THE POPULATION DYNAMICS OF THE APHIDS, *MACROSIPHUM AVENAE*, *METOPOLOPHIUM DIRHODUM*, AND *RHOPALOSIPHUM PADI* ON OATS, *AVENA SATIVA* CV FRASER

By

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ABSTRACT

Fraser oats were used to study populations of cereal aphids in 1972,1973 and 1974. The most commonly found species were Macrosiphum avenae (F.) (the English grain aphid), Metopolophium dirhodum (Wlk.) (Rose-grain aphid) and Rhopalosiphum padi (L.) (Oat bird-cherry aphid).

Aphid density was highest in 1972, lower in 1973 and lowest in 1974. Generally M. avenae had the highest population with M. dirhodum slightly lower. Rhopalosiphum padi was found infrequently with low numbers.

Fecundity trials, used to examine whether the difference between numbers of species was because of a difference in fecundity, did not substantiate field results but instead indicated that R.padi should have produced the highest population.

Differences were not found in the population dynamics when the oats were planted in solid blocks instead of rows.

A one month delay in the planting date did not change the total aphid population but did result in a higher proportion of M. avenae than found in any other plot.

Coccinellid numbers in two out of the three years were considered negligible. In 1972 rain was thought to destroy many coccinellid before they reached large enough numbers to greatly affect the aphid population.

No direct samples were taken of hymenopterous parasites but any found were collected and identified.

Water experiments were conducted to study the effect of water on the fecundity of *R. padi*. It was concluded that *R. padi* definitely preferred wet conditions.

Temperature and rainfall readings were used to show the effect of weather on aphid numbers. Weather was shown to be a major regulatory factor in the population dynamics of cereal aphids.

Considerations were made for aphid mortality caused by sparrows.

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INTRODUCTION

Regulated populations never increase indefinitely and rarely reach extinction. Factors contributing to population regulation fall into two categories - intrinsic and extrinsic. The former are characteristics of the organisms such as their behavior and physiology. Extrinsic or environmental factors are such things as weather, food, and predators and parasites. The importance of intrinsic and extrinsic factors in population regulation has long been a point of contention among population ecologists (general reference - Krebs (1972)). My study investigates the factors associated with the regulation of population numbers of the three dominant species of aphids found worldwide on oats, *Avena sativa*; *Macrosiphum avenae* (F.) (*Homoptera, Aphididae*) (The English Grain Aphid), *Metopolophium dirhodum* (Walker) (Rose-grain aphid) and *Rhopalosiphum padi* (L.) (Oat bird-cherry aphid) (Forbes and Frazer (1973), Forbes *et al*. (1973), Lambers (1939), Lambers (1947), Palmer (1952) and Richards (1960).

1. Economic Damage of Oat Aphids

Although records of economic damage by aphids on oats and extensive control programs do exist, Forbes (1962) found that these aphids did not reduce grain yields of oats and only slightly reduced straw yields in British Columbia. He thought that the economic injury level for the aphids would have to be higher than the 47 aphids per tiller observed in his study. Kolbe (1970) in West Germany however, reported that an average increase in yield of 15% was obtained by using chemicals to control the aphids on oats, var. Flamingskrone, when density on the untreated plots was 46 aphids per stem. He thought that the eradication of aphids was essential if there was suspicion that the cereal crops were infected by virus diseases.

Stern (1967) and Stern and Bowen (1967) studied the economic treatment level of aphids on barley in California, and concluded that the value of the extra yield resulting from chemical control exceeded the cost of treatment. Wood (1965) in Oklahoma found that even heavy infestations of *M. avenae* did not result in any loss of yield as the aphids were usually controlled by predators and parasites.

Zeclant (1969) in France found that *M. avenae* reduced yields by 600 Kg per ha, but he also thought chemical control unnecessary. He attributed the reduction in yield to a decrease in the number of grains rather than to weight loss of grains. As there was no reduction in the weight loss or in the baking quality it was not economically necessary to use chemical control. This conclusion is contrary to Wratten (1975), who said that aphids do not reduce either spikelet or grain number, as these are normally determined by pre-anthesis factors. He found that field caged populations of M. avenae and M. dirhodum reduced grain weight of wheat by 14% and 7%, respectively, and that both reduced grain protein by 1%. He thought the loss of protein was probably due to nitrogen drain for which the plant could not compensate. As little as a 1% reduction in grain protein can affect the suitability of wheat varieties for breadmaking.

In Finland, Rautapää (1968) found M. avenae reduced yields and changed brewing quality of barley, and that R. padi and M. avenae reduced the extract content of malt but had no significant effect on other brewing qualities (Rautapää, 1972). These aphids also reduced the yield of barley through a reduction in the weight of the grain. In 1966, Rautapää used outdoor cages around spring wheat and showed that heads severely damaged by aphids, yielded an average of 0.129 g/head compared with 0.999g for undamaged heads. Although starch quality was not affected, there was an adverse affect on gluten quality and on germination. Aphids infesting the head at flowering caused greater losses in yield than those infesting the plants only during the period of ripeness. In 1974, Kolbe and Linke found that 20-30 aphids per head of wheat can cause losses up to 10% compared to up to 30% for 150 aphids per head.

Apablaza and Robinson (1967) found in laboratory tests that aphids severely injured or killed seedlings of barley, wheat and oats, causing reductions in the kernel weight of grain even when placed on plants in advanced stages of growth. George (1924) concluded that aphids have little effect on yield until the grain begins to fill, when they can reduce yield. He determined that sampling with suction traps will give an adequate warning at the beginning of a crop infestation, thus making repeated visits and sampling unnecessary.

Grigorov (1967) studied the effect of chemical control on M. avenae. Because of high mortality to predators and parasites after the use of an organo-phosphate insecticide, M. avenae increased in density to high densities after an original 95% kill. Hamilton and Rieckhefer (1969) found in laboratory tests with malathion and parathion that predators were less vulnerable to the insecticides than the aphids, so they thought that an integrated program of control of cereal aphids using these materials had promise. (Forbes (1962) had stated that non-selective materials such as malathion and parathion should not be used, as they are toxic to predators and parasites, but that if chemical control became necessary systemics should be used).

2. Time of Planting

The time of planting has been thought by some to affect the extent of grain aphid infestation. Green (1966) found that barley sown in the early spring in Oregon developed smaller populations of *M. avenae*, but larger populations of *M. dirhodum*, than that sown late. Those two species as well as *R. padi* became established on plants at a later growth stage in early-sown plots than in those sown later. *M. avenae* peaked in numbers when the barley plants headed out but disappeared two weeks later in July. Green thought this disappearance was due to plant maturity accompanied by high temperature and low relative humidity. In his study, *M. dirhodum* also declined sharply in the later part of July, but *M. dirhodum* was not found until later in the spring and only reached population densities as high as *M. avenae* on the early-seeded field. Both species persisted later on plants in fields planted early or in midseason than on those planted later. *R. padi* entered fields later than the other species. Green thought *R. padi* might have preferred plants in which the lower leaves had begun to senesce and lose their chlorophyll. *R. padi* showed more erratic population trends generally, peaking in June when conditions were cooler than in July. This species was most numerous on young plants in late-seeded fields.

3. Population Dynamics

Jones (1972) used emergence cages to trap late aphids in Britain. The cages were large enough to accommodate ripening oat and wheat plants and were surmounted by a removable glass trap containing a cone to prevent the aphids from flying back to the plants. Macrosiphum avenae, S. fragariae, M. dirhodum and R. padi occurred in different proportions every year, but the timing of peak emergence was correlated with weather conditions. Generally, seasons with more sunshine and warmer weather had earlier development of peak numbers. She noted that predators, parasites and the indirect action of hyper-parasites have an important influence on yearly aphid population fluctuations.

Dean (1973) examined the initial colonization of cereals by oat aphids and their movement within the crop. He used suction and water traps to assess alatae numbers. Rhopalosiphum padi invaded the field first and remained the most common species until early June, when all species became more abundant. Metopolophium dirhodum was the first to become scarce in late July, while R. padi and M. avenae stayed until mid-August. After mid-June there was no apparent relationship between maximum aphid densities on the cereals and the number of alatae caught in the suction trap. Movement of M. avenae within the crop was studied by placing heavily infested potted plants within the field. The aphids moved in every direction and did not seem to be influenced by the direction of the wind, although (Dean, 1973) when distribution in relation to shelter was studied, aphid movement seemed closely related to wind direction. The adults mainly invaded areas shaded by hedges and woodland. Dean (1973) also studied the distribution of aphids on tillers and concluded that, until mid-June, when heading begins, the insects were all on the leaves. Thereafter, 76% of M. avenae were on the heads with a few on the flag leaf and two lower leaves. Eighty-five percent of M. dirhodum were on the lower leaves with a few on the flag leaf and head, while R. padi and M. festucae were only found on the lower leaves. Aphids seen moving up and down the stem were not probing or feeding. These results confirmed his earlier contentions that when studying cereal aphids, the entire plant must be collected in order to obtain an unbiased estimate because the different aphid species live on different parts of the plant (Dean and Luuring, 1970).

Dean (1974) found R. padi abundant in the air but not on the crop, and suggested that this discrepancy arose because in Britain the species is mainly a grass aphid. Jones (1972) also suggested that the higher number of that species in the fields she studied in 1971 might be due to the presence of a larger number of grasses between the wheat plants that year. Dean further suggested that changes in cereal varieties, farm practice or climate might be beneficial to R. padi.

Sparrow (1974) studied spring-sown cereals in non-sheltered sites. He, like Dean, found that populations did not peak until the crops had headed out in July or August, two to three weeks before ripening. He suggested that above average temperatures would be required in May and June for the aphids to have increased sufficiently by the end of June to significantly affect yields.

Malyk and Robinson (1971) studied the fates of individual field colonies of cereal aphids. Although large numbers of colonies were found prior to plant heading, many were destroyed by wind, rain and predators. Reproduction rapidly increased the total aphid population, but the proportion of infested plants decreased. Young plants could be killed by aphid infestations, but if the plants werenearly mature when infested, the aphid population declined as the plants ripened.

4. Insect Plant Relationships

Many factors, including the species, variety and age of the plant, the temperature, and predators and parasites, which may affect aphid numbers have been studied separately by many people. Eastop (1973) described insect/plant relationships and included plant preferences of aphids. Ten percent of the aphids listed alternate seasonally between two groups of plants which are often botanically distinct. The host range sometimes varies with temperature; e.g., at medium temperatures aphids are more specific than at high or low temperatures.

Hosts of cereal aphids in Great Britain are listed by

George (1974). The primary host of M. dirhodum is Rosa spp. on which it overwinters as the egg stage. Rhopalosiphum padi also overwinters in the egg stage on its primary host, Prunus padus, and in warm areas it overwinters viviparously on grasses and P. padus. Macrosiphum avenae has as its primary host various graminae on which it overwinters viviparously as well as in the egg stage. The apterous stage of R. padi was found to prefer oats to young bird cherry (P. padus) and actually survived best on oats, while the gynopae preferred bird cherry and only successfully produced offspring on the primary host, P. padus (Dixon, 1971).

Dean (1973) compared the bionomics of the three cereal aphids on barley, oats, and wheat. Metopolophium dirhodum and M. avenae were most abundant on barley, less on oats and least on wheat. Rhopalosiphum padi increased most rapidly on barley and least on oats. Metopolophium dirhodum and M. avenae had shorter generation times and higher survival rates on barley while R. padi did best on wheat. When given a free choice in large outdoor cages R. padi were found on barley. When M. avenae were reared (Apablaza and Robinson (1967)) on wheat, barley, and oats in the laboratory, the barley and wheat plants died before they produced seed. Concurrently M. avenae showed no preference of barley over wheat or wheat over oats.

Plant age was observed by Abernathy and Thurston (1969) as an integral part of insect/plant relationship.

In a study of the resistance of tobacco to *Myzus persicae*, the green peach aphid, a resistant exudate *Nicotiana* was only present in older plants. This demonstrates the importance of always using plants of the same age to study aphid/plant relationships, because the constituents of the plant are continually changing as the plant matures. If animals are simultaneously subjected to plants of varying ages in one experiment, biological differences could appear that were unrelated to the original interest of the test.

5. Temperature Relationships

Dean (1974) studied the effect of temperature on cereal aphids. He found development to be fastest at 25°C for *R. padi*, 20°C for *M. dirhodum* and 22.5°C for *M. avenae*, although the greatest number of nymphs were born at 20°C. Above 15°C, *R. padi*'s developmental rate accelerated faster than the others. The maximum temperature limit, at which all nymphs died before completing their development, was 27.5°C for *M. dirhodum* and 30°C for *R. padi* and *M. avenae*. In general, the pre-reproductive adult stage was longest in *M. avenae* and shortest for *R. padi*.

Dean (1974) reared cereal aphids on winter wheat sheltered from wind, rain and snow. *M. avenae* survived best, *M. dirhodum* less well and *R. padi* least. When exposed, none survived. He found the longevity of *M. avenae* varied inversely with temperature, and fecundity varied directly, with temperature.

In Alberta, Harper (1968) found R. padi actively infesting barley grain stored outdoors on polyethelene sheets at -17°C. They died from unknown causes in late March.

6. Predator and Parasite Relationships

The study of natural enemies is gaining recognition as a tool in understanding population dynamics. Dean and Wilding (1971) found the pathogenic fungi, Entomophthora aphidis, E. planchoniana and E. thaxteriana infecting M. dirhodum and M. avenae in Britain. High humidity and rainfall were thought to weaken M. dirhodum making it more vulnerable to attack. During that season fungus infection proved to be more important than predators or parasites in reducing aphid numbers. Although the attack was too late to prevent infection of the plants by virus, it did prevent aphid numbers from increasing sufficiently to reduce the grain yield. Further work (1973) showed that three species of Entomopthora killed 53% of the M. dirhodum, 60% of the M. festucae and 30% of the M. avenae on wheat. These fungi infected twice as many adult alatae as old nymphs and apterous adults, and seemed to increase after heavy rains.

Three imported parasites of the spotted alfalfa aphid, Therioaphis maculata (Buckton) obtained from Europe and the

Middle East,(Van den Bosch et al., 1959) were successfully mass produced and released in many areas throughout California. Despite interference from insecticides, coccinellids and aphid diseases, the parasites established themselves and are helping to control this aphid.

A detailed account of the impact of natural enemies has been given by Hagen and van den Bosch (1968). They discuss the use of pathogens, parasites, and predators as agents of natural controls and cite many examples from the literature. They stress the importance of collecting data to follow up insect releases and conclude that of the mass of literature only a half a dozen papers had significant information.

Methods of rearing natural enemies of aphids for studying their potential impact are discussed by Frazer et al. (1974). Campbell and Mackauer (1973) found that *Aphidius ervi ervi* (Haliday) and *A. smithi* (Sharma and Subba Rao) two introduced parasites of the pea aphid, *A. cyrthosiphon pisum* were affected by climate. *A. smithi* is dominant in hot and dry conditions, whereas *A. ervi* is dominant in wet and mild conditions. Dean (1974) studied the effects of parasites and predators on *M. dirhodum* and *M. avenae*. Coccinellids and syrphids were the most numerous predators. Parasites generally gave better control than predators. Predators, particularly syrphids, become more important in July.

Small populations of the black bean aphid, *Aphis fabae* (Scop.), are at greater risk from predators than large ones, (Way and Banks (1968)). The smaller populations of aphids remain crowded on a few colonized shoots which allows a few natural enemies to destroy them before many alatae are produced. Larger aphid populations disperse more widely on the plant.

7. Aim of this Study

The most commonly found species of aphids on oats in British Columbia are: *M. avenae* (F.), *M. dirhodum* (Walker) and *R. padi* (L.) (Forbes (1962)). Seasonal differences in populations have been noted, and factors such as weather, vegetation, predators, parasites and disease are known to affect the aphid numbers, but not necessarily to control them.

These seasonal differences in field aphid populations and some of the factors known to affect them were examined. Some hypotheses arising from the field studies were tested by laboratory experiments.

SECTION I

POPULATION DYNAMICS - 1972

1. Introduction

A plot of oats, *Avena sativa* cv Fraser, planted on May 12, 1972 on the campus of the University of British Columbia, was used to study the population dynamics of cereal aphids. The University is located in southwestern British Columbia at 49°11' latitude and 123°10' longitude. Fraser oats, developed for this area was chosen because of its ability to resist lodging. The plot consisted of 34 rows, one metre apart and 26.5 metres long. The oats were sampled for aphids at irregular intervals from June 10 until August 23. The interval depended on the weather, but usually was approximately one week. Sampling could not be done during or immediately after a heavy rain, as the rain washed the aphids off the plants and they required one to two days to re-establish themselves.

2. Materials and Methods

Sampling consisted of choosing three, 7.5 cm long sampling sites per row by using a table of random numbers. Samples from three adjacent rows were combined to make one sample unit of nine 7.5 cm sites. The outer two rows on each side of the plot and the 2 m at the end of each row were excluded from sampling to reduce border influences. Those found to be infested were cut at soil level, placed into cardboard cartons initally, and into plastic bags later in the season when the plants were larger. In the laboratory, a small paintbrush (#000 sable) was used to transfer the aphids from the tillers to a vial of 80% ethanol/5% lactic acid solution for preservation.

Each week the height of a randomly chosen tiller from each sampling site was measured and the number of leaves counted. Later, the area, length of leaves, and height of 20 tillers were measured and the relationships between these variables was used to estimate the leaf area in all other samples. The 20 tillers were carefully selected to represent all sizes of tillers present in the field at sampling time.

Fewer tillers were examined when the numbers of aphids increased (Table 1). Sampling continued until August 23 when the population of the aphids was decreasing sharply.

The aphids in each sample were separated into nymphs and adults under a microscope. The aphids were further divided into the three most commonly found cereal aphid species: Macrosiphum (sitobium) avenae (F.), Metopolophium dirhodum (Walker), and Rhopalosiphum padi (L.).

Counts were made of aphidophagous coccinellidae, (ladybird beetles) by recording the total number of larvae and adults observed while walking up and down the rows at a standard rate.

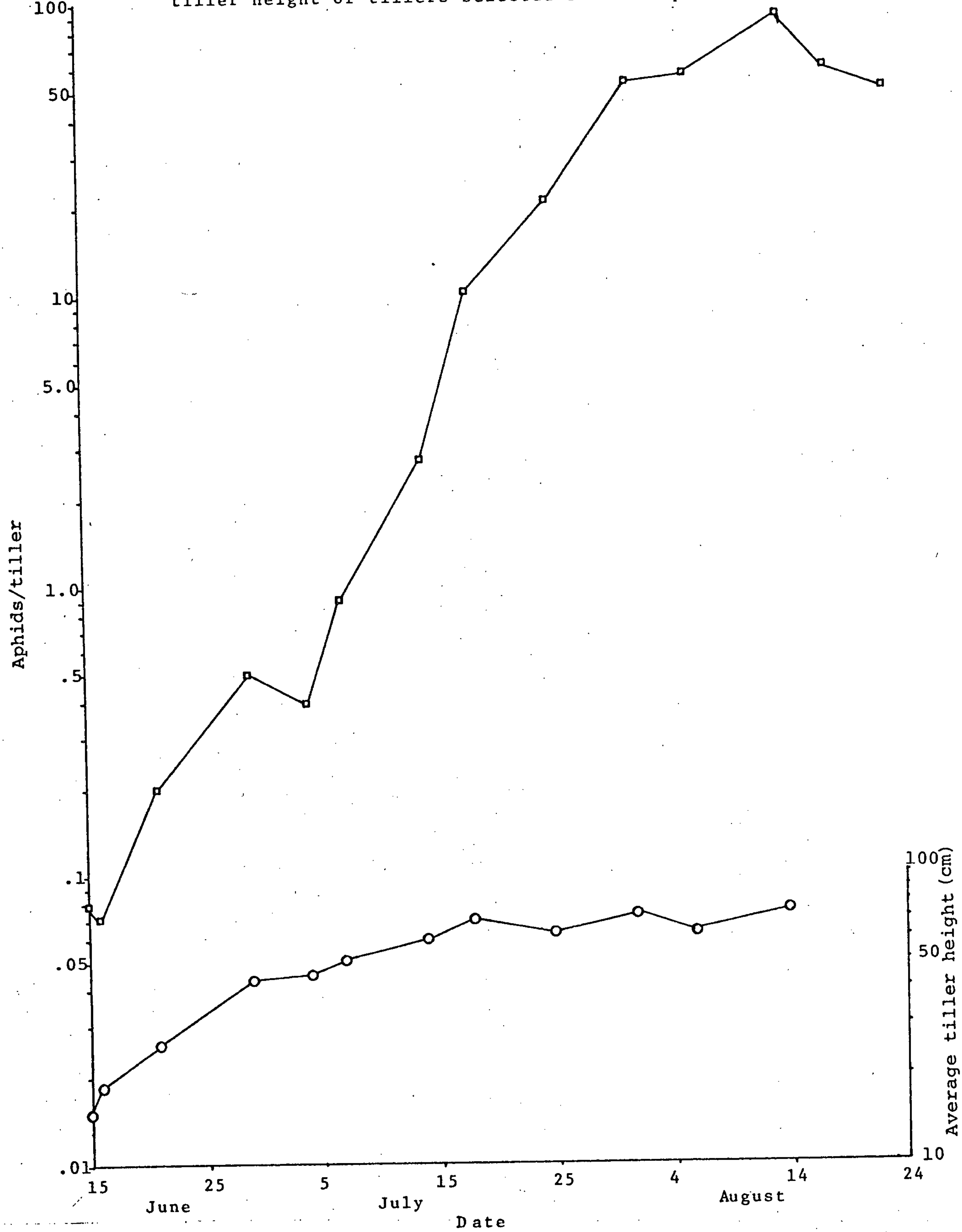
Table 1. Number of oat tiller sampled for aphids on each sample date in 1972

Date	No. of Tillers
June 15	3222
June 16	957
June 21	796
June 29	907
July 4	1088
July 7	1069
July 14	1019
July 18	210
July 25	210
Aug. 1	60
Aug. 6	60
Aug. 14	30
Aug. 18	30
Aug. 23	20

3. Results and Discussion

Aphid numbers increased throughout the season from 0.07 aphids/tiller on June 16 to a maximum of 88.8/tiller on August 14, after which time they began to decline (Fig. 1). There was also a slight decrease in numbers between June 29 and July 4. This decrease may have resulted from the abrupt change in weather at the time. June had been overcast almost every day with frequent precipitation until June 30 when the sky cleared and remained clear until July 6. The average temperature of 71°F $\pm$ 2.83

Fig.1. Total cereal aphids/tiller found in an oat plot, (*Avena sativa* cv Fraser) in 1972, and the average tiller height of tillers selected from the plot.



was 9.5°F higher during these six clear days than the 61.5°F ± 1.59 reached the six previous days.

When the population size was expressed as aphids/cm of tiller height, a similar pattern was followed with .004 aphids/cm on June 16 to 1.22/cm on August 14.

The relative abundance of the three species remained constant throughout the season (Fig. 2). Macrosiphum avenae accounted for 63.5% of the adults found, ranging from .005 per tiller on June 16 to 3.67 per tiller on August 14. Metopolophium dirhodum accounted for 33.5% of the adults per sample, ranging from .003/tiller on June 16 to 1.63/tiller on August 14. Although R. padi arrived earliest in the field with 0.01/tiller on June 15, it reached a peak of only .23/tiller on August 14 and accounted for only 2.94% of the total aphid population. (The "total" aphid population includes the population of all three species).

The numbers of coccinellid larvae observed in the plot on a per hectare basis ranged from 669 on July 25 to 4,909 on August 1 (Fig. 3). Thereafter the numbers decreased. The density of adults was 711.5/ha on the first sampling date of June 21. The adult numbers then decreased to 85.4/ha on July 18, after which they rose to 45,849/ha by August 18. Only one additional

Fig.2. The number of adults/tiller of three species of aphids; Macrosiphum avenae, Metopolophium dirhodum and Rhopalosiphum padi; on a plot of oats, (Avena sativa cv Fraser) during 1972

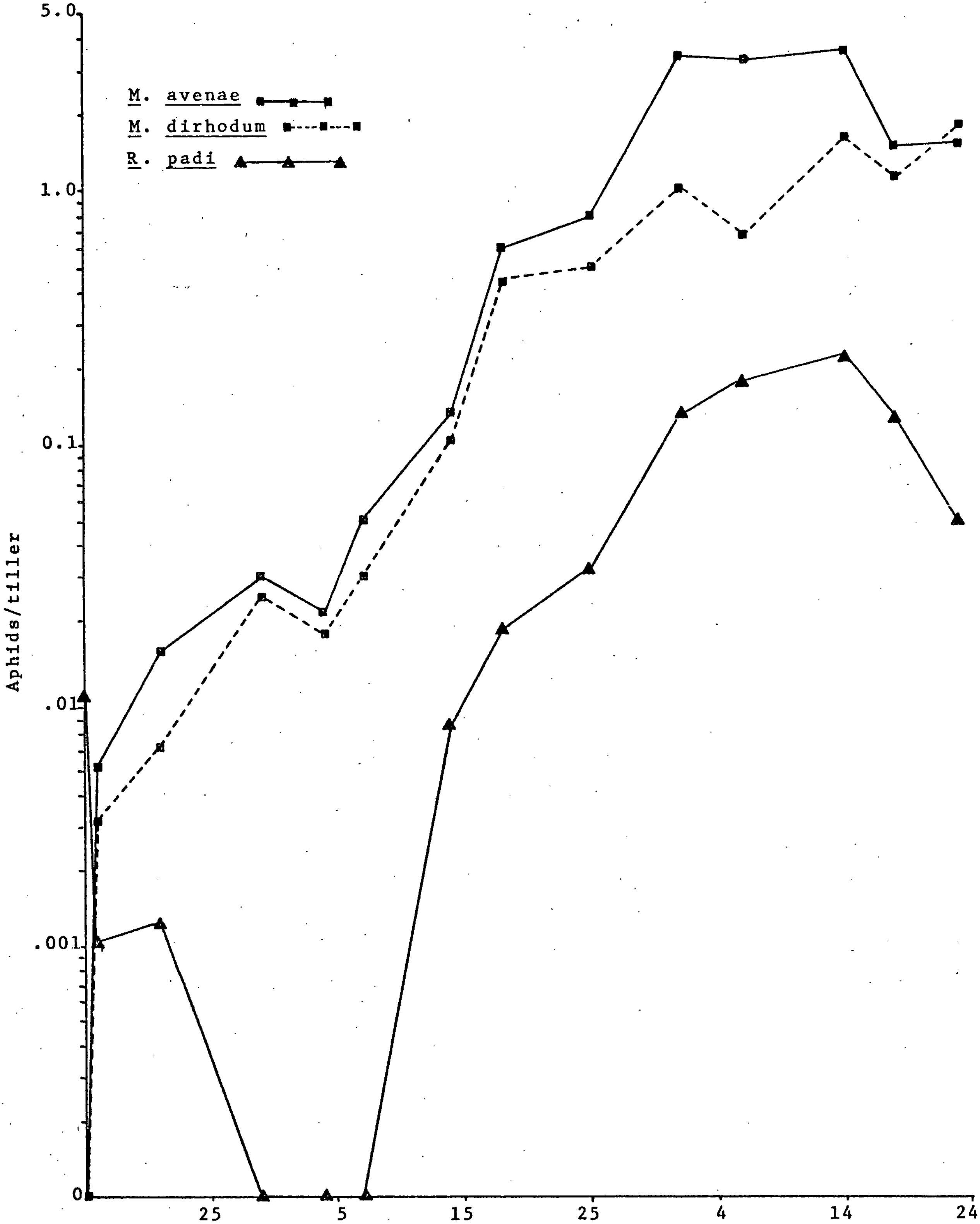
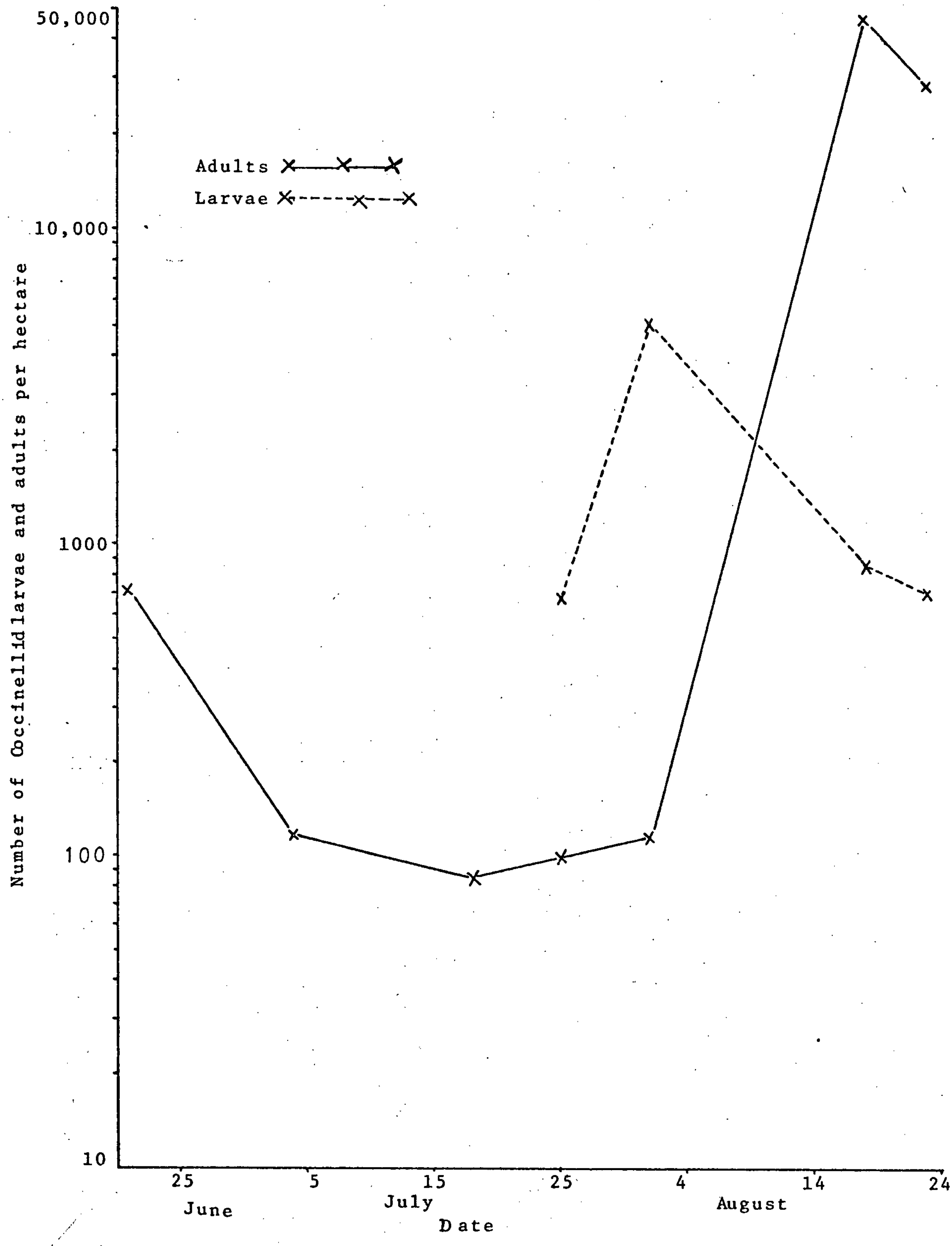


Fig.3. The number of coccinellid adults and larvae found per hectare in a plot of oats, (*Avena sativa* cv Fraser) in 1972



sample was taken on August 23, which indicated a decrease to 28,004.6 adults/ha. The decrease in adult coccinellid density from July 5 to July 18 may be explained by the continuous rainfall from July 7 to July 12 with particularly heavy rain on July 11 and 12 (Fig. 4).

When the number of coccinellid/cm^2 of leaf is compared with the total aphids/cm^2 of leaf, it is evident that the rapid increase in aphid density from July 7 to August 3 coincides with a decrease in beetle density (Fig. 5). Possibly the rain had a more detrimental affect on the beetles than on the aphids, and the resulting decline in beetle numbers then allowed the aphids to increase. The decline in larval coccinellid density coincided with the increase in the number of adults which implies that new eggs were not hatching (Fig. 3).

Figure 6 shows through the division of each weekly unit sample into its ten separate samples that the aphid population was never distributed evenly throughout the field. Each weekly unit sample is a combined total of samples from 3 adjacent rows. During most of the sampling season, the East side of the plot had more aphids. The prevailing westerly wind may have encouraged a movement in this direction but it seems more likely, when compared with Fig. 7, that as the plants were taller, lusher, and healthier in this area, they were able to

Fig.4. The precipitation at U.B.C. weather station for May, June, July and August in 1972

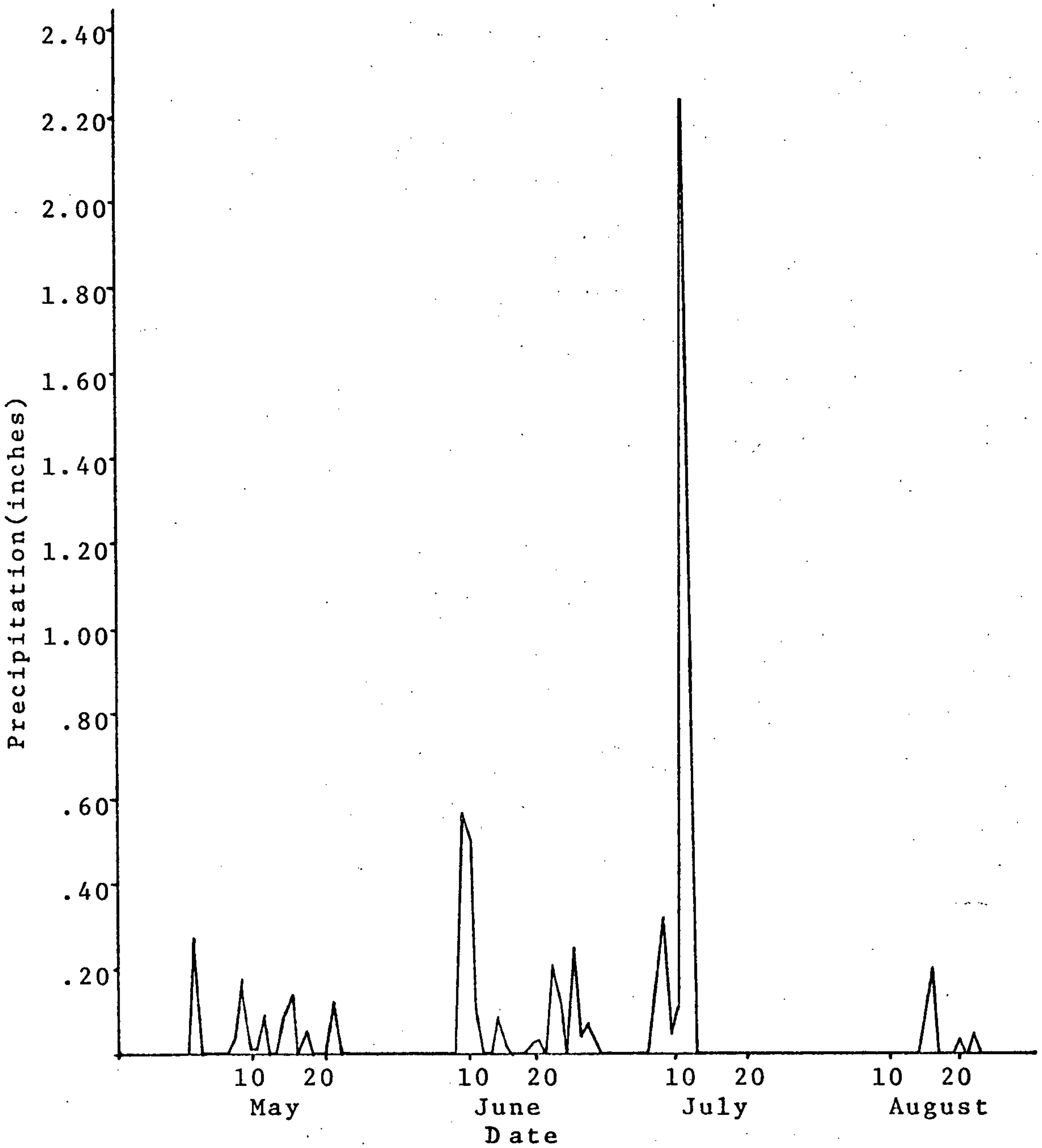


Fig.5. The total number of aphids and the number of coccinellid larvae and adults per cm^2 of leaf found in a plot of oats, (Avena sativa cv Fraser in 1972

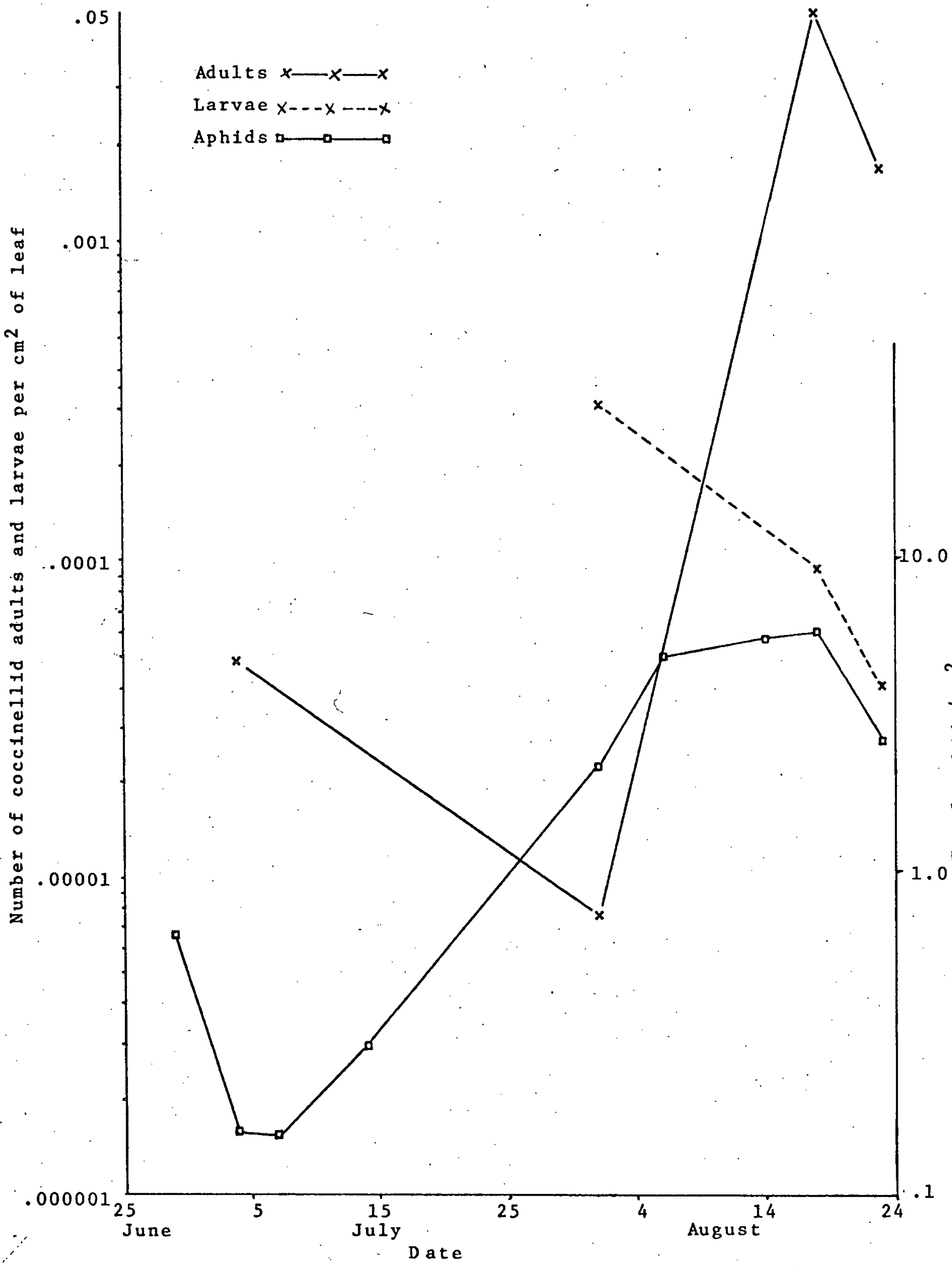
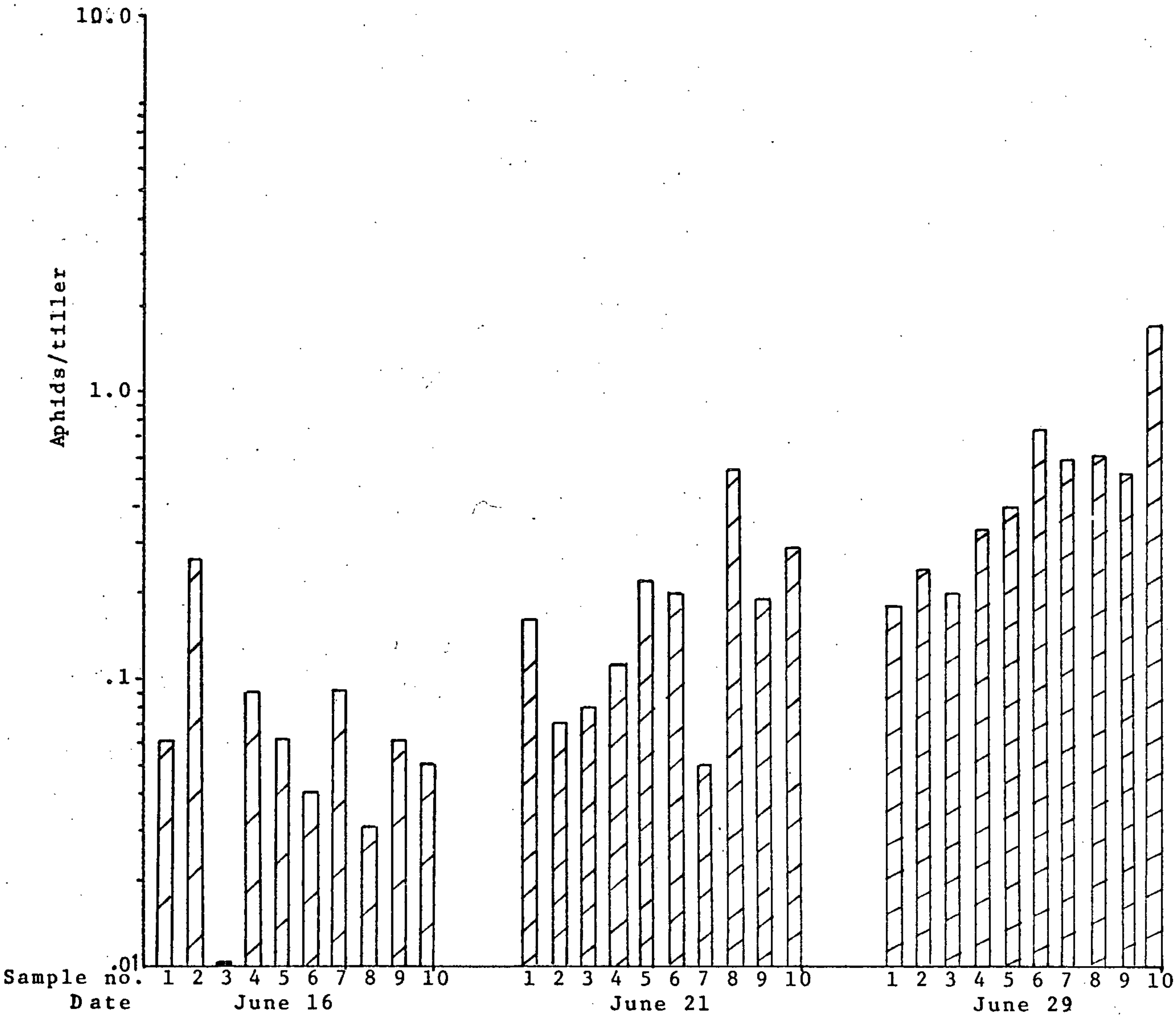


Fig.6. Total aphids/tiller/individual sample of an oat plot, (*Avena sativa* cv Fraser) sampled in 1972



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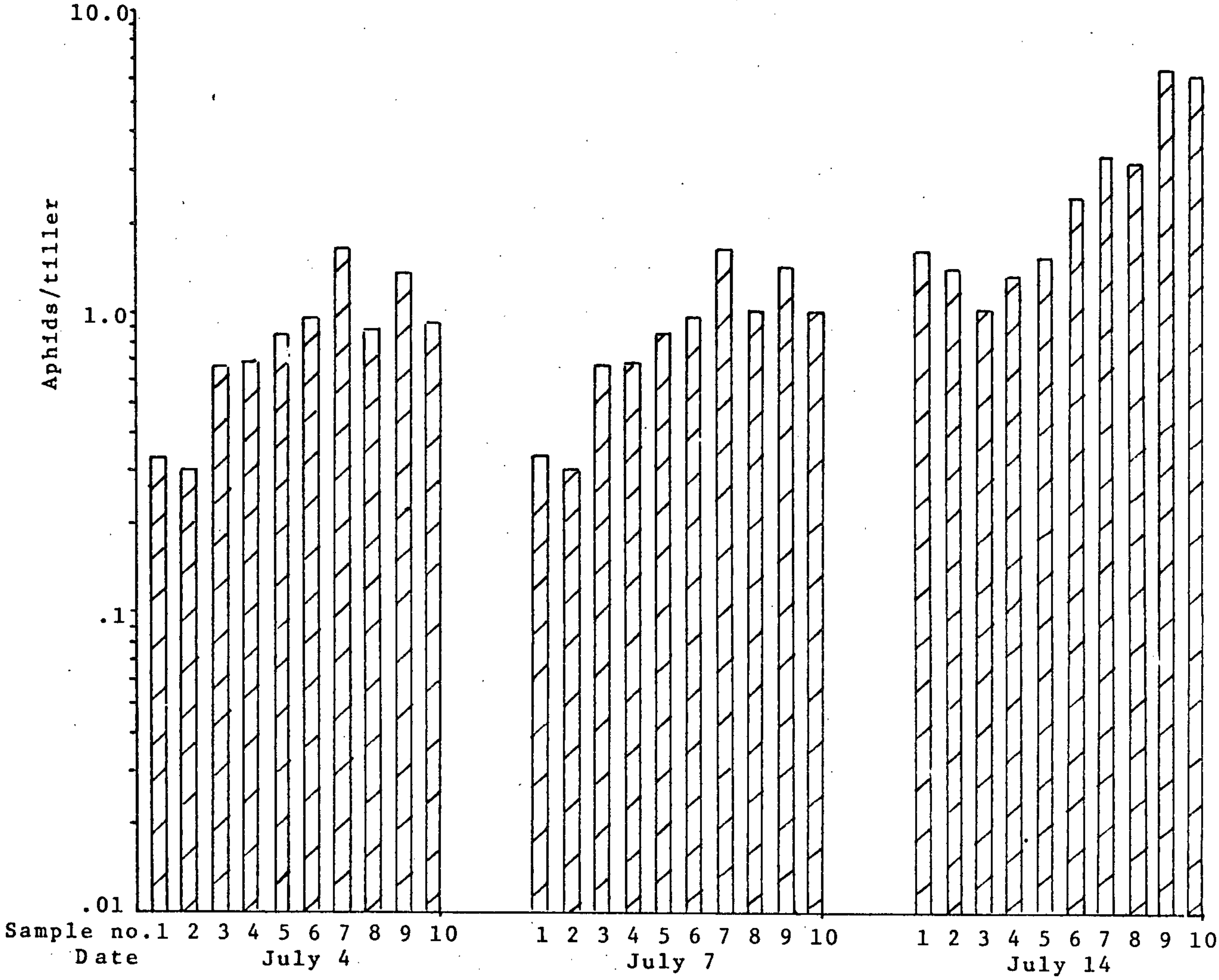

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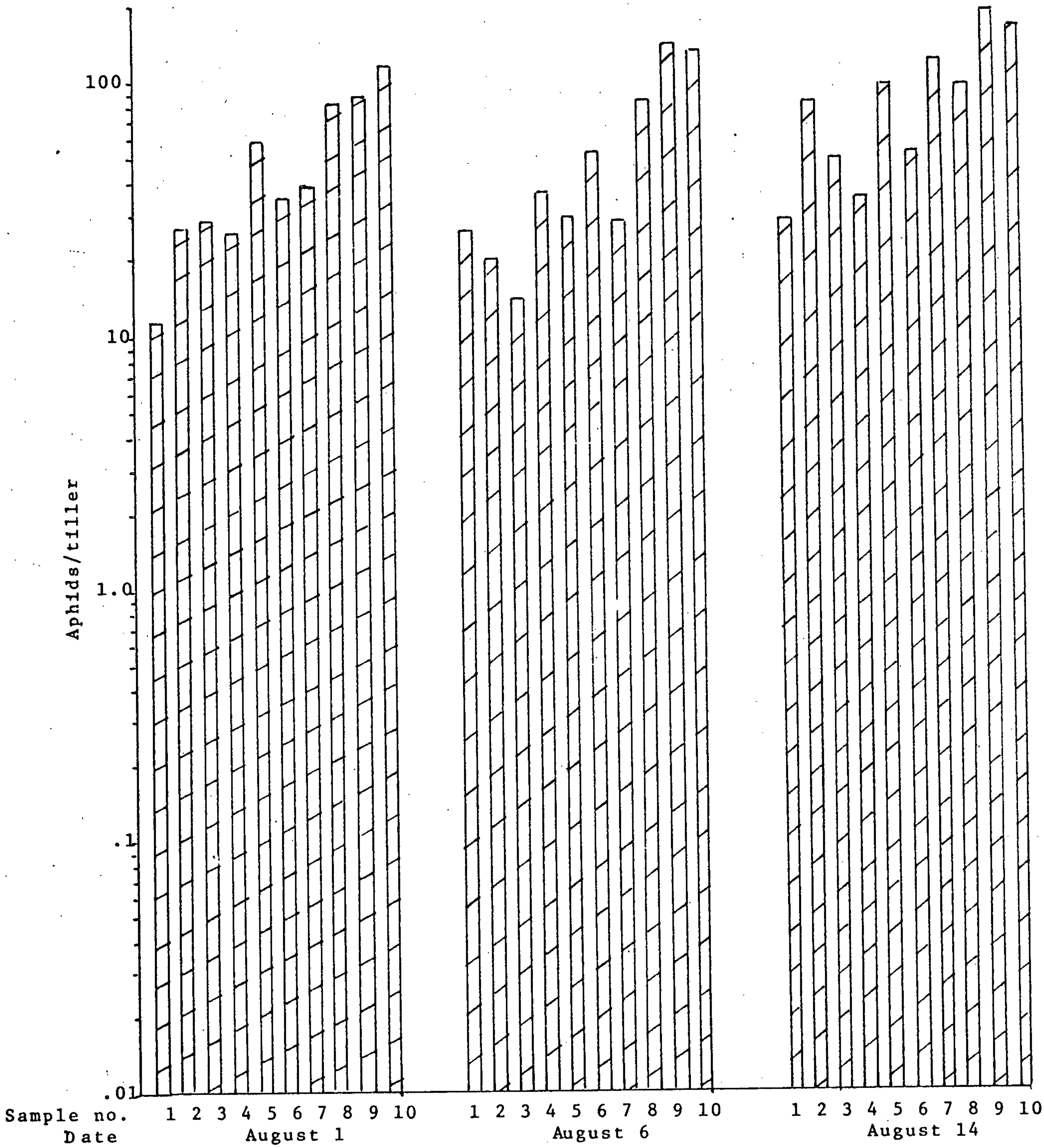

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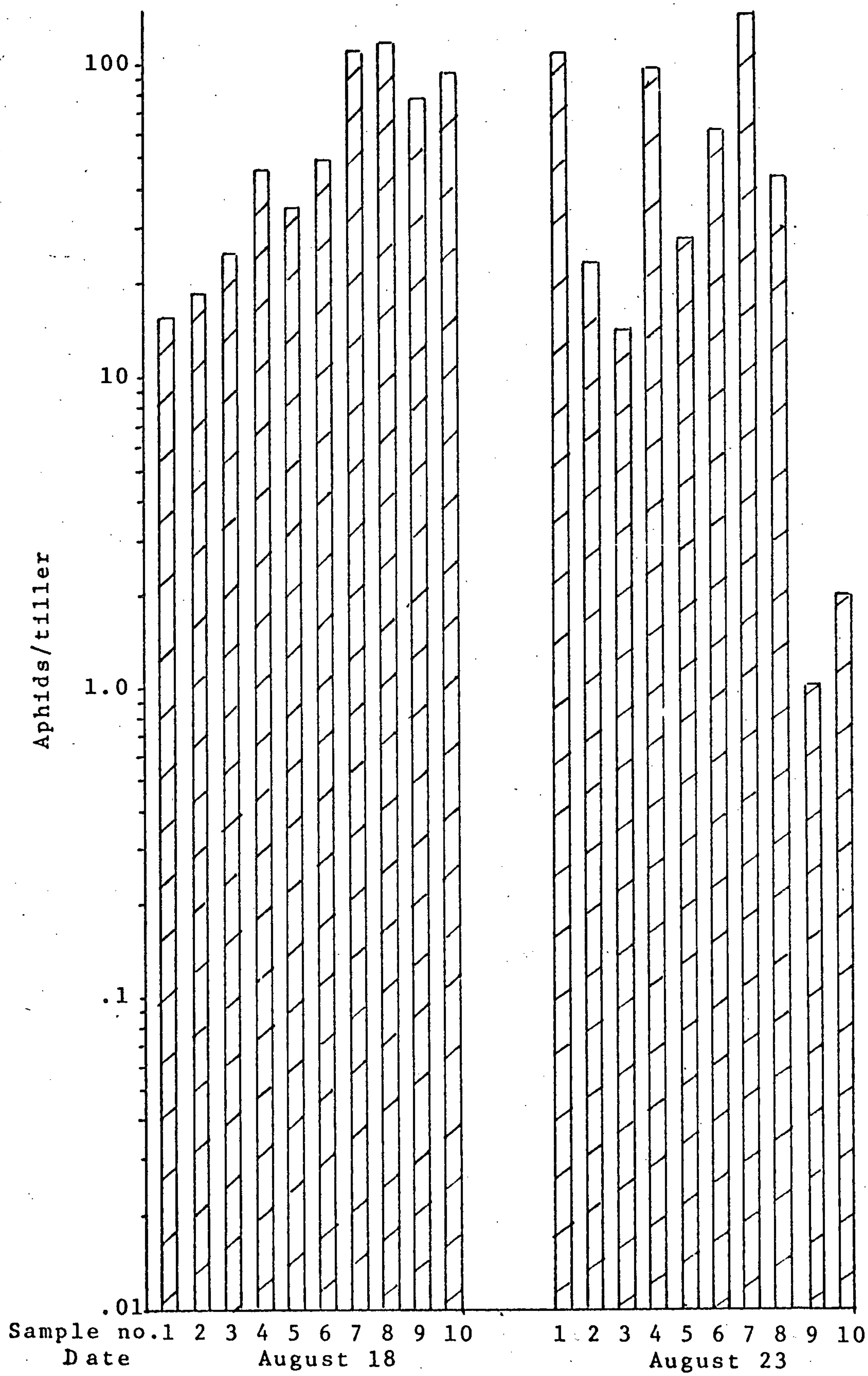


Fig.7. Average tiller height/individual sample in 1972 of an oat plot, (<u>Avena</u> <u>sativa</u> cv Fraser) sampled in 1972

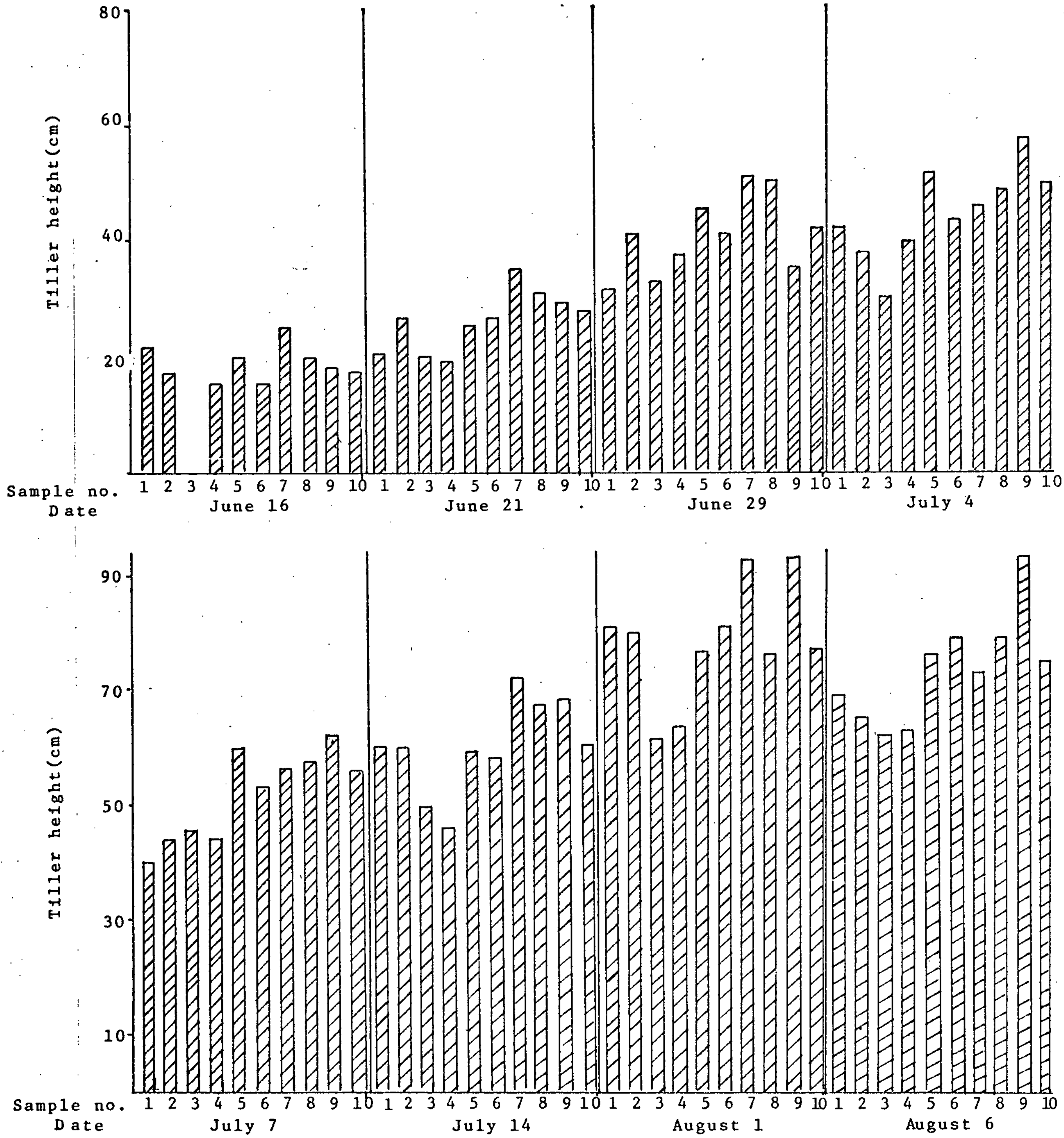
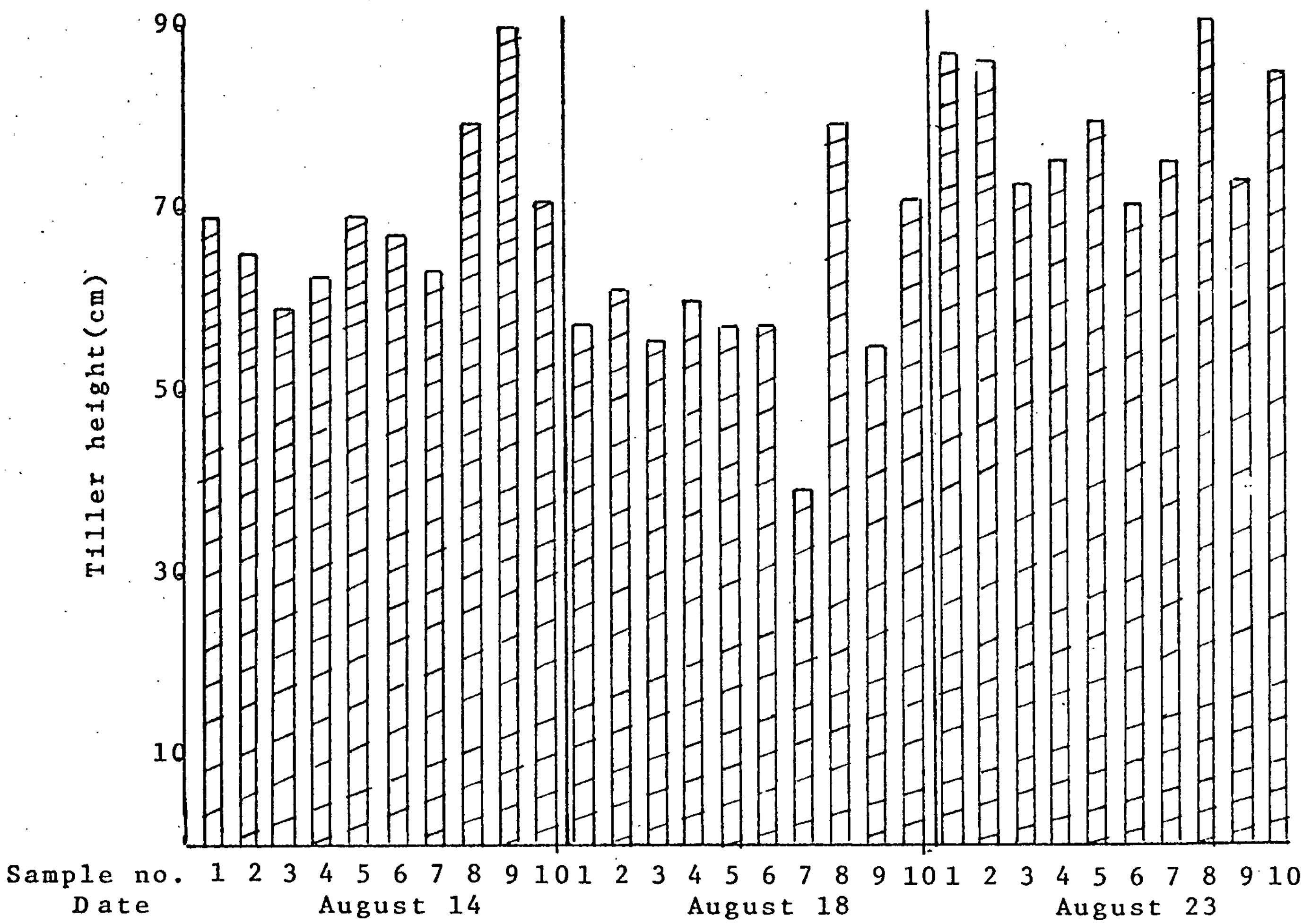


Fig.7. Average tiller height/individual sample in 1972 of an oat plot, (*Avena sativa* cv Fraser) sampled in 1972.



support a higher population. Observations at the time noted that the westernmost rows matured earlier, becoming dry, yellow, and seemingly unattractive to the aphid. The rest of the plot was slightly lower in topography, and the plants grew taller, remained green and lush longer, and probably created a higher humidity more suitable for the aphids. The plant heights had evened out across the plot by August 23.

The effect of plant growth on the aphid population is shown by comparing the total aphids/tiller with the plant height (Fig. 1). The aphid population increased rapidly until August 1, and thereafter at a reduced rate to reach its peak on August 14. On August 1 the plants were growing more slowly than before.

4. Conclusions

Through the season populations of the three species of aphids increased steadily and peaked only once.

Rhopalosiphum padi was the first species recorded in samples in the spring, but remained at low numbers and became even lower on July 4 and July 7. *Macrosiphum avenae* was always the most abundant, with *M. dirhodum* only slightly less abundant.

The rapid increase in aphid population during the season may have been aided by the effects of heavy rain on the beetles in July, as it appears that the beetle population thereafter never attained high enough numbers to greatly affect the aphids.

An increase in temperature and a lack of precipitation may explain the sudden decrease in aphid numbers between June 29 and July 4. Cooler conditions accompanied by some precipitation which followed the decline prompted a continuous increase in aphid numbers.

The higher aphid numbers on the eastern side of the plot may have been due to the better conditions afforded by the taller plants. The numbers of aphids levelled out later, when the plants were growing more slowly. Nutrients may have been less available to the aphids at this time as the plants were reaching maturity and becoming drier. This continued maturation of the plants probably caused the eventual decline in aphid numbers.

These results differ from those obtained at U.B.C. on Victory oats from 1957 to 1960 (Forbes (1962)). Macrosiphum avenae reached two definite peaks instead of one. Metopolophium dirhodum had one peak only but had appreciably lower populations in two years than did M. avenae. Rhopalosiphum padi occurred in appreciable numbers in only two out of the four years. In all cases, the highest densities were recorded in July, one month earlier than the present observations.

Results from England showed R. padi to be the most numerous and with two periods of peak abundance, while *M. avenae* reached its highest density only once, in August. Again the populations of both *M. avenae* and *M. dirhodum* were declining by the end of July (Dean (1973)). Populations of *M. avenae* on barley in Oregon also declined by the end of July (Green (1966)), even though four different planting dates ranging from April 2 to May 10 were used in this study.

Further work might show whether some of these differences result from different planting dates on different varieties of oats.

SECTION II

FECUNDITY

1. Introduction

The population dynamics in 1972 showed constant differences in field densities between the three species of oat aphids. Factors possibly responsible for the differences which were examined at that time were plant growth, coccinellid numbers and weather conditions, but they offered few explanations for the observations. The following experiments on the fecundity of the aphids therefore, were conducted to determine whether the relative abundance of the three species could be explained by differential fecundity. Fecundity trials were also used to evaluate the role of competition, by obtaining information about the reproductive potential of each species reared separately and in conjunction with one another.

2. Materials and Methods

A code devised during the experiments will be used throughout the discussions to represent the eight treatments for studying the fecundity of the three aphid species (Table 2).

Table 2. The identifying code of treatments used to study the fecundity of the three aphid species

Treatment No.	Number of Adult Aphids/Plant	Species	Code
1	1	*M. avenae*	a-1
2	2	*M. avenae*	a-2
3	3	*M. avenae*	a-3
4	1	*M. dirhodum*	d-1
5	2	*M. dirhodum*	d-2
6	3	*M. dirhodum*	d-3
7	1	*R. padi*	p-1
8	1	*M. dirhodum*	pd-1
	1	*R. padi*	

One Fraser oat seed was planted in each of two hundred 5 cm (2") diameter plastic pots. The soil used was acquired locally and had nutrients added to it. Seeds were allowed to germinate and grow to a height of approximately 7 cm in a greenhouse. Twenty plants were selected for each treatment and placed together in a plastic tray containing water where they were kept constantly damp. One adult of each species was then removed from the rearing stock and allowed to produce young. The stock colonies had been started from field collected aphids no more than two months earlier. A 5 cm (2") plastic tube covered with saran screening (40 x 60 mesh/inch) was placed over each plant to cage the aphids. When an adult produced several nymphs it was removed. Depending on the treatment, one, two or three numphs were left on the plant, and when they reached maturity, their daily fecundity was recorded as follows.

Each day every plant was carefully examined for first-instar nymphs which were removed and counted. This procedure was repeated until the adult died. For treatment #8, the fecundities of the R. padi adult and M. dirhodum adult on the same plant were recorded separately. Plants were trimmed regularly to a height of 20 cm. Weak plants were replaced, but in most cases only one plant was needed for the entire life of the aphid.

A Fortran program written by Frazer (1972) was used to calculate Ro, the net reproduction rate (in ♀/♀/generation); T, the generation time, (in days); r, the finite rate of increase, (in ♀/♀/day); rm, the intrinsic rate of increase, (in ♀/♀/day); and DT, the doubling time, (in days). All treatments were analyzed at the 5% level of significance.

3. Results and Discussion

A. Treatment Effects Within Species

i) M. avenae

a) M. avenae (a-1) reached maturity between 10 and 11 days from birth (Table 3). The maximum mean daily fecundity of 1.63 ♀/♀/day occurred on the 13th day with the first adult dying one day later (Figs. 8 and 9). Eighty per cent of all progeny

Fig.8. Daily age - specific survival for Macrosiphum avenae
(The English grain aphid)

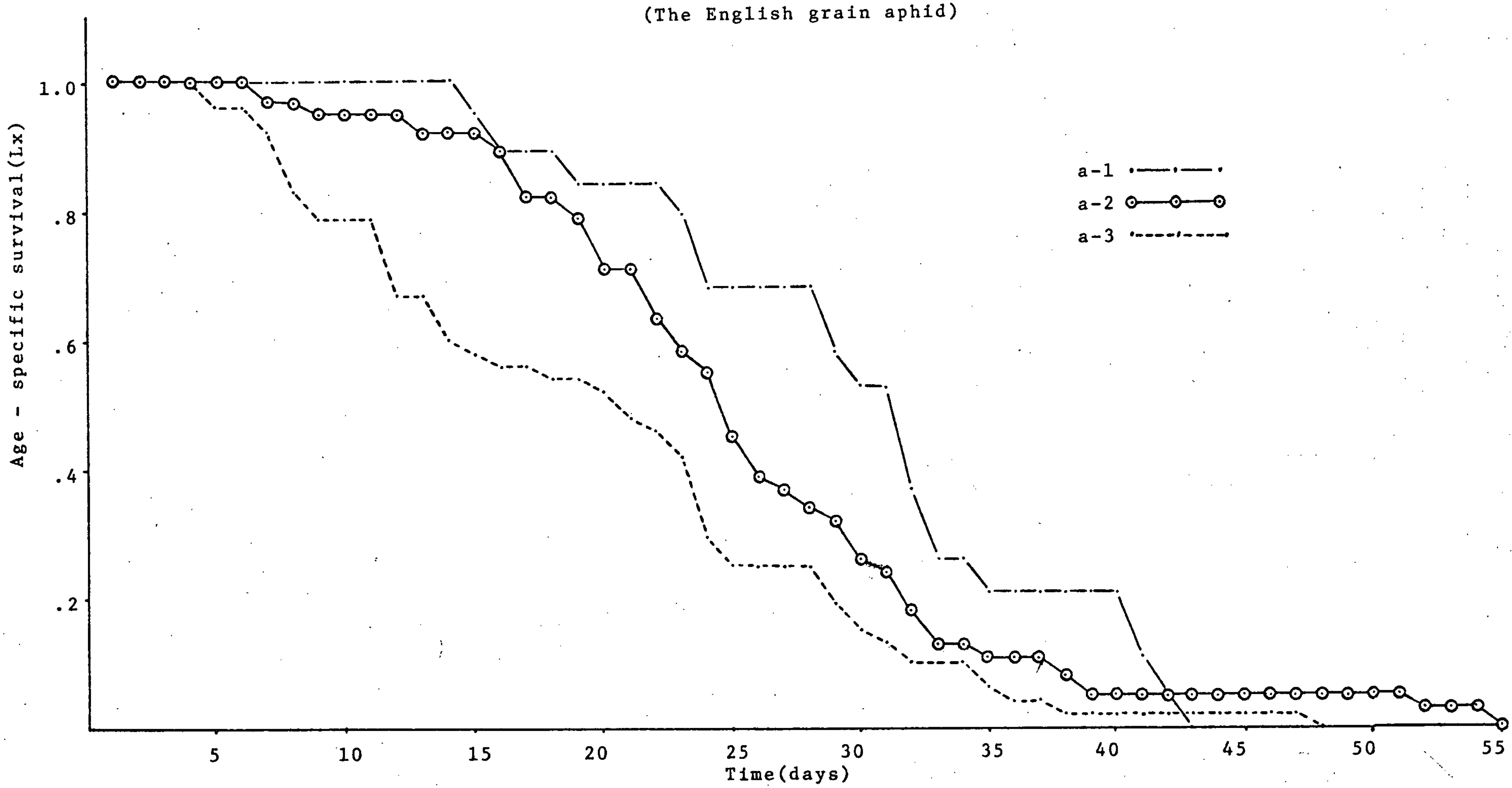
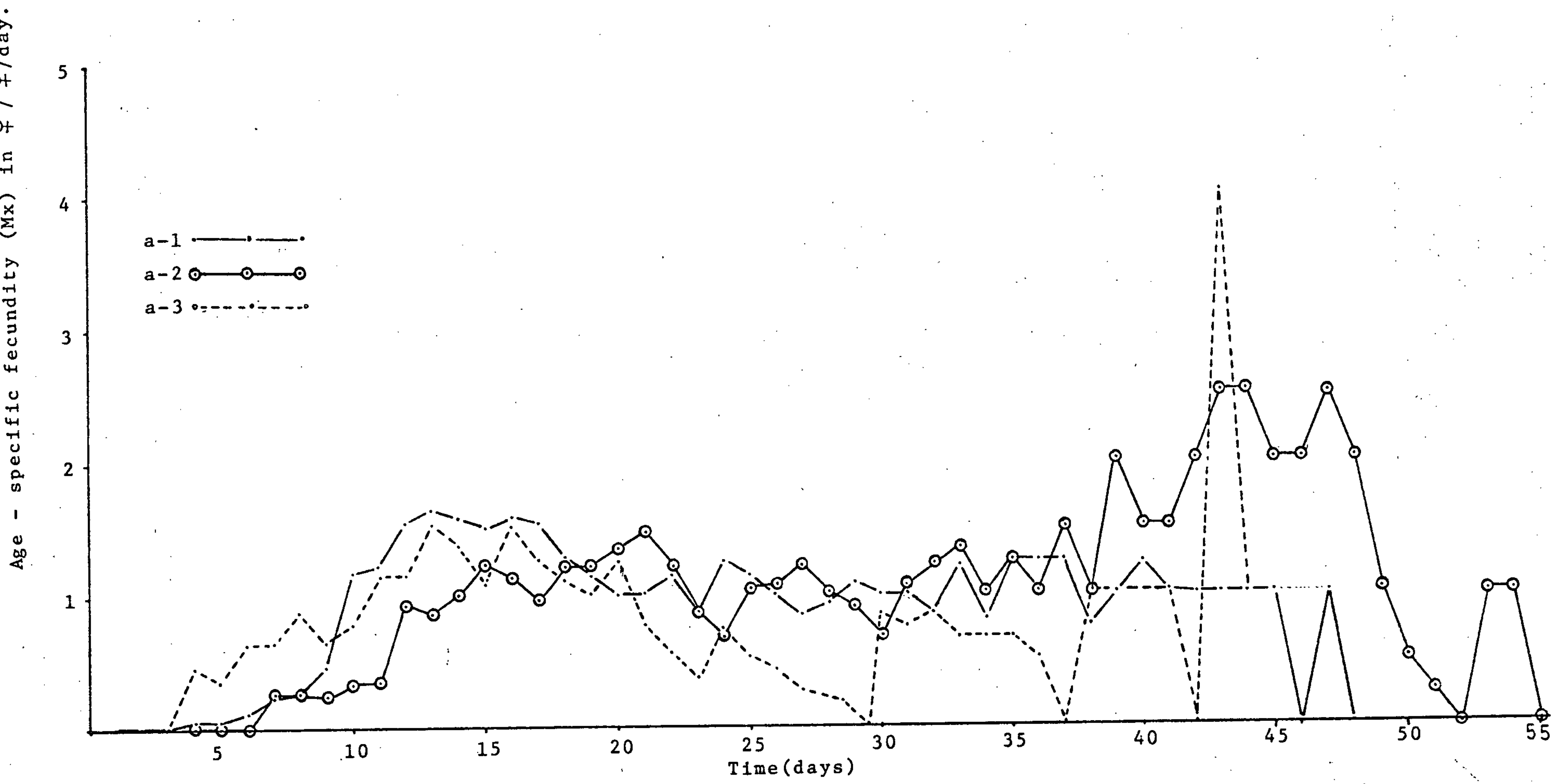


Fig. 9. Daily age - specific fecundity for <u>Macrosiphum</u> <u>avenae</u>
(The English grain aphid)



were produced by the 38th day, when only 16% of the adults were still alive. Reproduction ceased by the 47th day with the last adult dying on the 48th.

b) M. avenae (a-2) did not reach maturity until the 13th and 14th days, which was later than (a-1) (Table 3, Fig. 8). The lower maximum mean daily fecundity of 1.34 ♀/♀ /day was not produced until the 21st day, when 37% of the adults had died (Fig. 9). A higher mean progeny production of 2.5 ♀/♀ /day occurred on the 43rd, 44th and 47th days, but was not as representative a mean, as only two out of the 19 females were still alive at this time (Fig. 9). Eighty per cent of their progeny were not produced until the 45th day, when only 10% of the adults were still alive. (A-2) reproduced longer than (a-1) and did not cease reproduction until the 55th day, when the last adult died, (Fig. 8).

Table 3. Pre-reproductive period, reproductive period and post-reproductive period for various treatments of the oat aphids

Treatment code	Pre-reproductive period (days)	Reproductive period (days)	Post-reproductive period (days)
a-1	10.68±3.42[1]	19.58±8.16	.158±.335
a-2	13.21±2.79	17.21±6.62	1.58±1.94
a-3	6.44±1.53	17.5±5.06	2.63±2.15
d-1	9.06±1.43	16.4±6.05	2.89±2.66
d-2	9.72±.95	22.33±4.0	2.94±2.08
d-3	9.0±.82	26.1±4.98	3.28±2.36
d with p	9.2±2.13	17.67±4.53	1.73±.929
p-1	5.95±2.33	19.0±5.58	3.0±3.09
p with d	8.93±2.17	17.73±8.07	2.4±.888

[1]Mean ± standard deviation

c) M. avenae (a-3) had the shortest pre-reproductive period of the three M. avenae treatments. They reached maturity on the average of 6 to 7 days from birth, which was four days less than (a-1) and 7 days less than (a-2) (Table 3). The first adult died on the 5th day, earlier than (a-1) and (a-2) (Fig. 8). On the 13th day, as with (a-1), the maximum mean daily progeny production of 1.52 ♀/♀ /day was reached when 69% of the adults were still alive (Figs. 8 and 9). Again a higher mean of 4 ♀/♀ /day occurred on the 43rd day, but cannot be considered representative as only one female was alive at this time. Eighty percent of the progeny was produced by the 40th day, when only 6% of the adults were still alive. Reproduction ceased by the 45th day and the last adult died on the 48th (Fig. 8).

d) Comparison between M. avenae treatments

An analysis of variance and a chi square test showed that (a-3) had a significantly lower pre-reproductive period than (a-1) and (a-2) and a significantly longer post-reproductive period. It produced the highest intrinsic rate of increase, (Table 4) probably because of the lower pre-reproductive period (Table 3). The generation time and doubling time are also lowest in this treatment. The net reproductive rate of 13.38♀/♀/generation is lower than both (a-1) and (a-2) with 25.49 and 17.03♀/♀/generation respectively. These data strongly suggest that competition does exist even at a low density of 3/tiller.

Table 4. The intrinsic rate of increase in ♀/♀/day, the generation time in days, the doubling time in days, and the net reproductive rate of eight treatments imposed upon 3 species of oat aphids

Treatment	Intrinsic rate ♀/♀/day	Generation time (days)	Doubling time (days)	Reproductive rate
a-1	0.22	14.43	3.09	25.49
a-2	0.18	16.16	3.95	17.03
a-3	0.26	10.11	2.70	13.38
d-1	0.32	12.27	2.18	49.44
d-2	0.27	14.20	2.61	43.58
d-3	0.30	12.86	2.31	47.11
pd-1(d)	0.32	12.36	2.20	49.20
p-1	0.50	7.88	1.39	51.14
pd-1(p)	0.33	12.10	2.13	51.51

ii) M. dirhodum

a) M. dirhodum (d-1) reached maturity between 9 and 10 days from birth (Table 3). All the adults were still alive when the greatest mean progeny production of 5.72♀/♀/day was reached on the 11th day (Fig.10). The first adult didn't die until the 13th day, and over 83% of them were still alive on the 21st day, when 80% of the progeny had been produced (Figs. 10 and 11). They ceased reproduction on the 32nd day, but the last adult didn't die for another six days.

b) M. dirhodum (d-2) also reached maturity

Fig. 10. Daily age - specific fecundity for Metopolophuim dirhodum.
(The Rose - grain aphid)

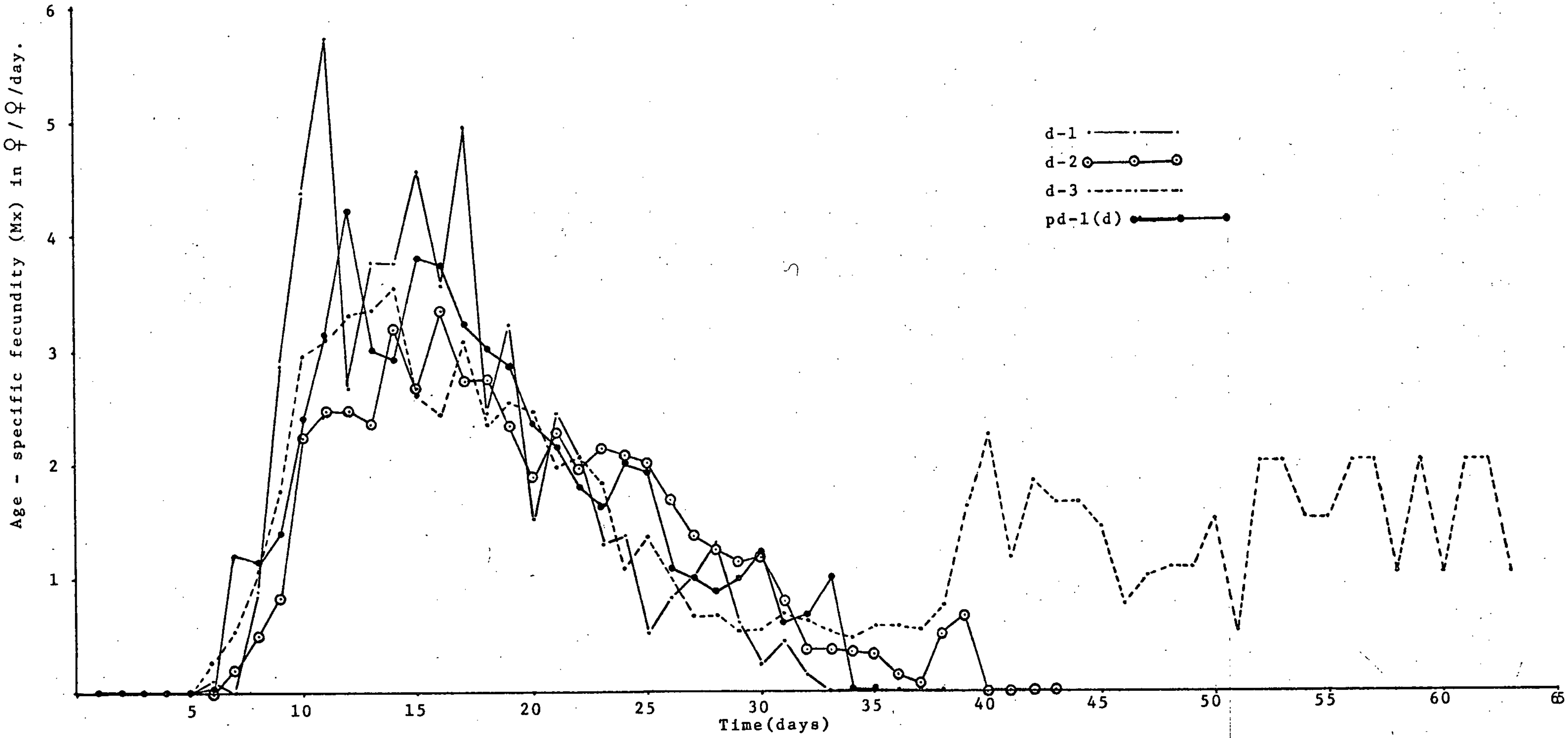
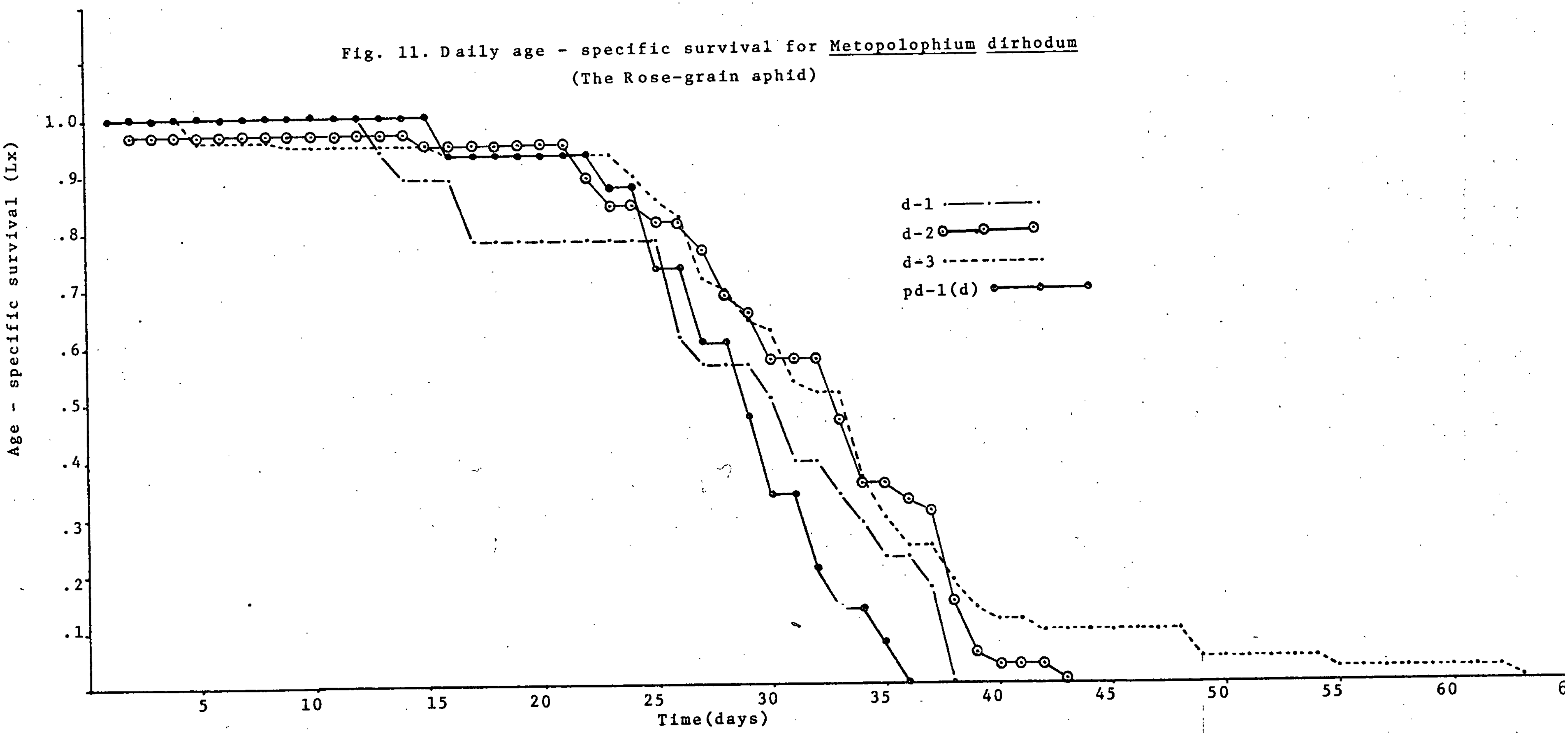


Fig. 11. Daily age - specific survival for <u>Metopolophium</u> <u>dirhodum</u>
(The Rose-grain aphid)



between the 9th and 10th days from birth (Table 3). Eighty-nine percent of the adults were still alive on the 16th day when the mean daily progeny production of 3.33♀/♀/day was reached. D-2 took longer than (d-1) to attain a lower mean progeny production. The lower fecundity of this treatment might have been due to an adult dying in its second day. Eighty percent of the progeny production occurred within the first 26 days when 67% of the adults were still alive. All adults had ceased reproduction by the 40th day, and all had died by the 43rd day (Fig. 11).

c) *M. dirhodum* (d-3) also reached maturity on average by the 9th day (Table 3). The greatest mean daily progeny production of 3.54 ♀/♀/day was attained on the 14th day (Fig. 10) when only two adults (10.5%) had died (Fig. 11). It took twice as long, 53 days, compared with (d-2) to produce 80% of the nymphs. Eighty-eight percent of the progeny had died by this time. The last adult lived for 53 days and had stopped reproduction a day earlier (Fig. 11).

d) *M. dirhodum* with *R. padi* (pd-1(d)).

The fecundity of one *M. dirhodum* adult when reared with one *R. padi* adult was the same as the other three *M. dirhodum* treatments. Average maturity was again reached between 9 and 10 days from birth (Table 3). The greatest mean progeny production of 4.2♀/♀/day occurred on the 12th day when all *M. dirhodum* adults were still alive (Fig. 11). This maximum mean daily progeny production was higher than (d-2) and (d-3) but lower than (d-1). Eighty percent of the progeny were produced by the 24th day, when 87% of the adults were still alive. Reproduction ceased on the 33rd day and the last adult died three days later.

e) Comparison between *M. dirhodum* treatments

An analysis of variance and a chi square test showed only one significant difference between *M. dirhodum* treatments. The reproductive periods of (d-1), with 16.4 days, and (dp-1(d)) with 17.67 days, were significantly less than (d-2) and (d-3) (Table 3). D-2 had a lower intrinsic rate of increase than the others, as well as a lower net reproductive rate (Table 4). It took longer to produce a new generation and longer to double its population, but the observed differences were not great enough to be statistically significant. Therefore crowding *M. dirhodum* on a plant did not alter its fecundity, but did increase the reproductive period which in turn decreases the intrinsic rate of increase.

iii) R. padi

a) R. padi (p-1) reached maturity between 5 to 6 days earlier than any other treatment (Table 3). It reached its maximum mean daily fecundity of 4.76 ♀/♀/day on the 8th day, also earlier than the other treatments, and when all the adults were still alive (Figs. 12 and 13). Eighty percent of the progeny were produced by the 18th day, when 90% of the adults were still alive. Reproduction ceased on the 41st day and the last adult died one day later.

b) R. padi with M. dirhodum (pd-1(p)) reached maturity three days later than (p-1). Its maximum mean daily fecundity, reached three days later than (p-1), was similar to the 4.27 ♀/♀/day noted earlier. A higher mean daily fecundity of 5 ♀/♀/day was reached on the 37th day, but was not representative, as only one (10%) of the adults was alive at that time. Eighty percent of the progeny were not produced until the 24th day, 6 days later than (p-1), when only 60% of the adults were still alive. Reproduction ceased by the 42nd day and the last adult died on the 45th.

c) Comparison between (p-1) and (pd-1(p))

The pre-reproductive period of (pd-1(p))

Fig. 12. Daily age - specific fecundity for <u>Rhopalosiphum padi</u>
(The Oat bird-cherry aphid)

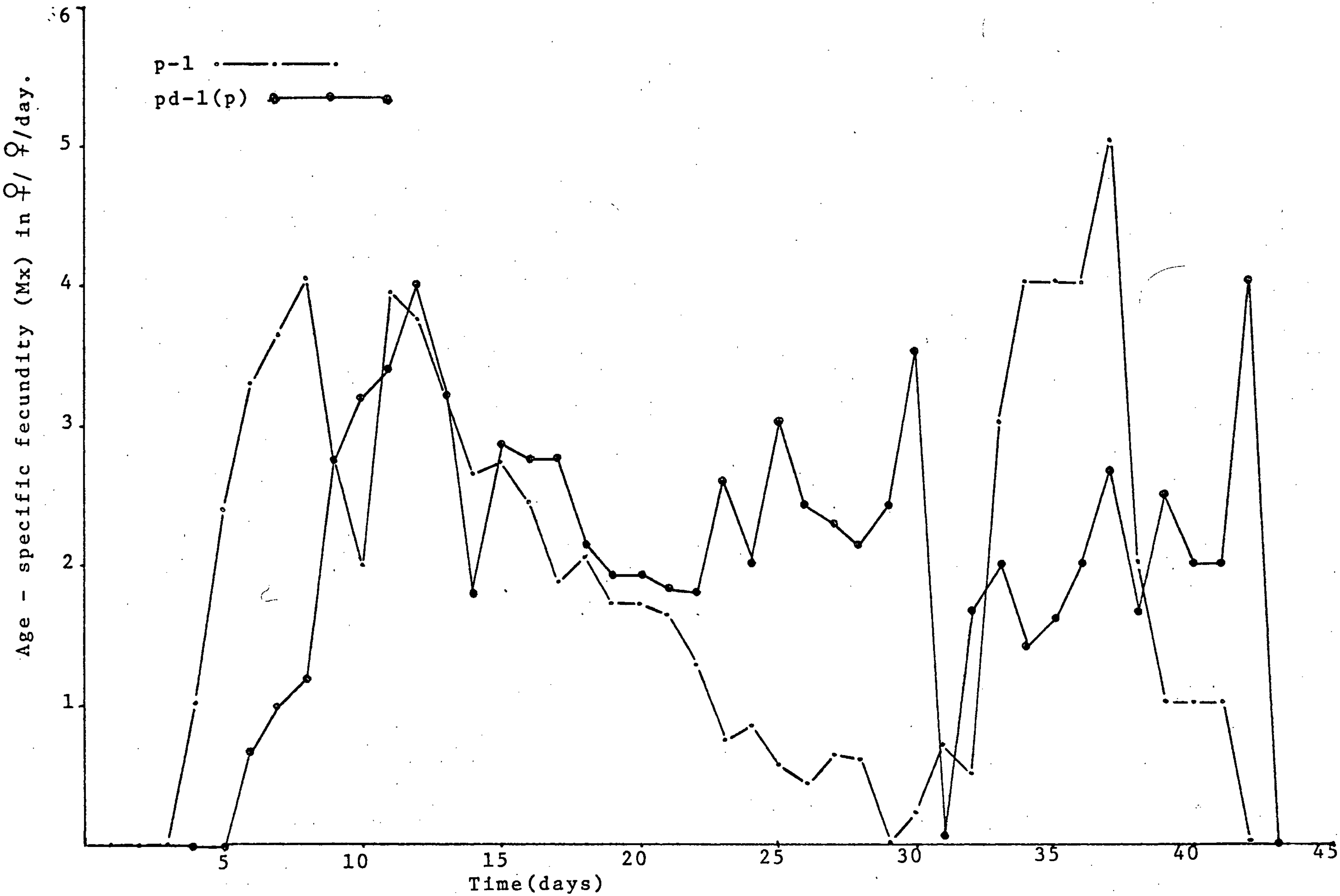
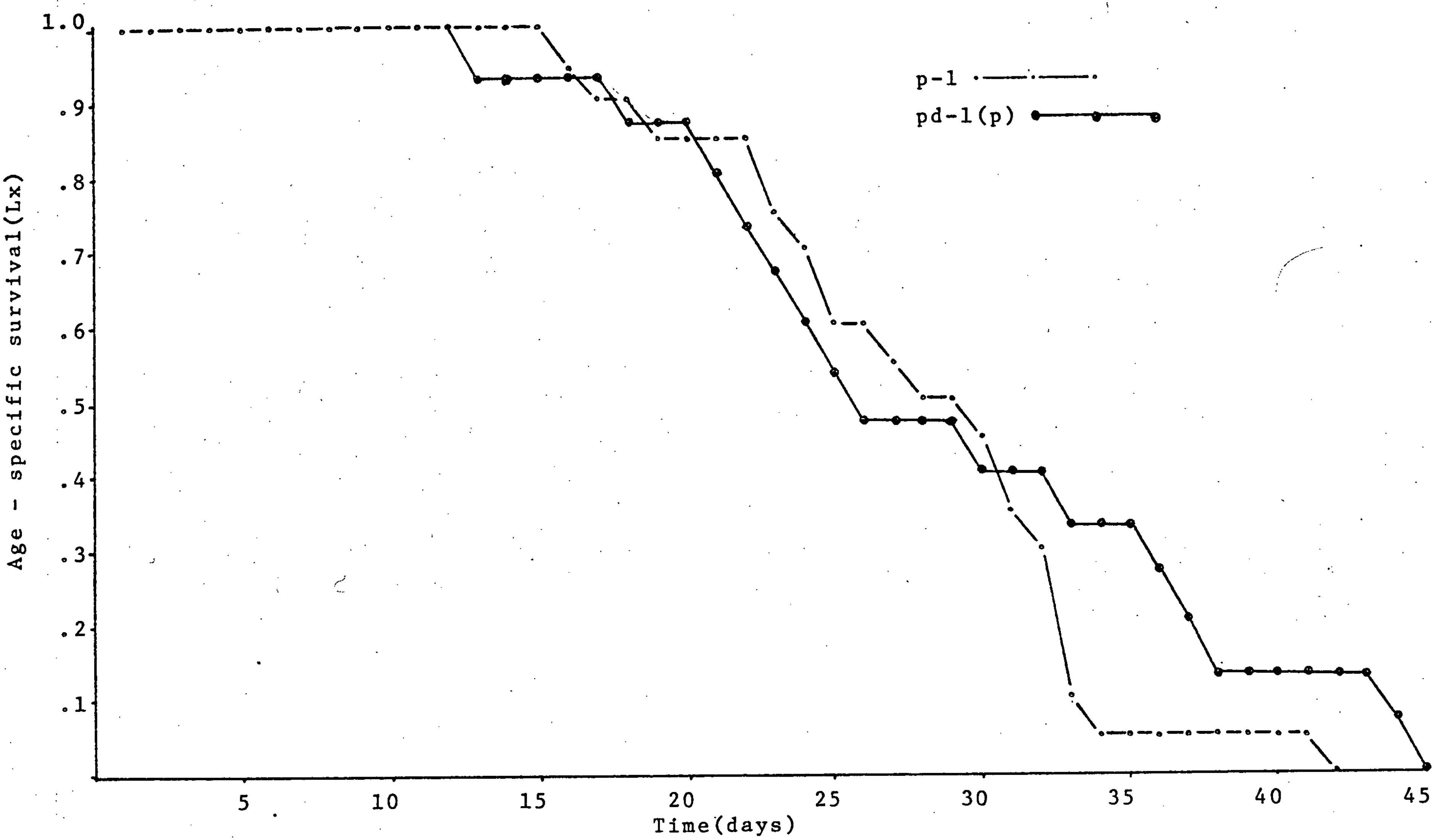


Fig.13. Daily age - specific survival for <u>Rhopalosiphum</u> <u>padi</u>
(The Oat bird-cherry aphid)



tested with a t-test at the 5% level was significantly longer than (p-l) (Table 3). This in turn affected the intrinsic rate of increase, which was lower in (pd-l(p)) than (p-l) (Table 4). The generation time and doubling time were longer in (pd-l(p)) but the net reproductive rate was the same. Thus competition between one R. padi adult and one M. dirhodum adult was evidenced by a lengthening of the generation time, though the net reproductive rate did not change.

B. Treatment Effects Between Species

A t-test at the 5% level showed some significant differences between species. The pre-reproductive period period for M. avenae was longer than that for either M. dirhodum or R. padi. Metopolophium dirhodum's pre-reproductive period was also significantly longer than that of R. padi. Macrosiphum avenae had a lower intrinsic rate of increase and a lower net reproductive rate. It took longer for M. avenae to produce a new generation and longer to double its population than the other two species. The post-reproductive period of M. avenae was significantly shorter than that of either M. dirhodum or R. padi.

The lower pre-reproductive rate of M. dirhodum compared with R. padi's resulted in a lower intrinsic rate of increase. But the net reproductive rate, generation time, and doubling time of M. dirhodum were all higher than R. padi, though lower than M. avenae.

R. padi thus had the highest intrinsic rate of increase and the shortest generation and doubling times, which gave it the highest net reproductive rate of the three species (Table 5).

Table 5. The intrinsic rate of increase in ♀/♀/day, the net reproductive rate, the generation time in days and the doubling time of three species of oat aphids, M. avenae, M. dirhodum and R. padi

Treatment	Intrinsic rate ♀/♀/day	Net Reproductive rate	Generation time (days)	Doubling time (days)
$\bar{x}$ M. avenae	0.21	17.22	13.42	3.27
$\bar{x}$ M. dirhodum	0.30	48.12	12.93	2.31
$\bar{x}$ R. padi	0.43	51.48	9.09	1.60

The mean total number of nymphs produced per female for each treatment is shown in Table 6. These means are supported by those of Dean (1973), which also showed R. padi highest and M. avenae the lowest. Dean reported 54.6 R. padi nymphs/female, 52.9 for M. dirhodum and 36.8 for M. avenae on

Blender oats in controlled conditions.

Table 6. The mean number of nymphs produced per female for each treatment

Treatment	Mean total young per female
(a-1)	25.74
(a-2)	25.63
(a-3)	21.39
(d-1)	51.56
(d-2)	47.71
(d-3)	52.75
(pd-1(d))	47.88
(p-1)	49.12
(pd-1(p))	54.69

C. Conclusion

Competition results when more than one aphid is present on a plant irrespective of the second aphid.

An increase in the number of adults of M. avenae is correlated in a decrease in the pre-reproductive period and a significantly longer post-reproductive period.

The reproductive period of one M. dirhodum adult treated alone or with one R. padi adult was significantly shorter than with more than one M. dirhodum adult.

When the fecundity of one R. padi adult was examined with one M.dirhodum adult, its pre-reproductive period was longer than when it was tested alone.

The pre-reproductive period for M. avenae was longer than that of M. dirhodum or R. padi. Dean (1974) also found that the pre-reproductive stage was shortest in R. padi and longest in M. avenae.

The pre-reproductive period for M. dirhodum was also shorter than R. padi's.

These results do not support the field results from 1972, which showed large populations of M. avenae, slightly lower populations of *M. dirhodum*, and very few *R. padi*. The laboratory results show *R. padi* with the highest fecundity, *M. dirhodum* slightly lower, and *M. avenae* still lower.

Further samplings of field populations and laboratory work were designed to examine environmental factors affecting the aphids and to determine factors other than fecundity that might influence the population dynamics of *R. padi*, *M. avenae* and *M. dirhodum*.

SECTION III

POPULATION DYNAMICS - 1973

1. Introduction

Field sampling in 1972 revealed large differences in population numbers between the three species of oat aphids. The fecundity trials negated the hypothesis that R. padi was lowest in field abundance because of low fecundity. The field plot work of 1973 was done to see what differences could occur between years and to formulate additional hypotheses.

2. Materials and Methods

A. Plot Descriptions

Three plots, each 930 m^2 were planted with Fraser oats.

i) Plot A was planted on May 2 and sprayed with 2-4D ester form on May 28 to combat weeds. Planting was done in 25 rows, each one metre apart so as to duplicate the previous season's work as closely as possible.

ii) Plot B was seeded on May 3 with a herbicide application on May 28. The plot was drilled in solid blocks, each 2.25 m wide, with one metre between them to represent normal farming practices. Each block consisted of 13 drill rows.

iii) Plot C was planted in 8 solid blocks on May 28, approximately one month after the other two plots. The purpose of the plot was to determine whether the time of planting would have a bearing on the ratio of the three aphid species present. No herbicide was applied.

B. Aphid Sampling

i) Plot A - A random number table was used to choose three, 8 cm long sections from each row. All plants in each section were examined for aphids. If aphids were present on a plant, it was cut at soil level, put into a cardboard carton or plastic bag and taken to the laboratory. The aphids were then transferred, with a small # 000 sable paintbrush, to vials of an 80% alcohol/5% lactic acid solution for identification. Sample size decreased as the numbers of aphids increased as in 1972.

ii) Plot B - Sampling followed the same method as for plot A. Eight of the 12 blocks were chosen at random for sampling with 12 sampling sites in each block making up one sample. When the aphid population became very dense, plants were taken, either from a diagonal strip across the whole plot including only the 8 randomly chosen blocks, or of a diagonal strip across each separate block.

iii) Plot C - Sampling followed the same procedure as that used in plots A and B. Irregular plant growth did not permit a satisfactory diagonal sample across the whole plot, so the blocks were always sampled separately.

C. Plant Samples

i) Size

Tillers from each sample were collected and measured on each sample day. The length and number of leaves were recorded.

ii) Percentage Moisture

Representative plants that had been measured were weighed and oven dried to calculate their moisture content.

iii) Sparrow Damage

Field observation in 1972 indicated that sparrows ate the oats as soon as the seed matured. The majority of aphids were on the heads at this time so the sparrows could have had a great influence on aphid numbers. In 1973, as soon as sparrows became evident, a count was made each sample day of the number of grainless husks, to obtain an estimate of sparrow damage.

D. Natural Enemies

i) Coccinellidae

One hundred randomly selected samples, each .3m in length, of plants were searched for coccinellid adults and larvae, three times in plot A and twice in plots B and C. Sampling was then stopped when the numbers became negligible.

ii) Parasites

Hymenopterous parasites were not directly sampled for although an estimate of the parasites present in the field was obtained. All stems collected for aphid samples were checked for parasitized aphids (mummies). Each mummy collected was put separately into a # 3 gelatin capsule. After the parasite had emerged, it was mounted with the mummified aphid and then identified.

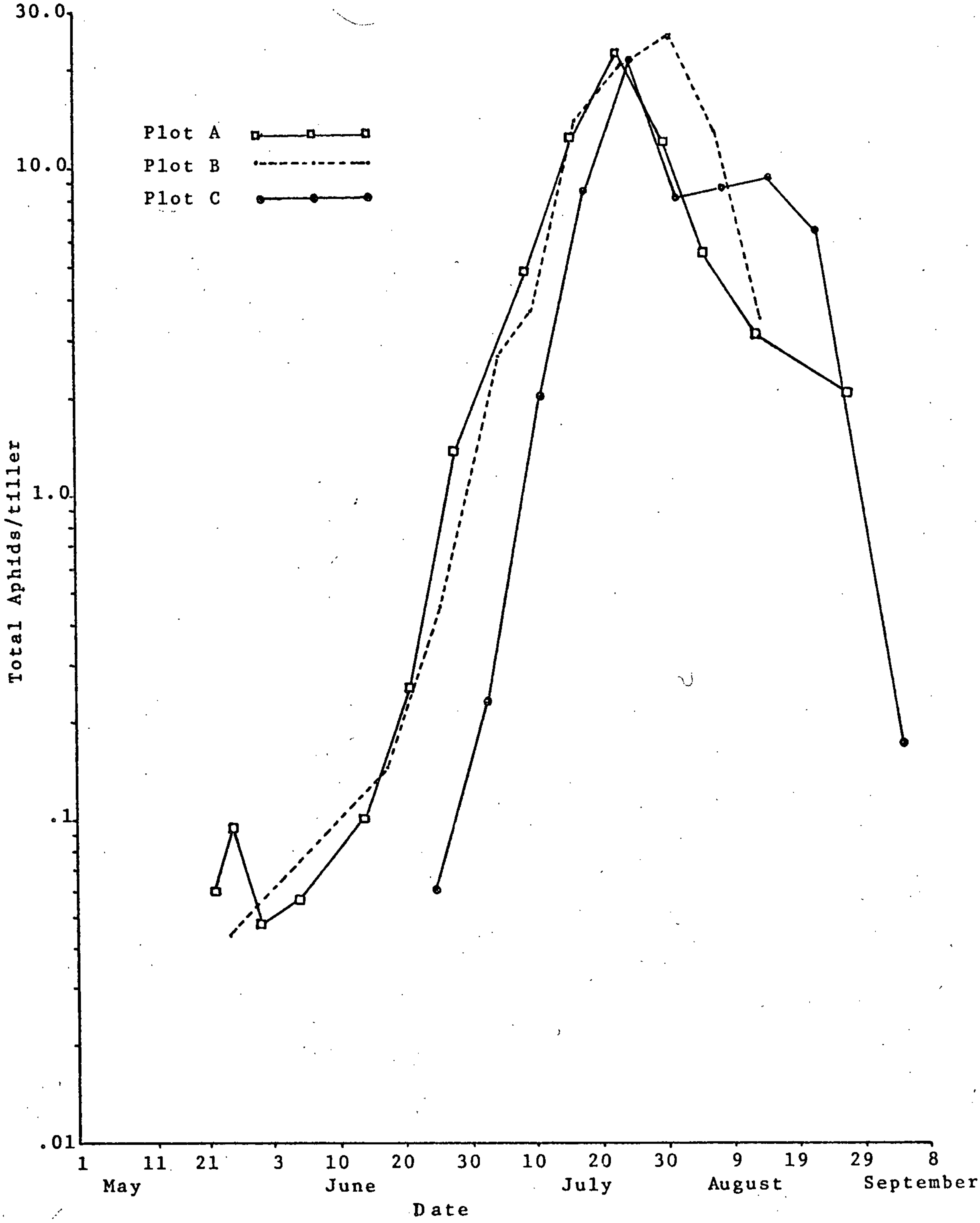
3. Results and Discussion

A. Plot A

i) Aphids

Aphids were first found in plot A on May 22 when .06 aphids/tiller were recovered (Fig. 14). The plants averaged 10.61 cm height at the time. Numbers decreased to .04 aphids/tiller on June 1 and reached a peak of 21.9 aphids/tiller on July 23. No change in pattern was found when aphid numbers were calculated as aphids/cm of tiller height. The decrease in numbers from May 5 to June 7 may have been due partly to a low average grass minimum temperature at that time of 37.38 ± 1.54 ^{o}F, compared to 45.5 ± 1.35 ^{o}F averaged over the eight days

Fig.14. Total cereal aphids/tiller found on 3 plots of oats, (Avena sativa cv Fraser) in 1973

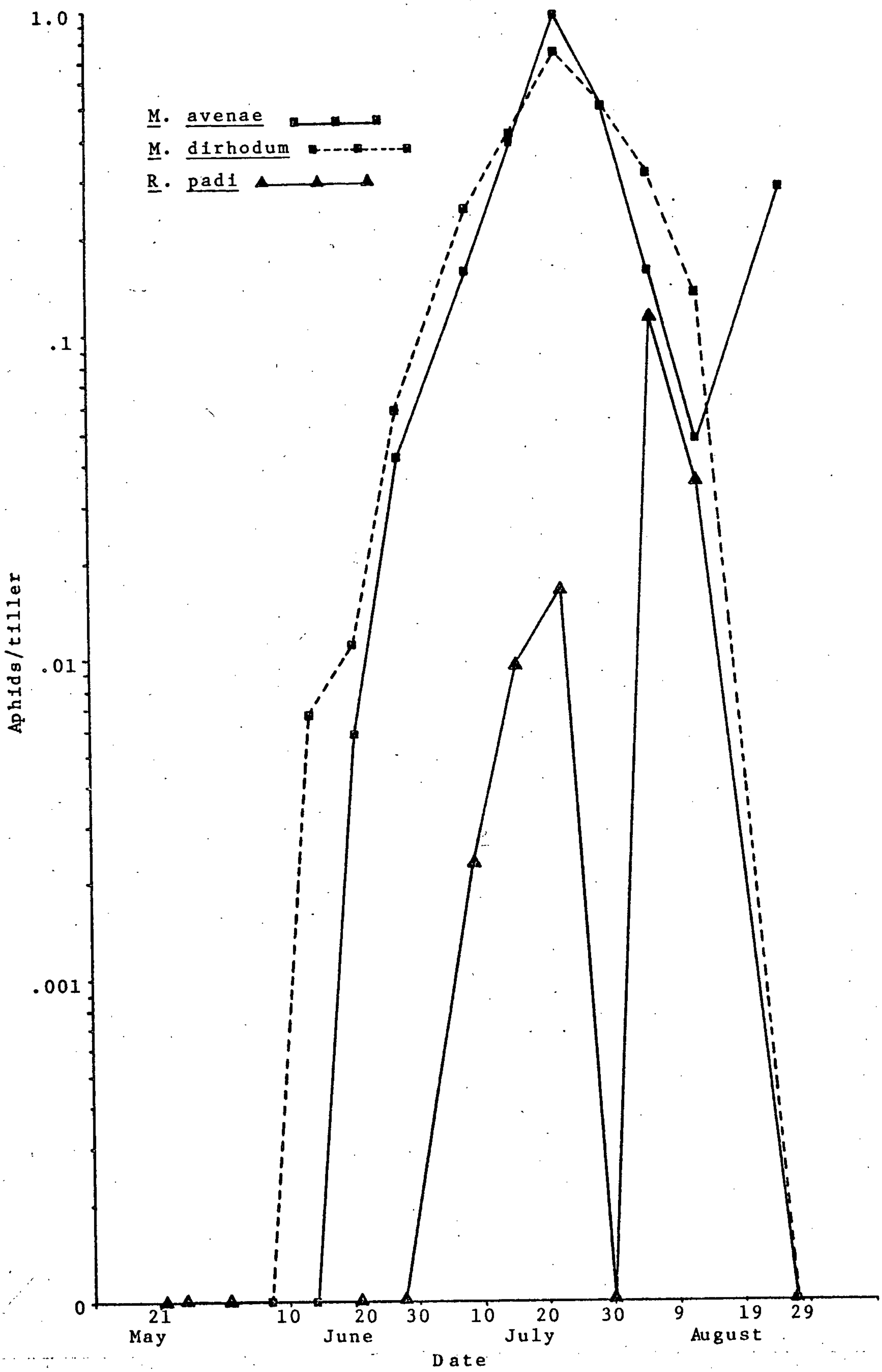


previous to the decrease, and an average of 43.88 ± 2.35 °F over the eight days following the decrease. Dean (1974) reported that these three aphid species produced most nymphs at 20°C (68°F), and M. dirhodum (which was the prodominant species early in the season) at 10°C (50°F). Because the aphids were on small plants, and near the ground, they would have been affected by the grass minimum temperature (which was as low as 32°F (0°C) on May 28). These low temperatures may have caused some aphids to drop off and therefore not be collected in the samples and would have inhibited potential nymph production.

ii) Species Difference

Metopolophium dirhodum produced the first adults and had .007/tiller by June 14 (Fig. 15). They continued to predominate until July 23, when the peak of .7302 adults/tiller actually was lower than that of M. avenae. Metopolophium dirhodum disappeared by the last sample date of August 27.

Fig.15. The number of adults/tiller of three species of cereal aphids; Macrosiphum avenae, Metopolophium dirhodum and Rhopalosiphum padi found during 1973 in plot A, planted with oats, (Avena sativa cv Fraser)



Macrosiphum avenae was recorded next, and on June 21 had .006 adults/tiller. Their numbers were lower than M. dirhodum until July 23 when they reached their peak of .9683 adults/tiller. There were still .286 adults/tiller on August 27 when the last sample was taken.

No adults of R. padi were recorded until July 9, when .0023/tiller were found. They continued to be present in low numbers and reached two peaks, .016 adults/tiller on July 23 and .036/tiller on August 13. None were recorded on the last sampling date of August 27.

The 1973 adult aphid population in plot A was composed of 53.96% M. dirhodum, 43.17% M. avenae and 2.88% R. padi.

iii) Plant Effects

Movement of aphids throughout plot A was slow at first, as shown by the percentage of sampled tillers infested with aphids (Table 7).

Table 7. The percentage of oat tillers (*Avena sativa* cv Fraser) infested with aphids in 1973.

Date	Tillers with Aphids	Tillers without Aphids	Percentage of Tillers with Aphids
Plot A			
May 22	3	97	3.0%
May 25	14	188	6.93
June 2	3	81	3.57
June 7	17	711	2.34
June 14	27	730	3.57
June 21	60	630	8.70
June 28	234	442	43.79
July 9	296	132	69.16
July 16	103	2	98.1
July 23	63	0	100
July 30	34	8	80.95
Aug 6	63	0	100
Aug 13	84	0	100
Plot B			
May 25	7	217	3.13%
June 18	21	436	4.60
June 26	52	312	13.94
July 5	169	456	27.04
July 10	129	72	64.18
July 17	46	2	95.83
July 24	32	0	100
July 31	48	0	100
Aug 7	32	0	100
Aug 14	96	0	100
Plot C			
June 18	0	305	0%
June 25	9	469	1.88
July 3	54	527	9.29
July 11	221	260	45.95
July 18	64	8	88.89
July 25	48	0	100
Aug 1	21	3	87.5
Aug. 8	32	0	100
Aug 15	96	0	100
Aug 22	32	0	100

There was a rapid increase in movement from June 21 to June 28, when the percentage of tillers infested increased almost five times. Probably the increase in the number of adult aphids recovered, particularly M. dirhodum noted then would account for some of this increased infestation (Fig. 15). The plants increased steadily in height from 10.61 cm on May 22 to almost 90 cm by July 30 (Fig. 16). They averaged four leaves each throughout the season. The water content of the plants was 84.7% water on May 22 and it decreased to 57.7% by August 6 when they had headed out and were maturing

The plants were still growing on July 23 when the highest number of aphids/tiller were recorded. Their moisture content had decreased by more than 20% by this time and had produced seed heads. Observations had shown that plot A started to head out by June 27. The degree of maturity reached by July 23 could inhibit the aphid numbers from increasing further.

iv) Sparrow Damage

By July 30, 1973, flocks of sparrows were again eating the oat seeds and presumably any aphids on

Fig.16. The average tiller height of tillers selected from three plots of oats, (<u>Avena sativa</u> cv Fraser) in 1973

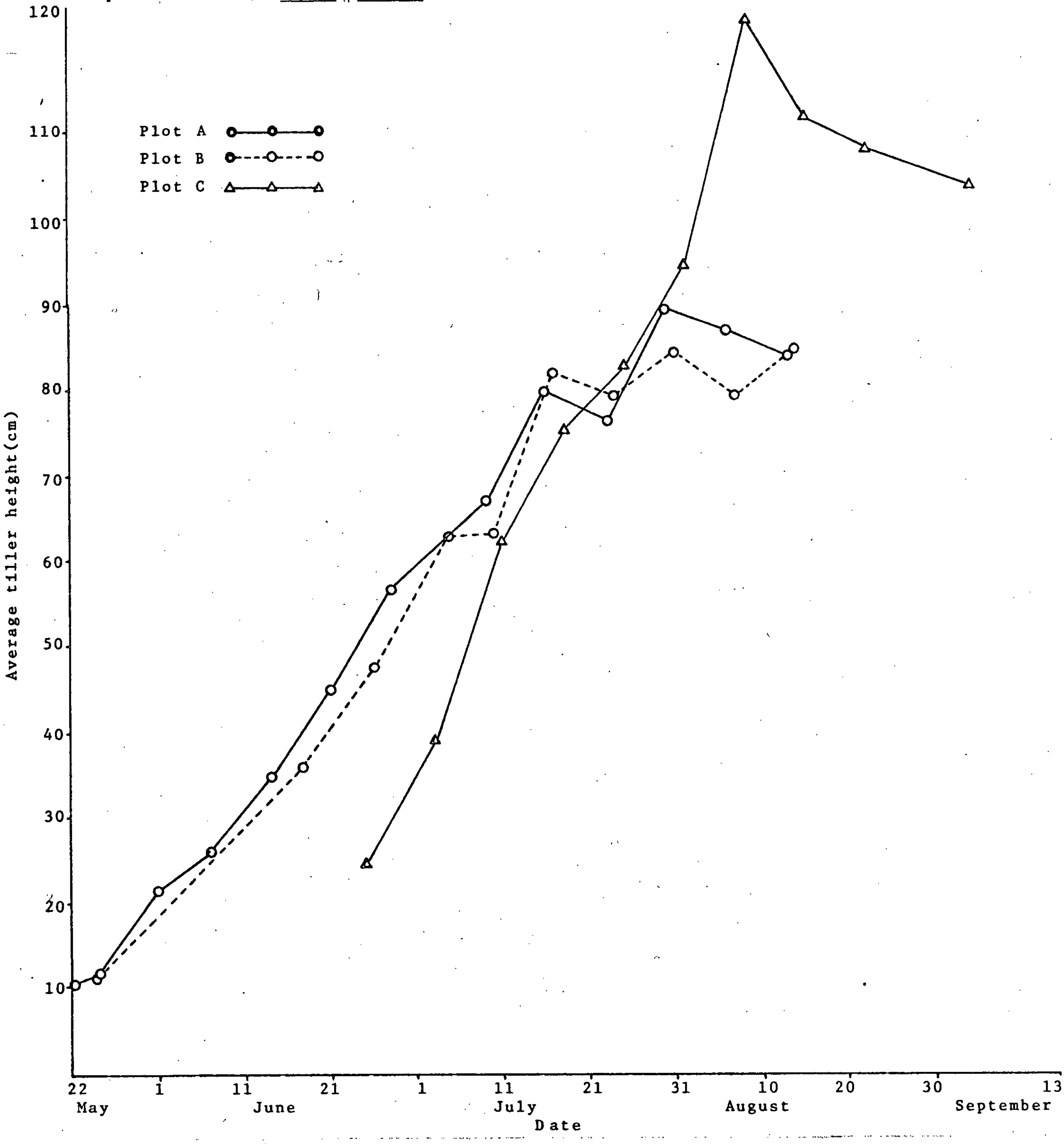
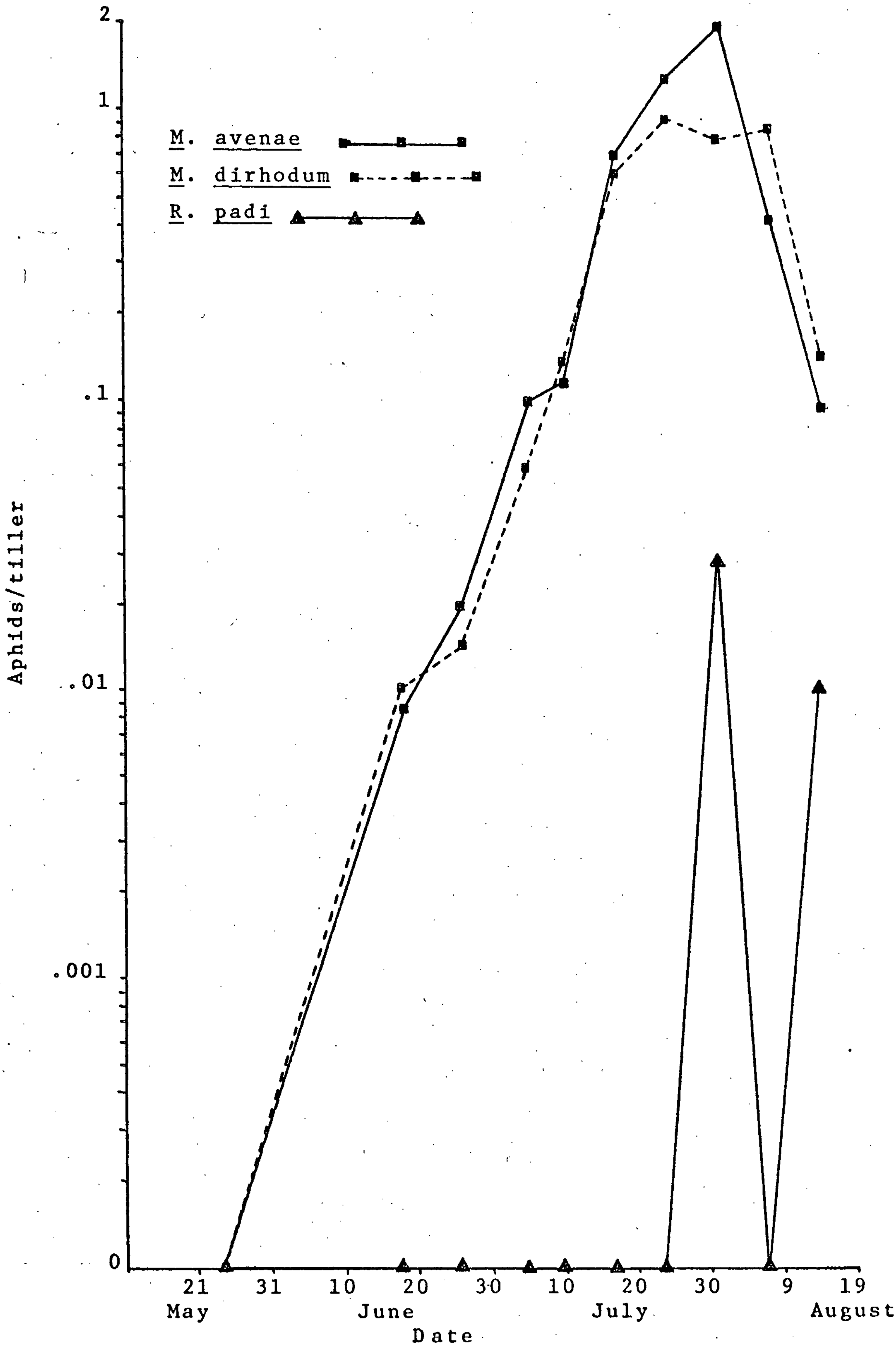


Fig.17. The number of adults/tiller of three species of cereal aphids; Macrosiphum avenae, Metopolophium dirhodum and Rhopalosiphum padi found during 1973 in plot B, planted with oats, (Avena sativa cv Fraser)



the seeds. Weekly counts of the number of husks that did not contain a seed showed that the percentage of husks without seeds increased from 22.65% on July 30 to 70.88% on August 13 (Table 8). When aphids on July 30 were recorded separately for the leaves and heads, 45% of the aphids were on the heads (Table 9).

Table 8. Oat husks with seeds, as normal, and oat husks without seeds due to sparrow damage in 1973.

Date	Husks with Seeds	Husks without Seeds	Percentage of Husks without Seeds
Plot A			
July 30	816	239	22.65%
August 6	837	830	49.79
August 13	428	1032	70.68
Plot B			
July 31	818	212	20.58%
August 7	567	255	31.02
August 14	804	387	32.49
Plot C			
August 8	701	5	.71%
August 15	1223	486	28.44
August 22	601	453	42.98
Sept 4	21	62	74.70

Table 9. The percentage of the aphid sample located in the head of the oat tillers, *Avena sativa* cv Fraser selected randomly from 3 plots of oats in 1973.

Date	Plot No.	Leaves	Heads	% in Heads
July 30	A	233	188	44.66
July 31	B	516	687	57.12
Aug 1	C	57	133	70

These observations indicate that sparrows in Plot A decreased the peak population, even though they did not affect the time of the peak (Table 10).

Table 10. The number of aphids/tiller sampled and the number of aphids/tiller estimated if sparrows had not been present in plot A in 1973.

Date	Aphids/Tiller (with Sparrows)	Aphids/Tiller (without Sparrows)
July 30	11.69	12.88
Aug 6	5.49	6.72
Aug 13	3.18	3.5

v) Natural Enemies

a) Coccinellidae

Numbers of Coccinellid adults and larvae were low, never exceeding .004/tiller all season. Species present were *Cycloneda polita* (Casey), *Coccinella trifasciata* (Mulsant), *C. californica* (Mannerheim), *C. undecimpunctata* (L.) and *Adalia bipunctata* (L.).

b) Parasites

Parasite species present were *Aphidius obscuripes* (Ashmead) and *Praon americanum* (Ashmead).

Hyperparasites present were *Charips* sp., *Coruna clarata* (Walker), *Asaphes* sp. and *Asaphes vulgaris* (Walker).

B. Plot B

i) Aphids

Aphids first appeared in plot B on May 25. The population was then .045 aphids/tiller, increasing to a peak of 25.06/tiller on July 31 (Fig. 14). Numbers decreased to 3.48 aphids/tiller by the last sampling date of August 14. When the population is plotted as aphids/cm of plant a similar pattern is evident with .004 aphids/cm on May 25, a peak of .297 aphids/

cm on July 31 and .041 aphids/cm August 14, the last sampling date.

ii) Species Difference

Macrosiphum avenae was the first species to be recorded, and had .009 aphids/tiller on June 18 (Fig. 17). Their numbers rose until July 31 when they reached a peak of 1.86 adults/tiller. On August 14, the last sampling date .094 adults/tiller were recorded.

Metopolophium dirhodum adults were found first on June 18 when .011 adults/tiller were recovered. They reached a peak of .917 adults/tiller on July 24, decreasing to .146 adults/tiller on the last sampling date of August 14. In all only two R. padi adults were found in plot B and were expressed as .028 adults/tiller on July 31 and .0104 adults/tiller on August 14.

Of the 1973 total adult aphid population, in plot B 56.12% were M. avenae, 43.09% were M. dirhodum and .80% were R. padi.

iii) Plant Effects

Although plot B was planted in solid blocks, the rate of movement of aphids through it was similar to plot A (Table 7), as indicated by the percentage of tillers infested with aphids on each sample day. Aphids moved gradually throughout plot B, so that all plants were infested by July 24, one week before the aphid population peaked.

The oat tillers grew from 10.76 cm on May 25 to 81.89 cm by July 17 when growth levelled off until August 14, when they reached 85.26 cm in height (Fig. 16). They averaged four leaves throughout the growing season.

The water content of the plants was 83.93% on May 25 but had decreased to 54.97% on August 14, when they were mature. The rate of plant growth slowed down two weeks before the aphids peaked. Seed heads started to form by June 30, when more than 24.18% of the plant moisture had been lost.

iv) Sparrow Damage

Large flocks of sparrows were observed eating oat seeds in plot B by July 25. Succeeding samples had the number of husks with and without seeds recorded separately (Table 8). Far fewer seeds were eaten by sparrows in plot B than in plot A, probably because plot B was adjacent to buildings and a busy parking lot. The percentage of husks without seeds increased from 20.58% on July 31 to only 32.49% on August 14.

Plants from the July 31 sample had the aphids on the seed head recorded separately, revealing that 57.12% of the aphids were found on the heads (Table 9). Damage from sparrows changed the peak number of aphids from 25.06 aphids/tiller to a potential of 28.00 aphids/tiller, but was not enough to delay the peak date (Table 11).

Table 11. The number of aphids/tiller sampled and the number of aphids/tiller estimated if sparrows had not been present in plot B in 1973.

Date	Aphids/Tiller (with Sparrows)	Estimated Aphids/Tiller (without Sparrows)
July 31	25.06	28.00
Aug 7	12.94	15.23
Aug 14	3.48	4.13

v) Natural Enemies

a) Coccinellidae

Few Coccinellid adults or larvae were found in plot B in 1973. The highest number recorded was only .0007/tiller. Species present were Coccinella californica (Mannerheim), C. undecimpunctata (L) and Coccinella trifasciata (Mulsant).

b. Parasites

Parasite species present were Aphidius obscuripes (Ashmead) and Praon americanum.

Hyperparasite present were Charips sp., Coruna clarata (Walker), Asaphes sp. and Asphes vulgaris (Walker).

C. Plot C

i) Aphids

The first samples to contain aphids in plot C were taken on June 25, with .061 aphids/tiller (Fig. 14). The population peaked with 21.06 aphids/tiller on July 25 and decreased to .17 aphids/tiller on September 4. The aphid population followed a similar trend when calculated as aphids/cm of tiller height with .0025 aphids/cm on June 25, a peak of

.03 aphids/cm on July 25 and .0016 aphids/cm on September 4, the last sampling date. In both cases the population decreased from July 25 to August 1 and increased again to a second smaller peak on August 15.

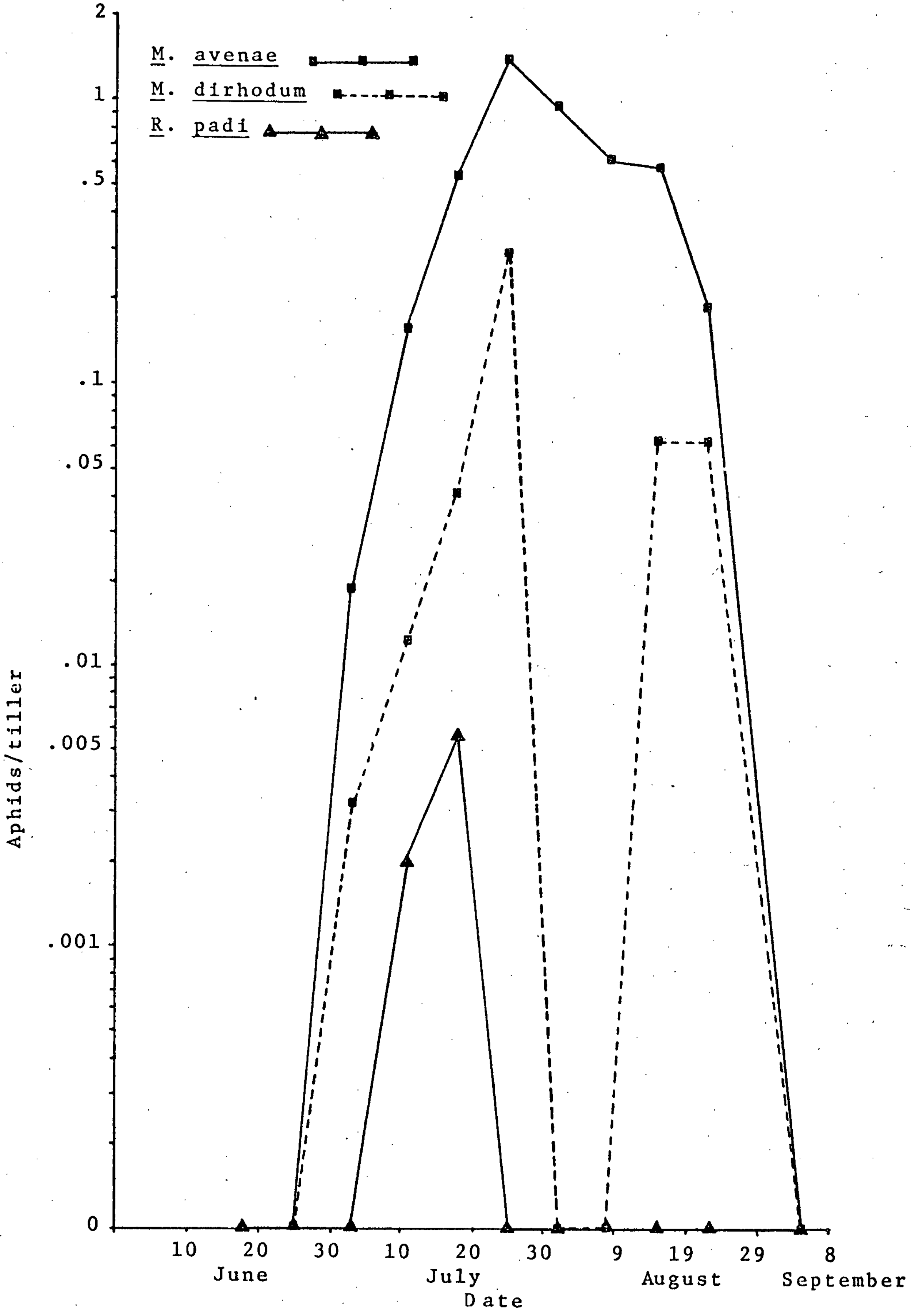
ii) Species Differences

Macrosiphum avenae and M. dirhodum adults were found on July 3, with populations of .019 and .003 adults/tiller respectively (Fig. 18). Macrosiphum avenae maintained the highest number of adults throughout the sampling season and peaked with 1.40 adults/tiller on July 25. The last sample, on September 4 contained no adults of any species. Metopolophium dirhodum peaked with .29 adults/tiller on July 25, had no adults in the next two samples, and then again increased to .063 adults/tiller for two weeks.

Rhopalosiphum padi adults were recovered only twice in the sampling season. On July 11, .0002 adults/tiller were counted in the sample.

The 1973 adult aphid population in plot C was composed of 88.62% M. avenae, 9.88% M. dirhodum and 1.5% R. padi.

Fig.18. The number of adults/tiller of three species of cereal aphids; <u>Macrosiphum avenae</u>, <u>Metopolophium dirhodum</u> and <u>Rhopalosiphum padi</u> found during 1973 in plot C, planted with oats, (<u>avena sativa</u> cv Fraser)



iii) Plant Effects

Plot C was difficult to sample because of irregular plant growth. The height of plants side by side differed as much as 150 cm. While plot C was growing, there was no rain and the plants became wilted

Eventually the aphids were found only on the tall lush plants and then only in the southeast corner, where the plants were healthiest because of a leaking irrigation pipe. A single water sprinkle was set in the southwest corner for one hour on each of two days, August 13 and August 20. The addition of the water may have been advantageous to aphid development, as there was an increase in the population of *M. dirhodum* adults on August 15 and 22.

The aphids spread throughout plot C within one month.

The average height of the plants increased from 24.94 cm on June 25 to 122.99 cm by August 8 (Fig. 16). Although seeded one month later, they started to head out and reached their maximum height only one week after plots A and B. *Macrosiphum avenae* moves to the heads when they are formed, (Forbes (1962)) and as plot C had heads longer than the other two plots, this habit may account for the large number of *M. avenae* in this plot.

The moisture content of the plants decreased from 86.91% on June 25 to 65.8% by August 22 They had lost only 8.64% moisture from June 25 to July 25 when the aphids peaked.

iv) <u>Sparrow Damage</u>

No sparrows were in plot C when the aphids peaked (Table 8). They eventually ate 74.9% of the seed, but as there were only .17 aphids/tiller by then their effect on the aphid population would have been negligible (Table 12).

Table 12. The number of aphids/tiller sampled and the number of aphid/tiller estimated if sparrows had not been present in plot C in 1973.

Date	Aphids/Tiller (with Sparrows)	Estimated Aphids/Tiller (without Sparrows)
Aug 8	8.62	8.67
Aug 15	9.13	10.94
Aug 22	6.38	8.29
Sept 4	.17	.254

v) Natural Enemies

a) Coccinellidae

The numbers of Coccinellidae adults were low throughout the sampling season and .0037 adults/ tiller recorded on July 12 was the highest population found. No coccinellidae larvae were found in the plot but adult species present were *Coccinella trifasciata* (Mulsant), *C. trifasciata* and *C. undecimpunctata* (L).

b) Parasites

Parasite species present were *Aphidius obscuripes* (Ashmead) and *Praon americanum* (Ashmead).

Hyperparasites present were *Charips*, sp., *Coruna clarata* (Walker), *Asaphes* sp. and *Asaphes vulgaris* (Walker).

D PLOT COMPARISON (CONCLUSIONS)

Throughout the 1973 season, one peak was reached by the three aphid species in each plot. Plot B peaked latest but had the highest total aphid population, while plots A and C were almost the same.

The population decrease in plot A from May 25 to June 7 was possibly due to the combined effect of a drop in maximum and low grass minimum temperatures. Plot B showed no increase in aphids/cm during this time, while plot C had not yet been sampled.

The total adult aphid population in the three plots was comprised of 59.02% M. avenae , 39.17% M. dirhodum and 1.82% R. padi. The percentage of adults per plot was similar for all three plots, although plot A was highest with 7.94%, whereas plot B had 7.85% and plot C, 7.76%.

The first adults found were the M dirhodum located in plot A. Four days later, both M. avenae and M. dirhodum were found at the same time in plots B and C. Only in plot A did M. dirhodum have a higher population than the two other species. Macrosiphum dirhodum also entered the field first, so it is possible that the species to enter the field first would have the eventual highest population. It is also possible that the potential number of M. avenae was decreased as a result of sparrows eating the seeds, as M. avenae was found on the seeds and sparrows had emptied 70.6% of the husks by August 13. In plot B, only 32.49% of the seed husks were damaged by sparrows at this time, and only 28.44% in plot C. Almost seventy-five percent of the husks were without seeds by the last sampling date of September 4 in plot C, but this level of damage would have had minimal affect on the aphid population, as very few aphids were left.

The population dynamics of M. avenae and M. dirhodum differed little in plot B.

Although plot C was planted one month after plots A and B, the aphid population in the former reached their peak numbers at the same time as those in the latter plots. The numbers of each species in relation to each other was very different in plot C, as 89% of the adults found were M. avenae, 10% were M. dirhodum and 1.5% were R. padi, compared with 43.17% and 56.12% M. avenae, 53.96% and 43.09% M. dirhodum, and 2.88% and .80% R. padi respectively. Rhopalosiphum padi entered all three plots late in the season and their numbers remained low throughout plots A and B.

In plot C, however, many _R. padi_ were observed after the last sampling date in the vicinity of the leaky irrigation pipe. Thus they appeared to prefer wetter conditions than were generally available in 1973.

The planting of plot C one month after plots A and B stimulated faster development of both the aphids and the plants. Plot C had the fastest growth rate, with the maximum height being reached only one week after the other two plots. The plants were taller, with more leaves. They contained more moisture, with 73.4% after 86 days of growth although they appeared very wilted throughout the growing season. After 96 days, plot A had 57.8% moisture and plot B had 57.2% moisture in the plants. The fast growth rate of plot C may possibly have been a result of fertilizer added to the plot area during the previous season. The aphids spread faster throughout plot C than in the other plots, so they infested 100% of the tillers there similtaneously with the 100% levels in the other plots.

No difference between plots could be attributed to the method of planting. Aphids moved throughout the plot faster in plot C, planted in blocks, but so was plot B. Plot A had more ladybird beetles than plots B and C, but the numbers were negligible in all three plots in 1973.

In summary, *M. dirhodum* was first to enter plot A in the spring and was followed after one week by *M. avenae*. During the same week, *M. dirhodum* and *M. avenae* together entered plot B, entering plot C two weeks later.

Sparrows lowered the potential aphid density in all three plots.

When *M. dirhodum* entered a field first, as in plot A, it had the higher population of the three species.

The method of planting, solid blocks or rows made no difference to the population dynamics of the three species.

A later planting date, as in plot C, did not change the total population of the aphids, but changed the ratio of the three species to one another.

The herbicide applied to plots A and B did not enhance the aphid numbers as suggested by Adams and Drew (1965). They reported that a herbicide application will increase the aphid population by depressing coccinellid adults and killing the larvae.

SECTION IV

THE EFFECT OF PLANT AGE AND WATER STRESS ON RHOPALOSIPHUM PADI (L.)

1. Introduction

During two consecutive summers, 1972 and 1973, three species of aphids were found in samples of oats at U.B.C. *M. avenae* and *M. dirhodum* were the most abundant species, with *R. padi* appearing rarely and irregularly in the samples. In 1972, *R. padi* was the first species to enter the field in the spring when the plants were only 20-25 cm high. They were present in low numbers for three weeks, and then were not observed or collected until the middle of July, after which time they remained in low numbers throughout the season.

Rhopalosiphum padi were not recorded in 1973 until July 9, when some were picked up in samples in plot A. Samples from plot C contained *R. padi* by July 11, and plot B by July 31. Again they remained in low numbers throughout the sampling season.

It was thought that the two main factors influencing the *R. padi* populations could be weather conditions and the species of host plant. Many authors mention that *R. padi* prefers other crops to oats. Dean (1974) found *R. padi* to be abundant in the air but not on the crop, and suggested that crop varieties grown in England may not be palatable to R. padi as it is mainly a grass aphid. He further suggested that changes in cereal varieties or climate might encourage it to become a pest.

Dixon and Glen (1971) say that the appearance of immigrants of R. padi seems to be related to the cessation of the spring growth period of bird cherry (Prunus padus L.), the primary host. They say R. padi will stay on sucker growth throughout the summer months and leave for grasses only in the absence of such suckers.

Dean (1973) found that R. padi, under controlled conditions, produced fewer nymphs on oats than on both wheat and barley.

Greene (1966) observed R. padi on more plant species than M. avenae and M. dirhodum and also mentioned that R. padi prefer cool conditions and were even observed alive and crawling in snow.

Jones (1972) mentioned that an increase in R. padi in plots in 1971 was probably due to the presence of other grasses between the wheat plants.

Dean (1973) found R. padi to have low numbers in the field but to increase when caged as a result of the more humid conditions.

It was observed in field experiments in 1972 (Section I) and 1973 (Section III) that R. padi returned to the oat plots in the late summer when the surrounding grasses became very dry but the oat plants were still succulent. It was also observed in 1973 that one wet section of an oat plot (see Section III) had an increasing number of R. padi living on it late into the fall.

Watering experiments were proposed to determine whether moisture was a limiting factor in the development of R. padi. The effect of plant age could also be examined by initially applying three different water treatments to three ages of plants.

2. Experiment # 1 (Controlled Conditions - caged)

A. Materials and Method

Two Fraser oat seeds were seeded into 9 cm diameter plastic pots filled with 32 g of mica-peat (a commercial peat moss-vermiculite soil mix) and set in a petri dish. This mix was used in laboratory studies because of its uniformity. Two seeds were sown in each of ninety pots. Thirty pots were sown on January 19, 30 on February 19 and 30 on March 12. Each pot was given 50 ml of water at each watering and given equal amounts of water until the plants had grown to 10 cm in height. The first seed to germinate was kept and the other, if it germinated was discarded. The plants when 10 cm high were segregated into the following treatments:

1. Wet - Pots sat in water at all times.
2. Damp - 50 ml of water was applied to the soil whenever all trace of water had disappeared from the petri dish.
3. Dry - 50 ml of water was applied to the soil when the plant showed signs of wilting.

All added water was recorded.

The 30 plants in each watering treatment were subdivided into groups of ten plants from each seeding date so that there were three plant-height treatments (Table 13).

1 Mature - The plant had headed out.
2. Medium - Averaged 30 cm in height.
3. Short - Averaged 25 cm in height.

Table 13. The nine treatments applied to *Rhopalosiphum padi* and oats, *Avena sativa* cv Fraser, in controlled conditions.

	Wet	Damp	Dry
Mature	Mat - wet	Mat - damp	Mat - dry
Medium	Med - wet	Med - damp	Med - dry
Short	Short - wet	Short - damp	Short - dry

Nine plants, one from each treatment, were placed randomly in each of ten flats. The flats were moved daily under a light bank (which was on for 16 hours each day) to ensure equal lighting.

When the plants had reached the required test height, each one received an R. padi adult chosen randomly from the rearing stock, which had been maintained for four months. Each plant was then covered with an 8 cm plastic tube (open at the top because R. padi will stay at the base of the plant, Belvett et al (1965)), where the adult was allowed to deposit one nymph before it was removed. When this nymph reached maturity, its fecundity was recorded for 16 consecutive days. Preliminary fecundity studies (see Section II) had shown that most R. padi adults had produced 80% of their progeny during the first 16 days.

B. Results and Discussion

When analyzed at the 5% level of significance, the results showed that significantly different fecundities of R. padi were produced by giving the plants different amounts of water. Significant differences were also shown when plants of different ages, as measured by their heights, were used to rear the aphids (Table 14). The mean and standard error of the mean are listed in Table 15.

Table 14. An analysis of variance of the mean number of nymphs produced by each of nine treatments described in Table 13.

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Squares	F
Treatment	18220.889	8	2277.611	6.54*
Water	2974.689	2	1487.344	4.27*
Height	12443.889	2	6221.944	17.86*
Water x height	2802. 311	4	700.578	2.01
Block	3314.011	9	368.223	1.06
Experimental Error	24390.889	70	348.441	
Total	45925.789	81		

* Significant at the 5% level.

Table 15. The mean and standard error of the mean of populations of *R. padi* raised on three sizes of plants which had been treated with three different amounts of water.

Treatment	Standard Error of the Mean	Mean
Small-dry	5.98	30.1
Small-damp	4.46	38.4
Small-wet	7.16	44.1
Medium-dry	5.88	47
Medium-damp	2.45	40.1
Medium-wet	5.90	44.5
Large-dry	1.98	2.2
Large-damp	6.47	14.7
Large-wet	7.04	32.2
Combined -small	3.60	37.53
Combined-medium	2.94	43.87
Combined-large	3.95	16.27
Combined-dry	4.43	26.43
Combined-damp	3.46	31.07
Combined-wet	4.01	40.27

Further analysis by Duncan's New Multiple Range Test showed there was a significant difference in the number of *R. padi* produced between all three watering treatments; wet > damp > dry, and between all three height treatments; medium > small > large.

Twenty-one percent of the water was given to the dry treatments, which produced 27.04% of the progeny. The damp plants received 34.98% of the water and produced 31.78% of the aphids, whereas 44.3% of the water was used by the wet plants, which produced 41.19% of the aphid young.

More water did not result in a higher fecundity when plant size was considered. The small plants received 18.39% of the water and produced 38.39% of the progency. Twenty-eight percent of the water was given to the medium plants to produce the most progeny (44.87%), whereas the large plants with 53.81% of the water produced only 16.74% of the young.

C. Conclusions

These results support the initial hypothesis that *R. padi* prefer wet conditions. The least numbers of aphids was produced on the large plants, possibly because they had headed out and had reached maturity by the end of the experiment. It was shown earlier, (see Sections I and IV) that the water content of the plants decreased as they matured, regardless of precipitation. The plants of medium height produced more than the smaller plants, possibly because the nutrient content of the small plants was not enough to support a large aphid population.

3. Experiment # 2 (Controlled Conditions - not caged)

A. Materials and Methods

In the first experiment the plants were caged to prevent the aphids from escaping. The purpose of this second experiment was to see whether similar results could be obtained if the aphids were free to choose any available plant. Only water relations were tested on plants of similar size. (Plants averaging 30 cm in height were used because they had produced a higher fecundity in experiment # 1).

Two Fraser oat seeds were planted in each of 15, 8 cm diameter plastic pots filled with 47 g of mica-peat, to which 50 ml of water were added. Additional water was added to all pots as required. The pots were left to germinate under a light bank in the greenhouse. Forty days later they were placed in a random design under the same controlled conditions as those in experiment # 1. A petri dish was placed under each pot to contain the water, and the pots were set about 30 cm apart. The plants in the dry treatment were given water only when they showed signs of wilting. The damp plants were given 50 ml whenever the petri dish dried, and the plants in the wet treatment sat constantly in water. Water was always added from the top.

Although no oat plants or visible residues of oat plants had been in this room for over two months, *R. padi* alates began to appear on the plants within two or three days. No aphid was removed from the plants until all residents were counted on the 43rd day.

B. Results and Discussion

Records show that *R. padi* alates moved initially to the dry plants from unknown sources.

After 43 days, the wet plants averaged 214 aphids/plant, whereas the damp plants had an average of 150 aphids/plant. These contrasted with an average of only 20 aphids/plant on the dry plants (Table 16).

Table 16. The mean number with standard error of *R. padi* on plants which had been treated with three different amounts of water.

Treatment	Mean No. Aphids	Standard Error of the Mean
Dry	20	4.33
Damp	150	15.37
Wet	214	19.46

An analysis of variance and a Least Significant Difference Test showed that the wet and damp treatments supported significantly more aphids than the dry treatments (Table 17).

Table 17. An Analysis of variance of the mean number of nymphs produced by *R. padi* during three water treatments under controlled conditions.

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Squares	F test
Treatment	89757.51	2	44878.76	8.898*
Experimental Error	56112.2	11	5101.11	
Total	145869.71	13		

* Significant at the 5% level.

C. Conclusions

These results support those in experiment # 1, in which the dry plants also had a statistically lower fecundity. In addition, this experiment shows that these results will occur when the aphids are able to select the plant as well as when they are forced to live on a particular plant. The high density of aphids on the plants initiated the production of alate adults, so even though the plants were not touching, the aphids could move away from them.

4. Experiment # 3. (Uncontrolled Conditions)

A. Materials and Methods

Experiment # 3 compared the plant preference of field aphids with those used in experiments 1 and 2, which had been reared for several generations in the laboratory.

Two oat seeds were planted in each of fifteen, 9 cm diameter pots filled with mica-peat. Only the first seed to germinate was kept. The experiment was carried out from July 12 until August 21 on the inside window sill of an East-facing laboratory. The light and heat therefore were provided naturally and were uncontrolled. Water was added as in experiment # 2.

"Nursery" plants for rearing aphids were kept about three metres from the test plants and all instars of R. padi brought in from the field were raised on them. The aphids had to reach the test plants unassisted. Forty days after the test plants had been placed on the window sill, the live aphids remaining on them were counted.

B. Results and Discussion

An average of 460.4 aphids/plant and 436.4 aphids/plant were respectively maintained by the wet and damp treatments. The dry plants produced an average of only 59.4 aphids/plant (Table 18).

Table 18. The mean and standard error of the mean of populations of R. padi established on plants which had been treated with three different amounts of water.

Treatment	Mean (No. Aphids)	Standard Error of the Mean
Wet	460.4	19.46
Damp	436.4	15.37
Dry	59.4	4.33

The numbers of aphids recorded on the wet and damp plants were significantly higher than on the dry ones (Analysis of Variance and Duncan's New Multiple Range Test (Tables 19 and 20)).

Table 19. An analysis of variance of the mean number of nymphs produced by *R. padi* during three water treatments under variable conditions

Source of Variation	Sums of Squares	Degrees of Freedom	Mean Squares	F Test
Treatment	505843.333	2	252921.7	19.32*
Experimental Error	157093.6	12	13091.133	
Total	662936.933	14		

* Significant at the 5% level.

Table 20. Duncan's New Multiple Range Test showing significant water treatments under variable conditions

Treatment	Wet	Damp	Dry
Wet	-	ns	*
Damp	ns	-	*
Dry	*	*	-

* Significant at the 5% level.

These results with field-collected aphids support those obtained with laboratory reared aphids in experiments # 1 and # 2, where R. padi populations on wet and damp plants were also significantly higher than those found on the dry plants.

C. Conclusions

These three experiments all support the hypothesis that R. padi prefer wet conditions. Their preference for wet conditions would be a partial explanation to their presence in oat plots mainly in the early spring and late summer when cooler night temperatures produce heavy dews and more humid conditions. These results are contrary to those of Adams and Drew (1969) in which, when water was applied to plants, _R. padi_ decreased reproduction and increased longevity, but they are supported by Dean's (1973) results which showed that the fecundity of _R. padi_ increased when it is caged, a condition that would increase the humidity.

Plants of medium height (averaging 30 cm) supported the largest _R. padi_ populations. Taller ones were probably too mature and dry, even when sitting in water, and the smaller ones were too small to support large aphid populations. Greene (1966) reported that _R. padi_ appeared in fields in Oregon later than _M. avenae_ and _M. dirhodum_. He says this difference may result from the plants becoming more favorable when the lower leaves begin to senesce and lose their chlorophyll.

SECTION V

POPULATION DYNAMICS - 1974

1. Introduction

Two plots of oats were planted in 1974. Plot A was planted in rows in the same location as in 1973. Plans were made to irrigate sections of plot A to field test the assumptions that R. padi preferred wet plant conditions, but the plants never became dry enough in 1974.

Small cages, 30 cm x 30 cm in diameter and 90 cm high, were put in the field to attempt fecundity trials, but were discarded when the rain kept washing the aphids off the plants, while the plants became infected with mildew making them impossible to use.

In 1972 and 1973 large numbers of sparrows were eating the oats,so to test their effect, two cages 2.4 m x 3 m in diameter and 1.8 m high, designed to keep sparrows off the plants, were placed over two sections of three rows.

Plot B was located in the same area as 1972 to see whether the large aphid population of 88.8 aphids/tiller recorded in 1972 would recur. (The population density in 1972 was almost four times that of 1973, but it was not known whether the higher population stemmed from a difference in location or an annual difference in numbers).

In 1974, more time was available for identifying species at all developmental stages.

2. Materials and Methods

A. Plot A

i) Description and Aphid Sampling

On May 13, 1974, Plot A was seeded in 47 rows, one meter apart and 32.2 m long. The outer two rows on each side and one metre at the end of each row were excluded from the sampling. Aphid populations were sampled in the same manner as in previous years.

ii) Sparrow Cages

Plants within the two sparrow cages were included in the plot samples until sparrows were seen in the plots and then they were sampled separately, each time by taking two stems per row or six per cage.

B. Plot B

i) Description and Aphid Sampling

On May 27, plot B was planted in 13 rows, one metre apart and 7.5 m long. It was located about one mile south of plot A in the same area as the 1972 plot. Again one metre around the plot was left as a guard area and not sampled. Aphid populations again were sampled in the same manner as in the previous two seasons. All instars were immediately separated into species instead of being stored in vials.

C. Plant Sampling

A sample of six to ten stems was collected each week for recording the height in cm and the number of leaves. These tillers were then weighed, oven dried and weighed again to obtain their moisture content.

D. Soil Samples

Five samples of soil were collected at a depth of 10-15 cm in both plots at various times, usually, on aphid sampling days. The soil was put in airtight aluminum containers, weighed, oven dried and weighed again to estimate the moisture content of each plot at approximate root depth.

E. Parasites

All sampled oat stems were checked for parasitized aphids (mummies) and any found were put in gelatin capsules, allowed to emerge, mounted and later identified.

3. Results and Discussion

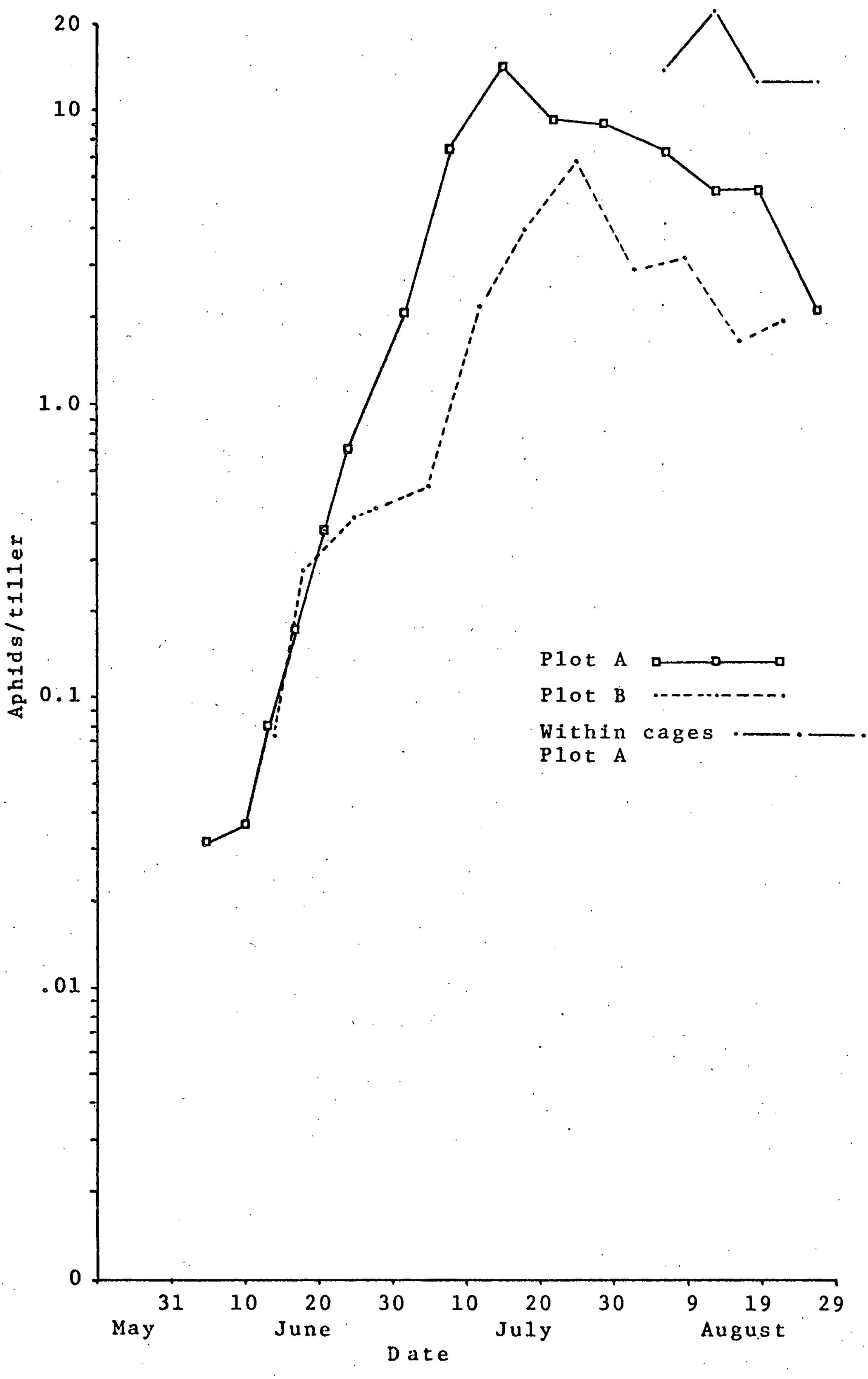
A. Plot A

i) Aphid Samples

Aphids were first found in plot A on June 5 when there were .003/tiller. They increased to a peak of 14.29 aphids/tiller by July 15 and had decreased again to 2.10/tiller by August 7, the last sampling date (Fig. 19). The population follows similar trends when expressed as aphids/cm of tiller height.

Movement of aphids throughout the plot was measured by the percentage of aphid infested

Fig.19. Total cereal aphids/tiller found on two plots of oats, Avena sativa cv Fraser) in 1974



tillers on each sampling date (Table 21). On June 5, the first sampling date, only 1.74% of the tillers were infested with aphids. By July 2, the last date on which the number of infested tillers was counted, almost 50% had aphids on them.

Table 21. The percentage of oat tillers (*Avena sativa* cv Fraser) infested with aphids in plot A in 1974.

Date	Percentage of Tillers with Aphids
June 5	1.74%
June 10	2.14
June 13	3.90
June 17	5.07
June 24	20.44
July 2	49.14

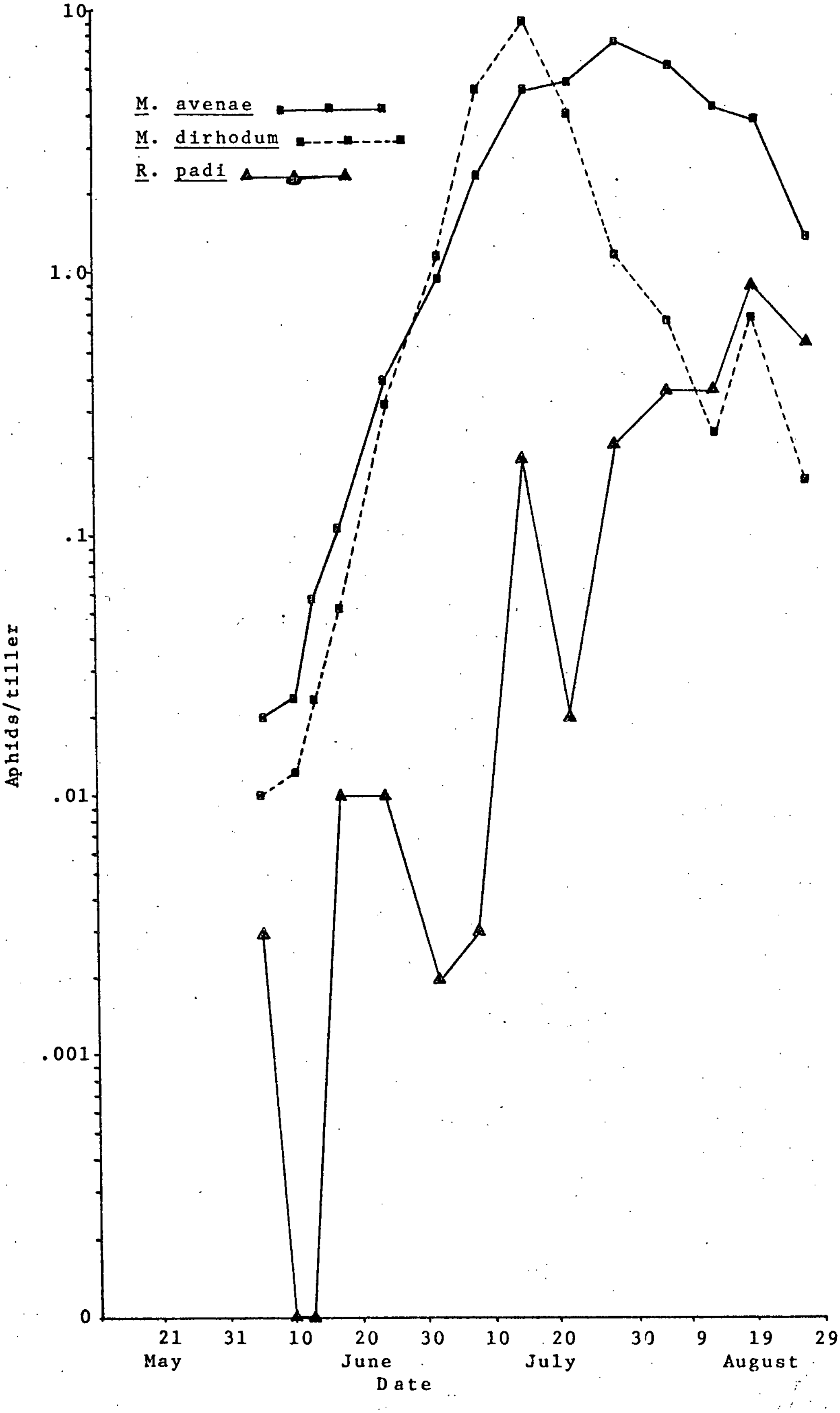
ii) Species Difference

Over half (51.65%) of the aphid population was M. avenae (Fig 20). They were first recorded on June 5, with .02/tiller, and had increased to a peak of 7.67/tiller on July 29. By the last sampling date of August 27, only 1.38/tiller were left.

The M. avenae were distributed uniformly throughout the plot, and did not produce many alates until August 19 when 51% of the 4th instar aphids were alates. There were 1.05 4th instar aphids/tiller collected that day. Few alate adults were recovered in the samples; presumably they had left the plot.

Metopolophium dirhodum made up 46.49% of the total aphid population only slightly lower than M. avenae. There were fewer M. dirhodum recovered in the first sample, (.01/tiller) but they increased more rapidly to reach a higher peak of 9.14 /tiller on July 15, two weeks earlier than M. avenae peaked. The M. dirhodum decreased more rapidly than M. avenae, only .167/tiller by August 27, the last sampling date. There was a slight increase in population between August 9 and 19 which might have been due to

Fig.20. The population/tiller of three species of oat aphids; Macrosiphum avenae, Metopolophium dirhodum and Rhopalosiphum padi found during 1974 in plot A, planted with oats, (Avenae sativ cv Fraser)



.38 cm of rain on August 11 and 12 after a lengthy dry period. Out of a population of 2.24 4th instar/tiller, over 56% were alates on July 15, when *M. dirhodum* peaked. The total aphid population peaked at that time with 14.30 aphids/tiller, which was probably high enough to overcrowd the *M. dirhodum*, inducing them to produce alates. Sixty-four percent of the total aphid population then was *M. dirhodum*. As with *M. avenae*, only a few alate adults were recovered.

The population of *R. padi* was low throughout the sampling season, accounting for only 1.86% of the total aphid population. On June 5, there were .003/tiller, but none were recovered in the next two samples. The fluctuating population increased to .905/tiller by August 19 and then decreased to .548 aphids/tiller by August 27, the last sampling date.

The fluctuating behavior of the *R. padi* population was due to their low numbers. Prior to July 15, the highest number of collected stems infested with *R. padi* was only 5 out of 1065 stems, too low to provide a representative sample. There were .032 *R. padi*/tiller on July 15 and 32.35% of these were 4th instar alates. No adults were recovered in the next sample. Presumably they had left the plot. Rhopalosiphum padi initially do seem to prefer other grasses to oats, Dean (1974), Greene (1966), Jones (1972), but many of the nearby uncultivated grasses such as Orchard grass (Dactylis glomerata (L)), had ripened by August, causing the R. padi to move onto the oats, which were greener and more succulent. The R. padi population continued to increase, produced very few alates (43% of 4th instar at the most) and by August 27 made up 26.14% of the total aphid population.

iii) Sparrow Cages

The data from both cages are combined to give a larger sample. The cages were large and covered only in 3/4" chicken wire, so except for excluding sprarrows, the conditions inside the cage should have been the same as those outside.

The caged oats supported a larger population than did the open plot (Fig. 21). On August 13, when the total aphid population had decreased to 5.38 aphids/tiller, the population inside the cages had risen to 21.92 aphids/tiller, which was 1.53 times higher than the peak population of the whole plot. On the last sampling date of August 27, the caged population was still 12.5 aphids/tiller, whereas outside the cage it had decreased to 2.10/ tiller.

Most of the caged aphid population was M. avenae, as in the whole plot, but the population of M. avenae was larger inside the cages. This difference was greatest on August 19, when 70.90% of the total aphid population in plot A was M. avenae, whereas inside the cages, M. avenae made up 90.67% of the aphid population. Fifty percent of the caged 4th instar were alates by August 27 when the oats were very ripe and dry. On that date only 46.67% of the aphids inside the cages were M. avenae, whereas in the open plot 65.91% were. Presumably, the M. avenae population had increased too much to be supported on the dry heads, so the alates that were produced had left.

There were fewer M. dirhodum inside the cages than outside. By August 27, only 1.33% of the aphids inside the cage were *M. dirhodum*, whereas there were 7.95% outside.

There were also fewer *R. padi* inside the cages than outside, with the exception of the last sample when *R. padi* had higher numbers inside the cages. On August 19, while the *R. padi* population outside the cages had increased to 16.63% of the aphid population, there were only 4.67% inside. By August 27, the last sampling date, the uncaged *R. padi* population had increased to 26.14% while inside the cages it was 52%. As *R. padi* are usually found at the base of the plant it seems unlikely that the sparrows could have affected the population that much, but the presence of cages might have changed some unknown environmental condition.

iv) Plant Effects

The first plant measurements were taken on June 5. Tillers then averaged 13.53 cm high, with 2.86 leaves. They grew until July 22, reaching a height of 102.34 cm with 4.86 leaves. The plants, already headed out, continued to grow a little more, reaching 107.06 cm on August 13.

The plants were still growing when M. dirhodum peaked, but had levelled off by the time M. avenae and R. padi peaked. This levelling did not appear to inhibit the growth of the M. avenae or R. padi populations.

The plants had an average moisture content of 85.07% on June 5, rising to 91.18% by June 10. Rain amounting to 3.7 cm from June 5 to June 10, would have caused this increase. Rain up to 2.05 cm a day prevented the moisture content of the plants from decreasing as it had in 1973 so that it was still 80.46% on July 15, when M. dirhodum peaked. As M. dirhodum prefer the succulent oat leaves to the drier head this higher moisture content may have allowed them to increase more rapidly than M. avenae, which appears to be less influenced by the moisture content of the plant. The higher nutrient content of the head attracts the M. avenae more than do the succulent leaves.

v) Soil Sample Results

The highest soil moisture content (22.91%) was measured on July 18 after ten days of nearly continuous rain amounting to 6.4 cm.

The first sample, taken on June 26, contained 6.96% soil moisture and the last, on August 27, had the lowest (5.52%). None were low enough to induce wilt, which would have allowed the necessary irrigation to field test the water relations hypothesis from Section V.

vi) Parasites

Of the 119 mummies (parasitized aphids) collected in plot A in 1974, 111 or 93.28% of them emerged. The parasite species present consisted of one *Praon americanum* (Ashmead), one *Ephedrus californicus* (Baker), 8 *Aphidius avenaphis* (Fitch) and 68 *Aphidius obscuripes* (Ashur).

The hyperparasites present consisted of one *Coruna clarata* (Walker), three *Dendrocernus niger* (Howard) and 35 *Asaphes* sp.

B. Plot B

i) Aphid Samples

The total aphid population was lower in plot B than plot A (Fig. 19). Plot B had .073 aphids/tiller when first sampled on June 14. It peaked on July 25, with 6.78 aphids/tiller, and had decreased to 1.94/ tiller by August 22, the last sampling date. When expressed as aphids/cm of tiller height the same trends appeared with .006 aphids/cm on June 14, increasing to .08/cm on July 25 and decreasing to .019 aphids/cm by August 22.

Aphid movement throughout the plot was slow, with 2.44% of the stems infested on June 14 and only 24.65% infested by July 5 (Table 22). In plot A, almost 50% of the tillers were infested with aphids by July 2. The slower movement in plot B was probably because of the lower plant density (6.83 tillers/7 cm compared to 9.68 tillers/7 cm in plot A).

Table 22. The percentage of oat tillers, *Avena sativa* cv Fraser, infested with aphids in plot B in 1974.

Date	Percentage of Tillers infested with Aphids
June 14	2.44
June 18	11.65
June 21	14.23
June 25	22.60
June 28	22.63
July 5	24.65

ii) Species Difference

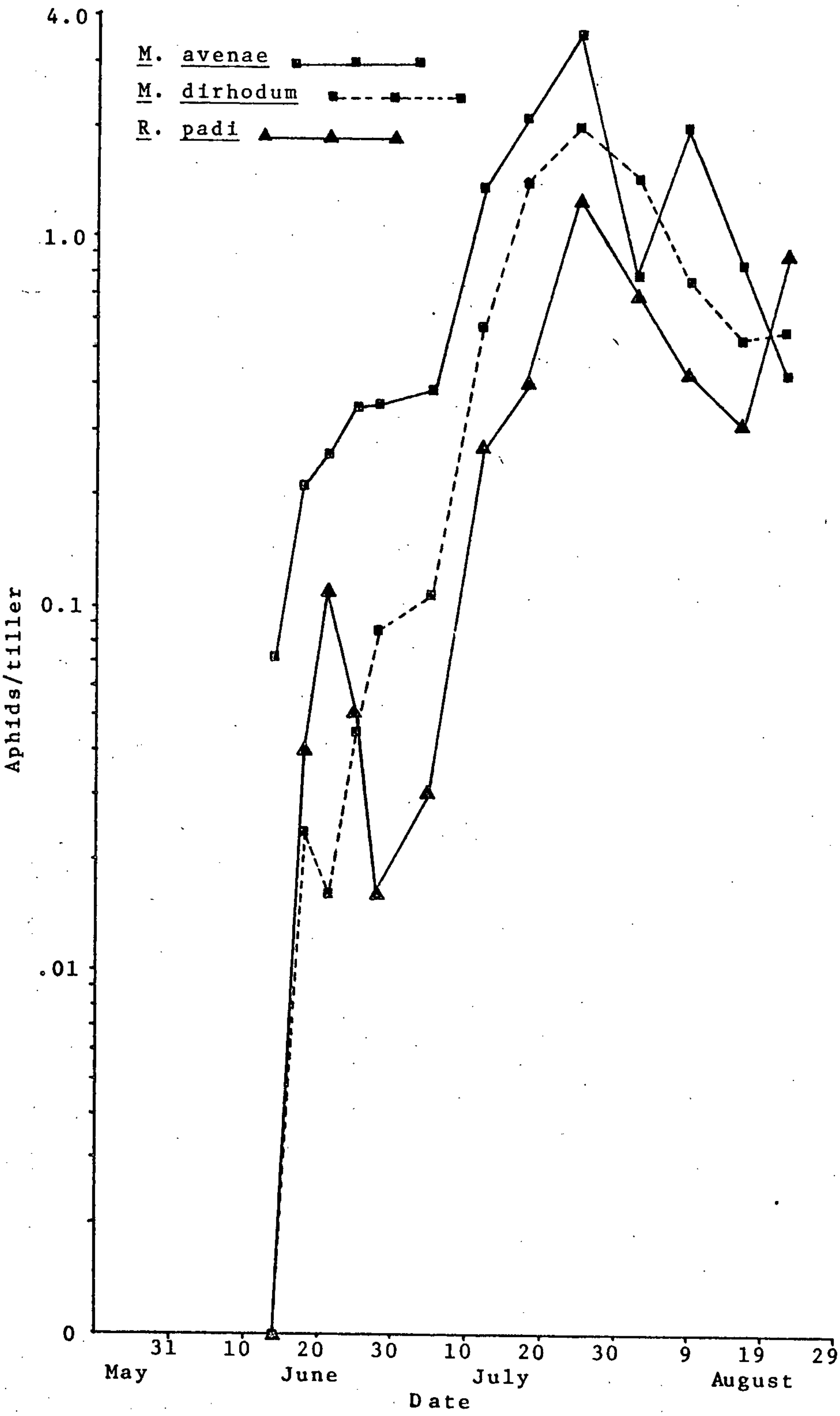
Macrosiphum avenae contributed 59.23% to the total aphid population. It was the first species to enter the field and had .073 individuals/tiller recorded on June 14 (Fig. 21). The population increased to 3.57/tiller by July 25 and had decreased to .444 M avenae/tiller on August 22, the last sampling date. The increase in numbers of M. avenae from August 2 to August 9 cannot be explained by any recorded data.

Macrosiphum avenae was recorded uniformly throughout the plot and produced a large proportion of alate adults throughout the sampling season.

On the first and last sampling dates the one M. avenae adult recorded was an alate, and on July 12, 85% of the adults recorded were alates. Although winged M. avenae were also produced in plot B, they did not appear to leave the plot.

Metopolophium dirhodum entered the plot June 18, when .024/tiller were recorded. The population increased to a peak of 1.97/tiller on July 25 and then decreased to .556/tiller by August 22. Metopolophium dirhodum contributed 26.36% to the total aphid population.

Fig.21. The population/tiller of three species of oat aphids; Macrosiphum avenae, Metopolophium dirhodum and Rhopalosiphum padi found during 1974 in plot B, planted with oats, (Avena sativa cv Fraser)



They were also distributed uniformly throughout the crop and 40% of their 4th instars were alates. Only 24% of the adults recovered were alate so apparently some were leaving the plot.

In plot B, R. padi contributed 14.41% to the total aphid population, compared with only 1.86% in plot A. It had entered the plot by June 18, when .048 individuals/tiller were recorded. Rhopalosiphum padi also peaked on July 25 with 1.24/tiller, decreased to .333/tiller by August 16 and then increased again to .889/tiller by August 22.

Rhopalosiphum padi also was uniformly distributed throughout the plot, but produced very few alates. Fourteen percent of all 4th instar aphids and 15% of adults were alates, indicating that a higher proportion of R. padi were staying in the plot than either of M. avenae or M. dirhodum.

iii) Plant Effects

Although plot B was planted two weeks after plot A the plants grew at similar rates to similar heights. They averaged 12 cm in height with 3 leaves when measured first on June 14. They reached their maximum height of 108.2 cm with 4.17 leaves by August 2 and so were still growing when the aphid population peaked on July 25.

The plants in plot B had a slightly higher moisture content than in plot A, which may have been sufficient to encourage the greater development of *R. padi* in plot B.

iv) Soil Sample Results

The soil in plot B had a higher moisture content throughout the entire growing season than did plot A. The average soil moisture of 15.64% in plot B compared to 11.68% in plot A may have produced an environment around the base of the plants humid enough to promote development of *R. padi*.

v) Parasites

Fifty of 51 mummified parasitized aphids (98.04%) emerged. The parasite species collected consisted of two *Praon americanum* (Ashmead), four *Aphidius avenaphis* (Fitch) and 19 *Aphidius obscuripes* (Ashmead). The hyperparasite species present were two *Charips* sp. and 24 *Asaphes* sp.

4. Conclusions

Plot A in 1974 produced more aphids than plot B so the high aphid population of plot B in 1972 was not a result of plot location alone.

Movement of aphids throughout both plots was faster in plot A, probably because of its denser plant growth.

The higher aphid population in plot A resulted in the production of alates through crowding. Plot B with fewer aphids, had very few alates.

A higher aphid population was recorded inside than outside the protected cages, indicating that sparrows did decrease the aphid population as much as 61%.

The higher *R. padi* population and lack of *R. padi* alates in plot B probably resulted from the higher soil moisture and plant moisture content on that plot.

Many parasitized *R. padi* never emerged. Some colonies set up in controlled conditions were completely parasitized.

SUMMARY

The population dynamics of three aphid species studied on Fraser oats in 1972, 1973 and 1974 varied considerably over the three sampling seasons. The total aphid population peaked once during each season with the peak densities ranging from 88.8 aphids/tiller in 1972 to 6.76 aphids/tiller in the same area in 1974.

The relative abundance of the three aphid species remained constant throughout each season and between seasons. *Macrosiphum avenae* was the most abundant species with *M. dirhodum* only slightly less so. *Rhopalosiphum padi* was found in every plot each season, although its numbers were very small except in 1974, when it contributed 26.14% to the total aphid population of plot B.

With the exception of 1972, when the peak numbers for all species occurred on August 14, the populations of each species usually peaked in late July or early August. In 1974, *R. padi* did not reach peak numbers until August 19 in plot A. In all cases the longer a species took to attain its peak, the higher that peak was, so the later peak in 1972 undoubtedly contributed to the higher aphid density recorded that year.

Every season the populations' peak occurred at about the same time as the plants reached their full height and were maturing.

Forbes (1962) had also found M. avenae to be the most abundant species at U.B.C., with M. dirhodum next most abundant and R. padi very scarce. He recorded M. avenae with two peaks, three out of the four years sampled, one in June and one in July, M. dirhodum with one peak each year, once in June and three times in July, and R. padi with one peak one year and two peaks the other year it was recorded, all in July. Substantially higher aphid densities were recorded one year than the other three.

Jones (1972) does not arrive at the same relative abundance of the species over a five-year record of alates, but instead finds M. dirhodum to be most abundant, with M. avenae next and R. padi still the lowest. She also records densities of one year to be much higher than the others.

Dean (1973) found R. padi to be the most numerous species in the air but the least numerous on the cereal crops. He suggested that cereal varities grown in Britain were unpalatable to R. padi and thus not attractive to migrants. In 1970, he found R. padi arriving first in the field, but later becoming scarce.

The only relationship found between tiller height and aphid density is that the plots with the shortest tillers appear to have the highest aphid numbers per tiller and per cm of tiller height.

The later planting date of plot C in 1973 produced a higher proportion of M. avenae and an increase in development of both aphids and plants, but did not substantially change any other aspect of the population dynamics.

Greene (1966) suggested that the time of planting influences aphid populations and found populations of M. dirhodum to be much higher in early seeded fields.

Sparrow (1974) also suggested that significant populations would have to occur before the end of June for cereal aphids to be a problem and that late seeding might prevent this.

Different planting methods; i.e. solid blocks vs rows, did not affect the population dynamics.

Fecundity trails which produced large numbers of R. padi and small numbers of M. avenae did not support observations from field sampling which showed the opposite results.

Results strongly indicate that weather plays a significant role in regulating the aphid numbers. In 1972, heavy rains on the beetles in July prevented their populations from reaching high enough numbers to greatly affect the aphids. In the same year, an increase in temperature and lack of precipitation may have caused a sudden decrease in aphid numbers from June 29 to July 4, whereas cooler conditions accompanied by some precipitation following the decline prompted the aphid numbers to increase.

In 1973 a population decrease in plot A from May 25 to June 7 was thought to be due to a $6^{O}F$ drop in maximum temperature on May 25, accompanied by low grass minimum temperatures of between $35^{O}F$ and $32^{O}F$ from May 25 to May 28.

Rhopalosiphum padi was used to study one aspect of weather (water) on the aphid populations. Watering experiments supported the hypothesis that _R. padi_ do prefer wetter conditions than the other species.

Dean (1973, 1974) and Jones (1972) and many others suggest that grasses are the preferred hosts of _R. padi_.

The combination of water preference and non-preference to oats would explain the behavior of *R. padi* in the field. Imigrants would enter the field in the spring, find the oats unpalatable, and continue moving to surrounding preferred grasses. As these grasses ripened and dried, the *R. padi* would return to the less ripe and more succulent oat crop. Although *R. padi* do not prefer oats, fecundity trials have shown that they certainly can live on them. Available data do not explain the success of *R. padi* when caged (see also Dean (1973)), other than the condusive effect of the increased humidity within the cages.

The yearly variations cannot be explained soley by differences in weather patterns and coccinellid numbers did not seem to have a controlling effect. The effect of other natural enemies could not be determined, as no direct samples of them were taken.

The fecundity trials did not explain the relative abundance of the three species, but the experiments on water relations supported the irregular timing of *R. padi*.

It would be interesting to explore further the role of the plant as a controlling agent for cereal aphid populations through its moisture content, size, vigour, nutritional and varietal make-up.

Further studies should consider the mortality inflicted by sparrows.

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