials newly-emerged insects were used).

On the tenth day, the plants were removed from the cages and the number of eggs laid per plant and the sites where the eggs were laid were recorded.

Results

a) *Geomyza tripunctata*. On very young plants one to two weeks old, and at the one-to two-leaf stage of growth, *G. tripunctata* laid most eggs (87.4%) on the coleoptile surface near the base, about three to five millimetres above soil level. The remaining eggs (12.6%) were laid higher up underneath the first coleoptile, which at this growth stage of the plant was closely attached to the main stem. In older, but still non-tillering, plants (3-4 weeks), at the three- to four-leaf stage, 64.9% of total eggs were laid under the now-withering coleoptile.

By contrast to the situation which obtained on younger plants, fewer eggs (35.1%) were laid on the surface of the coleoptile. In much older plants which were actively producing secondary tillers, G. tripunctata laid most eggs under the withered leaf sheath (53.5%) and in the crevices formed between the stems of the main plant and that of the newly emerging secondary tillers (29.6%). Occasionally, eggs were also found on the bases of, and underneath the leaf sheaths of, secondary tillers which had already separated from the main plant.

b) Oscinella frit L. and O. vastator. The selection of oviposition sites by females of these two Oscinella spp. was similar to that of G. tripunctata. On very young plants at the one- to two-leaf growth stage, O. frit L. and O. vastator laid 76.3% and 87.5% respectively of all eggs, singly or in pairs, on the coleoptile 3-5 mm above soil surface. As the plants grew older (3-4 leaf stage) and cracks appeared on the surface of the withering coleoptile, the situation was reversed and O. frit L. and O. vastator laid 89.9% and 78.2% of their eggs, respectively, underneath the coleoptile. The rest (10.1% and 21.8% respectively) were laid on stem surfaces. By the age of 8-12 weeks, the layers of leaf sheaths have been produced and the development of secondary tillers within has caused the leaf sheath to crack, and the exposed bases of tillers are visible through these crevices. O. frit L. and O. vastator now laid 3.8%. 7.3% on the basal shoot surface, 70.9% and 76.8% underneath the leaf sheath, and 25.3% and 15.8% respectively in crevices between tillers (Table 4).

Discussion. Studies by various workers on the egg-laying habit of Oscinella frit L. in cereal hosts showed that the sites where eggs were laid varied with the growth stage and the species of the host plant (Riggert, 1935a; Hemer, 1959; Le Berre, 1959; Ibbotson, 1960; Smith, 1962; Shapiro and Vilkova, 1963; Jones, 1969).

Hemer (1959) showed that in young seedlings of barley, at the one-leaf stage of growth, O. frit L. laid most eggs on the outside of the coleoptile, and that on older plants at the 3-4 leaf stage 21% of the eggs were laid behind the coleoptile, 32% on the outside of it and 41% behind the leaf sheath. Smith (1962) also showed that the position where the eggs of O. frit L. were laid in oats changed as the plant grew. All the eggs were laid on the outside of the coleoptile before it had loosened and from this stage onwards, until the coleoptile had just begun to wither, many eggs were found between the coleoptile and the primary shoot. Once the leaf sheath had withered completely, the eggs were all laid in crevices formed by the loose leaf sheaths and the newly formed tillers. Ibbotson (1960) made similar observations on oats and in addition, noted that, in the absence of suitable oviposition sites, eggs were laid in soil near the plant. Shapiro and Vilkova (1963) also found that in maize, barley, wheat and oats, O. frit L. may lay eggs in these sites and on leaf blades. According to these workers the proportion of eggs laid at various sites depended on the species and growth stage of the host plant, and also on climatic conditions, particularly wind and rainfall.

In no-choice experiments carried out with perennial ryegrass, Lolium perenne var. S24 at various growth stages (Table 1), O. frit L., O. vastator and Geomyza tripunctata laid eggs on the surface of the coleoptile, beneath the coleoptile and the primary shoot, underneath the leaf sheath, in cracks in the leaf sheath layers, and in crevices between the partially attached 'stems' of the main plant and the newly emerging secondary tillers. As the other above-mentioned authors found with cereals, the proportion of eggs laid at the various sites depended on the growth stage of the plant. In contrast to the situation in cereals, eggs were not laid on or in the soil around the plant, or on the leaf blades. Several suggestions have been put forward by some workers to explain the source of eggs found on leaf-blades or in soil around cereal host plants. Some of the eggs might have been dislodged from the original oviposition sites by wind or rain under field conditions, or through handling in the glasshouse. They could also have originated from the last egg to be laid by the fly, such an egg still being attached to the tip of the ovipositor as the fly took off from the site of oviposition (Riggert,1935a), or as it cleans itself up at the end of oviposition (Ibbotson, 1958).

It could also be due to lack of suitable oviposition site on the cereal host plants. Ibbotson (1960), Korting, (1934) and Riggert and Korting (1934) and Riggert (1935a) found that the eggs of *Hydrellia griseola* Fall. were similar to those of the frit fly and could be confused with the same.

More recently Jepson and Southwood (1960) also showed that the eggs of *O. frit* L. may be confused with those of other flies such as *Elachiptera cornuta* and *Chlorops* spp. whose eggs are found in young oats. Hemer (1959) observed eggs laid outside young barley plants being washed off by rain. Even under laboratory conditions overhead watering of plants could also result in eggs being washed down the plants into the soil. Such eggs would appear to have been laid in soil by the flies.

This failure to find eggs in the soil is in agreement with Ibbotson (1958), who found no oviposition on soil near ryegrass plants but thought that this was due to the fact that the plants (in a cereal plot) were few and scattered and had few tillers. My findings are based on observations with plants at relatively high densities in pure stands, with and without secondary tillers.

However, in ryegrass, even before tillering begins some of the suitable oviposition sites are already formed on the plants and the number of such sites increases as the plants grow. Under these conditions of abundant plant oviposition sites, flies are unlikely to prefer soil crevices. Shapiro and Vilkova (1963) showed a high proportion of the larvae of O. frit L. emerging from eggs laid more than 0.5 cm away from the host either failed to reach the plant, or if they did, they failed to become established in it. Jones (1969) also observed that such eggs were eaten by predators such as the carabid beetles Bembidion lampros (Herbst), Agonorum dorsale (Pont), and Notiophilus biguttatus (Fab.). The evidence therefore suggests that eggs are not laid in soil if other sites are available, and that eggs laid in soil have a much poorer chance of survival.

The biochemical stimulus, which originates entirely from the host plant, elicits oviposition behaviour in the insect. Once the flies are ready to lay eggs, the second, tactile stimulus plays a more prominent role (Ibbotson, 1960). Such tactile stimuli are provided by the cracks and crevices distributed at various parts of the host plant. Whether or not eggs were laid on the plant and where such eggs were laid would depend upon the presence and the distribution of such crevices in the plant. These cracks and crevices are present on the ryegrass plant as from the 2-leaf stage onwards. Even in the very young seedlings, the surfaces of the stem near the base was used as an oviposition site. This particular site was found to be more attractive when such seedlings were in close contact in pots sown at high densities, more eggs being placed at the junction of the stems of such seedlings.

To summarise, eggs are laid at five main sites on L. perenne (S24): on the coleoptile surface near the base, between the coleoptile and the primary shoot, on the surface and underneath the leaf sheaths and in crevices between tillers. The proportion of eggs laid at the various sites by O. frit., O. vastator and Geomyza tripunctata depends upon the growth stage of the host plant. Under glasshouse conditions eggs were not laid in soil or on the surface of leaf blades and the presence of eggs at such sites in the field is probably due to dislodgment by rain or other agencies.

(b) Intensity of oviposition

Experiment IIa. The effect of host plant age

Method. Seedlings of S24 perennial ryegrass of five different ages, 1, 3, 6, 9 and 12 weeks were re-planted in seed trays 15 x 15 cm. Each tray contained five plants of each age group randomly arranged. Secondary tillers were produced by plants from the age of 6 weeks onward. In half of the trays those plants old enough to produce secondary tillers were pruned so that only the oldest tiller remained. In the remaining trays the secondary tillers were left intact.

Pairs of trays, one of each type, were exposed to a small colony of ovipositing flies for a period of one week. The number of flies alighting, resting or performing egg-laying movements was recorded four times daily, and the result summarised in Table 1. The number of eggs laid on each plant was also recorded at the end of the week. This procedure was repeated four or five times with each of the three insect species.

Result

G. tripunctata: In the trays of pruned plants, eggs were laid on plants of all ages. In the trays of intact plants eggs were laid on plants of all ages except the youngest (1-2 weeks).

On the intact plants the number of eggs laid per plant increased with plant age reaching a maximum on the oldest plants (2.5 eggs/plant on 12-13 week-old plants). On those plants reduced to a single tiller the number of eggs per plant increased with plant age to a maximum of 2.6 eggs/plant at age 6-7 weeks, and fell off thereafter (Table 5).

The proportion of plants in each age group receiving eggs closely followed this trend, reaching 100% in intact and pruned plants at 12-13 weeks and 6-7 weeks respectively.

Oscinella spp.: Both species of *Oscinella* differed in egg-laying pattern from *G. tripunctata* in that host plants of all ages received eggs, regardless of the removal of secondary tillers. They are, however, similar to *G. tripunctata* in that the number of eggs laid per plant again increased with plant age, the maximum number again occurring on 6-7 week-old plants where plants were pruned, and later (9-13 weeks) where they were not. (Figure IV).

In plants in which secondary tillers have been removed, *O. frit* L. and *O. vastator* both laid 0.2 eggs per plant on the youngest plants, and 3.6 and 3.0 eggs/plant respectively on plants 6-7 weeks old. In much older plants (12 weeks) the number of eggs laid per plant by *O. frit* L. fell to 1.4 and that of *O. vastator* declined to 1.3.

The proportion of plants selected for oviposition in treated and untreated plants followed trends similar to that of *G. tripunctata* (Table 5, Figure IV).

Discussion. The results of this experiment showed that once the insects have settled on the plants, their subsequent behaviour, particularly that regarding egg laying, will probably depend on the suitability of the plant.

The oviposition behaviour of the frit fly has been shown to be influenced by (a) a biochemical stimulus and (b) a tactile stimulus, which act either singly or in unison (Ibbotson, 1961; Le Berre, 1959). The biochemical stimulus originated mainly from the host plant and elicited the egg-laying behaviour as the insect moved about on the plant. Once the insect had received the threshold level of the stimulus necessary to initiate egg-laying, the second, that is the tactile stimulus, took up a more prominent role, and determined where the eggs were laid. Crevices and cracks present on the plant are the main source of the tactile stimulus. The flies are stimulated as they push their extended ovipositor into cracks and crevices in search of suitable oviposition sites. Most eggs would therefore be laid on the plants which provided the greatest number of these sites. In experiment I, it was shown that the distribution of these sites changed and their number increased as the plant grew. The number of eggs laid per plant increased as the plant grew, probably because the number of potential oviposition sites increased simultaneously. More eggs were therefore laid on the older plants, particularly on intact plants where the secondary tillers were retained. The removal of the secondary tillers in a batch of plants consequently reduced the number of potential oviposition sites, (e.g. the surface and under-surface of the coleoptiles of younger tillers, the crevices between partially attached tillers, etc.). Also, in the much older tillers (9-13 weeks) the leaf-sheaths were already growing up the shoot. In the oldest tillers, they have a strongly erect pseudo-stem structure around the shoot-base and the smoothness of this pseudo-stem therefore renders the very old tillers less suitable for oviposition under the experimental condition provided. The intensity of oviposition therefore reached an optimum in single-tiller plants at the 6-7 weeks-old stage. These results showed that in grass, the intensity of oviposition depends not only upon the age of the plant but also on the number of secondary tillers with suitable ovipositional sites, which constitute the entire plant.

It is therefore not surprising that in grass the suitability of the plants for frit fly oviposition is very different from that which obtains in cereals.

Generally, in cereals, young plants (one- to four-leaf stage) are the most attractive for oviposition. (Zhukovskii, 1932; Cunliffe and Hodges, 1946; Ibbotson, 1958; Le Berre, 1959; and Shapiro, 1963). The main difference in the effect of host age on oviposition intensity on both types of plants could be explained in terms of the differences in growth patterns in grass and in cereals.

For most of the time during growth, the cereal plant is represented predominantly by a single tiller. The age and stage of growth of this tiller therefore represents that of the entire plant. By contrast, in grasses the plant is composed of either one tiller when it is very young, or of many tillers of different ages and growth stages as it grows. Similarly, the production of potential oviposition sites in the cereal plant or the one-tiller grass plant is considerably limited by its age. The number of oviposition sites reaching an optimum much earlier in the life of the plant. By contrast, the number of potential oviposition sites continues to increase in the multi-tiller grass plant, as it grows and as more tillers are produced. Consequently, the intensity of oviposition increases as the grass plant grows. In this work, the decreased suitability for oviposition in the older grass plants, whose secondary tillers had been removed, could be likened to that which occurs in normal growth in cereals.

Experiment IIb. To examine the effect of the presence of leaf sheaths on the intensity of oviposition on tillers of the same age.

Method. Plants were grown from seed in 15 cm diameter pots to the age of 6 weeks, by which time they had produced one secondary tiller each, and were attractive for oviposition. All secondary tillers were removed. The layers of coleoptile or leaf sheath were removed from half of the single-tiller plants so produced.

Three male and three female flies were then confined on each pot with cylindrical cages for five days after which the number of eggs laid per plant was recorded. Four or five trials were made with each insect species.

Results

Geomyza and Oscinella species: Each of the three species of flies laid more eggs in plants in which the leaf sheath was retained, than in plants in which the leaf sheath was removed.

The mean number of eggs laid per plant by G. tripunctata was 1.8 on the intact plant and 0.5 on the naked plant.

Similarly O. frit L. and O. vastator laid 2.6 and 2.3 eggs per plant respectively on the plants with intact leaf sheath whereas they laid 0.4 and 0.2 eggs per plant on those from which the leaf sheath had been removed.

For each species of insect, significantly more eggs were laid on plants with intact leaf sheaths than in plants in which the leaf sheath was removed.

The proportion of plants selected for oviposition was higher in the intact plants, but the difference was statistically significant in Oscinella species only (Table 5b).

Discussion

The result of this experiment showed that the presence or absence of loose coleoptiles and leaf sheaths may modify the intensity of oviposition in tillers or plants of the same age. Plants in which the leaf sheath was left intact received significantly more eggs than control plants of the same age in which leaf sheaths had been removed. This is because loose coleoptiles and leaf sheaths are the main sources of the cracks and crevices which provide the necessary contact stimulus as the flies move their extended ovipositor in search of suitable oviposition sites.

These findings agree with those of other workers who studied the oviposition of the frit fly in cereals. Korting (1934) rendered young oat seedlings less attractive for frit fly oviposition by covering coleoptiles of the plants with a pile of soil. Fewer eggs were laid on these plants than on the control.

Cunliffe and Hodges (1946) loosened some of the tight coleoptiles of young oat plants and compared frit fly oviposition on these with that on control plants in which the coleoptiles were left intact. They found that significantly more eggs were laid in the treated plants. Also, Ibbotson (1960) found that the intensity of oviposition by frit fly on oats was drastically reduced when he coated the base of the shoot with wax, or wrapped it with cotton wool. In all the three instances fewer eggs were laid on the treated plants because there were no cracks and crevices on them to provide the fly with the necessary amount of contact stimulus.

Experiment IIc. To examine the effect of plant age on oviposition intensity in the absence of secondary tillers and leaf sheaths.
Method. Plants 3, 9, 12 and over 16 weeks old, obtained as in experiment IIa were used. All the secondary tillers produced by each plant, and the layers of dead leaf sheaths formed around the main tillers were removed. This produced single-tiller plants of different ages which did not possess dead leaf sheaths. Three tillers each from the four age-groups were transplanted into a ten-centimetre diameter pot almost filled to the brim with soil. The plants thus transferred were arranged at random in a circle, 3 cm away from the centre of the pot, and left for two days during which the plants were re-established. The plants were then caged with mated flies (three couples) of the species under consideration. Trials with each species were conducted separately and each trial was replicated five times with flies from the same colony. The tillers of different ages were marked by pushing identifying pins into the soil near the plant. The number of eggs laid on each plant was noted. The mean number of eggs laid on plants of different ages were as shown in Table 5c.

Results

Geomyza and Oscinella spp.: In the absence of the leaf sheath the number of eggs laid per plant by G. tripunctata, O. frit L. and O. vastator decreased as the tiller-age increased. The proportion of tillers in each age group selected for oviposition also decreased as the age of the tillers increased. Except in the case of G. tripunctata, tillers older than 13 weeks were not selected for oviposition when a choice was permitted (Table 5c).

The difference between the number of eggs laid per tiller of different ages, and the proportion of these tillers selected for oviposition was highly significant for each insect species.

Discussion

The intensity of oviposition in tillers of different ages indicates that in the absence of tactile stimulus the intensity of oviposition decreased with tiller age. This is probably because a different type of stimulus is now involved, and that its effect decreased as tillers grew.

As pointed out earlier two types of stimuli produced by the plant, biochemical and tactile, influence egg-laying. The source of the tactile stimulus, and how its intensity changes with the development of the tiller and plant has been dealt with. The chemical stimulus originates in the plant and probably acts first, eliciting oviposition behaviour in the fly. Ibbotson (1960) showed that in the absence of oat extract, O. frit L. did not lay eggs on artificial models over a period of six weeks, although the models provided suitable tactile stimulus. By contrast, Le Berre (1959) was able to induce egg-laying on chemically inert artificial models by providing the necessary tactile stimulus. This apparent contradiction was attributed to probable differences in the qualities of light used in the experiments (Ibbotson, 1960).

In experiment IIb (where a choice of tiller types was offered), it was shown that even in the absence of cracks and crevices some eggs were laid on the tiller surface. This implies the existence of another stimulus, present on the tiller surface. However, it may be argued that flies provided with a choice of intact and treated tillers would probably have received enough of the tactile stimulus from the intact tillers to induce oviposition on smooth tillers. That this may not be the case was shown in experiment IIc in which all the tillers were treated. The main differences in the tillers now lay in their age and probably in the strength of the biochemical stimulus each tiller was able to provide. The result of this experiment indicates that in the absence of the tactile stimulus, the intensity of oviposition decreased as the tillers grew. This was probably because the intensity of the biochemical stimulus originating from the tillers decreased as they became older. This result is exactly opposite that obtained using intact plants, as in experiment IIa, where the intensity of oviposition was higher in older tillers (9-13 weeks) than in younger tillers. The implication is that the tactile stimulus becomes more important than the biochemical one as the plants age and produce more crevices.

Although Le Berre obtained oviposition on artificial models in the absence of the host plant, the results of experiments which I carried out with the three insect species suggest that the presence of the host plant or its extract was vital to successful egg laying. Various artificial models were tried, such as dead hardened stems of ryegrass, strips of cardboard, and rolls of filter paper, pushed vertically into wet sterilised sand. The models were treated either with sap of ryegrass or distilled water. In a non-choice situation, eggs were not laid in models treated with distilled water, but a small number of eggs were laid on the models treated with ryegrass sap (Table 5d). This strengthened the suggestion that the biochemical stimulus was critical to the eliciting of oviposition behaviour and probably, to the laying of eggs.

It may therefore be concluded that both biochemical and tactile stimulus act in concert to influence the egg-laying behaviour in flies.

Experiment III. To determine the effect of the host plant density on the intensity of oviposition.

Method. *Lolium perenne* S24 was sown in twenty (10 cm diameter) plastic pots at the rate of twenty seeds per pot. Three weeks after germination the pots were divided into five batches of four pots each. Plants in the first, second, third and fourth batches were thinned down to 2, 4, 8 and 16 plants per pot, respectively. The plants removed were lumped together and carefully transplanted into the pots in the fifth batch such that each pot in the fifth batch contained thirty-two plants. Ultimately, there were five batches of pots at five different densities but all the plants were of the same age and at the same stage of development. The pots were arranged randomly inside the observation cage. Small colonies of mated adult flies (fifteen couples) of the species under study were introduced into the observation cage. The number of eggs laid per pot after one week was recorded (Table 6). Also, the number of adults resting, crawling or performing oviposition movements on the plants within each pot were observed and recorded four times daily at 9.00, 12.00, 15.00 and 18.00 hrs. The effects of shoot-density on the various activities of the insects were presented in section (ii). In this way, the ovipositional responses of *Geomyza* 30 *tripunctata*, *Oscinella vastator* and *Oscinella frit* L. to different densities of young host plants were studied separately. This experiment was repeated four times with each of the three insect species, different colonies being used in each replicate.

Results

G. tripunctata: The mean number of eggs laid per pot increased as host-plant density increased from a minimum of 2.6 eggs/pot at the lowest plant density, to a maximum of 19.4 eggs/pot at the highest plant density. The intensities of oviposition at the intermediate densities were as shown in Table 6.

Oscinella spp.: In both O. frit L. and O. vastator, the intensity of oviposition per unit area also increased as shoot density increased. In the case of O. frit L. the mean numbers of eggs laid at the lowest and highest plant densities were 4.8 and 20.8 eggs/pot respectively. O. vastator laid a mean of 3.3 eggs/pot at the lowest plant density and 21.3 eggs/pot at the highest shoot density. The intensity of oviposition at the intermediate plant densities is also presented in Table 6.

Statistical analysis showed that for each insect species, there was a significant regression between plant density and the number of eggs laid per pot. (Fig. V). However, the mean number of eggs laid per plant and the percentage of plants selected for oviposition decreased gradually as plant density increased (Table 6, Fig. VI).

Discussion

Table 6 shows that for each of the three species of flies, O. frit L., O. vastator, and Geomyza tripunctata, the total number of eggs laid per pot increased as the density of host plants increased. This was probably because the total number of suitable oviposition sites available increased as the number of plants increased. By contrast, the total number of eggs laid per plant decreased as the plant density increased. In this instance the high plant density appeared to prevent the flies from gaining access to suitable oviposition sites. This finding partially agrees with the observations of Perron (1972) who found that in the field, the onion maggot, Hylemya antiqua laid more eggs over a given area where a high seed rate was used than where a low seed rate was used. The number of eggs laid per plant, however, remained almost constant under all rates of seeding with a slight tendency to a decrease at the highest seeding rate. Jones (1969) tested the effect of the density of oat seedlings on the oviposition of the frit fly in the laboratory. She used oat seedlings at the two-leaf stage at five densities (2, 4, 8, 16 and 32/pot) and found that more eggs were laid in pots with eight or sixteen seedlings than in pots with two, four or thirty-two seedlings. Although all the oat plants were of the same age, the form of growth was altered by the seed rate. In dense stands the plants grew straight up and the coleoptiles did not spread. Thus, favourable oviposition sites were fewer than the number of shoots at the maximum density of 32 plants/pot. This explained why the number of eggs laid at highest plant density was fewer than expected. In the sparse stands, (2 or 4 plants/pot) she suggested that the plants were possibly less attractive to the flies than in the denser stand, but did not explain why this was so. This could not be due to reduction in number of suitable oviposition sites but may have been because the plants grown under less competitive conditions were at a more advanced stage of growth, and may have passed the critical stage favourable to oviposition.

In my experiments, this source of variation in plants was removed or at least reduced by raising all the plants at the same density and thinning them to the required densities just before exposure to the flies. That my results showed a gradual decrease in the number of eggs laid per plant as plant density increased was therefore not due to variation in the conditions of the plant but was because the number of suitable oviposition sites available to the flies fell.

It was also found that the incidence of oviposition movements increased as plant density increased (Section ii, Table 2). As in the case of ovipositional movements, the rate of increase of ovipositional intensity is not directly proportional to the rate at which plant density increased. Consequently, both the number of oviposition movements and the number of eggs laid per plant decreased as plant density increased. In field observations Van Emden (pers. comm.) found that adult O. frit were preferentially attracted to bare areas within a grass crop. Adjacent areas will be areas of low plant density where one will expect an egg-laying female to deposit the greatest number of eggs per plant, because it is under such situations that the movement of the fly is least hindered by the presence of other plants and possibly other insects. In this trial, most of the largest egg masses were also found on plants growing at the lowest density. But since all the plants in sparse stands were not selected for oviposition, the total number of eggs laid was lower than the total number of eggs laid at higher plant densities where a greater number of oviposition sites occurred. With an increase in the number of suitable oviposition sites, as well as an increase in the number of egg-laying flies, one would expect higher number of eggs per unit area if my laboratory observations are typical of the field situation. In this study, the inability of the flies to reach the crevices on most plants in densely sown pots, largely accounts for the decreasing number of eggs laid per plant (Fig. VI).

It could therefore be concluded that given a choice of plants at the same growth stage, but at different plant densities within the range used in this experiment, Oscinella spp. and G. tripunctata will lay the highest number of eggs per unit area in denser stands. But, on per plant basis, the number of eggs would decrease with increasing plant density because the flies could not reach the suitable oviposition sites present on some plants. It may be of interest to note here that the maximum experimental plant density of 32 per 78 cm^2 pot used is still higher than that which usually obtains during the establishment of a newly sown sward. The adverse effects of high shoot density on the intensity of oviposition may therefore not be marked until the sward becomes fully established (late July). By this time, however, most of the eggs of the first and second generation flies would have been laid, and the sward would be due for mowing.

Experiment IV. To determine the effect of host-plant species on the ovipositional preferences of the flies.

Method. Eight species of grasses were presented in free-choice to the egg-laying flies. The grass species were Lolium perenne, var. S24; Dactylis glomerata, Poa trivialis, Phleum pratense, Festuca rubra, Avena fatua, Holcus lanatus, and Agrostis tenuis.

Due to differences in the rates of germination and of development of various grass species, seedlings of individual grass species were raised from seeds in separate seed trays. At the three-leaf stage, equal numbers of seedlings of each grass species were transplanted into a common seed tray in which they were randomly arranged. The seedlings were watered and left for two days to re-establish. They were then exposed to ovipositing flies in the observation cage over a period of one week, after which the number of eggs laid on the various grass species was recorded. The ovipositional preferences of Geomyza tripunctata, Oscinella frit L. and O. vastator were studied in separate experiments.

Results

(a) Geomyza tripunctata: Although the plants offered to the flies were all at the same stage of development, the mean number of eggs laid per plant varied with grass species. Most eggs were laid on Lolium perenne L. S24 and Avena fatua (Wild oats), the mean number of eggs per plant being 1.9 and 1.7 respectively. The lowest number of eggs were laid on Festuca rubra, with a mean of 0.2 egg/plant. The intensity of oviposition on other grass species lay between these two extremes.

The proportion of plants of each species selected for oviposition followed a similar trend.

Although the adult flies showed these clear preferences in oviposition, they were observed to visit and move about on all plants, regardless of species (section (ii))

(b) The host preference of the two Oscinella species were similar to each other and to that of G. tripunctata. Thus, both laid most eggs on A. fatua and L. perenne L. S24. O. frit L. laid an average of 2.7 and 2.4 eggs per plant on A. fatua and L. perenne, respectively. O. vastator laid an average of 2.7 and 3.2 eggs per plant on A. fatua and L. perenne respectively. In both species of Oscinella, the least number of eggs were laid on Festuca rubra and Phleum pratense, an average of about 0.3 eggs per plant. The other grass species fell between these two extremes (Table 7).

As with G. tripunctata, there was little difference between the frequencies with which adults of Oscinella spp. visited the different plant species to rest or perform egg-laying movements.

Discussion

At the three to four-leaf stage the flies oviposited on all the grass species provided, but the intensity of oviposition varied with the species of grass involved.

The variation in the intensity of oviposition was probably due to variation in the relative number of suitable oviposition sites present. It may also be due to variation in the concentration of the biochemical stimulus produced by each species. The results of preceding experiments and those of other workers suggest that the role of the biochemical stimulus is mainly to trigger oviposition, whereas the number of oviposition sites in the plant determines the intensity of oviposition. In a situation providing free choice of hosts such as obtained in this experiment, flies moved about freely from one plant to the other, before and during the oviposition process. During this time, the flies could have received the necessary concentration of the biochemical stimulus from any or all of the plants. The intensity of oviposition on a particular plant would then depend primarily on the number of oviposition sites it provided. In grasses this appears to be the main cause of varietal differences in attractiveness for oviposition.

Observation on species morphology at the 3-4 leaf stage showed certain obvious specific morphological differences. Firstly, the seedlings at the same stage of differentiation (3-4 leaf) could be split into two broad categories based on size. Seedlings of Holcus lanatus, Poa trivialis, Festuca rubra, Phleum pratense, and Agrostis tenuis were small and less vigorous while those of Lolium perenne, Dactylis glomerata and Avena fatua were bigger and more vigorous. Secondly, the coleoptiles were already well formed at this stage in all species but the degree to which they had loosened or separated from the shoot varied slightly. In Lolium, Dactylis and Avena spp. the coleoptile was partially loosened, the tip having separated from the shoot. In Poa, Agrostis, Festuca and the remaining species, the coleoptile was still tightly wrapped around it. This dichotomy more or less reflects the relative growth rates of the grasses in the two groups. In experiment II it was shown that in Lolium perenne more eggs were laid on young plants in which the coleoptiles had loosened. This was also the case with all the grasses tested here.

It seems, therefore, that in the young plants (3-4 leaf stage) it is mainly the condition of the coleoptile which determines the intensity of oviposition.

Belyaev and Kharichenko (1936) attributed the resistance of wheat varieties to the frit fly to the presence of long dense hairs on the leaf sheaths or blades of certain varieties. However, the failure of the flies to achieve a high intensity of oviposition on the slow-growing grass spp. mentioned earlier, could not have been due to this host factor, because pubescence in the seedlings of these spp., and even in that of Holcus lanatus (a species known to be very hairy at later growth stages) was not more pronounced than in those of the fast-growing species.

Ibbotson (1960) showed that the frit fly laid more eggs on artificial models coated with the sap of oats, than on models coated with the sap of wheat or barley. He concluded that the extract of oats had a stronger stimulating influence on ovipositing frit fly than the extracts of barley or wheat. Hilliyer (1965) compared the stimulating influence of a range of plant species (Gramineae and Brassicae) on the rate of ovarial development in the virgin frit fly. On the basis of egg/ovariole ratio, crop-capacity and weight of flies, and the number of eggs laid, he concluded that Avena spp. had the greatest stimulating influence, and that Lolium perenne and Arrhenatherum elatius were more stimulating than Dactylis glomerata.

These results suggest that variation in the chemical constituent of various grass species may also influence the intensity of oviposition of the flies. This would be more so particularly where the attractiveness of species is not modified by morphological features. In a situation which provides a free choice of intact plants of different species at the same growth stage flies are probably able to receive sufficient biochemical stimulus from visits to the most biochemically active plant species, but most eggs will still be laid on plants which provide the greatest intensity of tactile stimulus. These are the plants which have the greatest number of suitable oviposition sites (crevices, etc.). This may explain the lack of correspondence in Hilliyer's data between the rate of ovary development and the corresponding ovipositional intensity of the frit fly in various grass species, which the same author observed.

The results described here agree with those of Hemer (1960), who studied the ovipositional preference of the frit fly on barley. Hemer (1960) found that in this crop, apparent varietal differences in the intensity of frit fly oviposition were due more to the stage of development than to the anatomical or morphological differences in the plants. Similarly, the slight variation in the growth rate of the different grass species used in this study, and its effect on the condition of their coleoptiles, greatly influenced the choice of the flies during egg laying. Other factors peculiar to each grass species such as pubescence, chemical composition, etc. appear to be relatively less important. The similarity in the ovipositional intensity between G. tripunctata and the two Oscinella species studied here, suggests that flies of both genera are responding to a common factor in the plants, in this case, the intensity of tactile stimulus.

Experiment V. To determine the effect of varietal differences on intensity of oviposition within two species of host plant.

Method. Three diploid cultivars of Lolium perenne L. (S23, S24 and Grasslands Manawa), and four of Dactylis glomerata, (S37, S21 and S321 and Commercial) were tested. Each grass species was tested separately. Three-leaf stage plants of the cultivars within the same grass species sown in the same seed tray were offered in free-choice to egg-laying flies. Trays containing five plants of each cultivar were offered to ovipositing flies on four occasions. The number of eggs laid per plant within one week was recorded. Each insect species was tested separately.

Results

G. tripunctata: The intensity of oviposition on plants of different cultivars but of the same species was about the same. The mean number of eggs laid per plant on cultivars of L. perenne L. ranged between 1.9 and 2.3 whereas the mean number of eggs per plant on cultivars of

Dactylis glomerata ranged between 1.7 and 2.0. The proportion of plants selected for oviposition followed a similar trend.

Oscinella spp.: O. frit L. and O. vastator also laid eggs with almost the same intensity on cultivars of the same species. On cultivars of ryegrass, O. frit laid between 2.5 and 3.1 eggs per plant, while O. vastator laid between 2.5 and 3.2 eggs per plant.

On cultivars of Cocksfoot, O. frit L. laid between 1.9 and 2.4 eggs per plant, and O. vastator laid between 1.7 and 1.9 eggs per plant.

The proportion of plants selected for oviposition within a grass species by either O. frit L. or O. vastator was not significantly different.

The numerical results of these experiments are summarised in Table 8.

Discussion

The intensity of oviposition did not differ significantly among cultivars of the same grass species, probably because growth rates and hence the rate at which oviposition sites appear did not differ significantly. Lolium varieties are more attractive for oviposition than Dactylis varieties, as was found where both species were offered together in free-choice tests (Experiment IV). Under these conditions marked differences between grass species are observed. However, within one species it appears that cultivars do not differ enough to alter the flies' oviposition behaviour, and this was the case with all three insect species tested.

Experiment VI. To determine the effect on oviposition of diploid/tetraploid genotypic differences within L. perenne.

Method. The diploid genotypes of Lolium perenne, S23 and S24, and the tetraploid genotypes, Barpatra and Reveille were used. Lolium multiflorum (a tetraploid species) was included for comparative purposes. The plants were raised from seeds in separate trays in view of the faster initial growth of Lolium multiflorum. At the three leaf stage, ten plants of each strain were transplanted into a common seed tray. The plants, evenly spaced out and randomly arranged in the tray, were later exposed to small colonies of egg-laying flies. The number of eggs laid per plant after one week was recorded, and the experiment with each species of insect replicated four times.

Results

G. tripunctata: the insects laid consistently more eggs on L. multiflorum than they did on any of the genotypes of L. perenne L. The mean number of eggs laid per plant on L. multiflorum was 1.6 whereas the various genotypes of L. perenne received only 1.1 and 1.2 on the diploids S23 and S25, and 1.3 and 1.1 on the tetraploids, Reveille and Barpatra, respectively. The proportion of plants selected for oviposition was also highest in L. multiflorum - 87.5% - while that in various genotypes of L. perenne ranged between 67.5 and 77.5%.

Both the mean number of eggs laid per plant and the proportion of plants selected for oviposition differed significantly between L. multiflorum and Lolium perenne, but no differences were found between the genotypes of L. perenne itself.

Oscinella frit L.: the intensity of oviposition of O. frit L. and the proportion of plants selected for oviposition followed similar trends to those of G. tripunctata, significantly more eggs being laid on L. multiflorum. The mean number of eggs laid per plant was 2.5 on L. multiflorum, 1.5 and 1.4 on the diploids L. perenne S23 and S24; and 1.5 and 1.6 on the tetraploids Barpatra and Reveille.

The proportion of plants selected for oviposition was highest on L. multiflorum at 85%. In the diploid and tetraploid L. perenne, the proportion varied between 70 and 75%. However, these differences could not be shown to be statistically significant (Table 9).

Discussion

At a given growth stage all the genotypes of L. perenne tested were equally attractive to ovipositing flies. This was because all provided similar numbers of oviposition sites. L. multiflorum, included as a check, did attract more eggs and more of the plants exposed received eggs. This can be explained in the same way since this species has a faster initial growth rate and provided more oviposition sites.

Genotypic differences are likely to be less important than specific ones in determining intensity of oviposition.

Experiment VII. To determine the effect of the growth habits of different cultivars of the same grass species on the intensity of oviposition of the flies.

Method. Two cultivars each of Lolium perenne and Phleum pratense were used. The cultivars having erect growth habits, L. perenne S24 and Phleum pratense S48, were compared with their corresponding cultivars with prostrate growth habits, L. perenne Grasslands Manawa, and P. pratense S50. Seedlings of the two cultivars of the same grass species were sown in the same seed tray, but were not exposed to ovipositing flies until the characteristic growth habits had developed, nine weeks after germination. A pair of cultivars of the same grass species was tested in free-choice and each insect species was studied separately.

Results

G. tripunctata: Flies laid eggs on both the erect and prostrate cultivars of either grass species. The mean number of eggs laid on the erect cultivars of the perennial ryegrass and timothy were 6 and 11 respectively. The mean number of eggs laid per plant in the corresponding prostrate cultivars of the two grass species were 5 and 9.

Although in total more eggs were laid in the prostrate cultivars, the difference between the mean number of eggs laid on the contrasting pairs of cultivars of either grass species was not statistically significant and may be accounted for by higher rate of tiller production in the prostrate cultivars.

Oscinella frit L.: Both the erect and prostrate cultivars of perennial ryegrass were attractive for oviposition, about the same intensity of oviposition being attained. The mean number of eggs laid per plant on the erect and the prostrate cultivars were 6 and 8 respectively. On timothy, O. frit L. laid more eggs on the prostrate cultivars than on the erect ones, the mean number of eggs laid per plant being 7 on the prostrate cultivar whereas that on the erect cultivar was 5. After giving allowance for the number of tillers per plant, the difference between the mean number of eggs laid per plant in both cultivars was not statistically significant. (Table 10).

Discussion

It appears that the growth habit of a grass, at least within one species, is a relatively unimportant factor influencing oviposition. Neither species of fly laid significantly more eggs on one cultivar than on another. There was some suggestion that G. tripunctata favoured the upright cultivars while O. frit L. preferred the prostrate ones. The importance of this is doubtful and does not agree with observations made on adult fly behaviour in cages (section (ii)) where G. tripunctata tended to spend more time in shaded areas near plants. With O. frit L. the situation was quite the reverse. Oviposition seems then to be a specialised aspect of behaviour and the habits of the flies alter during this time.

Experiment VIII. To determine the effect of sowing mixed species on the intensity of oviposition.

Method. 20 seedlings each of L. perenne and Dactylis glomerata, sown separately, were transplanted at the 3-leaf stage into a common seed tray. Here they were arranged alternately within rows and columns. Equal numbers of plants of each species arranged in this form were exposed to a colony of mated flies for four days. The number of eggs laid per plant was recorded. The experiment was replicated 4 times.

Results

G. tripunctata: the flies laid more eggs on Lolium perenne than they did on Dactylis glomerata. The mean number of eggs laid per plant on L. perenne was 1.4 whereas that on D. glomerata was 1.0.

The proportion of plants of each species selected for oviposition was not significantly different.

Oscinella spp.: Both O. frit L. and O. vastator laid more eggs per plant on L. perenne. In the case of O. frit L. the mean number of eggs per plant was 2.3 on L. perenne and 1.8 on D. glomerata. With O. vastator the mean number of eggs laid per plant was 2.7 on L. perenne and 2.2 on D. glomerata. Neither the number of eggs laid nor the proportion of plants of each species selected for oviposition differed between plant species (Table 11).

Discussion

It has been shown in earlier experiments that the intensity of oviposition of the three species of flies depends mainly on the stage of growth of the plant and hence on the amount of suitable oviposition sites present. The same factors operated here. Although both species of plants were at the 3-leaf stage, the coleoptile of the faster-growing Lolium species was in a condition more suitable for oviposition, because it had loosened from the shoot base. In the less aggressive Dactylis species, the coleoptile had begun to separate from the shoot only at the tip. The number of eggs which the flies are capable of depositing is therefore limited by the amount of crevices available.

In tests in which the two grasses were compared at the early two leaf-stage the apparent superiority which Lolium had over Dactylis disappeared because in both species only the smooth surface of the shoots were available for oviposition (Table 11b). When some shoots of Dactylis species at a more advanced two-leaf stage, with a partially-separated coleoptile were compared with those of Lolium species at an early two-leaf stage before coleoptile separation, more eggs were laid on Dactylis species (Table 11c). It therefore seems that while flies of all three species show marked ovipositional preferences, it is a preference for a stage of growth which furnishes suitable sites, rather than a preference for particular plant species.

(iv) LARVAL ESTABLISHMENT

Experiment IX

(a) To determine the effect of host plant age and density on the rate of larval attack and survival in the field.

Method. Pots of L. perenne grown from seed in the glasshouse were thinned to give five plant densities (4, 7, 15,20 and 35 plants per 15 cm diam. pot). Staggered sowing dates were used to produce plants of five age groups at the start of the experiment (3, 5, 7, 9 and 12 weeks-old). All secondary tillers were artificially removed so that only single-tiller plants were used. The pots were then transferred from the insect-free glasshouse to the field where they were exposed to infestation for a period of three weeks. The stems were later dissected and the number of larvae and pupae per pot was recorded. Each age and density was replicated four times and all the plants were exposed at the same time.

Results

G. tripunctata and Oscinella spp.

Effect of host age: at all densities the youngest plants were the most heavily infested, the level of larval infestation steadily falling with increasing plant age. The mean number of larvae of G. tripunctata decreased from 7.0 larvae per pot in the youngest plants to 1.0 in the oldest plants. That of Oscinella spp. declined from 4.1 larvae per pot in the youngest plants to 1.1 in the oldest plants.

Effect of plant density:

G. tripunctata and Oscinella spp.: at all ages the number of larvae per pot increased as the number of plants per pot increased. This effect was most pronounced in the youngest plants and least so in oldest plants. In the youngest plants the mean number of larvae of G. tripunctata per pot increased from 1.4 at the lowest to 5.2 at the highest plant density. That of Oscinella spp. increased from 1.2 at the lowest to 4.4 per pot at highest plant density.

Analysis of the data showed that both factors significantly influenced the number of larvae produced per unit area. Over the chosen ranges of plant age and density, the former factor was the more important, and there was a significant interaction between the two. (See Figure VII and Table 12).

Discussion

Various workers have studied the effect of sowing date on the amount of shoot attack by frit fly larvae in plots of cereals. Generally, they found that the shoots of late sown crops were more heavily attacked than those of early sown crops (Kleine, 1927; Cunliffe, 1929; and Smith, 1962). This was probably because the late sown plots contained younger plants which are the most susceptible to larval attack. However, fluctuations in the prevalence of frit at the different times, during the life of the plants may also affect the intensity of attack. Fryer and Collin (1924) and Cunliffe, Fryer and Gibson (1925) took care to eliminate the effects of fluctuations in the number of adult flies in the field. They planted oats on six different dates but prevented frit fly invasion by covering the plants immediately after sowing with fly-proof cages. The plots were exposed later on the same day to invading adult flies and larval damage assessed two or three weeks later. They also found that primary shoots at the two- or three-leaf stage were more heavily damaged than either younger plants at the one-leaf-stage or older plants at four- or more leaf stage. They concluded that shoots at the 2-3 leaf stage were the most susceptible to larval attack. Shapiro (1958) also studied the attack on maize by the larvae of the frit fly. He observed that the larvae infested and fed on the embryonal and poorly differentiated tissues at the growth point of young plants, and abandoned the vegetative cone once three or four leaves appeared.

In grassland, observations similar to those above have been made by several workers. Southwood and Jepson (1961) noted that the populations of the frit fly in grassland are more or less steady from year to year. They suggested that this was due to a relative shortage of sites for development. They suggested that the size of the larval population living in grass tillers is limited by the number of tillers in the correct state for colonization, and the difficulty experienced by young larvae in finding these tillers amongst the unsuitable ones. The same workers (1962) and Aldrich (1920) compared the rate of larval attack in cut and uncut grassland. They found that grassland that was cut or grazed regularly contained more overwintering larvae than that which was not. Southwood and Jepson (1962) concluded that the treatment and condition of the grasses have an overriding influence on the population of larvae in both situations. Jepson and Heard (1959) also found that there were generally more larvae, though not consistently so, in plots of grass that had been grazed continually than in those that had been cut for hay and then grazed. They suggested that the larval population in a sward depends largely on the growth form of the grasses at the critical oviposition period. They also examined the relationship between larval number and tiller numbers. Their results, though inconclusive, suggested that high larval numbers tended to occur where tiller density was highest, particularly in wheat and in Lolium species.

Van Emden (1966) states that the growth stage of the plant is extremely critical because as the grass stem grows entry by the young larva becomes increasingly difficult. However, the older stem contains more food to sustain to maturity a larva which has successfully entered such a stem. He also suggests that cutting or grazing the grass provides the larva with a second opportunity for successful entry of the stem.

From the foregoing it appears that age and density of tillers in grassland affect larval attack and number, but direct evidence of how the two factors operate is lacking.

The experiments described here attempt to clarify the operation of the factors influencing larval attack.

The effect of tiller age

The number of tillers attacked and the number of larvae which become established decreased as the tillers aged. This was probably because younger tillers had softer tissues which were more easily penetrated by the newly-hatched larvae. This would explain why the number of young larvae surviving from eggs laid on the plants artificially reduced to a single tiller steadily decreased as the tillers aged. However, this trend may be modified in the case of the complete plant, by the presence of young secondary tillers. In this, the normal situation, the immunity conferred by age on the entire plant is reduced by the continued production of new tillers: production of secondary tillers is stimulated by defoliation either by grazing or mechanical harvesting. Care was taken to reduce this source of error in the study, by removing the majority of the secondary tillers produced by plants before transferring them to the field. Although all the tillers at different ages produced secondary tillers during the period they were exposed to infestation, the rate of tillering was slightly higher in the younger plants and consequently the age structure of tillers originally intended was maintained during the period of attack.

Observations on the morphological changes in the tiller which take place during its development, showed that some of these changes were probably associated with the decreasing ability of the larva to penetrate the tiller. The most important among these changes was the accumulation of layers of dead leaf sheaths, the distance up the shoot to which they extend, and the degree of hardness of the stem proper. Within the age-range of tillers used, only the first two changes were operating markedly, because the elongation and hardening of the internode has not yet taken place. In young tillers 2-5 weeks old, no dead leaf sheaths were present, and the tillers remain fresh and soft. In 7-week-old tillers, one layer of leaf sheath had been formed but this reached only about one cm up the shoot. In 9-week-old tillers, the number of layers of dead leaf sheaths had increased to between 2 and 3, and extended further up the stem. In 12-week-old tillers, the number of layers of dead leaf sheaths varied between three and four per tiller and reached even further up the shoot, giving the lower half of the shoot the characteristic pseudo-stem structure. The effect of these morphological changes was to increase the toughness of the external tissues to be penetrated by invading larvae.

The greater the number of the covering layers of dead leaf sheaths, and the extent to which they have grown up the stem, the more difficult it is for the larva to penetrate and establish itself. Also, the greater the extent to which the pseudo-stem is formed up the shoot the more extensive the search which the larva has to make, looking for an entry point. Consequently, the larva is exposed to external hazards such as dehydration, larval parasites and predators for much longer periods than it would have been in young tillers in which the larva finds an entry point. These findings support the views advanced by the authors cited above. It also explains how the management practices adopted on grassland may affect the size of the stem-borer population. Regular cutting or grazing of grassland not only provides fresh entry points for the larvae but also stimulates the continuous replacement of old tillers with younger ones, whose presence permits easy penetration and establishment of newly-hatched larvae.

Stem-hardness was not measured in this experiment because this phase of development occurs at a later stage of development than examined here. Nevertheless, it may have begun to contribute to the inability of the larva to establish in such tillers because the results of regular field sampling showed that tillers in which the internode has elongated and the stem hardened are not attacked by the larva. In field situations, therefore, the progressive elongation and hardening of the internode in the later stages of development will probably contribute to poorer establishment of the larva in the same way that accumulation of the layers of leaf sheaths does in the earlier stages of growth.

The effect of tiller-density

The results show that the number of tillers infested and the number of larvae which established increased as tiller density increased. Increasing larval number with increasing tiller density was particularly obvious in plants 2- and 5-weeks old. This was because all tillers of this age were suitable for larval establishment.

The effect of increasing plant density became less obvious as older plants were used. This was due to the increasing resistance to larval penetration preventing the exploitation of the numerous potential hosts provided. In other words the age of the tiller has a more significant effect on the entry and number of larvae which can establish successfully in the plant. This explanation is compatible with the results of Jepson and Heard (1959) who found that in grazed grasslands, high larval numbers tended to occur where tiller density was highest, particularly in Lolium species. They could not, however, establish a similar relationship in other grass species probably because those grass species were not in growth stages suitable for larval entry and establishment. Similarly Bullock (1967) established a positive linear relationship between shoot density in barley and infestation of the shoot fly, Leptohylemyia coarctata, particularly in young plants at the one-shoot stage. As the plants grew and more secondary shoots were produced, the size distribution of shoots in the sample had to be taken into account. The size distribution of shoots is probably a measure of the ageing of plants, and it is this new factor (i.e. the host age) which obscured the effect of plant density on the number of larvae.

That this may be a general phenomenon is suggested by similar findings with other insects on other crops. The studies of Fitch (1932) on the infestation of corn by the corn-borer, those of Pimentel (1961d) on the animal community associated with Brassicae oleracea L., and finally those of Perron (1972) on the infestation of onion by the onion maggot, Hylemyia antiqua, indicate that when the host plants are at the growth stage suitable for pest attack, an increase in plant density results in an increase in the numbers of the pest.

In experiments on oviposition it was shown that the number of eggs laid per unit area increased as tiller or plant density increased at a given age of plant, although the number of eggs per plant inevitably decreases at the same time. This tendency for the number of larvae per plant to decrease as plant density increases could therefore be due to the rate at which eggs were laid per plant. This negative trend agrees with the results of all the afore-mentioned workers, including those of Way and Heathcote (1966).

Increasing plant density has the effect of reducing the number of larvae per plant but increasing the number of larvae per unit area.

Experiment X. To determine the effect of host plant species at different stages of growth on the rate of larval attack in the field.
Method. Ten grass species or varieties were sown on five dates in the glasshouse at the rate of 15 plants per 10 cm. diameter pot. Plants 3, 6, 9, 12, and 16 weeks obtained in this way were later transferred to the field and exposed to natural larval infestation as described earlier. The plants were removed from the field after three weeks and the stems dissected. Each grass species was replicated four times at each age and all the pots were exposed simultaneously.

Results

Oscinella spp larvae of *Oscinella spp.* attacked all grass species and became established in them all except *Dactylis glomerata*. Larval infestation was highest in *Poa trivialis* and *Agrostis tenuis*, the level of infestation remaining more or less steady as the plant grew. In *Lolium multiflorum* and various cultivars and genotypes of *L. perenne*, larval infestation was highest in the youngest plants and the infestation declined gradually as the plant grew. In *Holcus lanatus*, *Avena fatua* and *Phleum pratense*, only the youngest plants were heavily attacked, the level of infestation declining very rapidly as the plants aged. In these species larvae failed to become established in plants aged five weeks or more. In contrast to all the grass species mentioned so far, *Festuca rubra* did not support larval infestation until the later stages of its development, and only the older plants 9-12 weeks old were attacked. Finally, *Dactylis glomerata* suffered minimum attack. In this species, symptoms of attack were confined to the secondary tillers of very young plants, but larvae were not found in any of the older stems. Generally, the mean number of larvae per pot declined with age except in Poa and Agrostis spp. in which larval numbers remained almost steady, and in Festuca rubra in which the number increased with age. (Figure IX).

G. tripunctata: The intensity of attack and the mean number of larvae per pot followed a trend similar to that of Oscinella spp, except that again Festuca rubra was not infested by larvae. (Figure VIII).

The number of tillers produced by the various grass species at different ages, and the number of larvae which established in them were as shown in Tables 14–16.

Discussion

The number of tillers attacked and the number of larvae of either Geomyza or Oscinella species which established in the tillers varied with the species and stage of development of the plant. It has been shown that in perennial ryegrass, larval entry and establishment is much easier in young tillers. It was also shown that at the susceptible growth stage of the plant, the number of larvae which established successfully increased as the tiller density increased. In this experiment, these same host plant factors appear to determine the number of larvae found in the stems of other grass species.

The grasses tested could be divided into four groups depending upon their susceptibility to larval attack (Figs. VIII and IX). Firstly, those which continuously produced young tillers, and which consequently remained "young" for a considerable length of time, supported the highest number of larvae. In this category are P. trivialis and A. tenuis. By contrast, the less actively tillering but fast-growing species such as L. perenne and L. multiflorum supported fewer larvae. The faster rate of development of species in this second group ensured that the newly-produced tillers remain susceptible to larval attack over a shorter period.

The third category comprised those grass species which produced the least number of new tillers and which developed quickly enough to enable most of them to escape larval attack. The most important species in this category is *Avena fatua*, followed by *H. lanatus* and *P. pratense*, in all of which larvae failed to establish from the age of 5 weeks onwards.

The fourth group contains only one species, *D. glomerata*. It is less aggressive than any of the *Lolium* species, at establishment, but subsequently develops much more quickly although its rate of tiller production remains very slow. The newly-produced tillers therefore remain susceptible for a very short period (between the one and two-leaf stage). However, tillers invaded at this stage seem to be incapable of providing adequate food to sustain larval growth to maturity as typical stem-borer damage was often observed but larvae rarely encountered in samples.

Laboratory observation showed that the larvae of *G. tripunctata* and *O. frit* L. were able to establish in very young shoots (one- to two-leaf stage) of *D. glomerata* which had been subjected to moisture stress for two or three days after eggs had been laid on them. Such plants succumbed more quickly to attack and permitted larval establishment but they were unable to produce secondary tillers before they died and before the development of the larvae was completed. Consequently both the infested plant and the larva died.

Slow tiller production and rate of development may also account for the observed failure of larvae to infest the young stages of *F. rubra*.

Other factors such as the production of poisonous substances by *D. glomerata* in response to larval attack (antiobiosis) may account partly for the resistance of D. glomerata to larval attack and establishment, but the observation above suggests that this factor is less important.

Other specific characters which inhibit oviposition, such as the production of long dense hairs in H. lunatus may in addition reduce infestation to a lesser extent.

The apparent inconsistency noted earlier in the general review of literature, a resume of which is given in Table 16, may be due to variation in the age and growth stage of the plants, and it may also be due to variation in environmental conditions in which a given grass species was exposed to infestation by the different authors.

To conclude, it seems that the specific susceptibility of plants to larval attack depends not only on the rate at which the tillers are produced, but also on the length of the period during which the tillers remain suitable for larval entry. Given successful penetration of the tillers, the survival of the larva may still depend upon the availability of adequate food material to sustain it to maturity.

Experiment XI. To examine the effect of sowing mixed grass species, Dactylis glomerata and Lolium perenne, on the rate of larval establishment in the field.

Method. Small plots of perennial ryegrass were compared with mixed swards containing a similar amount of ryegrass and in addition from 5% to 27% cocksfoot. Trials were conducted in the field in 1973 (autumn and winter) and in 1974 (summer and autumn). The swards used in 1973 were sown in July, and sampled from September through to the following January. Those used in the 1974 trial were sown in April and sampled from June to September of that year. Core samples were taken at fortnightly intervals, and the percentage of cocksfoot and ryegrass tillers in each sample recorded. The stems were dissected and the number and species of larvae recorded (Table 17a).

Results

G. tripunctata: The number of larvae which established in the tillers was significantly higher in the pure ryegrass swards than in the mixed swards. The number of larvae per core gradually decreased as the percentage of cocksfoot in the mixture increased. During 1973 the number of larvae was greatest (3.3 per core) in the pure swards and least (0.8 per core) in the sward containing most (27%) cocksfoot. The corresponding figures of 1974 were 1.5 in pure swards and 0.6 in the sward containing most, (20%), cocksfoot.

Oscinella spp.: In both years, the mean number of larvae per core was highest in the pure swards. In 1973, the mean number of larvae per core was greatest (7.2 larvae per core) in the pure swards and 1.2 in the sowings containing most (27%) cocksfoot. Corresponding values in 1974 were 3.3 in the pure ryegrass sward and 0.5 in the sward containing 20% cocksfoot.

The analysis of data during both years showed that there were significant negative correlations between the number of larvae which established in each sward and the number of cocksfoot tillers in that sward (Figures X and XI).

During 1973 and 1974 the addition of cocksfoot consistently reduced the size of the larval population of both genera which became established. The overall populations of larvae which became established in swards sown in the late summer of 1973 were greater than those which established in swards sown in the spring of 1974, in both the pure and mixed swards. This difference was due to the difference in the number of egg-laying flies invading the sward at the time of sowing rather than a year-to-year variation. The introduction of *D. glomerata* did not alter the species complex of stem-boring larvae and the same species were found in both the pure ryegrass and in the ryegrass/cocksfoot swards. The relative abundance of the species was also unaltered, being in descending order of abundance, O. vastator 41%, G. tripunctata 23%, O. frit L. 19%, O. frit ex Anthoxanthum 10%, O. frit ex Arrhenatherum 7%.

Discussion

The reduction in the number of larvae in mixed sowings could have been due to one or more factors. These include a reduction in the intensity of oviposition, and an increase in egg and larval mortality due to predation and parasitism. Mortality of the larvae would also be increased by their failure to penetrate the unsuitable cocksfoot tillers in the mixed swards.

In experiment IV it was shown that both the perennial ryegrass and cocksfoot were used for oviposition by the two genera of insects, although at the same growth stage the perennial ryegrass received more eggs. This would suggest that more eggs were laid in the pure ryegrass swards. However, here there was no significant difference between the mean number of ryegrass tillers per unit area in the pure and mixed swards. Hence, the intensity of oviposition induced by ryegrass tillers alone in both types of sward was probably similar. The overall number of eggs laid in the mixed swards could therefore be expected if anything, to be greater than the number laid in the pure swards because the cocksfoot provided additional oviposition sites.

If, however, a proportion of the eggs which would otherwise have been laid on ryegrass were laid on cocksfoot the survival rate of larvae would be adversely affected. Shapiro & Vilkova (1963), and Jones (1969) noted that eggs of Oscinella frit L. laid on the less suitable sites of maize and on oats tended to be dislodged and destroyed by predators.

Cocksfoot has relatively little leaf sheath and so provides fewer protected sites for eggs, so that higher losses may be expected. In addition, larvae emerging from surviving eggs would have more difficulty in becoming established due to cocksfoot's comparative resistance to penetration. Petherbridge (1917) and Nye (1959) showed that larvae of *O. frit* L. are capable of migrating from tiller to tiller, and also from plant to plant. Larvae moving to fresh tillers on cocksfoot will experience more difficulty in penetrating the stems, while those moving to adjacent ryegrass plants are exposed to desiccation and predation. This explanation draws support from the findings of Southwood and Jepson (1962) and of van Emden *et al*. (1966) who state that the key mortality factors operate before or during the entry of the larvae of *O. frit* into grasses.

The presence of a proportion of relatively unsuitable host plants appears to reduce overall larval infestation by increasing egg and larval mortality, and this reduction is related to the amount of unsuitable host present. It may be that the relatively unsuitable host, cocksfoot, acts as a trap crop by diverting a certain amount of oviposition from ryegrass and increasing the mortality of the eggs and larvae so diverted.

(v) Field Infestation

(i) Larval complex

Identification of the larvae obtained from the field samples on Rothamsted Farm during the period 1972-74, showed that the composition of the dipterous stem-boring larval complex infesting perennial ryegrass growing in pure and mixed sward was consistent and limited to five main species in the two genera, *Geomyza* and *Oscinella*. One species of *Geomyza*, *G. tripunctata*, and four spp. of *Oscinella*, *O. vastator*, *O. frit* L., *O. frit* ex *Anthoxanthum* and *O. frit* ex *Arrhenatherum* were found (Appendices I & II).

(ii) Estimation of damage

In newly-sown fields of the S24 perennial ryegrass, larval infestation of primary shoots and subsequent damage to shoots and tillers commenced soon after germination. The level of damage (estimated from the number of larvae plus the number of damaged stems found) then increased gradually as more shoots and young tillers appeared and as the population of larvae built up in the field. In 1972, the percentage of shoots and tillers damaged as a result of larval attack increased from 2.5% at the time of establishment in mid-June to about 7% in mid-July. The level of damage then declined to about 4.5% of all tillers in late July. Following the first mowing of the sward, and the resultant increase in number of susceptible younger tillers, a peak of damage was observed in late August (10.5%). In early November a second peak of infestation was recorded, 15.6% of all tillers containing larvae, reflecting the steady build-up of populations during the year. The corresponding peaks of damage during 1973 were 12.6%, 18.1% and 18.8% in June, August and November respectively.

In the older swards the trend of damage was similar. In 1972, the level of damage rose from 1.6% in mid-April to the first peak of 4.0% in late May, then declined to about 1% in late June. Following mowing operations in early June and late July, second and third peaks of 4.4% and 7.6% were observed early in August and in mid-October respectively.

In 1973, the three peaks of damage in the old sward were 6.2%, 15.1% and 20.2% in mid-June, late August and mid-October respectively. The first two peaks occurred following mowing operations and the third reflected the normal build-up in larval populations in the 3rd generation.

Damage tended to be slightly higher in the younger sward: this was most noticeable in 1972 when the disparity in age between 'young' and 'old' sward was greater (Appendices IA and IB).

(iii) Seasonal pattern of larval infestation

G. tripunctata: 1972: In the young sward, the mean number of larvae rose from 4/0.01 m^2 (ten cores) in late June to a peak of 8/0.01 m^2 in mid-July. A second and much higher peak of 14 larvae per 0.01 m^2 was detected again by mid-October.

The infestation of the older sward did not begin until after mowing in early summer. The first peak of about 11 larvae/0.01 m^2 was attained in late August. A second but lower peak of larval numbers of about 7 per 0.01 m^2 occurred in mid-October.

1973. In 1973, the trends of larval population build-up in both sward types were similar to those of 1972. The younger sward developed a higher population of larvae per unit area. Three peaks of population, 10, 10, and 30/0.01 m^2 were attained in mid-June, early July, and early October respectively.

In the older sward, the corresponding peaks of larval population were 2, 6, and 3 larvae/0.01 m^2.

O. vastator : 1972. In the newly sown sward, the number of larvae per 0.01 m^2 rose gradually from 2.0 in early July to a peak of 30 in late August, and then declined to 17 in early September. The population of larvae built up again later in the season giving rise to a second peak of 32/0.01 m^2 in mid-October. The larval population then declined gradually as winter mortality increased.

The infestation of the old sward did not become obvious until after the sward had been mown. The larval population built up from about 2/0.01 m^2 in early June to the first peak of 14 in late August, and declined to about half this size in early October. A second peak of 21/0.01 m^2 was attained by late-October and thereafter the population declined steadily as the season advanced.

In 1973, newly established early instar larvae were found in the younger sward very early in June, at the rate of about 2/0.01 m^2. A first peak of larval number, 22/0.01 m^2, was detected by the end of June. The population then declined and remained low until early August, after which it built up again. A second but higher peak of about 36/0.01 m^2 was attained by early September, and remained more or less steady at this level until early November.

The infestation of the older sward by early instar larvae was not detected until after the sward had been mown in summer. Infestation built up from about 15 larvae/0.01 m^2 early in August and attained the first peak of 55 larvae/0.01 m^2 late in September. The population of larvae then declined, remaining steady at about 36/0.01 m^2 until late October after which a second peak of 53 larvae/0.01 m^2 was attained. From early November onwards, the larval population in the sward declined gradually.

<u>O. frit L. : 1972</u>

The infestation of the young sward by larvae of the first generation was detected early in June. The population built up in early June from a mean of 3/0.01 m^2, reached a peak of 7/0.01 m^2 in early July, and rapidly declined. Infestation was very low in August and September. A second period of infestation occurred later in the season reaching a poorly defined peak of about 2 larvae/0.01 m^2 late in October.

Infestation of the old sward commenced late in June, and remained low throughout (1 to 3 larvae/0.01 m^2). Two peaks of larval numbers, 4 and 5/0.01 m^2 occurred in early July and mid-August respectively.

In 1973, the larval infestation of the young sward started very early in May. The first peak of 17 larvae/0.01 m^2 occurred in mid-June. The population of larvae built up again after the mowing of the sward and led to a second and higher peak of 26/0.01 m^2 by mid-August. Thereafter, the number of larvae gradually fell to about 1 per 0.01 m^2 early in September. Another build-up in larval numbers occurred from mid-September and reached a third and final peak of about 10 larvae per 0.01 m^2 late in October, remaining at this level until regular field sampling was discontinued in late Autumn.

Again in 1973, infestation of the old sward did not commence until after the mowing of sward in early summer. The population of larvae establishing in the sward built up from about 3/0.01 m^2 in mid-June to 25/0.01 m^2 in the middle of August, and then declined rapidly to about 2/0.01 m^2 by mid-September. A second period of infestation occurred from early September and a second but lower peak, 14 larvae/0.01 m^2, was attained late in September. Thereafter the larval population in the old sward declined rapidly as the soil temperature fell. In contrast to the young sward, only two peaks of larval numbers were detected during the year.

O. frit ex Anthoxanthum

In 1972, the newly sown grass was infested by larvae as from early May. The first peak of larval infestation, 8/0.01 m^2 occurred late in September, and remained more or less steady at this level until it fell in late September to about 2/0.01 m^2. A second but slightly lower peak 6/0.01 m^2 occurred in mid-October, and declined steadily to about 3/0.01 m^2 as the season advanced.

Infestation of the older sward in 1972 was similar to that of the younger sward, commencing after the sward had been mown. Three peaks of infestation occurred, the first, 4/0.01 m^2 early in July, the second, 7/0.01 m^2 occurred in mid-August and the third, 6/0.01 m^2 was attained later in the season, about mid-October.

In 1973, newly-establishing larvae of O. frit ex Anthoxanthum infested the young sward from mid-June. The first peak of larval population of 9/0.01 m^2 was detected by early July declining to about 2/0.01 m^2 by the end of the month. A second period of infestation occurred as from early August, and gave rise to a second, but higher, peak of larval numbers 14/0.01 m^2 about the middle of September.

Infestation then declined to about 5 larvae/0.01 m^2 in autumn.

Again, the infestation of the older sward started only after the sward had been mown, resulting in two peaks, 13 and 17 larvae/0.01 m^2, early in September and mid-October respectively. By early November, larval populations had fallen to about 9/0.01 m^2.

O. frit ex Arrhenatherum

In 1972, the infestation of the young sward was first detected by mid-June, reaching the only peak of 10/0.01 m^2 later in the month. Thereafter larval population fell drastically, and larvae were not found as from late July onwards.

The older sward by contrast was infested throughout the season, the larval population becoming more noticeable after the mowing of the sward. Three peaks of larval population, 4, 11 and 7/0.01 m^2 occurred in late June, mid-August and late September respectively.

In 1973, the infestation pattern of the newly sown sward did not follow that of the previous year, but commenced in early June. Peaks of larval infestation of 3, 5 and 6/0.01 m^2 were detected at the end of June, mid-August and late October, respectively.

In the older sward, infestation by first generation larvae did not occur until the sward had been mown. Early instar larvae were found from mid-June, the population reaching the first peak of 7/0.01 m^2 by mid-July and declining to zero by mid-August. A second infestation occurred late in October giving rise to a small, poorly-defined peak of 3/0.01 m^2. The larval population remained steady at this level until the end of regular field sampling late in autumn.

From the foregoing it seems that infestation by the five species of stem-borer does not occur simultaneously. G. tripunctata begins the process three to four weeks before any of the Oscinella species. O. frit L. and O. frit ex arrhenatherum follow next, and the last to invade are O. vastator and O. frit ex anthoxanthum.

This sequence is determined by the time of adult emergence in spring, each of the three groups having critical temperature thresholds. If the rise in soil temperature in spring is very protracted the emergence of the species will be more widely separated. Large differences in rate of temperature rise are due to year to year meteorological variation, but the condition of the sward may modify this effect, e.g. soil temperature rises more quickly if the sward is close-cropped or ploughed.

The results also showed that except in the case of G. tripunctata, which preferred the newly sown sward, there appears to be no strict preference for old or young sward in the case of the Oscinella spp. Once the old sward produced young tillers in response to mowing, they become equally susceptible to larval infestation. The summaries of these results are presented graphically in Figures XII - XV.

(iv) Relative abundance of larvae of different species

In 1972, the relative abundance of the various species of larvae in the newly-sown sward was as follows, in decreasing order of abundance:- O. vastator (49.2%), G. tripunctata (28.2%), O. frit ex Anthoxanthum (9.7%) O. frit L. (6%) and O. frit ex Arrhenatherum (3.9%).

During 1973, the corresponding order of abundance in the newly-sown sward was O. vastator (42.7%), G. tripunctata (21.8%), O. frit L. (17.4%), O. frit ex Anthoxanthum (11.9%) and O. frit ex Arrhenatherum (6.2%).

In the old sward, the relative order of abundance of larvae was slightly different from that of the young sward, although O. vastator again remained the most numerous species.

In 1972, the number of larvae of various species was in the following decreasing order of abundance: O. vastator (39%), O. frit ex Arrhenatherum (22%), O. frit ex Anthoxanthum (15.6%), G. tripunctata (12.5%) and O. frit L. (10.9%).

In 1973, the corresponding values in larval abundance in the old sward was O. vastator (57.6%), O. frit ex Anthoxanthum (16.7%), O. frit L. (15.1%), O. frit ex Arrhenatherum (6%), and G. tripunctata (4.7%). This information is summarised in Table 18.

From the foregoing, it seems that the relative abundance of the various species of larvae varied with the age and the condition of the sward, especially the number of young tillers present, at the period of adult oviposition and larval establishment. In general, O. vastator consistently remained the most numerous species in both sward types, and in both years. Apart from G. tripunctata, which seems better adapted to conditions in the young sward, and thus remained second to O. vastator in order of abundance, the other three Oscinella spp. did not demonstrate any strict pattern of relative abundance.

These findings probably explain the contradiction between the results of Jepson and Heard (1959), and those of Southwood and Jepson (1962) who studied the relative abundance of the various larval species in grass leys and in permanent grasslands respectively. The former authors found that in grass leys, the larvae of O. frit L. were the most abundant, whereas the same species was rated third in order of abundance in permanent grassland by the latter authors. Southwood and Jepson (1962) suggested that the differences in the rating of O. frit L. could partly be accounted for by differences in floristic composition of the sward, the breeding efficiency of other stem-borer species rising as the proportion of unsown invading grasses increased.

(v) Comparative abundance of larvae in young and old swards

G. tripunctata: In both 1972 and 1973, the population abundance of larvae of G. tripunctata was significantly higher in the newly-sown sward (Table 19 and Figures XVI & XVIII). This was probably because it contained higher numbers of susceptible tillers for most of the oviposition period. The first generation of adults of this early-emerging species were able to deposit most of their eggs in the newly-sown sward. By the time the older sward had been mown and had begun producing susceptible new tillers these flies had finished ovipositing. The failure of subsequent generations of this species to establish in the older sward even after mowing may have been due to lack of synchronisation between their oviposition and the period of grass-regrowth. This contrasts with the situation found with *Oscinella* spp. It may also have been associated with the inherent behaviour of the adults of this species which, in laboratory tests at least, tend to prefer denser cover, and to avoid exposed situations such as would be found in older swards after mowing. Larvae of *G. tripunctata* appeared to be less mobile in laboratory tests, and this too may reduce their success in finding suitable young tillers in the mown sward relative to the *Oscinella* species.

Oscinella spp.: In contrast to the situation found in *G. tripunctata* infestations, *Oscinella* spp. all become equally numerous in young and in old swards (Table 19; Figures XVII and XIX). The rate of build-up of larval populations depends predominantly on the rate of new tiller production. This is high in newly-sown swards, and in older swards is stimulated by defoliation. Since the four *Oscinella* spp. are able to exploit both situations, the relative sizes of the larval populations in young and old swards will depend on the frequency of mowing in the latter, and the synchronisation between the oviposition period of the various *Oscinella* spp. and the regrowth of mown swards. The dominance of *O. vastator* from year to year may be due to the fact that its host range is restricted to grassland (cf. *O. frit* L. - grasses and oats), so the loss of ovipositing adults to cereals is relatively less in this species.

(vi) Winter mortality of larvae

Quantitative estimates of larval mortality in the newly-sown sward during winter were made by comparing the numbers of larvae of the various species found during four consecutive weeks in late autumn with those found in a similar period during the following spring in the same sward.

In autumn 1972, the mean number of larvae of *G. tripunctata* per ten (10-cm diameter) cores was 20.3 whereas the corresponding value in the same sward had declined to 6.0 by early March 1973.

In 1973, the larval population in autumn was 25 per ten cores and by March 1974 it had declined to 8 per ten cores.

The mortality of larvae during the winters of 1972 and 1973 was remarkably similar at 70.4 and 68% respectively.

Oscinella spp.: Larval mortality during winter was also high in these species.

In autumn 1972 the mean number of larvae was about 19 per ten cores and fell to 9.5 per ten cores in April of the following year. The corresponding values for autumn 1973 and spring 1974 were 56.5 and 27.5 respectively.

Larval mortality figures during the winters of 1972 and 1973 were therefore 50% and 62.5% respectively.

Discussion

Various authors who studied the population abundance of *O. frit* larvae in grasslands have found that considerable mortality occurred during the winter months (January - March). Coaker (1953) found that in *Lolium* the larval population of *O. frit* fell by about 50% as a result of winter mortality. Southwood and Jepson (1962) found that the mortality of overwintering *O. frit* L. larvae in short grass could be high, varying between 4.2% and 67.5%. Except in the case of the short grass in Silwood Bottom in 1957-58, the overwintering mortality of *O. frit*, (the 4.2% value referred to), was usually 50% or more in grasslands. However, Nye (1959) considered the dipterous stem borer complex in permanent grass suffered only a slight reduction in the winter months.

The discrepancies in the results of various authors may be due to the variation in the intensity and the extent of winter period in different years. It may also be due to variation in the condition of the sward sampled by the various authors.

(vii) Parasitism

Imms (1930) and Bhattacharyya (1957) established that the three major parasites of the larvae of *O. frit* L. were *Halticoptera fuscicornis* Walk. (Chalcidoidea), *Rhoptomeris eucera* Hartig (Cympoidea), and *Loxotropa tritoma* Thoms (Proctotrupoidea).

Preliminary investigations of parasitised borer larvae during 1972 showed that all three species were present, parasitising *Oscinella* spp., but that *G. tripunctata* was parasitised only by *H. fuscicornis*.

The number of parasitised larvae found in field samples was very low. In an attempt to get more information on parasite populations the numbers of adult parasites present in the field were also recorded. During 1973 this information was obtained from the suction samples taken regularly to estimate adult stem-borer numbers.

Results. In the newly-sown and old swards the number of adults of the various parasite species was very low for most periods of the year (Table 20).

H. fuscicornis. In the young sward, the number of adults was about one per square metre from early June to mid-August. Most of the adults were found in late August when a maximum density of $8.5/m^2$ was recorded. Thereafter, the number of adults declined to $0.5/m^2$ in late October.

R. eucera. The number of adults varied between 0.3 and $4.0/m^2$ in June, and declined to $0.8/m^2$ from early July until early September. In the third week of September, the number increased again to $4/m^2$, thereafter declining rapidly to 0.3 in late October.

L. tritoma. The number of adults of this species remained consistently low throughout the year, the highest number being $1.0/m^2$ in mid-August.

In the old swards, the number of adults of each species of hymenopterous parasite followed a trend similar to that in the young swards, although the peaks were usually lower than in the younger swards.

Generally, most of the adults were found between late August and mid-September, in particular those of H. fuscicornis and R. eucera (Table 20).

Throughout the sampling period June-October 1973 the larvae of only two of the four Oscinella spp., O. frit L. and O. frit ex Arrhenatherum, were parasitised. Larvae of G. tripunctata were also parasitised but only two such specimens were found: these are not discussed further.

Halticoptera fuscicornis (Walker) and Rhoptomeris eucera (Hartig) were the main parasite species and were found in equal numbers. Loxoptera tritoma Thoms was rarely found.

Generally, levels of parasitism were low in both young and old swards. In the young sward parasitised larvae were found only during discrete periods, i.e. during the early phase of establishment (June) and after mowing. In the old sward parasitised larvae were found only after the sward had been mown.

These brief increases in the number of parasitised larvae do not appear to be related to an increase in the host larvae numbers, or of the number of adult parasites present. They appear to be related to the condition of the sward, i.e. to a newly-sown sward or to a newly mown sward. Both situations tend to make the host larvae more accessible to the adult parasites.

The relative numbers of host larvae, parasitised host larvae and adult parasites present during the season are shown in Figure XX.

In view of the wide fluctuation in the numbers of host larvae sampled, percentage parasitism was not calculated because values so derived may be misleading when the number of host larvae in the field was naturally low.

It is noteworthy that the larvae of the most abundant species, O. vastator and the closely related species, O. frit ex Anthoxanthum, were not parasitised.

Discussion

Larval mortality due to parasitism was very low, regardless of the age of the sward. Various factors appear to limit the efficiency of the adult hymenopterous parasites associated with the dipterous stem-boring larvae in grass.

Firstly the adult parasites were not present in large numbers in the field until very late in the season (Fig. XX). The seasonal abundance of adult parasites is closely related to their emergence in summer from parasitised overwintering hosts. Their peak emergence generally occurred after the second mowing of the old sward. Most larvae of O. frit L. and O. frit ex Arrhenatherum of the first and probably the second generations in sown grass thus escape parasitism, because most of the parasites appeared late. The poor synchronisation between the phenology of the parasites and those of their hosts appears to be an important factor limiting the efficiency of the parasites, particularly in the newly-sown sward.

By the time of peak appearance of the adult parasites in August, the young sward has established further. Also, most of the host larvae have pupated, and the few larvae remaining were well established within the tillers, where they appeared well protected from the parasites.

Peaks of parasitism were therefore limited to the first few weeks of establishment in the newly sown grass. At this growth stage of the infested shoots, the tissues of the infested plants are still succulent. It is possible that this condition of the plant enables the parasites to locate the larval hosts. With further sward development, the efficiency of the parasites was probably reduced because the tillers were growing thicker, and the parasites could not get to their hosts.

After the swards had been mown, the level of parasitism increased again, probably because the protection offered to the larvae by the host plant was removed. Most of the larvae became more exposed and more accessible to the parasites.

The incidence of parasitism which occurred in the younger sward in late October may also be due to further exposure of larvae as the peak of natural mortality of tillers usually occurs during this period. Also, infested tillers probably succumbed more readily and decayed at a faster rate in the young sward during this period. The ultimate effect of these will be that of exposing the larvae in infested tillers to their natural enemies.

The results of various authors who studied the parasitism of the immature stages of O. frit in cereal crops and in grasses, showed that the level of parasitism varied considerably with the generation of frit fly and with the type of host plant.

Imms (1930) found that the parasitism of O. frit in oats ranged between 15 and 54%, increasing progressively as the season advanced. He found that O. frit infesting late-sown oats were more heavily parasitised than those on early sowings. He attributed this to the increase in the number of adult parasites which emerged as the season advanced. According to this author, most parasites emerged in August;

this appears to be the general trend as indicated in this work, and by the results of Jones (1968).

Although larval parasitism increased with the number of adult parasites present in late-sown oats, the abundance of the parasites appears to be relatively less important than the conditions of the host plants in determining the intensity of parasitism. The higher level of parasitism recorded by Imms on late-sown oats may have been related to the "youth" of the infested crop at the time of parasite abundance. The softer tissues of the late-sown crop possibly facilitated the location of the larval and pupal hosts as the parasites probed the tissues of the plant in search of their hosts.

Hemer (1959, 1960) also found that in Barley, most of the chalcid parasites failed to attack the immature stages of O. frit in the panicles. He recorded a low level of parasitism (10%). He suggested that this was because the ovipositors of the parasites were too short.

Although this author may be dealing with a different Oscinella sp. in barley (Southwood and Jepson, 1962), it seems that it was the hardened condition of the panicle at the time of appearance of the parasite which reduced the efficiency of the latter.

Similarly in oats, the hardened condition of the infested panicles or grains will probably reduce the efficiency of the hymenopterous parasites which emerge late in the season. This may explain in part the generally lower level of parasitism of the panicle generation than of the tiller generation of O. frit, as found by various authors (Bhattacharyya, 1957; Southwood and Jepson, 1962; Hemer, 1960; and Jones, 1968): Jones also found that only the early-emerging parasite species (July) could parasitise the immature host stages in the grain. Again, the success of these spp. was probably increased because they were able to reach their hosts before the panicles hardened.

In this work, the late appearance of the most important hymenopterous larval parasites in the swards appears to explain in part the low level of parasitism in the swards. Fig. XX shows that most of the adult parasites appear a few weeks later than the peak of appearance of their host larvae. However, in spite of the low number of parasites earlier in the season, the level of parasitism was equally high as later in the season when there were significantly higher numbers of adult parasites in the swards. Higher larval parasitism occurred in the younger sward during the establishment phase and in both young and older swards during a short period, after the swards had been mown. This was probably because the larvae of O. frit and O. frit ex Arrhenatherum were more accessible in the establishing younger sward and exposed to their parasites after mowing.

Van Emden (1966) observed that the parasites remain in permanent grassland for most of the time, and suggested that they may be more efficient in grassland than in oats. Jones (1968) also concluded that the late emerging parasites which are less efficient in attacking frit flies of the panicle generation in oats will be more efficient in grass because the parasites will be in phase with the final generation of the frit fly in grass. Although this may be so, the result of this study showed that the efficiency of these parasites in sown grasses in autumn is greatly reduced by the age and condition of the sward. In newly-sown, continuously grazed, and regularly-mown grassland, it is possible that the various species of hymenopterous parasites will be more efficient, because it is under such conditions that their larval or pupal hosts would be exposed and would be more vulnerable to attack.

From this study, the level of parasitism appears to be unrelated to the density of the larval hosts. This is in agreement with the findings of Jones (1968) who found that successful parasitism did not depend on the number of frit flies in oat grains. On this basis she concluded that the larval parasitism as a mortality-factor is density-independent. However, this apparent density-independent relationship between O. frit larvae and their hymenopterous parasites may have been influenced by the conditions of the host plant.

(viii) Comparative size of different generations

On the basis of the number of peaks of the population of the early instar larvae (first and second instars), in the newly-sown and old swards, three overlapping generations of larvae of the various spp. were detected in a season (April-October) (Figures XII - XV).

The size of the first and second generations of larvae of each species is about equal. The third generation is much more numerous than the two which preceed it. In the case of O. frit L., in which the third generation is the smallest, this is probably because the larvae of the first and second generations are relatively better adapted for survival under the warmer conditions of spring and early summer.

In general, the size of larval population of each species did not vary very much from generation to generation within a year, the highest being about twice to thrice that of the lowest - Table 19.

With the onset of very low temperatures in winter, considerable mortality of larvae of the overwintering generation occurred. By the beginning of the following spring the number of larvae had been reduced to about 30% (in the case of G. tripunctata) and about 45% (in the case of Oscinella spp.) of the original number found at the end of the preceeding season.

Winter mortality therefore reduces the effective size of this large third generation to the same level as the other two. A relatively steady population level in grassland is the result.

These results partially explain the steady population density of different generations of adults in grasslands. This evidence also supports the findings of Southwood and Jepson (1958, 1961), Smith (1962) and Calnaido (1962) who all found that in permanent grasslands the population of adult flies of the three generations do not vary very much.

(ix) Year-to-year variation in larval numbers

Regular samples of field populations of larvae in ryegrass stems were taken during the period May-November in 1972 and 1973.

Generally populations in both newly-sown and in older swards were higher in 1973 than in 1972. The difference was least in the case of G. tripunctata, and most in the case of O. frit L. Data for the two years are summarised in Table 21.

The increased success of O. frit L. in building up a high larval population in 1973 may be due to climatic factors. In this species, unlike the others, the second generation, which appears in July-August, is the most prolific. Both temperature and rainfall at the experimental station were higher during 1973 than in 1972 between June and August (Table 22). These conditions would be favourable for larval survival and development. Conditions during the earlier and during the later part of the seasons were not very different in the two years. The other species of Oscinella, and G. tripunctata, which have their largest generation in autumn would have experienced fairly similar weather conditions during these two years.

The relative population stability of most of the species of stem borers in grassland is consistent with the findings of other authors. (Southwood and Jepson, 1958, 1962; Nye, 1960; Jepson and Heard, 1959). These authors found that in the U.K. the population of dipterous larvae in grasses did not vary much from year to year, although Mowat (1974) noted that in Northern Ireland, the larvae of O. frit L. overwintering in cut and grazed grass were uncommonly numerous during 1968. He suggested that this might have been due to the proximity of the previous cereal crops to the sward.

The evidence available is probably not adequate to explain exactly why O. frit L. populations are relatively so variable in grassland compared with the other species. I have suggested that small climatic changes may influence the success of O. frit in grassland more than other species. Mowat (1974) suggests that invasion from cereal crops causes variations in grassland populations. However, Calnaido (1962) found that small variations in temperature between years had a pronounced effect (five-fold annual variations) on O. frit L. populations in the cereal itself.

It appears that the species which are confined to grassland, a relatively stable environment, do not fluctuate widely in numbers from year to year. The species O. frit L. which here, and elsewhere, showed appreciable year to year fluctuation, breeds both in grassland and in cereals. However, unless the acreages of cereals were to fluctuate widely from year to year, it is hard to see how this aspect of their biology could account for variations in grassland populations. It seems more likely that climatic variation, which affects both host crops, is responsible.

(VI) Spatial and Temporal distribution of adult and immature stage

Eggs. Distribution was examined in laboratory experiments. In one series female flies were confined, in small cylindrical cages, singly with individual young ryegrass plants at the 3-leaf growth stage. In a second series flies were confined in colonies of ten in a large observation cage.

Tests were conducted separately with O. frit L., O. vastator, and G. tripunctata. The results were analysed by the statistical method described below.

Larvae. Field larval populations were assessed from examinations of 10 cm diameter cores taken during 1972 and 1973.

During 1972, 20 random cores were taken in a series of 25 weekly samples. Larvae of all species were considered together. Both young and old swards were sampled.

In 1973, 10 random cores were taken in a series of 20 weekly samples. The larvae found were separated to *Oscinella* spp. and *Geomyza tripunctata*. As in the previous year, swards of both ages were sampled and the appropriate statistical analysis made.

Pupae. The distribution of pupae obtained from the core samples above was determined, but only during the peak period of pupation, and for a few weeks before and after this. This was because the number of pupae was very low at other times, being usually one or two per ten or twenty cores.

Adults. The distribution of adult stages of *G. tripunctata*, and *Oscinella* spp. was obtained from regular suction sampling. Ten 0.5 m^2 areas in each sward type were sampled with a suction sampling device at weekly intervals during the period April-November 1973.

The four *Oscinella* spp. could not be separated in the adult stage with any confidence, so they were grouped together.

Statistical Analysis: For each set of data, a test of deviation of the spatial pattern of eggs, larvae, pupae or the adults, from a random distribution towards a more highly aggregated distribution was made, using the test statistic $\frac{\text{variance}}{\text{mean}} \times (N-1)$ (where N = number of samples)

This statistic, assuming a random distribution, should have a χ^2 distribution with N - 1 degree of freedom.

The degree of aggregation for each set of data was measured by an index of dispersion

$$D = \frac{(\text{variance} - \text{mean})}{(\text{mean})^2} \qquad \text{(Pielou, 1969, p. 94)}$$

which for the negative binomial distribution can be equated with the parameter 1/K and takes the value of zero when the distribution is random.

Significant departure from randomness at the 5% level is indicated by an asterisk (Tables 23-30.).

Results

Eggs

G. tripunctata: In most instances, the distribution of eggs laid by isolated individual flies appeared to depart from randomness. However, this departure was significant on only one out of five occasions.

In the case of eggs laid by colonies of the same insect species the distribution of egg batches did not depart significantly from randomness (Table 23).

Oscinella spp.: In both O. frit L. and O. vastator, the distribution of each egg-batch laid by isolated individuals departed significantly from randomness in all instances.

The distribution of egg-batches laid by small colonies of flies in most instances departed significantly from randomness.

In the case of colonies of O. frit L., four out of five distributions departed significantly from randomness. With O. vastator all the distributions significantly departed from randomness.

These results indicate that in both species of Oscinella the distribution of eggs laid by either individual flies or colonies tended to be more aggregated than was the case with G. tripunctata (Table 24).

Larvae

Larval Complex: The analysis of larval counts in 1972 showed that the distribution of the larvae in both swards generally departed from randomness. In each sward type, the distribution of larvae on thirteen out of twenty-five dates was significantly aggregated. The degree of aggregation appeared to be independent of the mean population (Table 25).

The dates on which larval distribution tended to be less aggregated coincided with the beginning and end of the first and second generations in the newly-sown sward; and also with the weeks following mowing operations in both sward-types.

Individual spp.

G. tripunctata: In 1973, the distribution of larval counts of G.tripunctata and Oscinella spp. were analysed separately (Table 26). Five out of 20 distributions were significantly aggregated in the case of G. tripunctata. These highly aggregated distributions occurred only during autumn, the main breeding period of this species. Again, the distribution of the larvae was markedly random in the young sward during the first two weeks of sampling in early summer.

Oscinella spp.: In contrast to the distribution of G. tripunctata, larval distribution departed from randomness on most sampling dates. Eleven out of 18 distributions were significantly aggregated. Larval distribution tended towards randomness after the sward had been mown.

From this, it seems that the larvae of G. tripunctata were less aggregated than those of Oscinella spp. for most of the breeding period. This reflects the basic pattern of egg laying observed in the laboratory. The tendency towards a more aggregated pattern during the main breeding period in autumn may be in response to the changes in the habitat as the distribution of suitable tillers for oviposition, and also for larval entry, may be less homogeneous later in the season. Most ovipositing adults would under such conditions compete for the suitable sites, and the distribution of the eggs and consequently of the larvae would tend to be aggregated in autumn.

In the case of Oscinella spp. the distribution of larvae on most dates in 1973 conformed to that of the eggs, as indicated by laboratory experiments.

The distribution of the larval complex in 1972 showed the effects of an interaction between distributions of the larvae of G. tripunctata and Oscinella spp. in both swards. During that year, the less aggregated pattern in both swards after they had been mown may be explained by either the dislodging and redistributing of larvae from their original sites, or by the peak pupation of larvae, shortly after moving. Thus, the few larvae left (that is, those which pupated late) would be distributed randomly.

Pupae. The distributions of pupae of both G. tripunctata and Oscinella spp. were random for most sampling dates. During the periods of peak-pupation the distributions were significantly aggregated (Tables 27 and 28).

The random pattern of distribution on most dates was probably due to individual variation in the rates at which larvae pupated in the various species.

The aggregated distribution at the peak of pupation, again conforms with the distribution of the larvae from which the pupae were produced.

Discussion and Conclusions

These results indicate that within each genus, the spatial distribution of the various stages of development did not differ much from one stage to the other, but intergeneric differences may occur. Thus, while the distribution of the various developmental stages of G. tripunctata was slightly aggregated for most of the season, those of the corresponding stages of the Oscinella complex were highly aggregated.

Within each species, it is the egg-laying behaviour of the adult flies which largely determines the pattern of distribution of the subsequent immature stages. This was so because all the immature stages are relatively sessile. In G. tripunctata, whose eggs are less aggregated, the distribution of the larvae and pupae were similarly less aggregated. With Oscinella spp. the strongly aggregated egg-distribution also gave rise to similar aggregation of larvae and pupae. Distributions which deviated from those of the eggs could be partly accounted for by the heterogeneity in space and time of the habitat. In this instance habitat heterogeneity was produced naturally as the sward established. It was also produced by management operations such as mowing. It was pointed out earlier that the mowing operations by dislodging and redistributing the larvae and pupae from infested tillers, may alter the basic patterns of distribution. This may also apply to the distribution of the immature stages under field conditions.

These findings are in agreement with the observations of other authors who studied other aspects of the ecology of the dipterous stem-boring larvae in grasses (Thomas, 1938; and Nye, 1955, 1959). They observed that the larvae usually occur in aggregates, particularly during the winter months. The results indicate that the egg-laying behaviour of the female rather than the preference of the larvae is the main cause of the distribution of the larval and pupal stages.

Thomas (1938) also observed that under laboratory conditions, G. tripunctata usually laid eggs singly, although two or three eggs were sometimes laid adjacent to one another on the same stem. Such ovipositional behaviour would tend to produce the less-aggregated pattern observed in this study.

These differences in the behaviour of the adult insects during oviposition and hence in the dispersion of eggs and larvae may be of biological significance. The less aggregated pattern of the larvae of G. tripunctata may reduce intraspecific competition among the larvae, whereas the more strongly aggregated situation within the genus Oscinella may increase intra-specific as well as inter-specific competition among the larvae of the various Oscinella spp. during establishment, particularly in an unmown, or ungrazed relatively old permanent grassland, where there may be a shortage of tillers suitable for larval entry and establishment.

Considering the complex as a whole, the differences in the spatial distribution of eggs and larvae in the two genera will probably reduce intergeneric competition between G. tripunctata and the genus Oscinella. This may be one of the underlying mechanisms of successful co-existence of the various species of dipterous stem-boring diptera in grassland.

IV. GENERAL DISCUSSION AND CONCLUSIONS

(i) The Larval and Adult Complex

These studies on the biology of dipterous stem-boring larvae revealed that two main genera, Geomyza and Oscinella, invaded and bred successfully in pure stands of ryegrass, and in mixed sowings of ryegrass and cocksfoot. In the genus Geomyza, the only species found was G. tripunctata Fall. whereas four species of the genus Oscinella, O. vastator Curtis, O. frit L., O. frit ex Anthoxanthum and O. frit ex Arrhenatherum were found.

These results are in agreement with those of several other workers in the U.K. already referred to, who found that many species of dipterous stem-borers infest ryegrass. In Northern Ireland, Mowat (1974) found that ryegrass was less heavily infested than some other grass spp. This may be because different species of stem-borers are involved. It may also be because most of his samples were taken during the winter months, by which time winter mortality would have taken its toll of both larvae and of the infested tillers too. An underestimate is inevitable in those grass species in which both the larvae and the infested tillers decayed very quickly during winter.

It is noteworthy that the composition of the larval complex remained consistent in both years in both the pure and in the mixed swards. Oscinella nitidissima & Meromyza variegata have been suggested to prefer Dactylis glomerata to other grass species (Nye, 1955) and this might have been expected to alter the composition of the species complex and to increase larval populations; but the inclusion of cocksfoot here did not encourage the establishment of any additional stem-borer species. This may be because these insect species, as in the case of others, are less efficient in a habitat containing mixed plantings of both the preferred and less attractive plant species.

The relative abundance of all stem-borer species except O. frit was similar in both years. The status of O. frit L. in this instance seems to be anomalous. As discussed later, this may be because the year 1973 was a more climatically suitable year for this species in particular. Mowat (1974) who sampled populations over five winters in N. Ireland also found considerable year to year stability except in the case of O. frit L.

(ii) Pupation of the overwintering larvae in spring

In Section (iii) it was shown that larvae of G. tripunctata required a minimum threshold of temperature much lower than any of the Oscinella spp. The ecological significance of the lower temperature requirements of G. tripunctata is that it enabled the larvae of this sp. to resume active development and to pupate in spring before any of the Oscinella spp. Although the pupae of Oscinella spp. were not separated into their spp., similar differences in their temperature requirements would result in differences in the time at which they resume active feeding and pupate in spring. This would be more obvious in intact sward (unmown or unploughed). If the sward is mown or ploughed in spring the soil temperature may rise so abruptly that all various Oscinella larvae pupate at about the same period and so make less distinct differences in the minimum threshold of temperature normally required for the pupation of the various Oscinella spp. The time of pupation of the various larval species in spring or summer therefore depends not only upon their minimum temperature requirements but also on how quickly the soil temperature rises above these minima.

(iib) Sward damage. In a newly sown ryegrass sward, damage commenced in early spring, when rising temperatures allowed shoot emergence and the breeding of the flies to begin. The number of larvae in the sward increased rapidly with the appearance of more young tillers, and reached equilibrium within the first year of the sward's life.

The old sward was mown twice a year and received Nitrogen fertiliser twice a year; the young sward received the same number of fertiliser applications but was mown only once. Under this condition, the level of damage in the older sward was similar to that in the younger sward. This was because, in response to mowing, the older sward produced young tillers which were in a very favourable condition for both entry and establishment. It seems that under continuous mowing or grazing the annual level of damage will be similar to that of the first or establishment year.

(iii) Adult emergence and sward invasion in spring

The time of emergence of adults of the various species in spring corresponded with those of their larvae, already discussed above.

The adults of *G. tripunctata* are the first to emerge in March/April from the overwintering immature stages. The newly-emerged adults, together with the few adults which survive the previous winter, invade the newly-sown sward, before any of the *Oscinella* spp., as from the time of shoot emergence, usually in early May.

The various *Oscinella* spp. emerge and invade the swards later in the season. *O. frit* L. and *O. frit ex Arrhenatherum* emerge and invade the sward a little earlier than the remaining two species, *O. vastator* and *O. frit ex Anthoxanthum*. During 1972/3 and 1973/4 these emergence periods were closely related to the rise in temperature in spring, and appear to reflect the different minimum thresholds of temperature required for eclosion of each species. This threshold is lowest in the earliest species to emerge (*G. tripunctata*) and highest for *O. vastator* and

O. frit ex Anthoxanthum, the latest to emerge (Fig. I). As is the case with larval pupation, the rate at which soil temperature rises in early spring (with regard to G. tripunctata), or in early summer (in the case of the Oscinella species), probably dictates the time of emergence of the various species, and hence the extent to which the specific invasion periods are staggered in spring.

(iv) Spatial and temporal distribution and its biological significance

From the above it is obvious that the invasion of a sward by the different species of stem-borer and the establishment of their first generation larvae take place in a well-defined succession. G. tripunctata emerged and invaded the sward before any other species. It therefore escaped interspecific competition during oviposition and larval establishment. Among the various Oscinella spp. O. frit L. and the closely related O. frit ex Arrhenatherum emerged next and invaded the sward before O. vastator and the closely related O. frit ex Anthoxanthum. Interspecific competition between these two groups would be similarly reduced during the establishment of the first generation.

Later in the season interspecific competition among larvae of the various species may not be pronounced because of the increased rate of tiller production.

The spatial distribution of the larvae, the actively-feeding stage, are slightly different in the two genera. Larvae of G. tripunctata are more evenly distributed than those of the Oscinella complex. Intra-specific competition would consequently be more reduced in the former species. The difference in spatial distribution of G. tripunctata and the Oscinella complex may also reduce inter-specific competition.

'It is suggested that separation in time and space during various developmental stages, and the consequent reduced competition, partly ensures the co-existence of the various species of dipterous stem borers infesting grasses.

(v) Seasonal variation in number of adults

Following emergence, the number of adults of G. tripunctata and the Oscinella complex built up gradually as the season progressed. Two distinct peaks of adult numbers were obvious. The first began in April in the case of G. tripunctata, and lasted until mid-July. With the Oscinella spp. the first peak began in May and lasted until July. This peak, as in the case of G. tripunctata, consisted of adults of the first and second generations, which overlapped sufficiently to give an apparent single peak. The second peak of adults occurred in August, and consisted mainly of adults of the third generation, supplemented by immigrant adults from neighbouring grassland, or, in the case of O. frit, from oats and grassland.

If allowance is made for the effect of the immigrants, the population size of the flies of the different generations produced by the swards remains relatively constant throughout the season.

As the field temperature began to fall there was an increase in the rate of natural mortality of flies, and the number of flies in the field declined gradually from late August onwards. The frit flies were the first to disappear in both years. Their disappearance was much earlier in 1972, occurring in late September, whereas in 1973 the flies were found until the end of October (Figs. XVI and XVII). This appeared to be closely related to the autumn fall in temperature during both years. Numbers of adult G. tripunctata also declined sharply as from the end of August, but in contrast to the former spp. adult flies were found in the field throughout the year. Between late August and early April of the following year, the number of adults remained at about one per square metre. It seems that the adult stage of G. tripunctata is better adapted to survive the winter cold than the Oscinella spp., and indeed it is the first species to start breeding in spring.

Most of the adults found during this winter period were females. In view of the fact that during the season the overall sex ratio was almost 1:1, it seems that the males do not survive as well as the females. Examination of the ovaries of adult G. tripunctata caught between late Autumn and early spring showed that most did not carry mature eggs during this period. However, when some of these flies were caged with males under adequate conditions of temperature, light and relative humidity in the glasshouse in winter, they soon resumed reproductive activities leading to successful egg laying. The duration of the breeding period of the flies is therefore determined by how soon temperature falls in autumn, and how soon it rises again in spring.

Although G. tripunctata survived through winter in the adult stage, while the Oscinella spp. did not, the former did not reproduce during this time. Effectively, it is the fall in temperature which stops breeding in both genera. It seems, therefore, that temperature is the most important environmental factor which regulates the number of the various species.

(vi) Breeding cycles and number of generations in a year

Within a year each species completes three breeding cycles producing at least three generations of larvae. Except in the case of O. frit, the third generation of larvae produced in autumn is usually the largest. With O. frit, the middle generation produced in mid-summer is the most numerous. The position of this species is anomalous regarding the size of the middle generation. It seems that O. frit, and probably the closely related O. frit ex Arrhenatherum, breed mainly during the warmest period in the middle of summer, whereas the other species utilised the cooler periods at the beginning and towards the end of each season. However, in years with very warm and prolonged summer temperatures, O. frit is also able to exploit the warmer conditions which prevail until late in the season. Perhaps as in cereal crops, it would be able to produce in some years, a partial (van Emden _et al_., 1961) or complete (Jones, 1970), fourth generation.

Again, temperature is the most important environmental factor determining the main breeding periods in the various species. In a sward where the suitability of the host plant for breeding is non-limiting, the difference between the reactions of the various borers to changes in field temperature also determines the extent of the breeding periods, and hence the possible number of generations within a year. Such slight differences in the temperature requirements of, and the consequent separation in time and space of the various insect species, would effectively reduce competition for both oviposition sites and for tillers suitable for larval entry and establishment.

(vii) Adult activity patterns

The general activities of the flies were observed in the field. On a typical warm and bright summer day, adults of the various species became active at sunrise. _G. tripunctata_ showed a bimodal pattern of peak activities during the day. Most adults were active between 8.00 and 12.00 and disappeared into sheltered places as ambient temperature approached a peak (13.00 hrs). Between 12.00 and 15.00, fewer adults were active, probably because of the high temperature and high light intensity. The flies resumed activities later in the day as the temperature fell and another peak level was recorded, usually between 16.00 and 18.00 hrs.

By contrast, the activities of the adult _Oscinella_ spp. increased as the day became warmer. Feeding, flying and mating activities increased and attained a peak between 13.00 and 15.00 hrs. There was a general decline in activities as the temperature fell and as it became darker later in the day. In both genera more adults settled on plant tips as from 18.00 hrs onwards.

Under standardised conditions in the laboratory, flies were active throughout the period of observation, without any obvious peaks of activities. The apparent rhythm of activities observed in the field, particularly those relating to mating, are probably induced by variations in temperature and light conditions which occurred in the field. It is therefore unlikely that the various activities are controlled by an internal clock mechanism.

The ability of the flies to respond to variation in the environmental conditions in the field suggests that temperature and light preferenda may differ between G. tripunctata and the Oscinella complex. The exhibition of such preferences in the field will possibly reduce interference between them, particularly during mating and oviposition. This temporal separation of essential activities may provide another mechanism by which interspecific competition is avoided or reduced under field conditions.

(viii) Courtship and mating behaviour

A detailed observation of the courtship and mating behaviour in G. tripunctata made in the laboratory showed that these were made up of a series of phases. The phases most critical to successful courtship were the body-gliding and antennal tapping phases during which the males signalled and appeased the females. Whenever the male omitted these phases, courtship was usually terminated. Any attempt made by the male to mate directly without passing through this phase was abortive. Detailed description of the courtship and mating behaviour of the Oscinella spp. were not given here, because they are essentially similar to those described earlier by other authors (Ibbotson, 1959; Southwood et al., 1961).

The notable differences between the courtship and mating behaviour in these species are more pronounced between Geomyza and Oscinella spp., than between the Oscinella spp. These are:

(1) the distinct absence of the body-gliding phase in the former species during courtship

(2) the absence of wing-locking phase during mating in the Oscinella spp.

(3) The more or less parallel positioning of the male on the female in G. tripunctata.

(With the Oscinella spp. the male is inclined on the female at an angle of about 45° during mating).

The precise significance of this is not understood, but merely reinforces the impression that these two genera are quite separate in many respects, the only real common factor being their utilisation of the habitat.

(ix) Plant factors affecting adult behaviour

Laboratory studies on the effect of the growth stage, density and species of the host plant, on the landing and resting behaviour and on the performance of oviposition movements, show that G. tripunctata, O. vastator and O. frit are influenced in a similar manner by the various plant factors. The frequency of performance of the various activities was greater on larger plants. This was because the flies received stronger visual, optomotor and tactile stimuli from these plants. In a young ley, shoot emergence is not usually uniform. Flies will naturally be attracted visually to and will lay most eggs on the bigger shoots (the first to emerge). Consequently, both the eggs and the larvae which hatch from them would be distributed in clumps during sward establishment.

The activities of flies also increased as the density of young shoots increased, although the performance of oviposition movements by G. tripunctata attained an optimum before the maximum experimental plant density was reached. Very high plant density, although it produced a stronger visual stimulus, seemed to have interfered with oviposition movements (section (iiib)). This probably explains why most of the larger egg masses per plant occurred at the lowest plant densities. It may also be because the more isolated plants produced a stronger optomotor attraction. Eventually, the stronger visual and tactile attraction produced by plants offered at higher densities resulted in a corresponding increase in the number of eggs laid per unit area.

At the three-leaf growth stage, the various grass species were equally attractive to the flies as the latter performed various activities preceding oviposition. The flies therefore landed and rested on, and performed oviposition movements equally well on the various grass species indicating that at this particular growth stage all species were equally attractive. Any obvious change in the response of the flies at later growth stages of the plant and during egg-laying will be determined by the size, the number of secondary tillers and by the amount of crevices present on the shoot, characteristic of the grass species. This is because these peculiarities of the shoot determine the intensity of visual, optomotor and tactile stimulus which the insect may receive while on the plant.

(x) Plant factors affecting oviposition

Studies on the effect of the various host factors on the intensity of oviposition showed that both biochemical and tactile stimuli influence oviposition, but that the latter stimulus is the more important. Shoots which have many crevices usually provide the strongest tactile stimulus. In ryegrass, the number of crevices increased as the shoot grew, consequently more eggs were laid on the older (bigger) shoots. The most attractive growth stage of the single tiller shoot was the one just before the separation of the secondary tiller, which until then is wrapped round the common leaf sheath with the main shoot. In the entire actively-tillering plant, the number of eggs laid increased as more tillers were produced. This is simply because the number of oviposition sites increased. Similarly, at the single-tiller stage, the intensity of oviposition increased with increase in the number of shoots per unit area.

This result on the effect of increased plant densities on the intensity of oviposition therefore contrasts with that of the host factor on the performance of oviposition movements. Although very high plant densities seem to interfere with the performance of oviposition movements, it does not reduce the intensity of oviposition per unit area. This apparent contradiction may have been due to an interaction between the attraction of the plant for performing various activities preceding oviposition, and its suitability for egg-laying.

In free-choice trials with various grass species at the three-leaf stage, the intensity of oviposition was highest in the fast-growing species such as *Avena fatua* and *Lolium multiflorum*, and lowest on the slow-growing ones *Poa trivialis* and *Festuca rubra* . Again, the intensity of oviposition was dictated by the rate of production of suitable sites, rather than by the species of grass. These sites occurred earlier in the fast-growing ones. At later stages of growth, such as when plants have commenced active tillering, the intensity of oviposition will be influenced by the rate of tillering. The most actively tillering species, although slow-growing initially, may later produce as many, or more, oviposition sites.

(xi) Larval survival

Laboratory studies showed that of the various host plant factors, shoot age (stage of growth) and shoot density influenced larval attack and establishment more than any other factors. The ability of the newly-hatched larvae of the various insect species to penetrate the tissues of the plant decreased as the plant grew. This is because the plant tissues become tougher, and the layers of dead leaf sheath which accumulate round the base of the shoot form a strong mechanical barrier through which the young larvae must pass before getting to the softer plant tissues within. However, the tiller is not completely immune to larval penetration until the basal internode has hardened. Under natural conditions, this occurs a few weeks before flowering.

In situations where the newly-hatched larva enters the young tiller, the survival of the larva still depends upon whether or not such a tiller provides adequate food materials to sustain the larva to maturity. The larva which penetrated very young shoots at the one- or two-leaf stage usually moved into another young shoot before completing its development. In the absence of another young shoot or young tiller very close to the infested tiller, the larva usually perished with the infested tiller. Again, the most suitable growth stage for larval success is the well-developed four-leaf stage in which the secondary tiller is still in the process of formation. This provides the best combination of adequate entry points and anchorage (cracks and crevices) during entry as well as adequate food materials after the larva has entered.

The number of larvae which become established increases as the density of suitable tillers increases. This increase probably reflects the increased oviposition intensity at higher shoot densities.

In the actively tillering plant, the positive association between tiller density and larval number becomes less marked as the plant grows. This is because the age of the individual tiller on the plant determines whether or not a larva enters and establishes in it.

The infestation of laboratory-raised plants of various grass species at different growth stages also shows that the level of larval infestation of a grass species depends upon the length of the period during which its tillers remain at the susceptible growth stage, and the number of such tillers present on the shoot. The most highly infested grass species are those which retain their youth for longer periods and which also produce the greatest number of secondary tillers, e.g. Poa trivialis and Agrostis tenuis. This is possibly because the tissues of most of the tillers remain soft for a longer period than other less susceptible species. In this situation larvae short of food in one tiller will have little difficulty moving to and establishing in the neighbouring tiller. It may be of interest to note here that in cereals, the actively tillering species may for the same reason remain more susceptible to infestation by frit larvae, than the fast-maturing less vigorously tillering varieties. This will be so particularly for the tiller generation of frit fly.

By contrast, the least susceptible grass species are those which grow most rapidly but which produce the least number of secondary tillers, e.g. P. pratense and A. fatua. These species therefore permitted larval entry for a relatively shorter period than the previous group.

The most resistant grass species was D. glomerata which, although it remained favourable for oviposition as it grew, was unsuitable for larval entry for most of the time. Although this grass species has a slower initial growth rate than most other grass species, it becomes more aggressive at later growth stages and produces very few young tillers. The very young tillers which were susceptible to larval attack did not sustain the larvae to maturity, probably because they did not contain adequate food materials (either qualitatively or quantitatively). As a result, both the tiller and the larva usually died.

From this it is obvious that the degree of susceptibility of a grass species will be determined by a combination of the attractiveness of the shoot for oviposition and its suitability for larval entry and further development. At a given growth stage the grass species which provide the best combination of these characteristics will be the most suitable for larval infestation. The same will apply to cereals during the tillering stage.

However, these infestation-determining characteristics may be modified by particular management practices or environmental stress, so altering the degree of susceptibility or resistance of a species, under field conditions. Poor growing conditions which reduce the speed of development of the plant may place them more at risk to larval attack by prolonging the susceptible period. Management practices such as regular mowing and grazing may also render the shoot more susceptible by providing direct entry points for the larvae at cut surfaces, and will promote larval establishment by increasing the number of young tillers.

From the discussion above, it seems that host preference of O. frit L. and those of other species, based on the number of larvae which established in each grass species, reflects more on the condition of the plant during larval establishment than on the preference of the flies during oviposition. A grass species less attractive for oviposition at the early growth stage (e.g. P. trivialis) is not necessarily the least susceptible at later growth stages. The interaction of oviposition with larval success in assessing the host preferences of the various insect species could therefore account for the apparent inconsistency noted earlier.

(xii) Infestation of single-species swards

In the field, where the number of egg-laying flies, as well as the number of young tillers increased throughout the season, various plant factors influenced larval infestation as discussed above. Thus in the newly-sown sward, the number of larvae increased as more shoots emerged, attaining the equilibrium level within the first year. This was because more eggs were laid, and because most tillers were at a susceptible stage. In the older sward, infestation by the newly hatched larvae did not begin until the sward had been mown. This was probably because although the tillers were attractive for oviposition, they were unsuitable for larval penetration. Consequently, the main difference between the degree of susceptibility of the young and older swards was more obvious earlier in the season, before the latter was mown. Whereas both early and late instar larvae were found in the newly sown sward, the older sward contained mainly overwintering third instar larvae until late June. This indicates that the older sward was less susceptible to attack by newly-hatched larvae during this period. In response to mowing the older sward produced a flush of young tillers and became as susceptible as the newly sown sward, to the various *Oscinella* spp. From then on, the number of *Oscinella* spp. larvae became similar in both sward types. The newly sown sward, however, remained more susceptible to infestation by larvae of *G. tripunctata* throughout the season. This trend was consistent during 1972 and 1973.

The degree of success of a particular insect species subsequent to sward mowing may depend on the degree of synchronisation between the reproductive activities of that species and the period of sward-regrowth. Thus in 1972, during which the older sward was about two years older than the newly established sward, *O. frit* L. and the closely related species *O. frit ex Arrhenatherum* were more successful on the older than on the younger sward. In 1973, during which the dates of sward establishment differed by only one year, all the species, except *G. tripunctata*, were as successful on the old as they were on the younger swards.

The consistent failure of *G. tripunctata* to exploit the renewed "youth" of the recently mown sward may be explained in terms of the behaviour of the adult flies. In laboratory studies flies oviposited equally on prostrate and on mown plants, but given a choice of prostrate or erect plants they spent more time on the latter. Adult flies therefore tended to avoid the relatively bare sward after mowing, and oviposition was consequently reduced.

Also the survival of larvae from what eggs were laid in the newly-mown old sward would tend to be adversely affected by the reduced cover and consequently drier and hotter, and hence more hostile environment.

These results also explain why the short (regularly mown or grazed) grassland supported higher numbers of larvae than the untreated grasslands, because it is the production of young tillers in response to defoliation that enabled the newly hatched larvae to establish. Larval infestation in grazed and mown swards would probably be similar. Any departure from this would probably be explained by the timing and intensity of the treatment with regard to periods of active breeding of the flies.

Similarly in permanent grasslands containing several species of grasses the timing of mowing or grazing and the response of each grass species to these treatments during larval establishment may influence the relative number of larvae supported by each grass species.

(xiii) Larval Parasitism

The results of regular sampling also showed that larval parasitism was very low. It is suggested that this was mainly due to the protection afforded the larvae by the host plant. Until the sward was mown, the parasites were unable to reach their larval hosts. Parasitism was therefore limited to the very early phase of sward establishment or to the short period of regrowth, subsequent to mowing. The late emergence of the adult parasites in summer and poor synchronisation thereafter must partly account for the low level of parasitism encountered. Parasite efficiency may be higher in continuously grazed or regularly clipped swards but those are the conditions most suitable for larval establishment and survival. Unless parasitism, under such conditions, operates as a direct density-dependent mortality factor, the proportion of larval mortality which would be accounted for by parasitism will continue to be insignificant.

(xiv) Winter mortality of larvae. The mortality of larvae during the winter months was very high and very similar during the winters of 1972-3 and 1973-4, being 70% and 68% in the case of G. tripunctata, and 50% and 63% in the Oscinella complex. These values are similar to those of previous authors who sampled the population of frit larvae in leys and permanent grasslands during winter. By the beginning of the next season winter mortality thus reduces the sizes of the large third generation to a level similar to the two previous generations. Low temperatures during the winter months therefore stabilise the population of larvae from which the first generation of adults are produced at the beginning of each sowing year.

(xv) Larval infestation in mixed-species swards

Studies on the relative attractiveness of ten grass species for oviposition, and susceptibility to larval entry, when sown either as pure or mixed seeds showed that D. glomerata was the most resistent species. The results of regular sampling of mixed swards of this species and Lolium perenne, a susceptible species, showed that mixed swards containing up to 27% of D. glomerata were significantly less heavily infested. This was very probably because D. glomerata, by being attractive for oviposition but unsuitable for larval entry and establishment, served as a trap-crop.

Jepson and Heard (1959) found that winter cereals which followed pure leys of cocksfoot and fescue were the least infested by dipterous stem-borers. They suggested that these grass species may be used in place of the more susceptible grass species in areas where stem-borers create serious problems on cereals following such leys. The findings here suggest that the total replacement of more susceptible grass species with cocksfoot may not be necessary because mixed-sowings of these species could effect a useful degree of stem-borer control.

It seems, therefore, that mixed sowing of cocksfoot (the hay variety in particular), is a promising tool for controlling larval infestation where stem-borers are having a serious effect on the establishment of leys, or of winter cereals following leys.

In Appendices IA and IB it was shown that a steady level of damage is caused by the dipterous stem borers to grass swards. Also, it is known that grasslands serve as the main source of O. frit L. which invade and cause considerable damage to cereal crops in spring and summer. The numbers of adult O. frit L. which establish in cereals determine the sizes of the populations in both habitats later in the year. In view of this, it seems that control of frit flies and associated stem-borers in grassland could improve the yields of both crops. The application of a simple form of habitat diversification such as mixed planting of cocksfoot with perennial ryegrass, could effect considerable control, without necessarily reducing the quality of the grassland habitat.

Reference has been made earlier to the use of pesticides for the control of pasture pests in general. In view of the toxicity hazards to livestock and hence the restriction in the use of chemicals, the integration of chemical and cultural control methods suggested above could be used to minimise the quantity of pesticides, which would have been used to control the stem-boring Diptera.

SUMMARY

1. Five species of stem-boring diptera invaded pure stands of perennial ryegrass or mixed plantings of ryegrass and cocksfoot.
2. In the year of sowing, these species were, in decreasing order of abundance, O. vastator, G. tripunctata, O. frit L., O. frit ex Anthoxanthum, and O. frit ex Arrhenatherum.
3. In subsequent years of sward-growth, O. vastator remained the most numerous, and G. tripunctata was supplanted by the four Oscinella spp.
4. G. tripunctata overwintered as adults, larvae and pupae, whereas the Oscinella species overwintered only as larvae and pupae. Low temperatures during winter prevented adults of G. tripunctata from breeding actively during this period.
5. In spring, the overwintering immature stages of G. tripunctata were the first to pupate and to emerge. This species was followed by O. frit L. and O. frit ex Arrhenatherum. The last species to emerge were O. vastator and O. frit ex Anthoxanthum. This sequence appeared to be dictated by the minimum temperature requirements of the various species, for pupation and emergence.
6. The number of flies in the field increased as the season progressed giving rise to two peaks during the year. The first peak consisted of adults of the overlapping first and second generations. The second peak consisted mainly of flies of the third generation.
7. In both genera, the female flies emerged slightly earlier than the males and were more numerous in the field at the beginning of spring and summer. With the appearance of more male flies later in the season, the overall sex ratio during the year reverted to approximately 1:1.
8. The time spent on the plant by adults of G. tripunctata, O. frit L. and O. vastator increased with increasing plant height and increasing plant density.

9. Oviposition was influenced by biochemical and tactile stimuli produced by the plants. The tactile stimulus was the more important factor. It is provided mainly by crevices on the plant.
10. Five main oviposition sites on the plants were distinguished: the surface of the coleoptile, the space between coleoptile and shoot surface, the leaf sheath surface, underneath the leaf sheaths, and crevices at the shoot base or between tillers.
11. The proportion of eggs laid at the various sites changes with the growth of the plant.
12. The distribution of eggs on the various grass species is similar but differed from that on cereal plants. On grasses, eggs are not laid on other parts of the grass plants (e.g. leaf blade) or in the soil around the shoot.
13. As was the case with landing and resting of flies, the number of eggs laid by flies of all species increased as plants grew and as tiller-density increased.
14. The intensity of oviposition on a grass plant was also influenced more by the size of the plant than by its species.
15. Larval survival was determined both by the tiller growth stage and by the tiller density, but the former factor was more important.
16. The susceptibility of a grass species was determined by the number of young tillers produced and the length of time during which they remained in the susceptible stage.
17. In a given grass species, the population of larvae attained was determined by larval survival rather than by oviposition.
18. The stem-borers were more successful in infesting some grass species than others: P. trivialis was the most susceptible whereas D. glomerata was the least susceptible.

19. Larval infestation of a newly sown sward began very early in the season as young shoots emerged. Infestation built up very rapidly as the number of young tillers increased and attained equilibrium within the same year.
20. Management procedures which encouraged the production of young tillers in the old sward (e.g. regular mowing) also favoured larval establishment, and made the level of infestation in this sward similar to that in the newly-sown sward.
21. Mortality of larvae during winter was high in both genera, and reached approx. 69% and 57% in <u>G. tripunctata</u> and <u>Oscinella</u> spp. respectively.
22. Larval parasitism was very low, and restricted to discrete periods when the plants were at the young stage or after the sward had been mown. The host plant provided protection for the larvae for most of the time.
23. The distributions of larvae and pupae in all species were aggregated: more so in the <u>Oscinella</u> spp. In each genus, the degree of aggregation of the immature stages was determined mainly by the egg-laying behaviour of the flies, and partly by the condition of the sward.
24. Larval infestation in the field was reduced by mixed plantings of ryegrass and cocksfoot. The more resistant grass species, cocksfoot, probably served as a trap crop for eggs and young larvae.
25. It is suggested that mixed plantings of the two grass species could be used to control stem-borers particularly during the establishment of a grass ley, and in cereals following such leys.

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List of Tables

Table No.

Table 1 a. Effect of shoot-age on the number of flies resting on plants*

Insect spp.	Age of single-tiller shoot (weeks) 1-2	3-4	6-7	9-10	12-13
G. tripunctata					
$\bar{n}$ flies/16 plants	0	1	2	4	10
O. frit L.					
$\bar{n}$ flies/16 plants	0	1	2	5	5
O. vastator					
$\bar{n}$ flies/16 plants	1	1	3	3	7

Table 1 b. Effect of 'stem' height on the number of flies resting*

Insect spp.	Height of artificial 'stem' (cm) 2.5	5.0	7.5	10.0	12.5
G. tripunctata					
$\bar{n}$ flies/10 'stems'	1	2	3	8	11
O. frit L.					
$\bar{n}$ flies/10 'stems'	<1	1	2	4	9
O. vastator					
$\bar{n}$ flies/10 'stems'	<1	1	3	5	8

Table 1 c. Effect of shoot density on the number of flies resting*

Insect spp.	Number of shoots per pot 2	4	8	16	32
G. tripunctata					
$\bar{n}$ flies/pot	1	2	3	3	12
O. frit L.					
$\bar{n}$ flies/pot	1	2	2	4	6
O. vastator					
$\bar{n}$ flies/pot	1	2	3	5	7

* Mean figures from 4 trials.

Table 2 a. Effect of shoot age on frequency of performance of oviposition movements*

	Age of single-tiller shoot (weeks)				
Insect spp.	2	5	7	9	13
G. tripunctata					
$\bar{n}$ flies performing	1	2	5	4	7
O. frit L.					
$\bar{n}$ flies performing	0	0	3	3	4
O. vastator					
$\bar{n}$ flies performing	1	2	2	3	5

Table 2 b. The effect of shoot density on frequency of performance of oviposition movements*

	Number of shoots/pot				
Insect spp.	2	4	8	16	32
G. tripunctata					
$\bar{n}$ flies performing	2	3	5	4	4
O. frit L.					
$\bar{n}$ flies performing	3	2	3	7	4
O. vastator					
$\bar{n}$ flies performing	2	3	3	5	5

* Mean of four trials.

Table 3 a. Effect of grass species on the number of flies resting

Grass spp. (3-leaf stage)

Insect spp.	Lolium perenne	Avena fatua	Dactylis glomerata	Agrostis tenuis	Poa trivialis	Holcus lanatus	Festuca rubra	Phleum pratense
G. tripunctata $\bar{n}$ flies/32 plants	8	9	12	7	8	7	6	8
O. frit L. $\bar{n}$ flies/32 plants	4	10	7	6	8	8	8	7
O. vastator $\bar{n}$ flies/32 plants	7	11	8	8	7	12	9	8

Table 3 b. Effect of plant spp. on the number of flies performing oviposition movements

Grass spp. (3-leaf stage)

Insect spp.	Lolium perenne	Avena fatua	Dactylis glomerata	Agrostis tenuis	Poa trivialis	Holcus lanatus	Festuca rubra	Phleum pratense
G. tripunctata $\bar{n}$ flies/32 plants	3	3	4	3	2	2	3	3
O. frit L. $\bar{n}$ flies/32 plants	2	2	3	3	2	2	3	3
O. vastator $\bar{n}$ flies/32 plants	3	5	3	4	4	2	2	2

Total number of plants of each grass sp. 32
Total number of each insect sp. under observation 120
All figures accumulated from four series of experiments with four different colonies of flies.

Table 4. Changes in oviposition sites with increasing age of host plant (L. perenne, S24).
*Actual number of eggs observed given in brackets.

PLANT AGE (weeks)	INSECT SPECIES	Percentage of Eggs laid:-								
		Coleoptile surface near base	Between Coleoptile and primary shoot	On leaf sheath surface	Underneath leaf sheaths	Between primary and secondary tillers	Between soil and shoot base	On or in soil	Elsewhere e.g. leaf blade	Total number of eggs
1-2	Geomyza tripunctata	86.4 (19)	13.6 (3)	0	0	0	0	0	0	22
	Oscinella frit L.	76.3 (29)	23.7 (9)	0	0	0	0	0	0	38
	O. vastator	87.5 (14)	12.5 (2)	0	0	0	0	0	0	16
3-4	G. tripunctata	35.1 (20)	64.9 (37)	0	0	0	0	0	0	57
	O. frit L.	10.1 (7)	89.9 (62)	0	0	0	0	0	0	69
	O. vastator	21.8 (12)	78.2 (43)	0	0	0	0	0	0	55
8-12	G. tripunctata	0	0	16.9 (12)	53.5 (38)	29.6 (21)	0	0	0	71
	O. frit L.	0	0	3.8 (3)	70.9 (56)	25.3 (20)	0	0	0	79
	O. vastator	0	0	7.3 (5)	76.8 (53)	15.9 (11)	0	0	0	69

Table 5a Effect of age and of presence of secondary tillers on the number of eggs laid on ryegrass

Plant age (weeks)	*Geomyza tripunctata*			*Oscinella frit* L.			*Oscinella vastator*		
	Mean no. eggs per 5 plants			Mean no. eggs per 5 plants			Mean no. eggs per 5 plants		
	Normal plants	Secondary tillers removed	Difference	Normal plants	Secondary tillers removed	Difference	Normal plants	Secondary tillers removed	Difference
1 - 2[+]	0.0	0.5	NS	0.3	0.8	NS	0.4	1.1	NS
3 - 4[+]	0.5	3.5	***	1.8	4.5	NS	2.3	4.8	NS
6 - 7	6.3	13.0	***	5.8	17.8	***	5.8	14.8	***
9 - 10	12.0	8.0	***	15.5	8.3	***	9.3	7.3	NS
12 - 13	12.3	6.5	***	20.3	6.8	***	10.0	6.5	**

[+] All plants are single-tiller until after 4-week-old stage.

Table 5b Effect of leaf sheath removal on intensity of oviposition

	$\bar{n}$ Eggs per Tiller		% Tillers selected	
Insect species	Sheath intact	Sheath removed	Sheath intact	Sheath removed
G. tripunctata	1.8	0.5*	65	50^{ns}
O. frit L.	2.6	0.5*	60	32*
O. vastator	2.3	0.2*	60	24*

*Effect of sheath removal significant at $p = 0.05$.

Table 5c Effect of tiller age on oviposition when leaf sheaths are removed.

Insect species		Age of Tiller (weeks)				F-ratio (p = 0.05)
		3-4	9-10	12-13	16-17	
G. tripunctata	$\bar{n}$ Eggs/plant	1.4	0.3	0.4	0.1	*
	% plants selected	80	33	33	7	*
O. frit L.	$\bar{n}$ Eggs/plant	1.6	0.5	0.3	0	*
	% plants selected	100	40	33	0	*
O. vastator	$\bar{n}$ Eggs/plant	1.3	0.1	0	0	*
	% plants selected	90	13	0	0	*

* mean of 15 plants

Table 5d The effect of treating artificial plant models on the intensity of oviposition

	Models moistened with Ryegrass-sap			Models moistened with distilled water		
Insect spp.	Dead stems	Rolled filter paper	Strip of cardboard	Dead stems	Rolled filter paper	Strip of Cardboard
G. tripunctata						
No. eggs laid per ten models	0	2	0	0	0	0
O. frit L.						
No. eggs laid per ten models	0	3	0	0	0	0
O. vastator						
No. eggs laid per ten models	0	0	2	0	0	0

Figures represent total number of eggs laid on ten models, by different colonies of flies (4 trials).

Table 6 Oviposition intensity;-effect of plant density

Density (Plants/ pot)	*Geomyza tripunctata* Mean eggs/ pot	*Geomyza tripunctata* Mean eggs/ plant	*Geomyza tripunctata* % plants oviposited	*Oscinella frit* Mean eggs/ pot	*Oscinella frit* Mean eggs/ plant	*Oscinella frit* % plants oviposited	*Oscinella vastator* Mean eggs/ pot	*Oscinella vastator* Mean eggs/ plant	*Oscinella vastator* % plants oviposited
2	2.6	1.3	70	4.8	2.4	70	3.3	1.6	62.5
4	4.6	1.3	65	6.8	1.7	70	5.5	1.4	53.3
8	7.6	1.0	67.5	11.0	1.4	60	9.5	1.2	53.1
16	13.4	0.8	62.5	14.0	0.9	46.25	12.8	0.8	39.1
32	19.4	0.6	48.75	20.8	0.7	40.12	21.3	0.7	39.1

Table 7 Ovipositional preferences of three insect species on plants offered at the 3-4 leaf stage in free choice trials

Insect spp.	Grass species								
	Lolium perenne	Avena fatua	Dactylis glomerata	Agrostis tenuis	Poa trivialis	Holcus lanatus	Festuca rubra	Phleum pratense	S. E. of Difference
G. tripunctata									
$\bar{n}$ Eggs/plant	1.8	1.7	1.0	0.5	0.5	0.5	0.3	0.2	0.18
% Plants selected	87.5	80	66	28	32	40	22	20	-
Oscinella frit L.									
$\bar{n}$ Eggs/plant	2.4	2.7	1.2	0.5	0.4	0.4	0.2	0.3	0.22
% Plants selected	84	97	53	36	22	28	19	16	-
O. vastator									
$\bar{n}$ Eggs/plant	3.2	2.7	1.8	0.8	0.6	0.8	0.3	0.3	0.40
% Plants selected	100	100	87.5	44	50	44	31	25	-

Table 8 Effect on oviposition of varietal differences within two species of host plant

	Lolium perenne Cultivars				*Dactylis glomerata* Cultivars				
	S23	S24	Grasslands Manawa	$\bar{n}$	S21	S37	S321	Commercial	$\bar{n}$
G. tripunctata									
$\bar{n}$ Eggs/plant*	1.9	2.3	2.0	2.1	1.7	2.2	1.8	2.0	1.9
% Plants selected	60	60	70	63.3	75	70	60	70	68.8
O. frit L.									
$\bar{n}$ Eggs/plant*	2.5	2.9	3.1	2.8	2.0	2.1	1.9	2.4	2.1
% Plants selected	60	55	60	58.3	65	60	60	55	60
O. vastator									
$\bar{n}$ Eggs/plant*	3.2	2.7	2.5	2.8	1.9	1.7	1.7	1.8	1.8
% Plants selected	75	60	70	68.3	60	65	65	55	61.3

* $\bar{n}$ not sig. diff. at $p = 0.05$.

Table 9 Effect of diploid/tetraploid plant genotype on oviposition

		Lolium perenne			
		DIPLOID		TETRAPLOID	
	L. multiflorum	S23	S24	Barpatra	Reveille
G. tripunctata					
$\bar{n}$ Eggs/plant	1.6	1.1	1.2	1.3	1.1
% Plant selected	87.5	67.5	77.5	70	75
O. frit L.					
$\bar{n}$ Eggs/plant	2.5	1.5	1.4	1.5	1.6
% Plant selected	85	70	75	75	75

Table 10. The effect of growth habit of grass species on the intensity of oviposition

	Lolium perenne		Phleum pratense	
	Erect (7)	Prostrate (10)	Erect (7)	Prostrate (13)
G. tripunctata $\bar{n}$ eggs/plant*	$^{+}6$	5	9	9
O. frit L. $\bar{n}$ eggs/plant*	6	8	5	7
O. vastator $\bar{n}$ eggs/plant*	6	9	4	6

Total number of plants - 16

(--) Figures represent mean number of tillers/plant

Table 11a Effect of mixed plantings of Ryegrass and Cocksfoot at the 3-leaf stage on the ovipositional preference of flies

* significant at p = 0.05

Insect spp.	*L. perenne*	*D. glomerata*	't' test
G. tripunctata			
$\bar{n}$ Eggs/plant	2.5	1.8	n.s.
% Plants selected	63	58	-
O. frit L.			
$\bar{n}$ Eggs/plant	2.3	1.8	n.s.
% Plants selected	75	60	-
O. vastator			
$\bar{n}$ Eggs/plant	2.7	2.3	n.s.
% Plants selected	80	75	-

Table 11 b Effect of mixed plantings of Ryegrass and Cocksfoot at the early 2-leaf stage on the ovipositional preferences of flies

Insect spp.	*L. perenne*	*D. glomerata*	't' test
G. tripunctata			
$\bar{n}$ Eggs/plant	0.5	0.4	n.s.
% Plants selected	40	30	-
O. frit L.			
$\bar{n}$ Eggs/plant	0.3	0.3	n.s.
% Plants selected	20	35	-
O. vastator			
$\bar{n}$ Eggs/plant	0.2	0.2	n.s.
% Plants selected	20	20	-

Table 11 c Effect of mixed plantings of early 2-leaf stage of Ryegrass and advanced 2-leaf stage Cocksfoot on ovipositional preferences of flies.

Insect spp.	*L. perenne*	*D. glomerata*	't' test
G. tripunctata			
$\bar{n}$ Eggs/plant	0.1	0.8	*
% Plants selected	10	60	-
O. frit L.			
$\bar{n}$ Eggs/plant	0.2	0.5	*
% Plants selected	20	40	-
O. vastator			
$\bar{n}$ Eggs/plant	0.5	0.8	*
% Plants selected	32	40	-

Table 12 Effect of plant age and density on the infestation of single-tiller plants by larvae of *Oscinella frit* L. and *O. vastator*, and by *Geomyza tripunctata*

OSCINELLA SPP.

No. Tiller /pot	4	7	15	20	35	$\bar{x}$
Tiller age	MEAN NO. OF LARVAE/POT					
2	1.0	1.8	2.5	4.3	10.8	4.1
5	1.8	2.5	2.8	3.3	4.5	3.0
7	1.3	1.8	1.5	1.8	3.0	1.8
10	0.8	1.0	1.0	1.8	1.8	1.3
12	1.3	0.5	1.3	0.5	1.8	1.1
$\bar{x}$	1.2	1.5	1.8	2.3	4.4	

GEOMYZA TRIPUNCTATA

4	7	15	20	35	$\bar{x}$	No. Tiller /pot
MEAN NO. OF LARVAE/POT						Tiller age
2.8	3.3	6.5	9.0	13.3	7.0	2
1.5	2.0	3.0	4.3	7.5	3.6	5
1.5	1.5	1.3	2.3	2.3	1.8	7
0.5	1.0	1.3	1.5	1.8	1.2	10
0.5	0.8	1.0	1.0	1.3	0.9	12
1.4	1.7	2.6	3.6	5.2		

Table 13 Variation in number of *G. tripunctata* larvae with plant species and age

AGE FROM SOWING (WKS.)	Number of larvae per pot (15 plants)									
	Poa trivialis	Agrostis tenuis	Lolium perenne S24	L. perenne Tetraploid	L. multiflorum	Avena fatua	Phleum pratense	Holcus lanatus	Festuca rubra	Dactylis glomerat
5	3.0	1.3	6.3	6.8	6.8	5.3	2·5	2·3	0	0
8	6.5	4.8	4.0	5.3	8.0	3.5	0	0	0	0
10	6.8	4.8	2.5	2.0	3.3	2.3	0	0	0	0
13	5.5	4.5	2.0	1.5	2.8	0	0	0	0	0
16	5.0	4.8	2.5	1.3	1.3	1.0	0	0	0	0

Table 14 Variation in number of Oscinella spp. larvae with plant species and age

AGE FROM SOWING (WKS.)	Number of larvae per pot (15 plants)									
	Poa trivialis	Agrostis tenuis	Lolium perenne S24	L. perenne Tetraploid Reveille	L. multiflorum	Avena fatua	Phleum pratense	Holcus lanatus	Festuca rubra	Dactylis glomerata
5	8.5	8.0	5.5	3.8	8.5	9.0	1.8	2.0	0	0
8	8.5	10.5	4.5	4.5	8.0	5.0	0	0	0	0
10	11.8	7.0	3.5	4.3	5.0	0	0	0	0	0
13	6.5	4.5	3.8	3.3	4.8	0	0	0	3.8	
16	4.8	5.3	3.0	0.8	1.5	0	0	0	4.5	0

Table 15 Variation in number of susceptible tillers* with plant species and age

AGE FROM SOWING (WKS.)	SUSCEPTIBLE TILLERS PER PLANT (mean of 60 plants)									
	Poa trivialis	Agrostis tenuis	Lolium perenne S24	L. perenne Tetraploid Reveille	L. multiflorum	Avena fatua	Phleum pratense	Holcus lanatus	Festuca rubra	Dactylis glomerata
5	7.5	7.0	4.0	2.3	4.7	2.5	2.5	2.7	3.3	1.9
8	7.2	5.7	3.9	3.6	5.3	2.3	2.4	3.2	6.0	1.9
10	4.8	4.6	3.8	2.1	4.1	1.9	2.4	2.3	6.0	1.9
13	5.1	4.7	3.5	2.4	3.2	2.1	2.3	1.8	5.9	2.1
16	4.7	4.5	2.9	2.5	2.2	1.9	1.9	1.5	5.8	1.9

* i.e. Tillers prior to hardening of base and internode elongation.

Table 16 Grass species most susceptible to attack by (a) *Oscinella frit* and (b) *Geomyza tripunctata* according to various authors

Grass Species	Agropyron repens	Poa pratensis	P. palustris	Lolium perenne	L. italicum	L. multiflorum	Agrostis tenuis	Festuca pratensis	F. rubra	Dactylis glomerata	Trisetum flavescens	Arrhenatherum elatius	Insect Species
Authors													
Aldrich 1920		X											OSCINELLA FRIT
Mayer 1926	X												
Vasina 1929	X												
Wilbur and Sabrosky 1936		X											
Roos 1937	X												
Jepson and Heard 1959		X											
Nye 1959				X					X^m				
Hemer 1960				X				X					
Southwood and Jepson 1962				X					X				
Taimr and Dielbek 1968				X								X	
Mühle and Wetzel 1969			X								X		
Thomas 1938				X	X								GEOMYZA TRIPUNCTATA
Jepson and Heard 1959				X^m									
Nye 1959				X	X^m								
Wetzel 1967												X	
Southwood and Jepson 1962				X									

X^m = Mixed Sward

Table 17. Effect of addition of cocksfoot to a perennial ryegrass ley on the infestation by larvae of *Oscinella* spp. and *G. tripunctata*

		Pure ryegrass	Ryegrass/Cocksfoot Mixture		
		I	II	III	IV
1973	$\bar{n}$ tiller/core, ryegrass*	67	59	60	57
	$\bar{n}$ tiller/core, cocksfoot*	0	7	12	21
	% Cocksfoot	0	10.6	16.6	26.9
	$\bar{n}$ larvae/core, *Oscinella* spp.	7.2	3.8^{+}	3.5^{+}	1.2^{+}
	$\bar{n}$ larvae/core, *G. tripunctata*	3.3	1.5	1.5	0.8^{+}
1974	$\bar{n}$ tiller/core, ryegrass*	53	48	46	45
	$\bar{n}$ tiller/core, cocksfoot*	0	6	8	11
	% Cocksfoot	0	11.1	14.8	19.6
	$\bar{n}$ larvae/core, *Oscinella* spp.	3.3	1.9^{+}	1.0^{+}	0.5^{+}
	$\bar{n}$ larvae/core, *G. tripunctata*	1.5	0.6^{+}	0.6^{+}	0.6^{+}

* $\bar{n}$ of 40 ten-centimetre cores

$^{+}$ $\bar{n}$ larvae/core signif. different from Pure ryegrass sward where $p = 0.05$.

Table 18 Relative abundance of larvae of each species in newly-sown and in old swards, 1972 and 1973

1972					1973				
SPECIES OF LARVAE	YOUNG SWARD		OLD SWARD		SPECIES OF LARVAE	YOUNG SWARD		OLD SWARD	
	n	%	n	%		n	%	n	%
1. *O. vastator*	292	49.2	147	39.0	1. *O. vastator*	382	42.7	445	57.6
2. *G. tripunctata*	167	28.2	47	12.5	2. *G. tripunctata*	195	21.8	36	4.7
3. *O. frit ex anthoxanthum*	75	9.7	59	15.6	3. *O. frit* L.	156	17.4	117	15.1
4. *O. frit* L.	36	6.0	41	10.9	4. *O. frit ex anthoxanthum*	106	11.9	129	16.6
5. *O. frit ex arrhenatherum*	23	3.9	83	22.0	5. *O. frit ex arrhenatherum*	55	6.2	46	6.0
TOTAL	593	100%	377	100%	TOTAL	894	100%	773	100%

Figures based on 200 (10-cm diameter) cores per sward-type taken during June-November 1972 and mid-May-October 1973.

Table 19 Comparative abundance of larvae in young and old sward, in different generations, and in different years.

INSECT SPECIES		*G. tripunctata*				*O. vastator*				*O. frit* L.				*O. frit* ex *Anthoxanthum*				*O. frit* ex *Arrhenatherum*			
YEAR		1972		1973		1972		1973		1972		1973		1972		1973		1972		1973	
SWARD TYPE		Y	0	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0
				MEAN NUMBER OF LARVAE PER 10 CORES																	
GENERATION OF LARVAE	I^{+}	6.6	-	7.3	2.0	-	-	8.2	-	4.7	2.3	7.5	4.8	1.5	-	2.3	-	5.8	2.0	1.3	4.5
	II^{+}	4.3	2.0	5.7	2.3	16.3	9.5	16.2	20.6	-	3.0	11.0	12.0	7.4	3.8	8.0	7.0	-	4.4	3.2	4.5
	III^{+}	14.4	4.1	20.0	2.0	20.2	11.0	32.3	39.5	1.7	1.7	6.5	4.0	3.8	4.7	5.3	12.7	-	5.6	4.3	2.5
	Total	25.3	6.1	33.0	6.3	36.5	20.5	56.7	60.1	6.4	7.0	25.0	20.8	12.7	8.5	15.6	19.7	5.8	12.0	8.8	11.5
Grand total		31.4		39.3		57.0		116.8		13.4		45.8		21.2		35.3		17.8		20.3	

$^{+}$Each Figure represents Mean of 8 consecutive weeks

Y = Newly Sown sward

0 = Old sward

- = Larvae not found

Table 20 Mean number* of adult hymenopterous parasites per square metre in suction samples

Parasite spp.	A *Haticoptera fuscicornis*		B *Rhoptomeris hexatoma*		C *Loxotropa tritoma*	
Sward type	Young	Old	Young	Old	Young	Old
Week						
June I	1.0	0.5	0.3	0.3	0.5	0.3
II	1.0	0.5	2.4	0.5	0.5	0.3
III	1.0	0.8	4.0	1.5	0.5	0.3
IV	1.0	0.8	2.0	0.3	1.8	0.3
July I	0.5	0.5	0.3	0.3	1.3	0.3
II	0.8	0.5	0.8	0.3	0	0
III	0.5	0.5	0	0.5	1.0	0
IV	0.5	0.5	0	1.8	0.5	0
Aug I	0.5	0.5	0.5	0.5	0.8	1.0
II	1.0	0.5	0.5	0.3	0.7	1.0
III	1.5	0.5	0.7	0.8	0.3	0.8
IV	8.5	2.5	1.0	1.0	0.4	0.3
Sept I	2.5	1.0	0.5	0.5	0	0
II	2.0	0.5	3.0	1.0	0	0
III	3.8	1.3	4.5	4.0	0	0
IV	0.8	0.5	0.8	0	0	0.5
Oct I	0.5	0.5	0.5	0	0	0.5
II	0.5	0.5	0	0	0	0
III	0.8	0	0	0	0	0
IV	0.5	0	0.3	0	0.3	0

* Mean of ten 0.5 m^2 areas sampled.

Table 21 Year to year variation in larval numbers of all species, 1972 and 1973

Sward Type YOUNG

Larval Species	*G. tripunctata*	*O. vastator*	*O. frit* L.	*O. frit* ex *Anthoxanthum*	*O. frit* ex *Arrhenatherum*	TOTAL
1972	167	292	36	75	23	593
1973	195	382	156	106	55	894

Sward Type OLD

1972	47	147	41	59	83	377
1973	36	445	117	129	46	773

Figures based on 200 (10 cm diameter cores) per sward type taken during June-November 1972 and mid-May to October 1973.

Comparison between years based on young swards *only*, because both are similar in all respects (e.g. age, management, etc.).

Old sward 1973 (sown April 1972) is younger than Old Sward 1972 (sown Autumn 1970).

Table 22 Mean monthly soil temperature (10-cm depth) under grass and mean monthly rainfall at Rothamsted Experimental Station. 1973 and 1974.

MONTH		MAY	JUNE	JULY	AUGUST	SEPT.	OCT.
	Year						
Temperature (°C)	1973	13.0	15.3	15.3	12.7	10.5	7.2
	1974	10.9	16.7	16.4	15.0	10.2	6.9
Rainfall (ins)	1973	44.0	36.7	29.1	36.0	31.2	28.7
	1974	54.7	83.4	54.6	41.0	64.0	30.6

Table 23. Distribution of eggs laid by (a) individual insect and (b) colonies of fifteen insects per colony (*G. tripunctata*)

(a)

Insect No.	$\bar{n}$ eggs/plant^{+}	s^2	χ^2	D	P = 0.05
1	1.3	0.9	5.5	0.24	
2	1.2	1.8	12.0	0.4	
3	0.9	0.7	6.2	0.3	
4	0.9	1.0	8.9	0.1	
5	0.8	1.4	14.0	0.9	
6	0.8	0.8	-	-	
7	0.9	1.7	15.1	1.0	
8	0.6	0.6	-	-	

(b)

Colony No.	$\bar{n}$ eggs/plant$^{\oplus}$	s^2	χ^2	D	P = 0.05
1	0.38	0.49	93.0	0.8	*
2	0.32	0.28	63.0	0.4	
3	0.22	0.18	58.9	0.8	
4	0.29	0.24	59.6	0.6	

$^{+}$ 8 plants (three-leaf stage)

$^{\oplus}$ 72 plants (three-leaf stage)

* significantly aggregated at P = 0.05

Table 24. Distribution of eggs laid by (a) individual insect and (b) colonies of 15 insects/colony (*O. vastator*)

(a)

Insect No.	$\bar{n}$ eggs/plant[+]	S^2	X^2	D	P = 0.05
1	1.2	4.7	19.6	2.4	*
2	1.2	1.7	7.1	0.4	
3	1.0	2.0	10.0	1.0	
4	1.4	6.8	24.3	2.8	*
5	1.8	6.2	17.2	1.4	*
6	1.4	2.6	9.3	0.1	
7	1.0	5.0	25.0	4.0	*
8	1.4	4.3	15.4	1.5	*

(b)

Colony No.	$\bar{n}$ eggs/plant[⊕]	S^2	X^2	D	P = 0.05
1	1.8	4.8	106.0	0.9	*
2	0.9	4.2	186.7	1.1	*
3	1.0	2.6	104.0	1.6	*
4	1.2	2.5	83.8	0.9	*

[+] 5 plants (three-leaf stage)

[⊕] 40 plants (three-leaf stage)

* significantly aggregated at P = 0.05

Table 25 Distribution of the larvae (all species) in 1972

OLD SWARD						YOUNG SWARD					
Dates	Mean+	Variance	X^2	D	P = 0.05	Dates	Mean+	Variance	X^2	D	P = 0.05
17/4	1.4	2.0	28.5	0.31		15/6	0.65	0.87	26.8	0.52	
25/4	1.6	5.3	66.3	1.4	*	22/6	1.2	2.8	46.7	1.11	*
3/5	1.0	2.2	44.0	1.2	*	29/6	1.7	2.0	23.5	0.10	
11/5	1.0	1.2	24.0	0.2		6/7	1.8	5.2	57.8	1.04	*
18/5	1.2	1.6	26.7	0.3		13/7	2.2	2.3	20.9	0.02	
25/5	1.6	3.4	42.5	0.7	*	20/7	1.0	1.9	38.0	0.9	*
1/6	1.3	1.4	21.5	0.06		27/7	1.6	2.7	37.8	0.43	*
8/6	0.30	0.32	21.3	0.02		4/8	2.7	4.9	36.3	0.30	*
15/6	0.2	0.27	27.0	1.75		11/8	2.8	6.2	44.3	0.43	*
22/6	0.15	0.24	32.0	4.0	*	18/8	3.4	4.9	28.8	0.13	
29/6	0.8	1.2	30.0	0.63	*	25/8	4.1	7.0	34.1	0.17	*
6/7	0.8	0.8	20.0	0.04		5/9	2.7	3.0	22.2	0.04	
8/7	0.4	0.46	23.0	0.38		11/9	3.0	4.6	30.7	0.18	
10/8	2.1	5.5	52.4	0.77	*	18/9	2.3	2.6	22.6	0.06	
19/8	3.04	5.83	38.4	0.21	*	27/9	3.4	4.8	28.3	0.12	
24/8	2.8	5.0	35.7	0.28	*	4/10	2.6	3.7	28.5	0.16	
1/9	1.40	2.14	30.6	0.36	*	11/10	4.8	12.2	50.8	0.32	*
11/9	1.80	1.9	21.1	0.03		18/10	3.1	3.5	22.5	0.04	
18/9	2.2	2.6	23.6	0.08		26/10	2.3	3.0	26.1	0.13	
29/9	2.6	6.3	57.3	0.55	*	3/11	4.0	7.7	38.5	0.23	*
4/10	2.3	4.7	40.9	0.45	*	10/11	5.4	13.8	51.1	0.28	*
11/10	3.5	8.2	46.9	0.38	*	31/11	2.5	5.6	44.8	0.50	*
18/10	3.8	7.3	38.4	0.24	*	17/12	2.5	3.7	29.6	0.19	
26/10	2.5	2.5	20.0	0.00		19/12	2.9	11.2	74.7	1.0	*
3/11	2.6	5.3	40.8	0.4	*	29/12	3.0	7.4	49.3	0.49	*

*Significantly aggregated (p = 0.05).

+ Mean of 20 Samples

Table 26 Distribution of larvae in young sward during 1973

	G. tripunctata					*Oscinella* complex				
Dates	Mean+	Variance	X^2	D	P = 0.05	Mean+	Variance	X^2	D	P = 0.05
May I	-					-				
II	-					-				
III	-					-				
IV	0.6	-	-	-		0.4	-	-	-	
Jun I	0.9	1.2	13.3	0.37		2.2	-	-	-	
II	1.0	0.88	8.8	-0.12		1.9	4.0	21.1	0.58	*
III	0.8	1.28	16.0	0.75		0.8	1.5	17.0	1.09	*
IV	0.4	0.48	12.2	0.5		2.9	14.77	50.9	1.4	*
Jul I	1.0	1.3	13.0	0.3		2.7	2.46	9.1	-0.03	
II	0.6	-	-	-		1.4	2.27	16.2	0.44	
III	0.1	-	-	-		0.6	0.49	8.20	-0.31	
IV	0.2	-	-	-		1.1	1.76	16.1	0.55	
Aug I	0.2	-	-	-		2.8	-	-	-	
II	0.2	-	-	-		4.0	8.22	20.6	0.26	*
III	0.1	-	-	-		3.1	2.5	8.06	-0.06	
IV	0.8	-	-	-		3.4	1.4	4.1	-0.17	
Sep I	0.8	1.5	18.78	1.1	*	4.9	12.3	25.1	0.31	*
II	0.9	0.66	7.33	-0.30		4.2	6.1	14.7	0.11	
III	0.8	-	-	-		3.4	7.6	22.4	0.36	*
IV	0.7	-	-	-		5.3	9.8	18.5	0.16	*
Oct I	1.0	-	-	-		4.6	11.15	65.5	0.31	*
II	1.7	2.01	11.8	0.11		4.5	14.6	32.4	0.50	*
III	2.0	3.6	17.8	0.40	*	4.6	8.5	18.45	0.18	
IV	3.0	6.4	21.5	0.38	*	5.4	14.5	26.8	0.31	*
Nov I	3.3	6.3	19.19	0.28	*	4.7				

*Significantly aggregated (P = 0.05).

\+ Mean of ten samples

Table 27 Distribution of Pupae (*Oscinella* spp.) 1973

Young Sward						Old Sward					
Period	Mean^{+}	Variance	X^2	D	P = 0.05	Period	Mean^{+}	Variance	X^2	D	P = 0.05
June II	0.7	0.5	7.1	-0.4		June II	0.4	0.7	17.5	1.9	
June III	1.7	8.7	51	2.4	*	III	0.9	0.8	8.9	0.01	
IV	0.6	1.6	26.7	1.8	*	IV	-	-	-	0	
July III	0.6	0.9	15.0	0.8		July III	0.2	0.2	10	0	
IV	0.9	0.8	8.9	0.1		IV	0.2	0.2	10	0	
Aug I	0.9	0.8	8.9	0.1		Aug I	2.2	9.1	41.2	1.4	*
II	0.7	0.7	10	0		II	0.4	0.8	20	2.5	
III	3.3	23.3	70.7	1.8	*	III	0.5				
IV	0.7	0.7	10	0							
Sept I	0.7	0.9	12.9	0.4							
II	0.3										

* Significantly aggregated (P = 0.05)

$^{+}$ Mean of ten samples

Table 28 Distribution of Pupae (*G. tripunctata*) 1973

Young Sward						Old Sward					
Period	Mean$^+$	Variance	X^2	D	P = 0.05	Period	Mean$^+$	Variance	X^2	D	P = 0.05
June II	0.2	0.1	5	2.5		Mar III	0.3	0.3	10	-	
III	0.3	0.5	16.7	2.2		IV	0.3	0.3	10		
IV	0.1	0.1	10			Apr I	0.7	1.6	22.8	1.8	*
July II	0.4	0.5	12.5	0.6		II	0.2	0.2	10		
III	0.3	0.5	16.7	2.2		III	0.2	0.2	10	-	
IV	0.3	0.3	10	-		IV	0.3	0.3	10		
Aug I	0.4	0.5	12.5	0.6		May I	0.3				
II	0.3	0.3	10.0	-		II	0.2				
III	0.3	0.5	16.7	2.2							
IV	0.1										

* Significantly aggregated (P = 0.05)

+ Mean of ten samples

List of figures

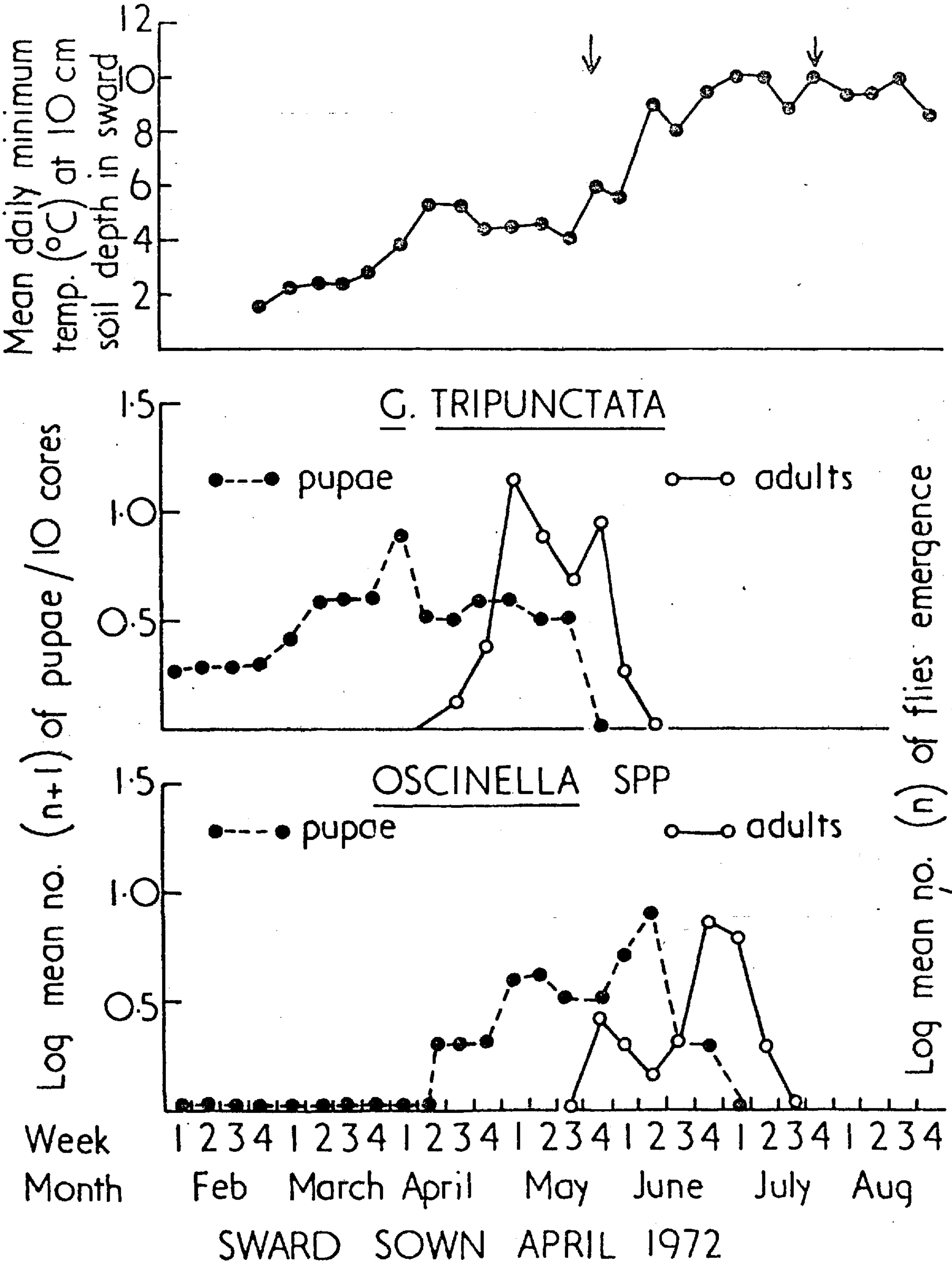


Fig I. Pupation of overwintering larvae (●- - - - -●) and the Emergence of first generation adults (○———○) of G. tripunctata and Oscinella spp. in spring and early summer, in relation to soil temperature.

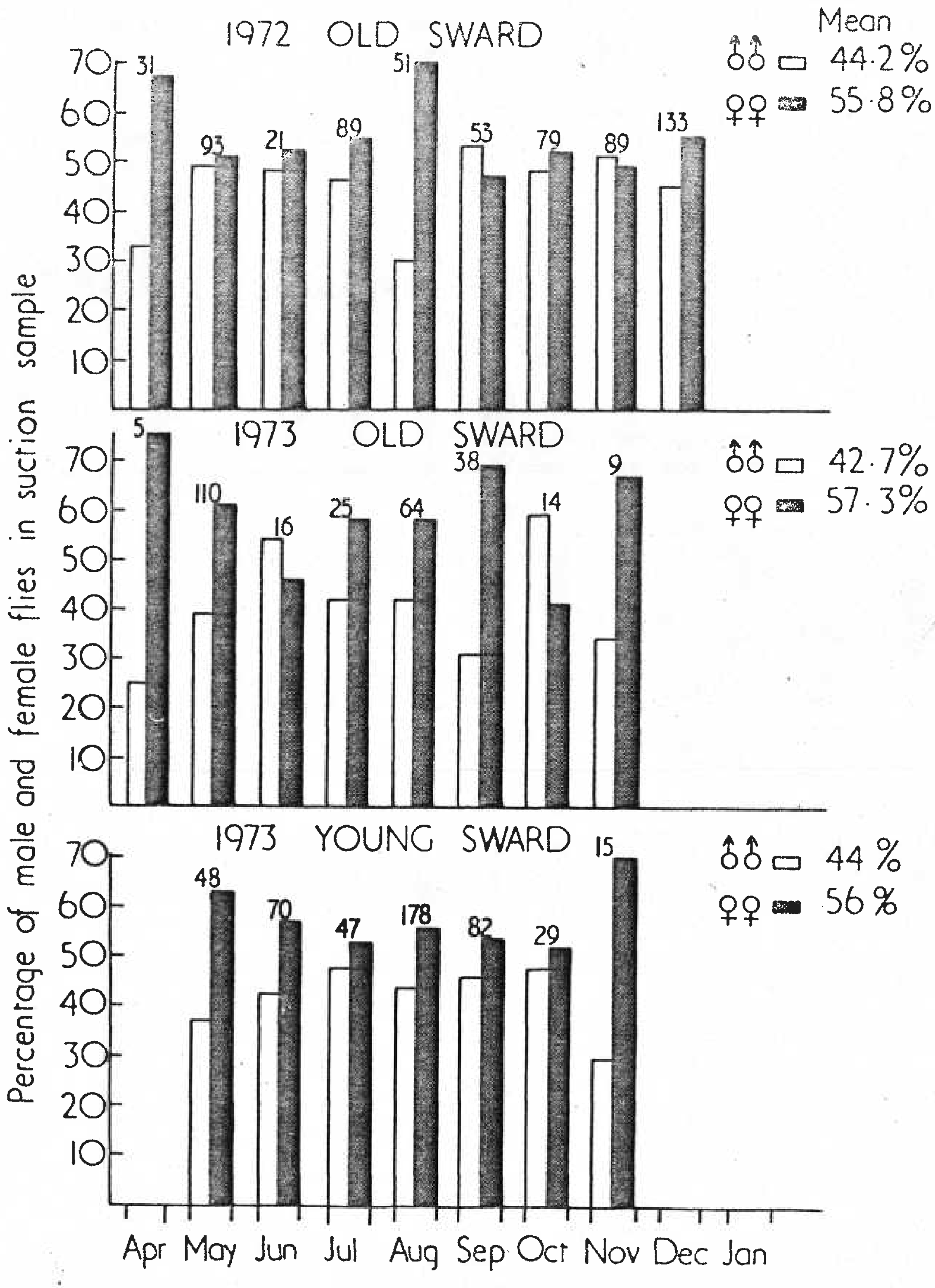


Fig. II. The sex-ratio of adult *G. tripunctata* in suction samples taken from old swards (1972 & 1973) and young sward (1973).

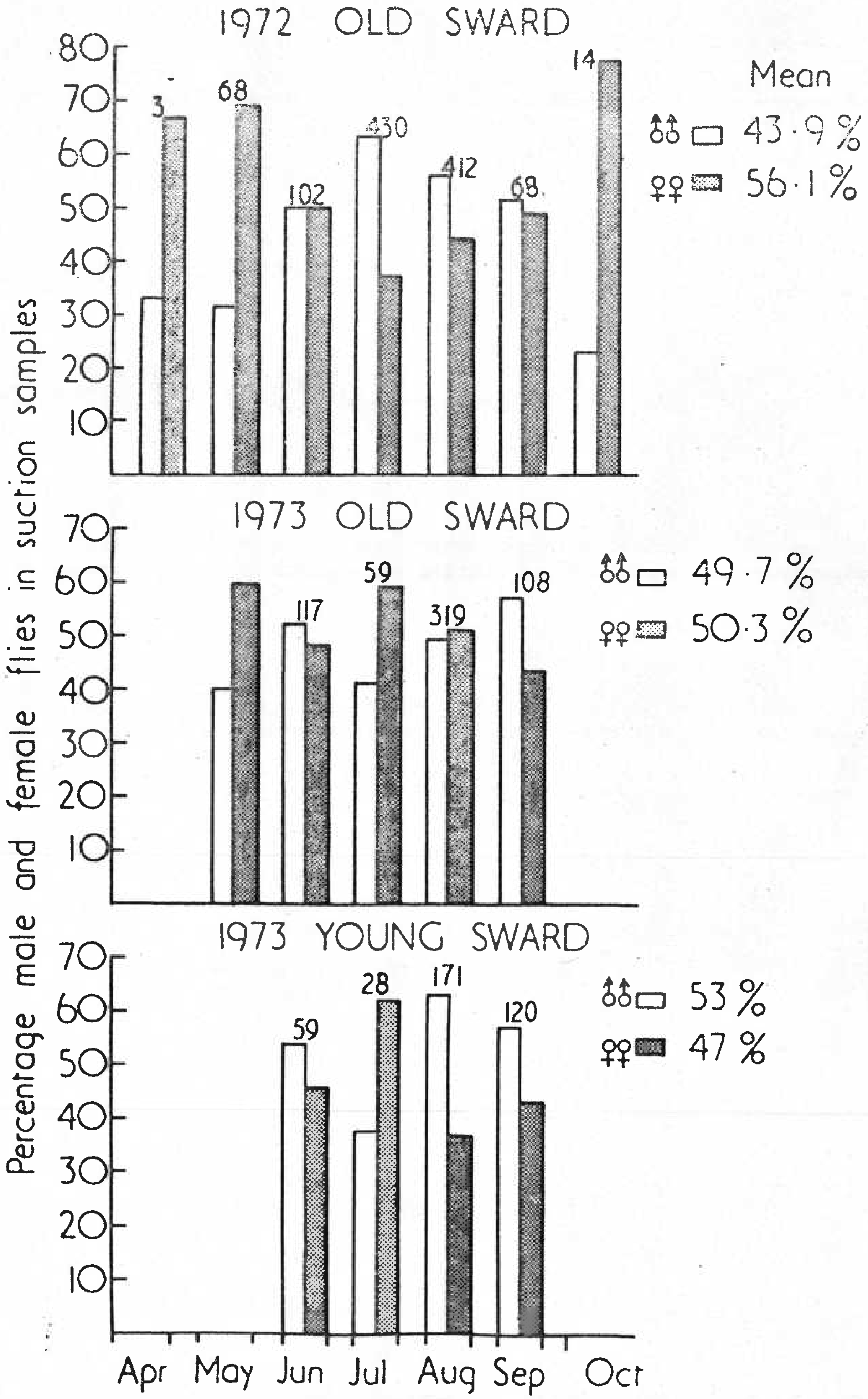


Fig. III. The sex ratio of adult *Oscinella* spp. in suction samples taken from old swards (1972 & 1973), and young sward (1973).

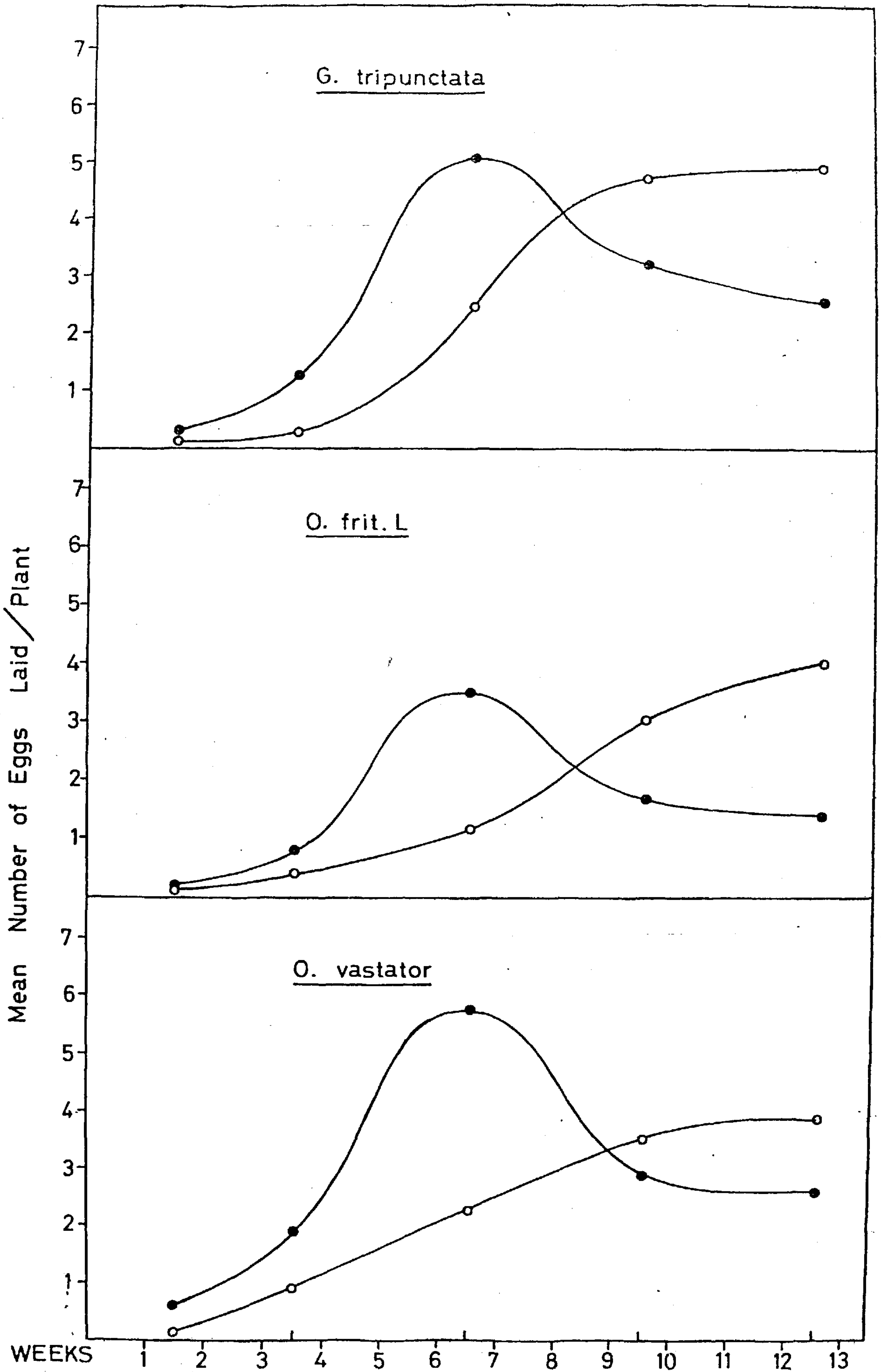
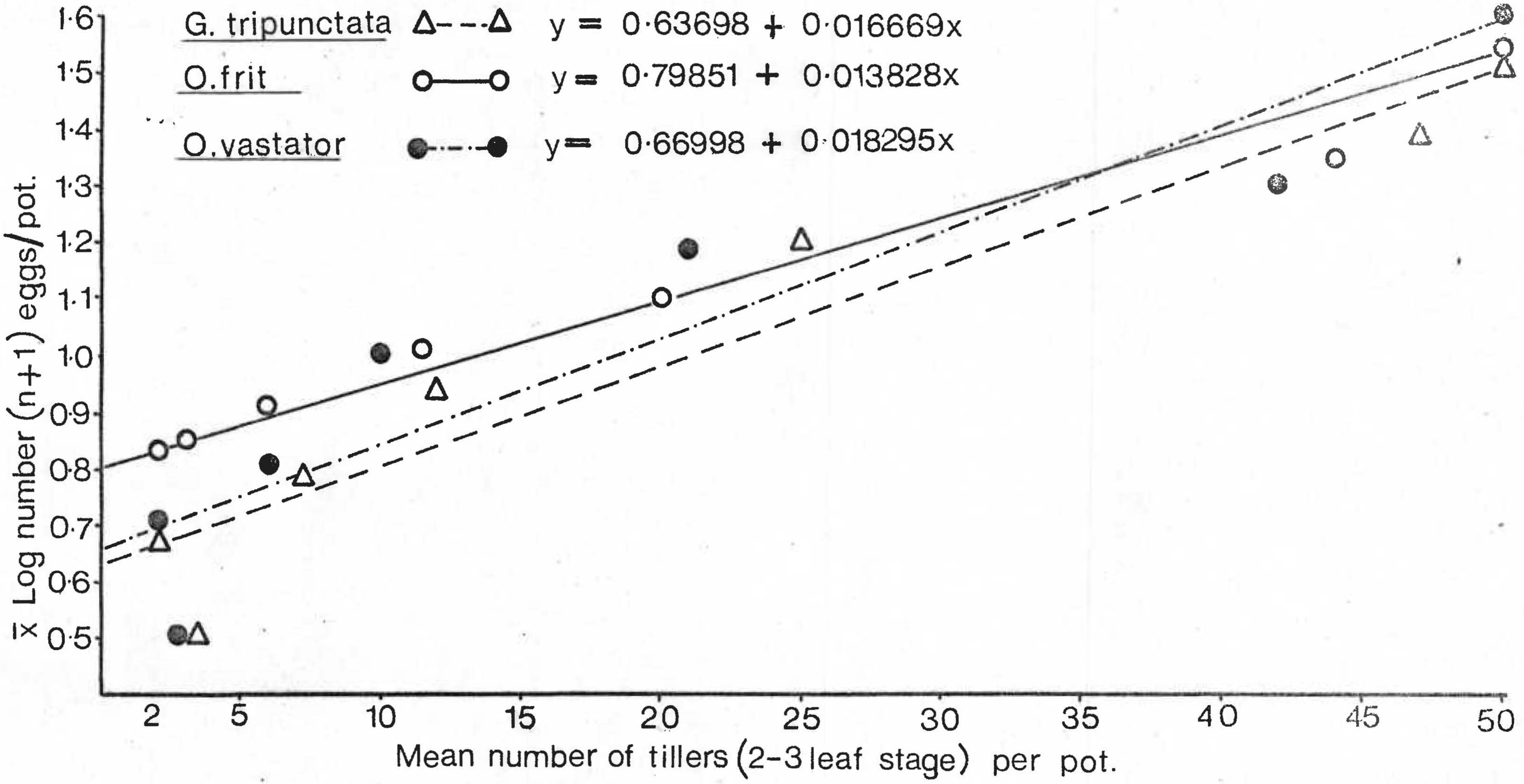


Fig. IV. Effect of plant age or tiller age on the intensity of Oviposition.

Fig. V. The effect of shoot-density(3-leaf stage) on the intensity of oviposition.



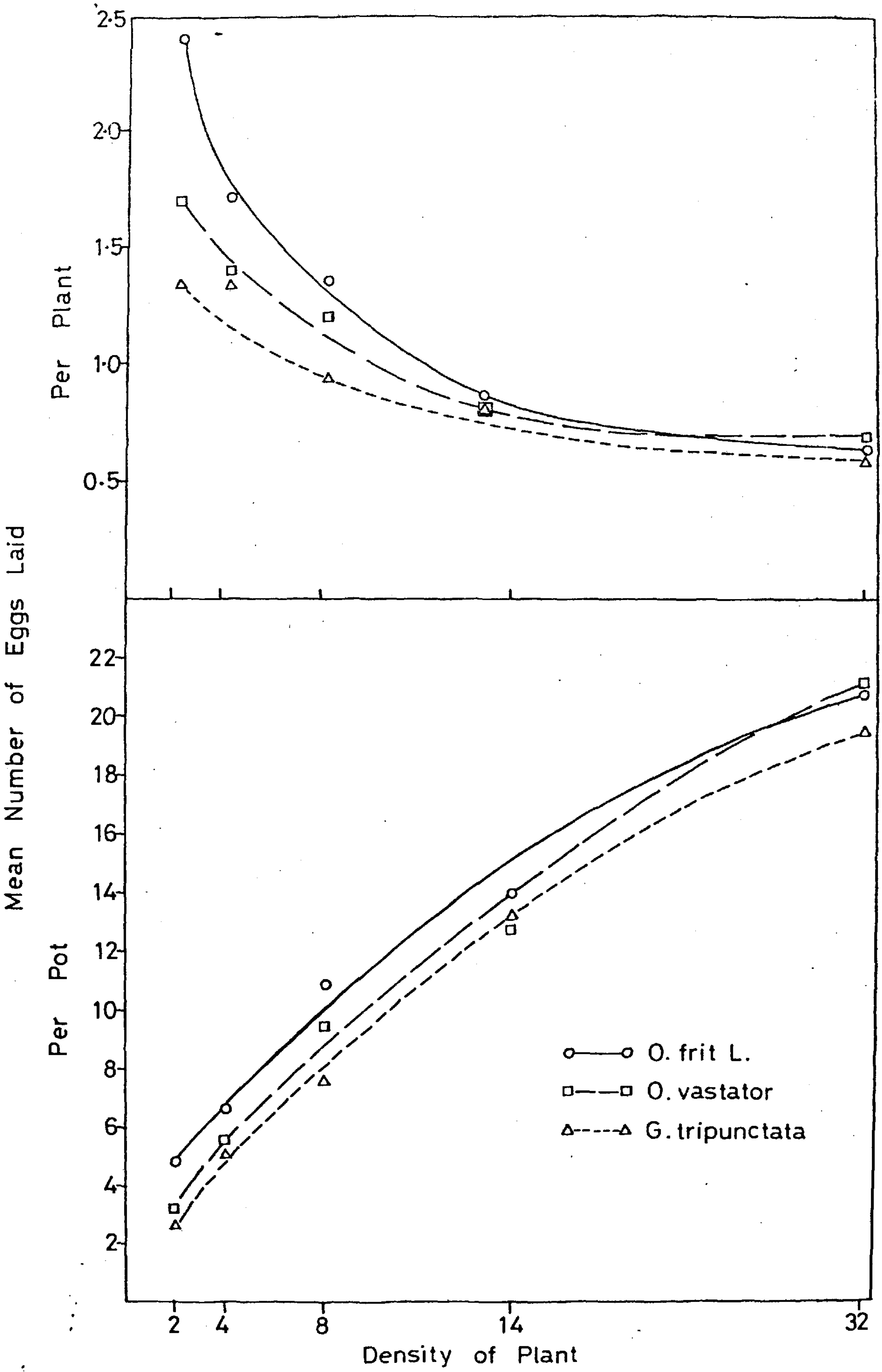


Fig. VI. The relationship between shoot density and the number of eggs laid by G. tripunctata, O. frit L. and O. vastator per plant and per unit area.

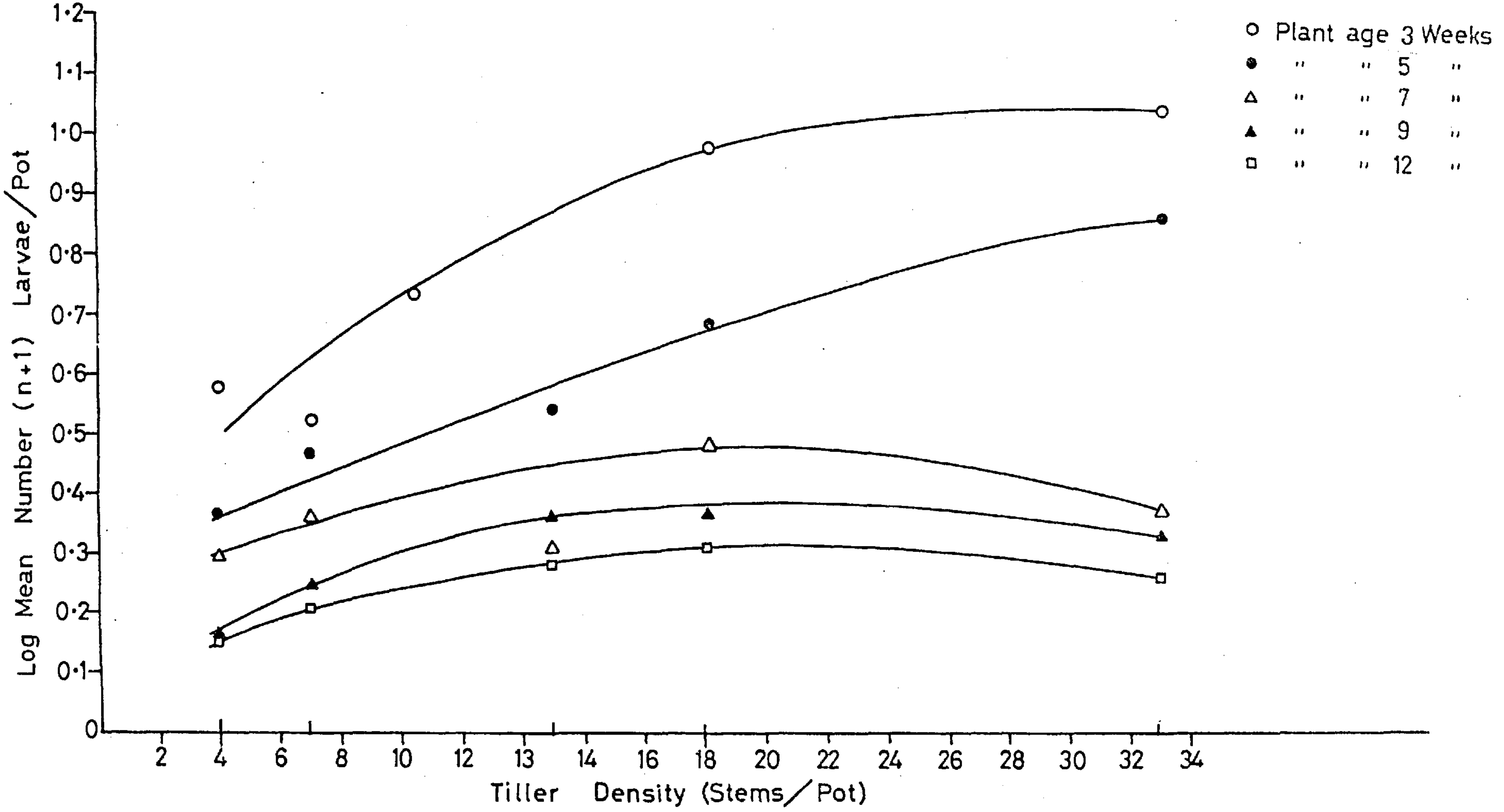


Fig. VII. The effect of age and density of ryegrass tillers on larval establishment in the field (all spp.).

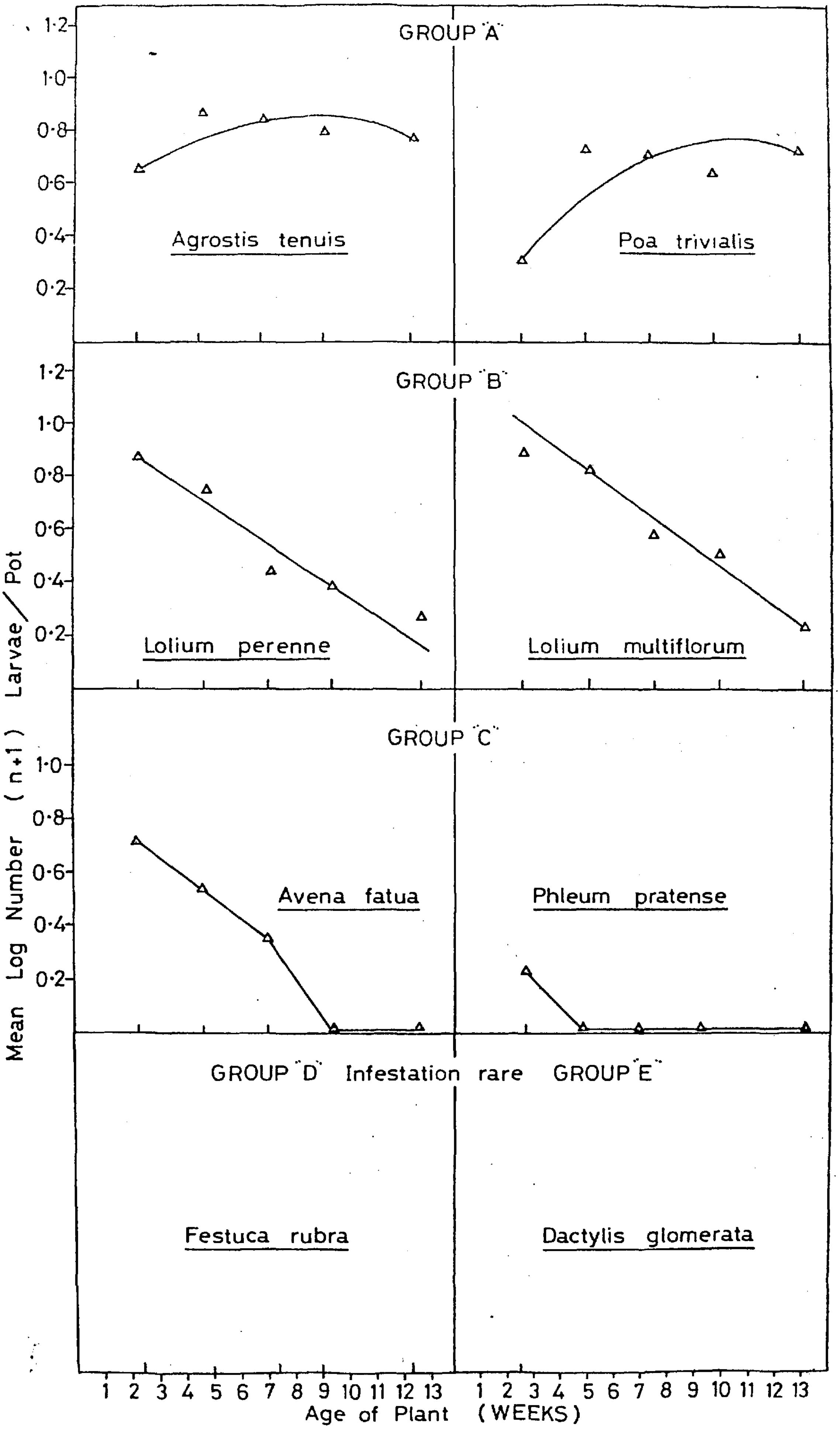


Fig. VIII. The effect of grass species and plant age on larval establishment in the field (*G. tripunctata*).

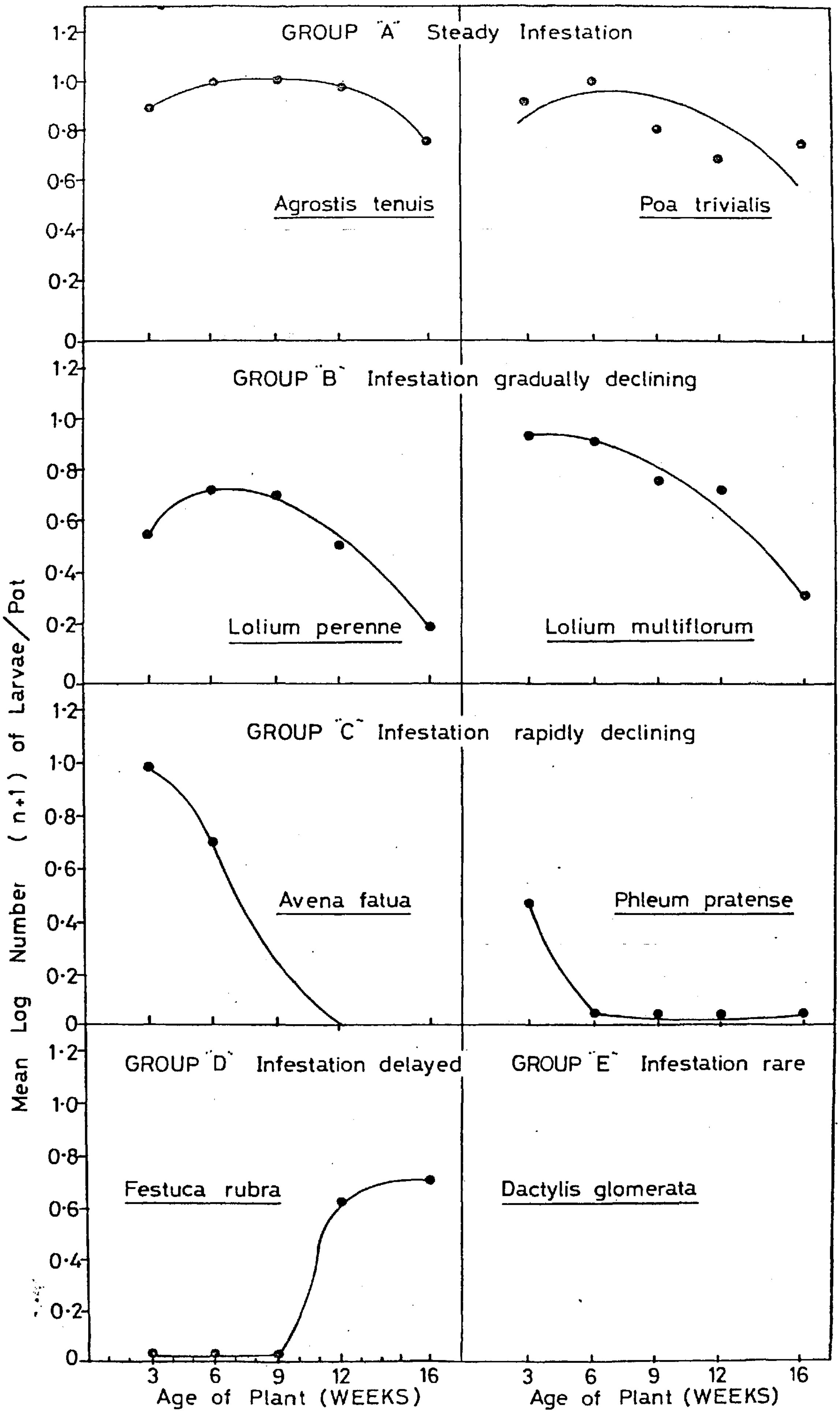


Fig. IX. The effect of grass species and plant age on larval establishment in the field (*Oscinella* spp.).

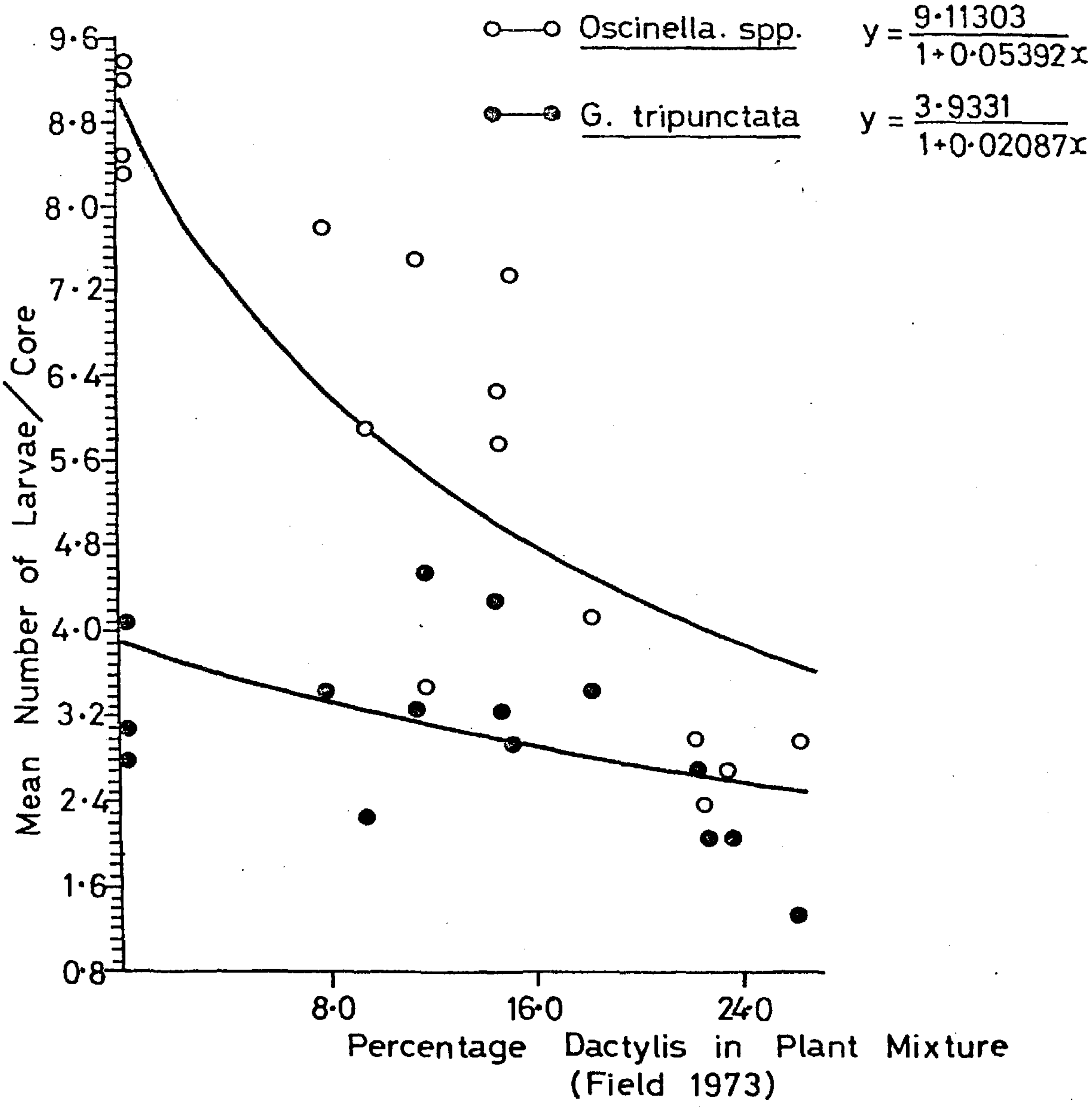
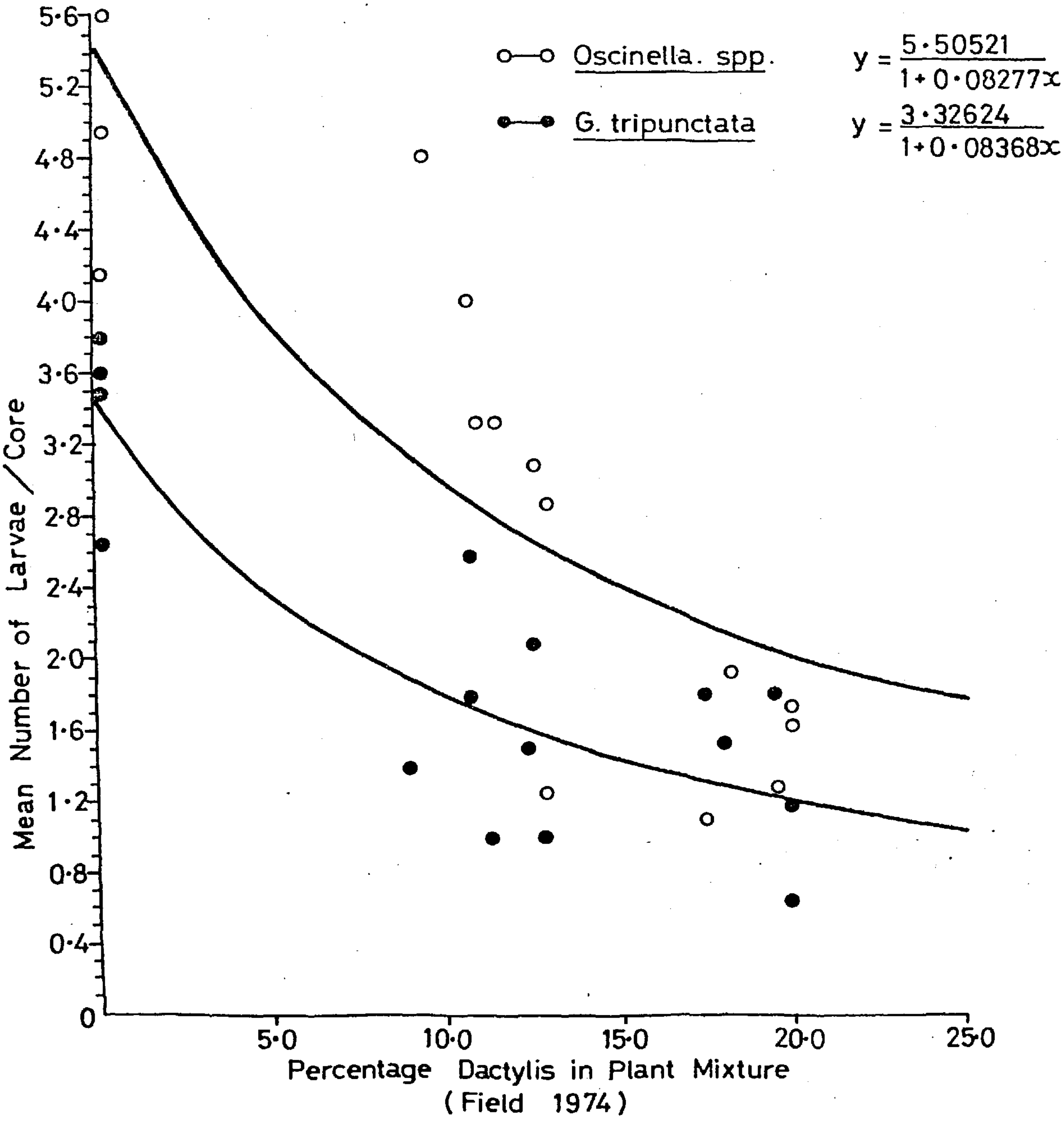
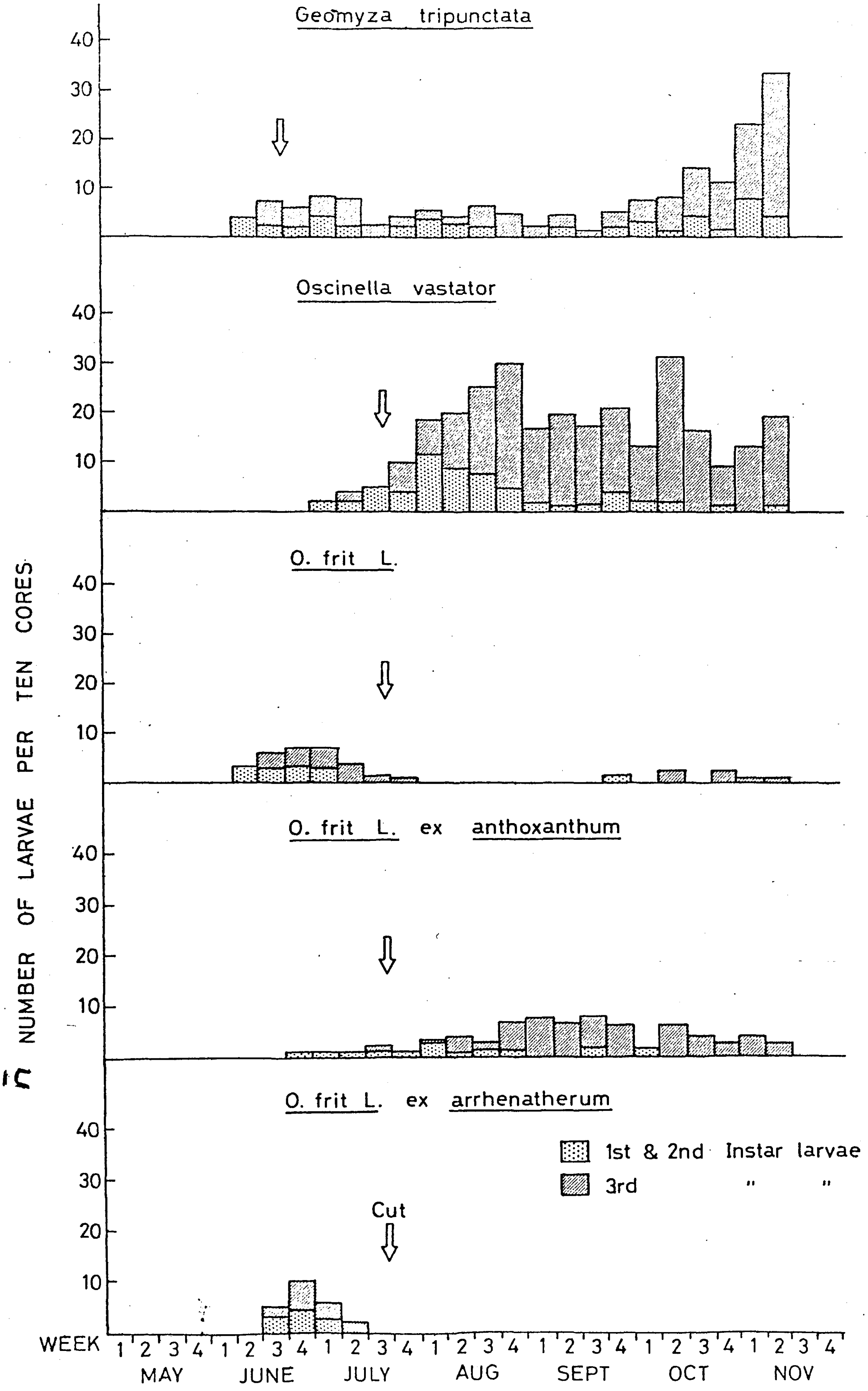


Fig. X. The effect of mixed planting of ryegrass and cocksfoot on the larval establishment of G. tripunctata and Oscinella spp. in the field (1973).



<u>Fig. XI.</u> The effect of mixed planting of ryegrass and cocksfoot on the larval establishment of <u>G. tripunctata</u> and <u>Oscinella</u> spp. in the field (1974).



g. XII. Seasonal distribution of larvae of different spp. in the newly sown sward, 1972. (Sowing date April, 1972).

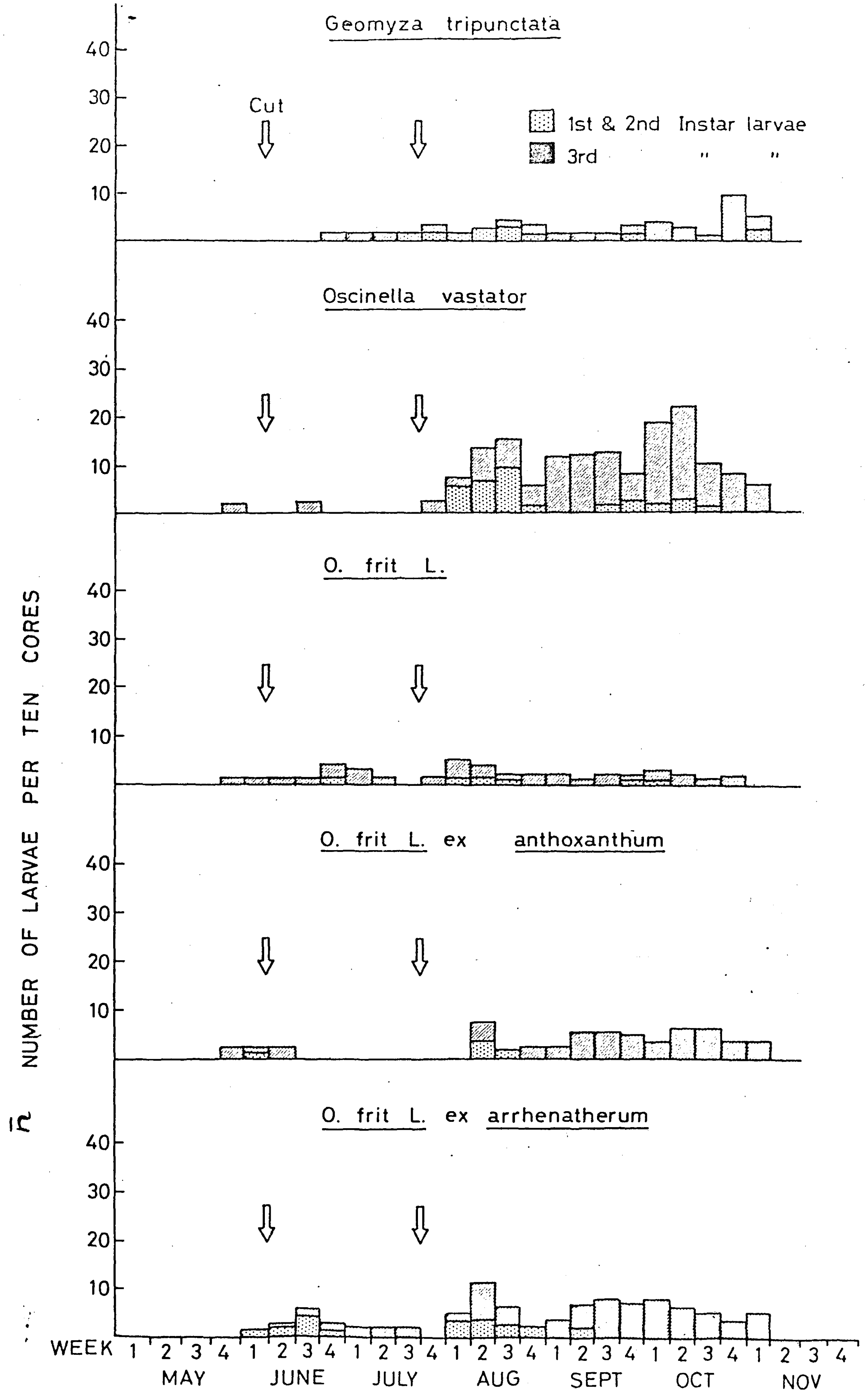


Fig. XIII. Seasonal distribution of larvae of different species in the old sward, 1972. (Sowing date, September 1970).

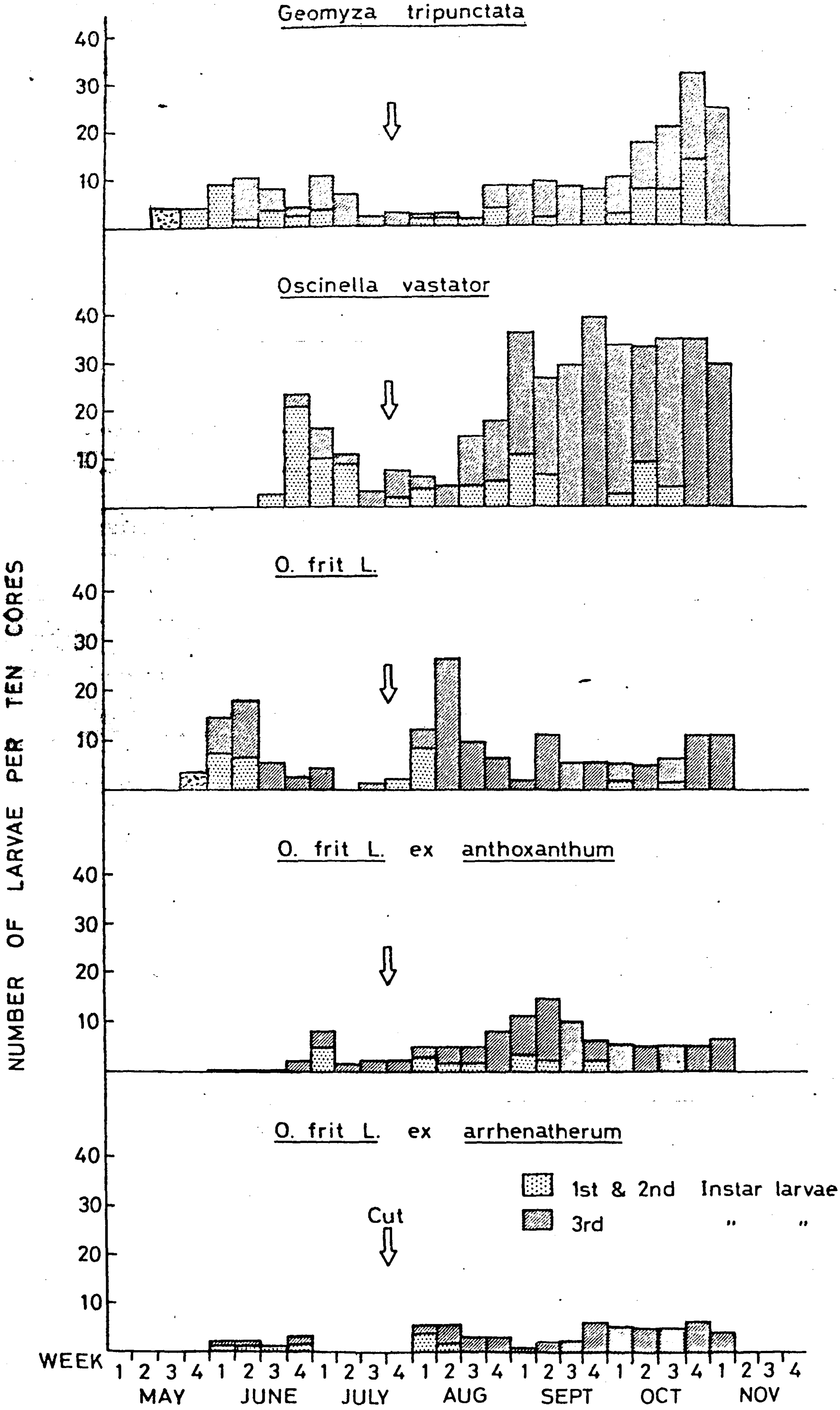


Fig. XIV. Seasonal distribution of larvae of different spp. in the newly-sown sward, 1973. (Sowing date April, 1973).

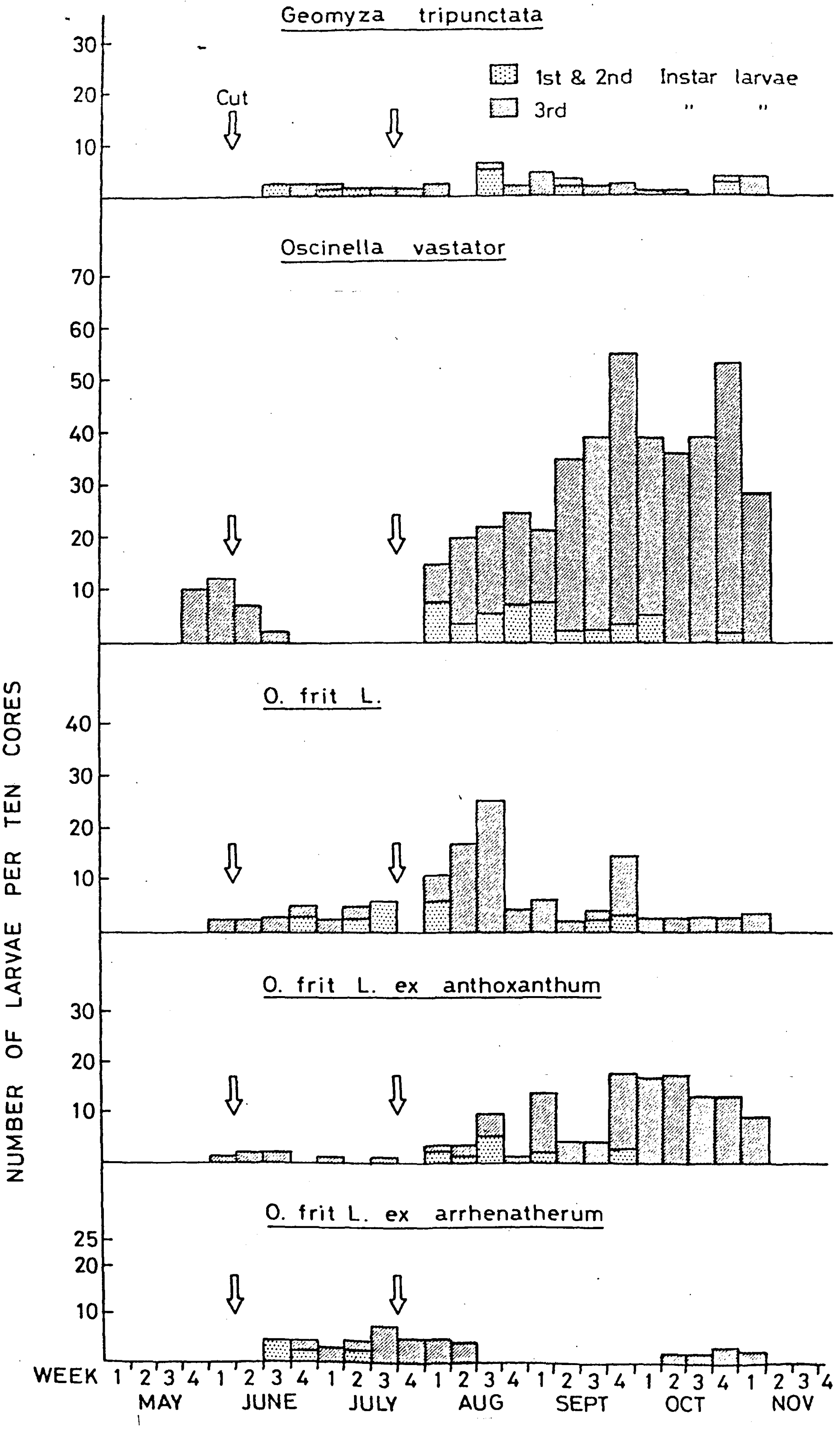
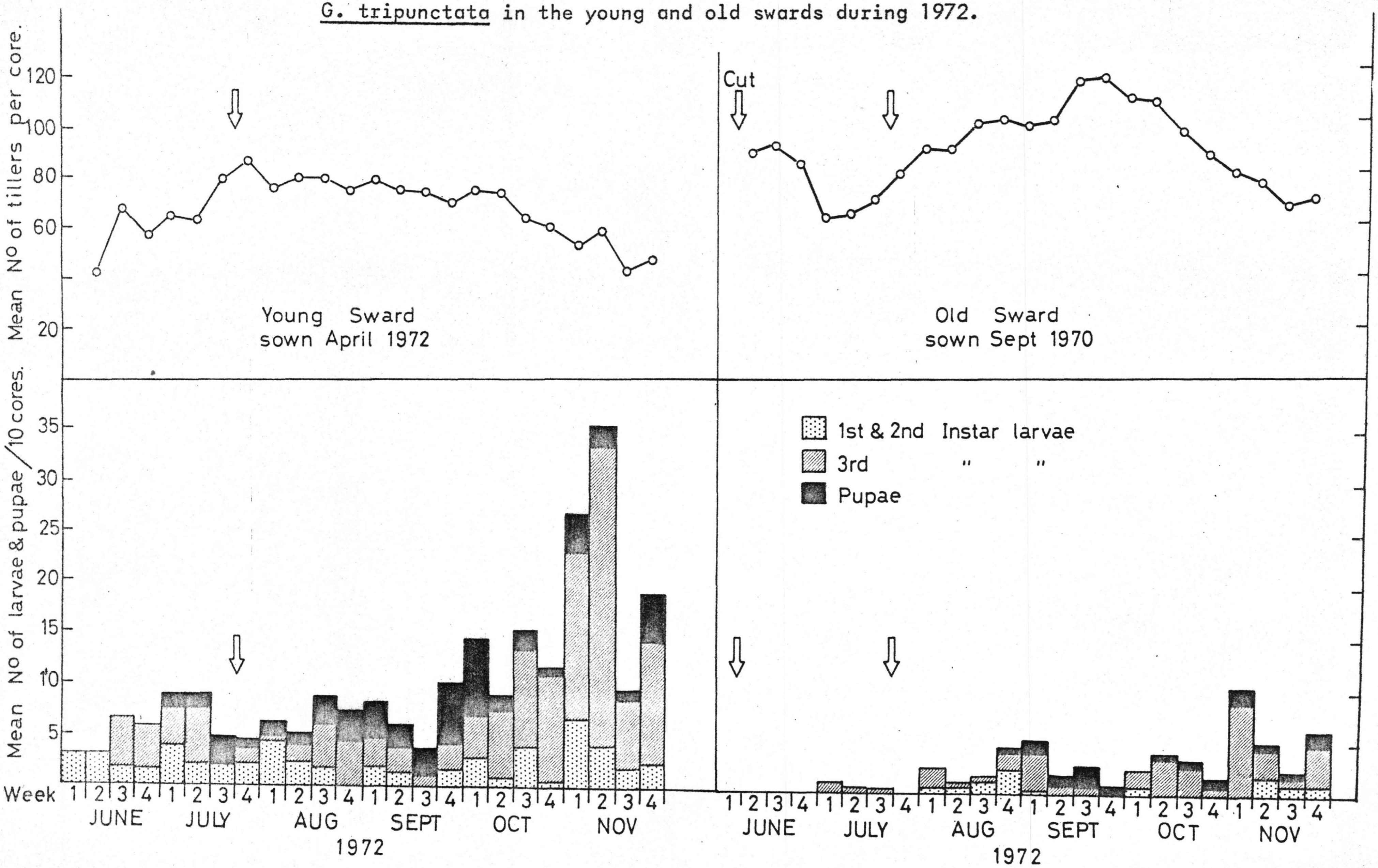
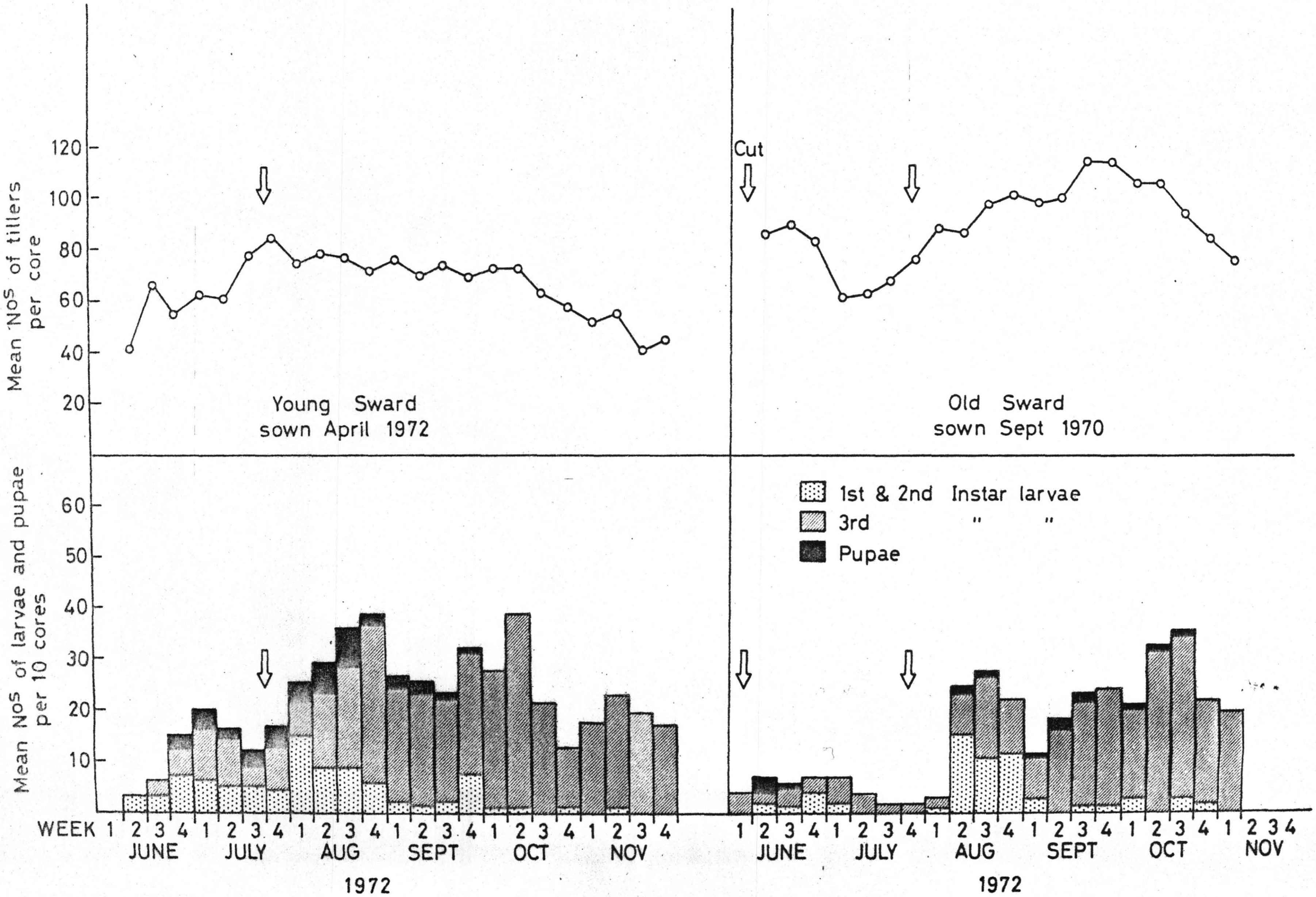


Fig. XV. Seasonal distribution of larvae of different species in the old sward, 1973. (Sowing date, April 1972.)

Fig. XVI. Tiller density and the comparative abundance of larvae of *G. tripunctata* in the young and old swards during 1972.





<u>Fig. XVII</u>. Tiller density and the comparative abundance of the larvae of *<u>Oscinella</u>* spp. in the young and old swards during 1972.

Fig. XVIII. Tiller density and the comparative abundance of the larvae of *G. tripunctata* in the young and old swards during 1973.

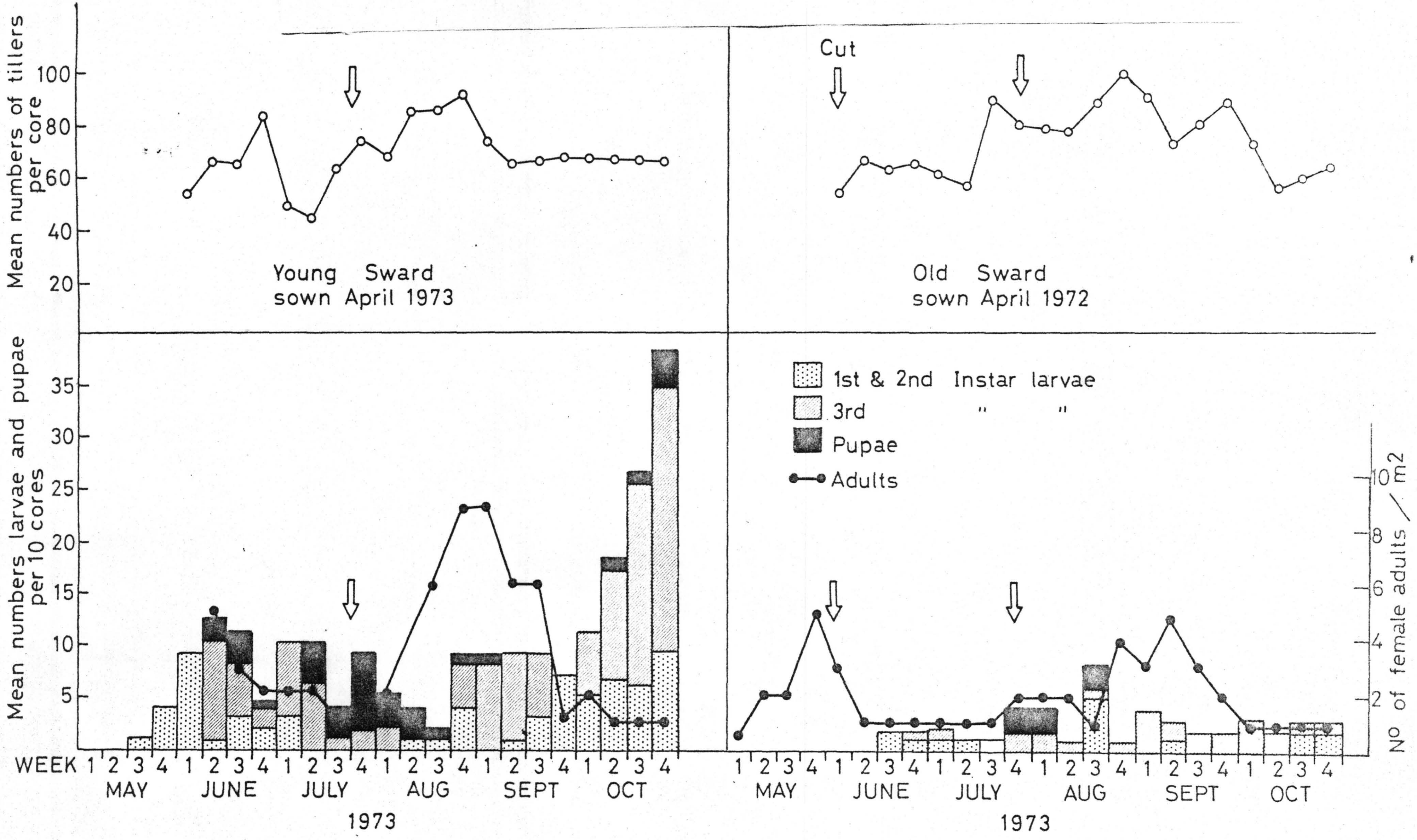
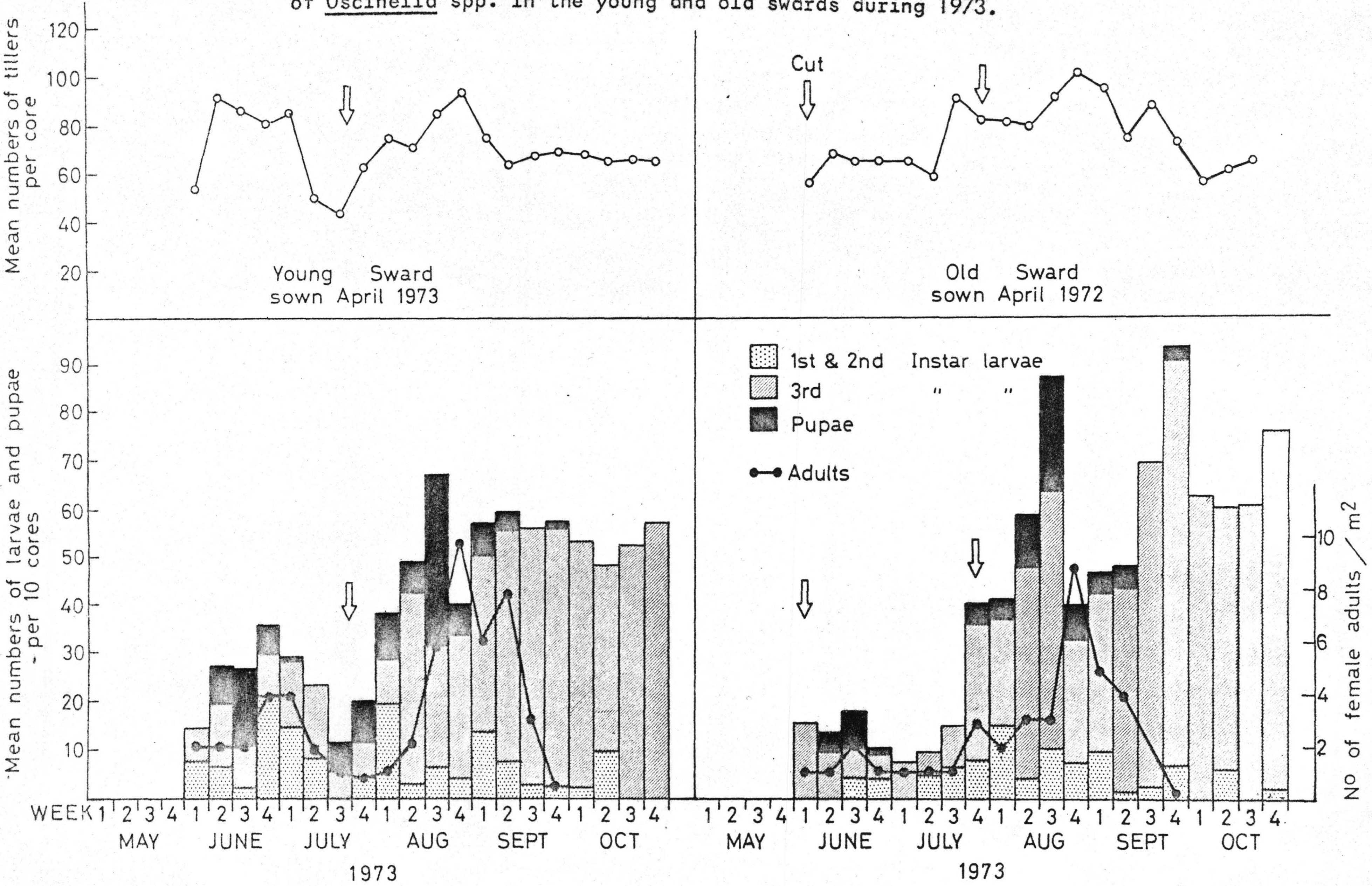


Fig. XIX. Tiller density and the comparative abundance of the larvae of *Oscinella* spp. in the young and old swards during 1973.



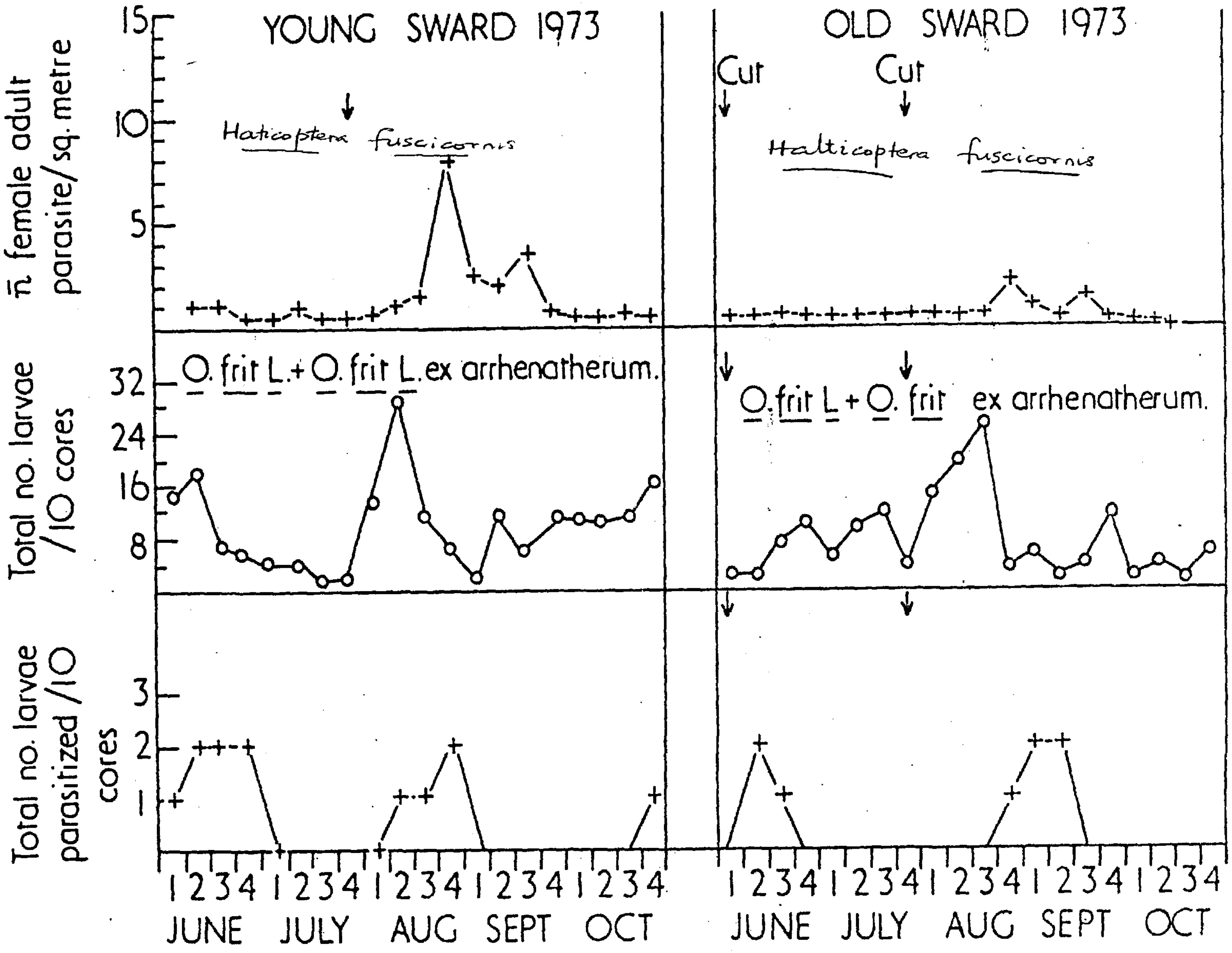


Fig. XX. Parasitism: numbers of host larvae, adult parasites and rasitized larvae in oung and old swards, 1973.

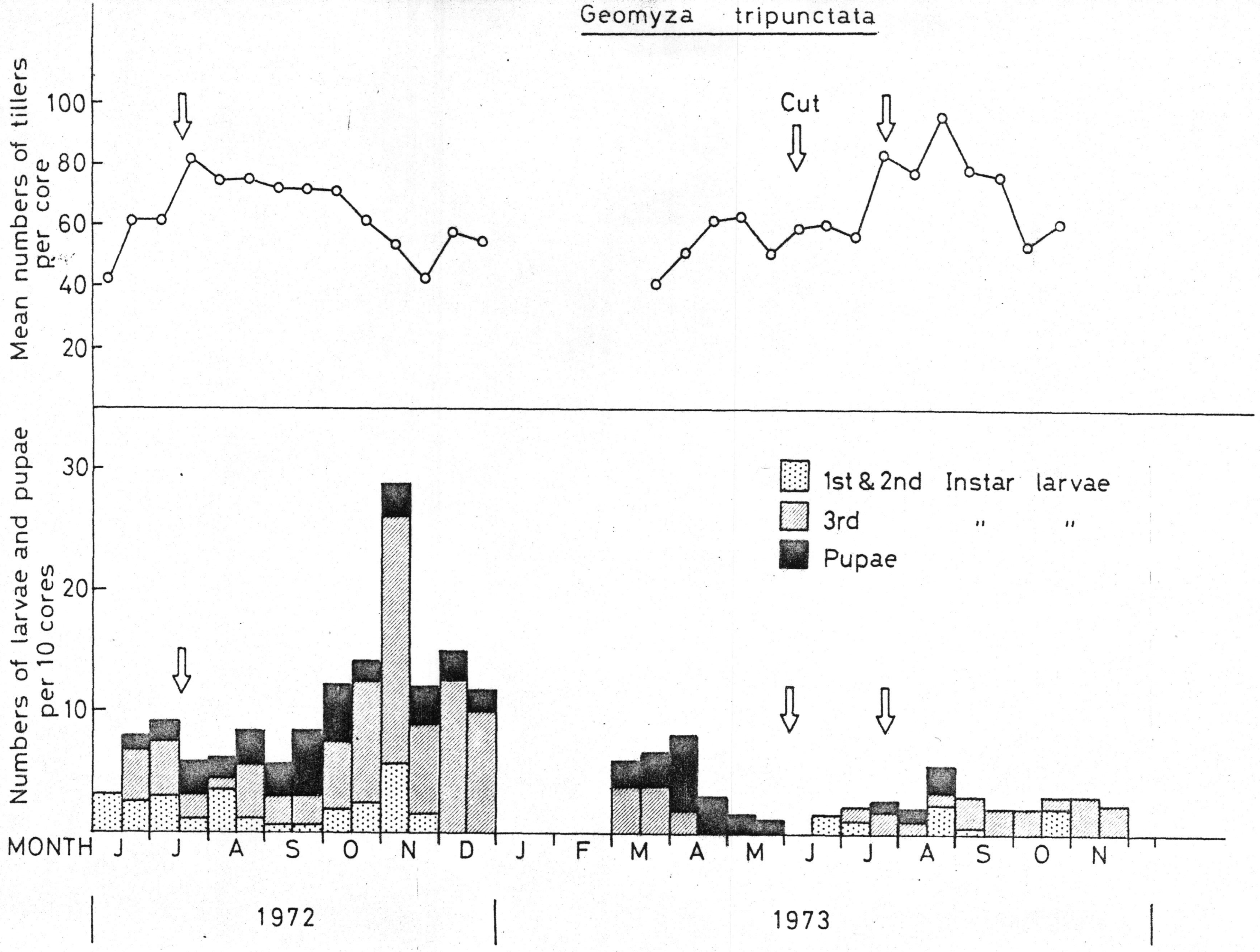


Fig. XXI. Changes in larval numbers of *G. tripunctata* during the first two years of a sward's life. (Sown April 1972).

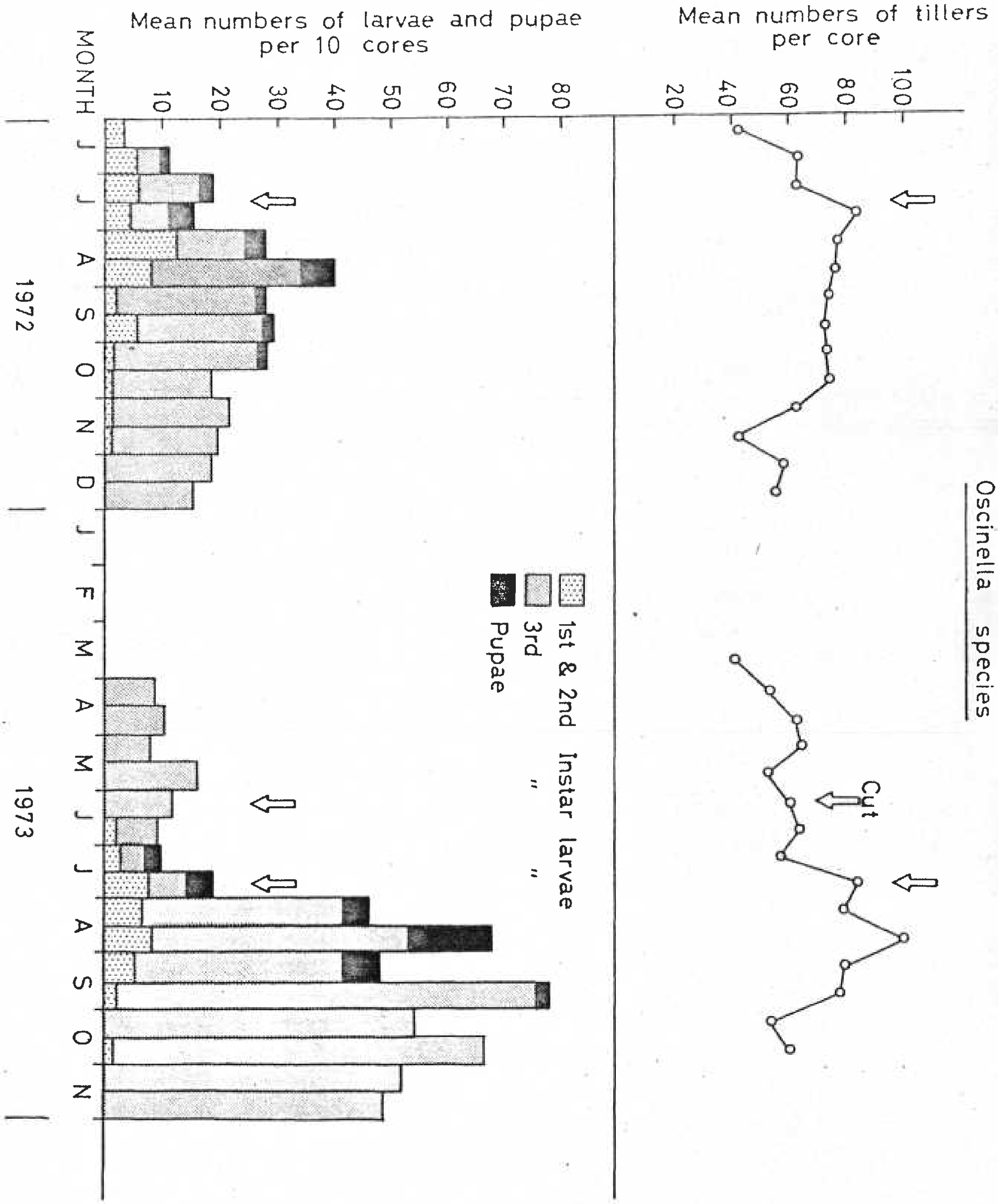


Fig. XXII. Changes in the larval numbers of Oscinella spp. during the first two years of a sward's life. (Sown April 1972).

APPENDIX 1A Seasonal distribution of various larval species, tiller numbers and percentage tiller damaged in young and old swards 1972.

Number of larvae/20 cores

LARVAL SPECIES	A		B		C		D		E		TOTAL		n tiller/ core		% tiller damage	
SWARD TYPE	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0	Y	0
Dates																
April II	-	2	-	14	-	2	-	16	-	2	-	36	-	93	-	1.6
III	-	0	-	12	-	2	-	17	-	3	-	34	-	106	-	2.2
IV	-	0	-	12	-	6	-	20	-	0	-	38	-	92.3	-	2.4
May I	-	0	-	11	-	1	-	5	-	6	-	23	-	108.4	-	1.6
II	-	0	-	15	-	0	-	5	-	0	-	20	-	95.4	-	2.2
III	-	1	-	25	-	1	-	10	-	0	-	37	-	84.0	-	3.2
IV	-	0	-	19	-	0	-	5	-	5	-	29	-	71.0	-	4.0
June I	-	0	-	2	-	2	-	4	-	2	-	10	-	72.0	-	2.8
II	8	0	0	0	6	2	0	4	10	4	24	10	40.2	85.7	2.5	1.0
III	14	0	0	4	12	2	0	4	20	8	46	10	66.3	88.2	3.5	1.0
IV	12	2	0	0	14	8	2	0	12	6	40	18	54.5	82.0	4.8	1.0
July I	16	2	4	0	14	6	2	0	4	2	40	16	61.2	60.4	6.7	1.0
II	16	2	8	0	8	2	2	0	0	2	34	10	60.0	62.5	6.3	1.7
III	4	2	10	0	2	2	4	0	0	2	20	6	77.6	68.2	3.4	2.0
IV	8	6	20	4	2	2	2	0	0	0	32	6	83.3	77.7	4.5	1.5
August I	10	4	36	14	0	10	8	0	0	8	54	12	72.6	88.6	6.9	1.5
II	8	4	40	26	0	8	8	14	0	22	56	36	76.1	87.0	6.4	4.4
III	12	8	50	28	0	4	6	4	0	12	68	74	76.1	97.4	7.5	3.9
IV	10	8	60	10	0	4	14	6	0	2	84	56	70.2	99.0	10.5	3.4
Sept. I	4	2	34	22	0	4	16	6	0	6	54	30	74.1	98.0	7.3	3.0
II	8	2	40	22	0	2	14	10	0	12	62	40	69.3	100.2	8.0	2.4
III	2	2	36	24	0	4	16	10	0	14	54	48	71.8	114.2	7.0	3.9
IV	10	6	42	14	2	4	14	10	0	14	68	48	67.5	114.3	10.0	3.9
October I	14	8	26	36	0	6	4	6	0	14	44	70	70.8	107.0	8.8	4.0
II	16	6	64	42	4	4	12	12	0	10	96	74	70.6	107.0	11.3	6.8
III	28	2	32	20	0	2	8	12	0	10	68	46	62.1	93.0	11.5	7.6
IV	22	18	18	16	4	2	4	8	0	6	48	50	58.7	84.0	8.2	7.3
November I	46	10	26	12	2	0	8	8	0	10	82	40	50.9	77.6	12.4	6.4
II	66	10	38	9	2	2	6	7	0	8	112	36	55.6	74.3	15.6	4.9

20 cores is approximately 0·02 m^2

APPENDIX IB. Seasonal distribution of various larval species, tiller numbers and percentage tiller damaged in young and old swards 1973

		Number of larvae/20 cores															
LARVAL SPECIES		A		B		C		D		E		TOTAL		$\bar{n}$ tiller/ core		% tiller damage ($\bar{n}$)	
SWARD TYPE		Y	O	Y	O	Y	O	Y	O	Y	O	Y	O	Y	O	Y	O
Dates	Week																
February	I	-	2	-	5	-	0	-	1	-	0	-	8	-	25.0	-	-
	II	-	7	-	3	-	0	-	0	-	0	-	10	-	33.0	-	-
	III	-	4	-	2	-	0	-	0	-	0	-	6	-	43.2	-	-
	IV	-	6	-	4	-	1	-	1	-	1	-	13	-	30.6	-	-
March	I	-	7	-	5	-	0	-	1	-	0	-	13	-	35.0	-	-
	II	-	1	-	5	-	0	-	0	-	1	-	7	-	33.5	-	-
	III	-	4	-	6	-	0	-	3	-	0	-	13	-	38.3	-	6
	IV	-	4	-	6	-	0	-	1	-	0	-	11	-	30.5	-	3.5
April	I	-	3	-	5	-	1	-	1	-	0	-	10	-	45.5	-	6.6
	II	-	0	-	6	-	0	-	1	-	0	-	7	-	43.7	-	4.6
	III	-	0	-	10	-	0	-	2	-	0	-	12	-	60.1	-	3.0
	IV	-	0	-	6	-	1	-	0	-	1	-	8	-	55.3	-	2.0
May	I	-	-	-	-	-	-	-	-	-	-	-	-	-	49.1	-	3.2
	II	-	0	-	6	-	0	-	0	-	0	-	6	-	44.4	-	3.0
	III	-	0	-	6	-	0	-	2	-	0	-	8	-	47.5	2.0	3.0
	IV	4	0	0	13	0	0	0	1	0	0	4	14	36.9	37.0	4.9	2.8
June	I	9	0	0	12	14	2	0	1	2	0	25	15	49.3	52.3	8.4	4.0
	II	10	0	0	7	17	2	0	2	2	4	29	11	87.9	64.1	7.2	2.1
	III	8	2	2	2	5	2	0	2	1	4	16	12	80.4	59.3	12.6	6.2
	IV	4	2	22	0	2	5	2	0	3	3	33	11	76.9	60.9	8.9	5.1
July	I	10	2	15	0	4	3	8	1	0	4	37	9	79.7	59.4	11.2	3.1
	II	6	1	10	0	2	5	2	0	0	7	20	10	46.4	54.2	5.0	3.0
	III	1	1	3	0	1	6	2	1	0	5	7	15	40.3	85.4	5.0	3.2
	IV	2	1	7	0	2	0	2	0	0	5	13	6	59.0	78.4	7.3	8.4
August	I	2	2	6	15	12	11	5	3	5	4	30	36	70.7	80.0	10.0	9.5
	II	2	0	4	20	26	17	5	3	5	0	42	44	65.1	75.5	12.5	11.1

APPENDIX IB cont.

LARVAL SPECIES		A		B		C		D		E		TOTAL		$\bar{n}$ tiller/ core		% tiller damage ($\bar{n}$)	
SWARD TYPE		Y	O	Y	O	Y	O	Y	O	Y	O	Y	O	Y	O	Y	O
Dates	Week																
August	III	1	6	14	22	9	25	5	9	3	0	32	62	81.9	94.3	13.3	15.1
	IV	8	1	17	25	6	4	8	1	3	0	92	31	88.4	73.7	14.2	6.1
September	I	8	4	36	21	1	6	11	13	1	0	57	44	67.7	87.4	13.0	12.1
	II	9	3	25	35	11	2	14	4	2	0	51	44	60.7	68.2	18.1	11.7
	III	8	0	27	38	5	2	10	4	2	0	42	52	60.2	73.0	15.6	12.5
	IV	7	2	37	55	5	14	6	17	5	0	60	93	63.3	82.7	16.2	14.9
October	I	10	1	32	38	5	2	5	16	4	0	56	57	59.5	75.8	16.5	15.8
	II	17	1	31	36	5	2	5	17	4	2	62	58	60.6	51.5	15.6	14.6
	III	20	1	33	38	4	2	5	13	4	2	66	56	58.5	63.8	16.5	17.0
	IV	30	3	33	53	10	2	5	13	6	3	84	74	61.7	59.5	18.8	20.2
November	I	33	3	28	28	10	3	6	9	3	3	80	46				

KEY TO APPENDICES IA and IB

Larval species:

A - *G. tripunctata*
B - *O. vastator*
C - *O. frit* L.
D - *O. frit ex Anthoxanthum*
E - *O. frit ex Arrhenatherum*

Sward Type Y - Young sward sown April 1972
O - Old sward sown September 1970