AN ABSTRACT OF THE THESIS OF

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Title *Biology Studies of Macrosiphum avenae* (Fabr.), *Acyrthosiphon dirhodum* (Walker), and *Rhopalosiphum padi* (L.) on Gramineae in Western Oregon.

Abstract approved [redacted]
(Major Professor)

Field biology studies of three grain aphids, *Macrosiphum avenae* (Fabr.), *Acyrthosiphon dirhodum* (Walker), and *Rhopalosiphum padi* (L.) were conducted near Corvallis, Oregon, from 1961 to 1964.

Populations of *M. avenae* were found on grain plants, and alatae entering spring barley may have been from wheat fields. Specimens were found more commonly on plants taller than six inches. Orchardgrass supported the largest numbers of *A. dirhodum* during the winter. Many grain and grass plants were inhabited by *R. padi* during mid-winter, and this species survived temperatures below freezing. Aphids of these three species were not found during August and September. Aphid flight was sampled using sticky traps which caught aphids from March 3 to November 14; the major flights of *M. avenae* and *A. dirhodum* occurred during July and *R. padi* during June.

M. avenae populations appeared on spring barley in May, peaked in July and declined to zero by July 31. The first appearance of M. avenae was related to planting dates of the barley. A. dirhodum appeared in the barley fields two weeks later than M. avenae and the populations reached less distinct and lower peak numbers. R. padi appeared later in the spring and in lower numbers than the other two species. The number of aphids per infested plant increased as the number of plants infested increased. M. avenae was found on all 200 plants for only one of 40 sampling dates. In conjunction with the abundance study, six life stages of M. avenae and A. dirhodum were recorded for all samples. Aphid populations consisted of progressively smaller numbers of specimens from the first to the fourth nymphal instar. There were more apterous aphids than fourth instar nymphs and the alate group was the smallest. The instar data were used to estimate the reproductive rate under natural field conditions. An estimate of 14.99 young were produced per adult M. avenae and surviving births averaged from 8.08 to 10.69 per adult. It was estimated that adults reproduced for 75% of the expected time and that 50% of the second, third, and fourth instar nymphs died under field conditions.

Four areas of the barley plants were sampled; M. avenae frequented the upper growing areas of the plant and migrated to the heads, A. dirhodum inhabited three areas of the plant, and R. padi occurred on the subterranean shoot and lower senescent leaves.

Statistical analysis indicated several distribution patterns. All aphids, species combined, were found to infest plants at random for most sampling dates. M. avenae and R. padi were randomly distributed from plant to plant for most samples, and A. dirhodum infested the plants at random in all samples. Specimens of M. avenae were randomly distributed across four quadrants of the fields during most samples. They were clumped within the quadrants, as were the A. dirhodum during 1963. The distribution of aphids per plant area, the number of aphids in each of six life stages, and the interaction of these two classifications showed M. avenae populations unequally distributed on the plant areas, and the number of specimens for each life stage was dissimilar. Estimates of 30,895 to 16,266,718 aphids per acre along with the confidence limits were given. The larger the means the smaller were the confidence ranges relative to the mean.

Coccinella trifasciata subversa LeConte and Hippodamia sinuata spuria LeConte were the most abundant Coccinellidae found and Scaeva pyrastri (L.) was the most common Syrphidae associated with the grain aphid populations, primarily M. avenae. From 100 parasitized aphids, 54 Aphidius obscuripes Ashmead emerged and 33 hyper-parasites. An undetermined entomophagus fungus was seen attacking A. dirhodum on orchardgrass.

The library recognizes that there are certain irregularities in the form of this thesis. As the Graduate School was unable to have the corrections made, the library is binding it as it was received from the Graduate School. Any questions should be referred to the Graduate School, Oregon State University.

CT

BIOLOGY STUDIES OF MACROSIPHUM AVENAE (FABR.), ACYRTHOSIPHON DIRHODUM (WALKER), AND RHOPALOSIPHUM PADI (L.) ON GRAMINEAE IN WESTERN OREGON

by

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BIOLOGY STUDIES OF MACROSIPHUM AVENAE (FABR.), ACYRTHOSIPHON DIRHODUM (WALKER), AND RHOPALOSIPHUM PADI (L.) ON GRAMINEAE IN WESTERN OREGON

I. INTRODUCTION

The biology of aphids in grain fields of western Oregon is of considerable importance because they transmit barley yellow dwarf virus. Since the description of the disease in 1951 by Oswald and Huston (68) it has been reported to damage 100% of barley plants (Dickason, Raymer, and Foote 17), and to reduce oat yields 50% in the Willamette Valley of Oregon (Raymer and Foote 73). The incidence of barley yellow dwarf virus and aphid populations were reduced by early seeding (Dickason, Raymer, and Foote 17), but avoidance of barley yellow dwarf virus by early seeding was unpredictable (Bruehl and Damsteegt 8).

The purpose of this study was to learn what insect species were associated with barley plants and how their populations were related to seeding date. Three insect species, *Macrosiphum avenae* (Fabr.), *Acyrthosiphon dirhodum* (Walker), and *Rhopalosiphum padi* (L.), in the family Aphididae of the order Homoptera were studied in barley fields near Corvallis, Oregon, from 1961 to 1964. Since the purpose was to gain knowledge on aphid biology, no attempt was made to include a study of the relationship of these vectors to barley yellow dwarf virus.

Aphid biology studies by Kennedy (48 and 49), Broadbent (6) and a monograph by Bruehl (7) indicated a need for additional work on host range, migration, and field population dynamics. Population studies of particular interest included seasonal abundance relative to planting dates and plant growth stages, types of aphids present (immatures and winged or wingless adults), field fecundity, and mortality under natural stresses. Several statistical approaches to aphid distribution patterns were followed in an attempt to determine population dynamics of the species of grain aphids present in Oregon.

II. REVIEW OF LITERATURE

Taxonomy

The binomial names of the three aphid species studied have been frequently changed, including a change for each of the species while this study was in progress. This fluctuation in nomenclature presented problems when reviewing the literature, and rendered many early works unusable because of questionable identifications.

The currently (1964) accepted scientific names for the three grain aphids studied are: *Macrosiphum avenae* (Fitch), Fitch 1855 (23); *Acyrthosiphon dirhodum* (Walker), Walker 1849 (87); and *Rhopalosiphum padi* (L.), Linnaeus 1758 (63). Several common names have been applied to these three aphid species, but do not appear in the list of "Common Names of Insects" by Laffoon (59); so common names will not be used in this thesis except for reference to the three species as grain aphids.

General references to aphid taxonomy were found in Theobald (83 and 84), Palmer (69), and Bodenheimer and Swirski (4). Dickson (18) published and cross indexed currently used names of aphid vectors of plant viruses.

Aphid Biology Studies

Aphid biology information relating to life cycles, host plants, predators, and parasites was mentioned by several early entomologists. Asa Fitch (23) 1855, Oestland (66) 1887, and Webster (90) 1894 mention grain being damaged by aphids. In 1904 Pergande (71) published a taxonomic bulletin on aphids (including M. avenae) that damage wheat, oats, barley, and grasses in the United States, and commented on their abundance for several years between 1870 and 1903. Webster and Phillips (91) in 1912 published biological studies of the spring grain-aphis Toxoptera graminum (Rondani). Davis (16) in 1914 reported Aphis avenae (Fabr.) (M. avenae Fitch) as the major pest of oats and a pest of wheat, and Phillips (72) in 1916 summarized the known information concerning Macrosiphum granarium (Kirby) (M. avenae). Phillips (72) and Baker and Turner (3) conducted biology studies of M. avenae under insectary conditions. Biology studies of grain aphids up to 1961 are summarized in Bruehl's (7) monograph "Barley Yellow Dwarf," and Orlob and Medler (67), present information on field biology studies of aphids infesting cereals and grasses in Wisconsin.

Biological studies of other aphid species were utilized in establishing this research and include studies of the cabbage aphid, Brevicoryne brassicae (L.) by Hughes in Australia (34 and 35), Hafez (28) in Europe, and Kennedy (45 through 56) and others in England. Hughes (35 related several life processes to field population studies, Hafez (28) discussed the effects of the predators and parasites on field populations in Holland, and J.S. Kennedy and co-workers (45 through 56) studied aphid behavior, aphid flight, aphid migration, and host plant findings.

Kennedy, Ibbotson, and Booth (55) divided plants into three regions by age: young, mature, and old or senescent, and related these plant regions to aphid feeding. These regions were discussed by Kennedy (46) when he indicated that too much emphasis had been placed on plant nutrition and not enough consideration given to the plant as a home and food source of aphids. Aphids probably can not distinguish areas of plants with or without certain amino acids but may be more influenced by cuticle thickness, internal cell arrangement, leaf surface color, and age when establishing on plant leaves (Kennedy 46).

Macrosiphum avenae

Gillette and Braggs (25) reported host alternation for M. avenae, with eggs being deposited on rose bushes in the fall and migration to wheat, oats, and grasses early in the summer. Phillips (72) in 1916 found eggs at Lafayette, Indiana, but had difficulty in obtaining living nymphs from the eggs. He believed that north of Indiana this aphid overwintered either in the egg stage or as ovoviviparae, or both, depending on the severity of the winter. Below the 35°N latitude in the United States eggs probably seldom occur (Phillips 72). In western Oregon and Washington ovoviviparous individuals were observed throughout the winter (Bruehl and Damsteegt).

Phillips (72) reported four nymphal instars, but the time required for each instar has not been determined. Phillips (72) recorded the average number of young per female, the average time from birth to first offspring and the average reproductive life of this species. Ito (37) found M. granarium (M. avenae) produced twice as many young when maintained on wheat plants as when maintained on barley plants.

Acyrthosiphon dirhodum

Walker (87) in 1849 found A. dirhodum feeding on rose in the spring and fall and stated, "In the summer it migrates to different species of corn and of grass (Secale, Triticum, Avena, Hordeum, Bromus, Dadylis, Holais and Poa), and it fixes itself on the blades of these plants." These comments suggest another aphid species, but A. dirhodum described by Walker has remained a valid taxon. Wilson and Vickory (93) list grass, grain and rose as hosts for the species. Gillette and Braggs (25) list Elymser sp. as the summer host and Rosa sp. as the winter host for this aphid. Bruehl and Damsteegt (9) observed this species on orchardgrass during the winter in western Oregon and Washington.

Egg production was reported by Orlob and Medler (67) but none of the eggs hatched. They suggest that this aphid species may be autoecious utilizing only plant species of the genus Rosa as hosts. No information on fecundity, length of life, or immature stages was found in the literature.

Rhopalosiphum padi

R. padi (L.) has been recorded from several species of Prunus and grasses (Richards 74). Cutright (13) 1925, Lathrop (61) 1928, and Andre and Tate (1) 1933 have reported viviparous colonies overwintering on species of Gramineae.

Rogerson (77) reported oviposition on bird-cherry in October and November. Eggs hatched in April and the nymphs moved to the buds of the plant where young were produced. In May the colonies produced alate forms which migrated, and by the end of June, corn and grasses were the principle hosts and parthenogenetic reproduction was common.

Baker and Turner (3) report the number of days spent in each of the four instar stages, average length of life, and the average fecundity. They reported a lower fecundity for aphids feeding on grain plants than for those on apple trees.

Distribution

Grain aphids are probably present wherever grains are grown throughout the world. In many areas they are of major economic importance, even though the species differ. Their cosmopolitan distribution on grains and grasses makes it impossible to designate specific areas of likely origin of the three species studied.

Macrosiphum avenae

This species has been reported from all continents with the exception of the Arctic Circle (Bodenheimer and Swirski 4). This wide distribution has been facilitated by a large and diverse host range including grasses, herbaceous plants and deciduous trees (Wilson and Vickery, 93; and Patch, 70). A listing of *M. avenae* distribution in the United States was given by Phillips (72) in 1916 and more recently by Bruehl (7), who includes reference to collections from California, Oregon, and Washington.

Acyrthosiphon dirhodum

A. dirhodum has been reported from Europe (Borner, 5 and Theobald, 83), the Middle East (Bodenheimer and Swirski, 4 p. 272), and North America as summarized by Orlob and Medler (67). Dickason, et al. (17) and Bruehl and Damsteegt (9) discuss its presence in Oregon and Washington.

Rhopalosiphum padi

R. padi has been so confused taxonomically it is difficult to be certain of the validity of distribution reports. It occurs in most

European countries and the Middle East (Bodenheimer and Swirski 4). Richards (74) lists R. padi from several sources in Canada, and states that many R. fitchii (Sand.) records refer to R. padi. This species has been reported from most states in the United States, Davis (16) and Bruehl (7). These papers cover R. fitchii (Sand.) and R. prunifoliae (Fitch) respectively, but undoubtedly refer to R. padi, either fully or in part. Lathrop (61) and Bruehl and Damsteegt (9) observed R. fitchii (R. padi) in grain fields of western Oregon and Washington during 1959 and 1960.

III. METHODS AND MATERIALS

General Description of Study Locality

The methods and materials used during this study were closely related to the types of investigations being conducted, therefore the more detailed descriptions of procedures will be included with the appropriate discussions and results.

The study was conducted near Corvallis, Oregon, where the winter temperatures seldom go below 20°F, and in the summer rarely above 90°F. The month with the lowest temperature is January, which averages 39.8°F, and July, the highest month, averages 66.6°F. The majority of the 38 inch average yearly rainfall comes during the winter months, while the total precipitation for the three summer months (June, July, and August) averages less than three inches. These averages were based on a thirty year period, 1931-60 (86).

Overwintering Host Plants

A large variety of plantings of agronomic species were present where the aphid host range and population studies were conducted. During the winters of 1961-62 and 1962-63 Gramineae plants were checked at weekly intervals at randomly chosen locations within fields. Wheat plants were observed in 10 randomly chosen one-foot sections of row so that the same plants were observed each week during the winter and spring of 1961-62.

During the autumn, winter, and spring of 1962-63 the number of aphids of each species on winter barley, wheat, rye, and orchard-grass were recorded. During the spring of 1963, oat fields were observed for aphid presence.

On hosts where aphid populations were observed, they were followed until the populations disappeared. These observations consisted of from 10 to 2,000 grain plants (generally 200 plants were observed) in a field, or of clumps of orchardgrass approximately one foot square in size. During the fall and winter of 1963-64 presence or absence of aphids on plants was noted.

Aphid Flight

Aphid flight was investigated by counting aphids caught on sticky traps during 1962 and 1963. In 1962 a variety of traps were set up in May, and checked for aphids until early June. During 1963 three solid cylindrical yellow traps were used from January 1 to December 31. Aphids were removed from the sticky material every 2-18 days during 1962, and approximately weekly during 1963. Specimens were placed in 70% alcohol and later washed in paint thinner to remove the adhesive material.

During 1962, traps were of two basic types. The first type consisted of rectangular traps 5 x 10 inches as suggested by Dickson

(19) and Kaloostian and Yeomans (44). These were constructed of either solid 1/8 inch masonite fiber board of 8/50 (eight squares to the inch) galvanized screen. The other type was a cylinder, 10 inches long and 4.5 inches in diameter. These were constructed from fiber sewer pipe, or the galvanized screen.

The adhesive material painted on the traps was Senco Bird repellent (Semewald Drug Co., Inc., 2723 Chauteau Avenue, St. Louis, Missouri). This viscous material was heated to approximately 250°F to facilitate application on the trap surface.

The traps were hung 12 feet apart in north and south rows on number 10 wire on six foot steel fence posts. The two rows were separated by barley plantings 150 feet wide (Figure 1). Fresh traps were placed in the field at approximately monthly intervals because of the accumulation of insects and debris in the sticky material of old traps.

During 1963 three traps were placed 150 feet apart on the south margin of the barley fields used for the 1962 and 1963 plant observations (Figure 1). Trap height was five feet, as used by Johnson (41), and Johnson and Eastop (43).

Spring Barley Studies

Location and Arrangement of Study Area

The spring barley fields observed during this study were located 10 miles northeast of Oregon State University on the Hyslop Agronomy Farm at Granger, Oregon. This farm is managed by the Farm Crops Department which kindly made all mechanical and agronomic facilities available. The fields studied were located approximately one-half mile from the Oregon State University weather recording station. Other plots on the 240 acre farm were used for host range and winter host observations.

The 1963 studies included commercial fields of barley, wheat, and oats approximately 35 miles north of the study area. These fields were located in an area reported to have been free of barley yellow dwarf virus in previous years.

The spring barley studies on the Hyslop Farm consisted of following aphid populations in four fields, three during 1962 and one during 1963.

1962

Early season planting date	April 12	Field I
Mid-season planting date	April 26	Field II
Late season planting date	May 9	Field III

1963

Late season planting date May 3 Field IV

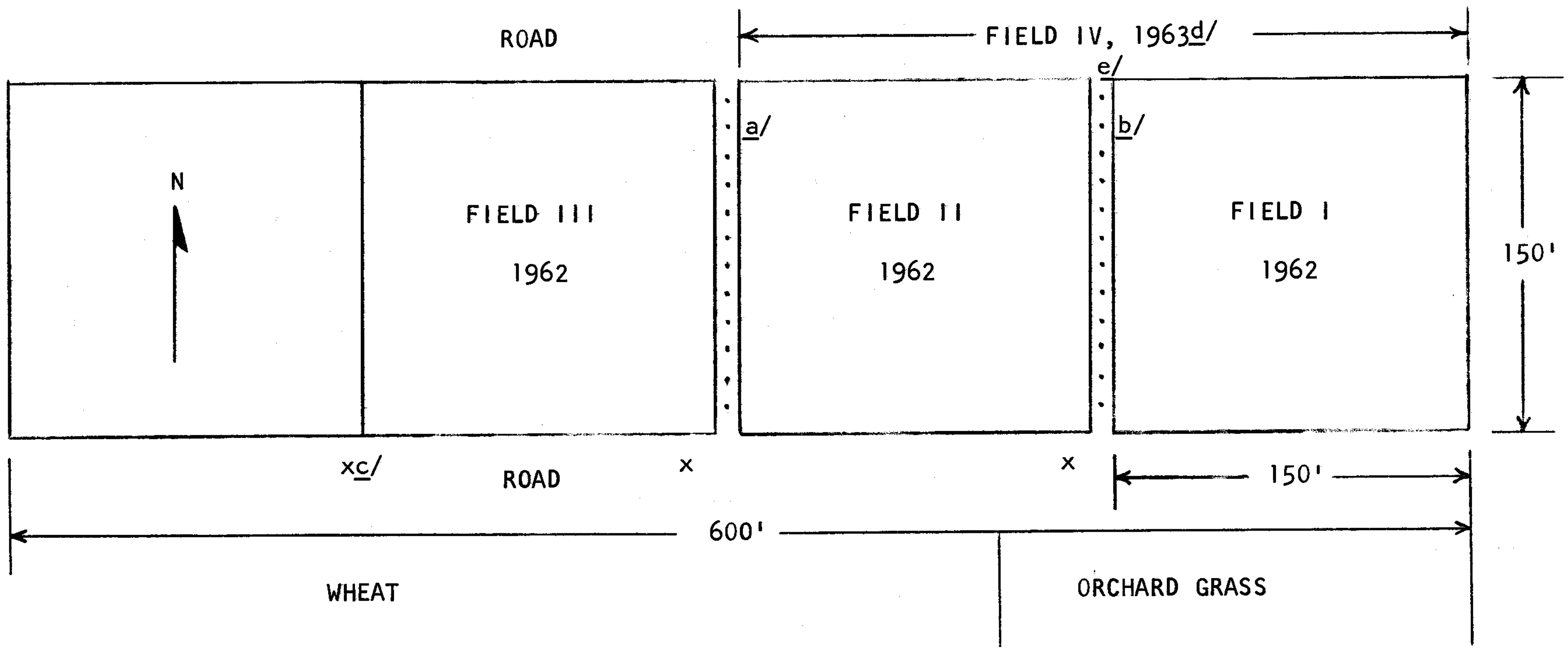
Figure 1 shows the arrangement of the fields used in 1962. Each of these fields were 150 by 150 feet separated by a barren alley 10 feet wide. During 1963 a single field was used (150 by 300 feet) which occupied the same area as fields I and II during 1962. Only one field of barley could be planted in 1963 because of wet spring weather.

On the north and south sides of each field were grass road ways, and the west two-thirds of the study area was bordered by wheat to the north and to the south (Figure 1). Orchardgrass was grown on the east one-third on the south margin, and mixed grasses and legumes in a cover crop study were grown on the east one-third of the north margin.

Sampling Plan

Sampling in the barley fields followed a randomized plan (Li 62, p. 196) shown in Figure 2. Each of the 100 sampling stations and the row to be sampled (numbers inside the small blocks) was chosen by using a random numbers table.

Range and section divisions were marked on the south and west sides of each field providing an easy to follow pattern for locating sampling areas in the fields. Each of the 17 ranges (Figure 2) was a nine foot drill swath consisting of 15 rows of barley plants, and each



a/ Dots represent sticky traps, replication one of 1962.
b/ Dots represent sticky traps, replication two of 1962.
c/ "x" stands for location of the three 1963 sticky traps.
d/ Field IV occupied twice the area of the 1962 fields.
e/ A ten foot barren strip was left between fields I and II, and fields II and III, 1962.

Figure 1. General layout of the 1962 and 1963 experimental area located on the Oregon State University, George Hyslop Agronomy Farm near Corvallis, Oregon.

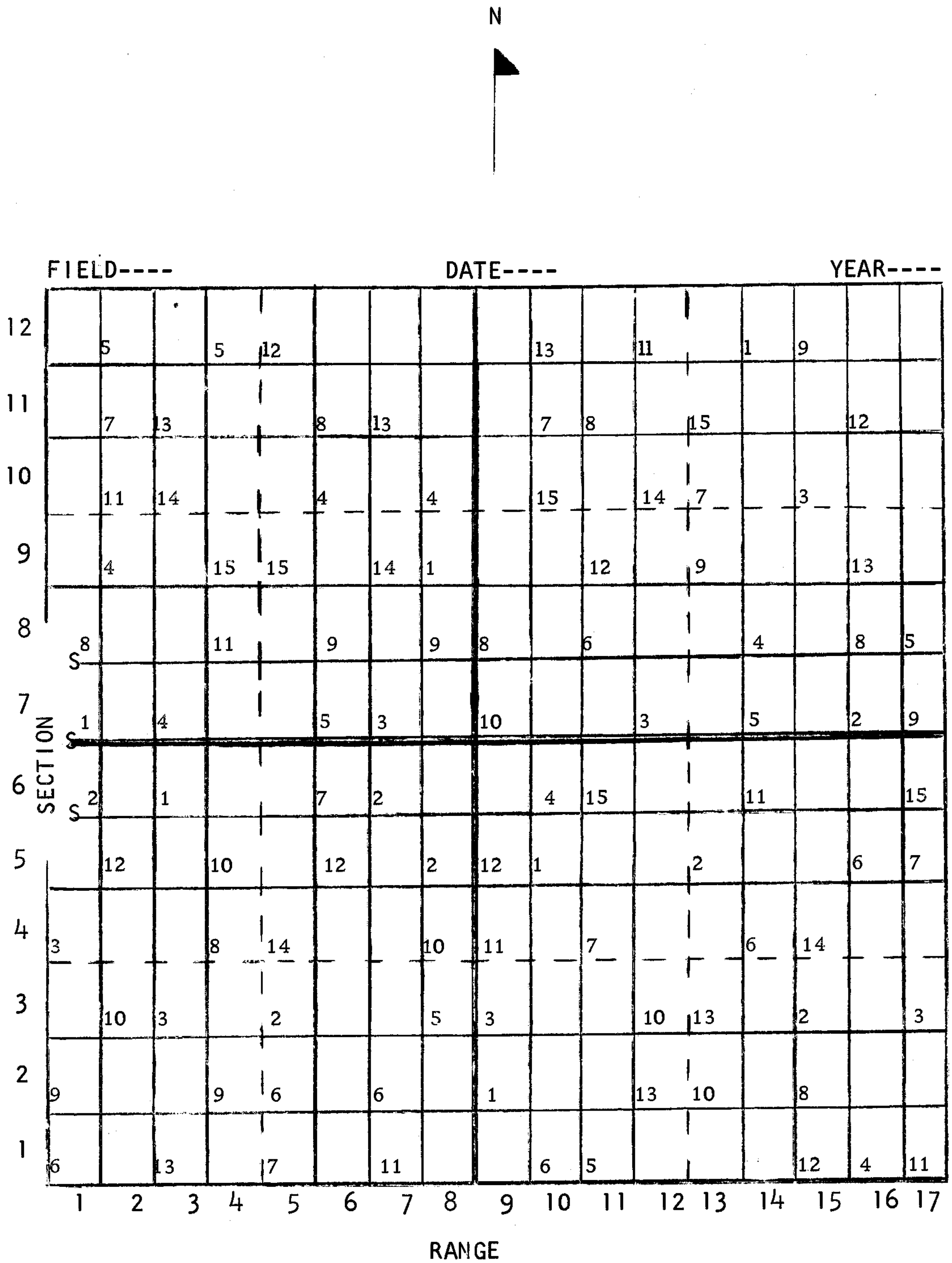


Figure 2. Plot design used during 1962 and 1963 when making randomized field samples and recording field data. Scattered numbers in the small blocks refer to the row number, 1 through 15, where two adjacent plants were sampled.

section contained 12 feet of rows.

The procedure followed when sampling, consisted of entering a range, proceeding to the section containing a number on the data sheet, selecting the designated row, and sampling at random two adjacent plants. Hence, samples were taken from the same 12 feet of row each date, but not necessarily the same plants. For each date there were 200 plants sampled from each field from 100 sampling stations.

The master plan (Figure 2) was reproduced on sheets of paper for recording the field data at approximately weekly intervals from early May until late July, the period of barley plant growth and maturation. Information was gathered concerning seasonal occurrence of aphids by species, population densities during the season, morphological form (instars and adults), plant area [redacted]ccupied by aphids, field distribution of the aphids, and biologically associated organisms including predators, parasites and host plants. More detailed discussion of the methods used for these studies is included in the appropriate sections dealing with these data.

Statistical Methods

Previous to gathering field data a conference was held with members of the statistics department, Oregon State University. The sampling procedure and the number of plants to be sampled per field was established as outlined in the discussion of Figure 2.

Part of the data gathered during the spring of 1962 and 1963 was entered on IBM punch cards; M. avenae data from all four fields and A. dirhodum data from field I. The calculation of statistics from the data cards was done with the aid of the Oregon State University Statistics Laboratory and their 1420 and 1410 computors.

Predators and Parasites

Observations of predators and parasites were recorded when sampling the 200 plants in the four barley fields. These observations were not sensitive to insect species, therefore collections were made at random (separate from the field plant counts, but at the same time) and these specimens used for insect species determinations.

Aphid predators, primarily Syrphidae, were gathered from plants in the larval stage and reared on aphids under laboratory environments, or leaf pieces with pupae were collected and adults from the pupae preserved for identification. Coccinellidae were collected in the adult stage with a sweep-net. Predators were also collected from the sticky traps used for the aphid flight studies.

Aphid parasites were collected by removing the piece of leaf to which the mummified aphids were attached. Specimens were placed one per vial and taken to the laboratory to await emergence.

IV. OVERWINTERING HOSTS

General

Observations were conducted to find overwintering host plants of grain aphids in western Oregon and to determine the relative importance of the different host plants. During the fall, winter, and early spring of 1961-62 a wide range of plant species were checked and a number of aphid hosts found. During 1962-63 the observations were concentrated more on the known host plants.

The occurrence of the three species of grain aphids by months of the year during the 1961-62 and 1962-63 seasons is summarized in Figures 3, 4, and 5. The most striking feature of these figures is the absence of the three species of aphids in the field during the months of August and September. At this time of the year the spring cereals have been harvested, fall growth has not begun and the perennial grasses are dry. Thus, there were no cultivated hosts in a suitable condition to support aphid populations. An attempt was made to find aphids on some other hosts, such as corn, rose, blackberry, apple, and roadside plants, during this period of the year, but aphids were not found until they appeared on overwintering hosts.

Aphid Species

Macrosiphum avenae

M. avenae was found only on grain plants during this study (Figure 3). During 1961-62, barley, rye, and wheat plants were observed weekly from November 16, 1961 to April 5, 1962 without seeing M. avenae. On February 15, 2,000 wheat plants were observed to confirm the validity of the 200 plant sample size.

During the winter of 1962-63, M. avenae were found on most sampling dates between December, 1962 and August, 1963. M. avenae appeared on the taller wheat plants during March, 1963. Alate aphids were found on these plants during April and May at the time wheat plants were heading. Winter wheat may have been a major source of the alate M. avenae which entered the spring barley fields. An oat field was investigated which had two plantings of oats, one seeded early in the fall and the other in late fall. The few early seeded plants that survived were taller and were infested with M. avenae more often than were the shorter late seeded plants.

The presence of overwintering M. avenae on plants appeared to be associated with the growth pattern of the plants. Specimens were more likely to be found on vigorously growing plants over six inches tall, than on shorter plants in the same field. The barley, rye, and wheat plants observed during 1961-62 that did not have

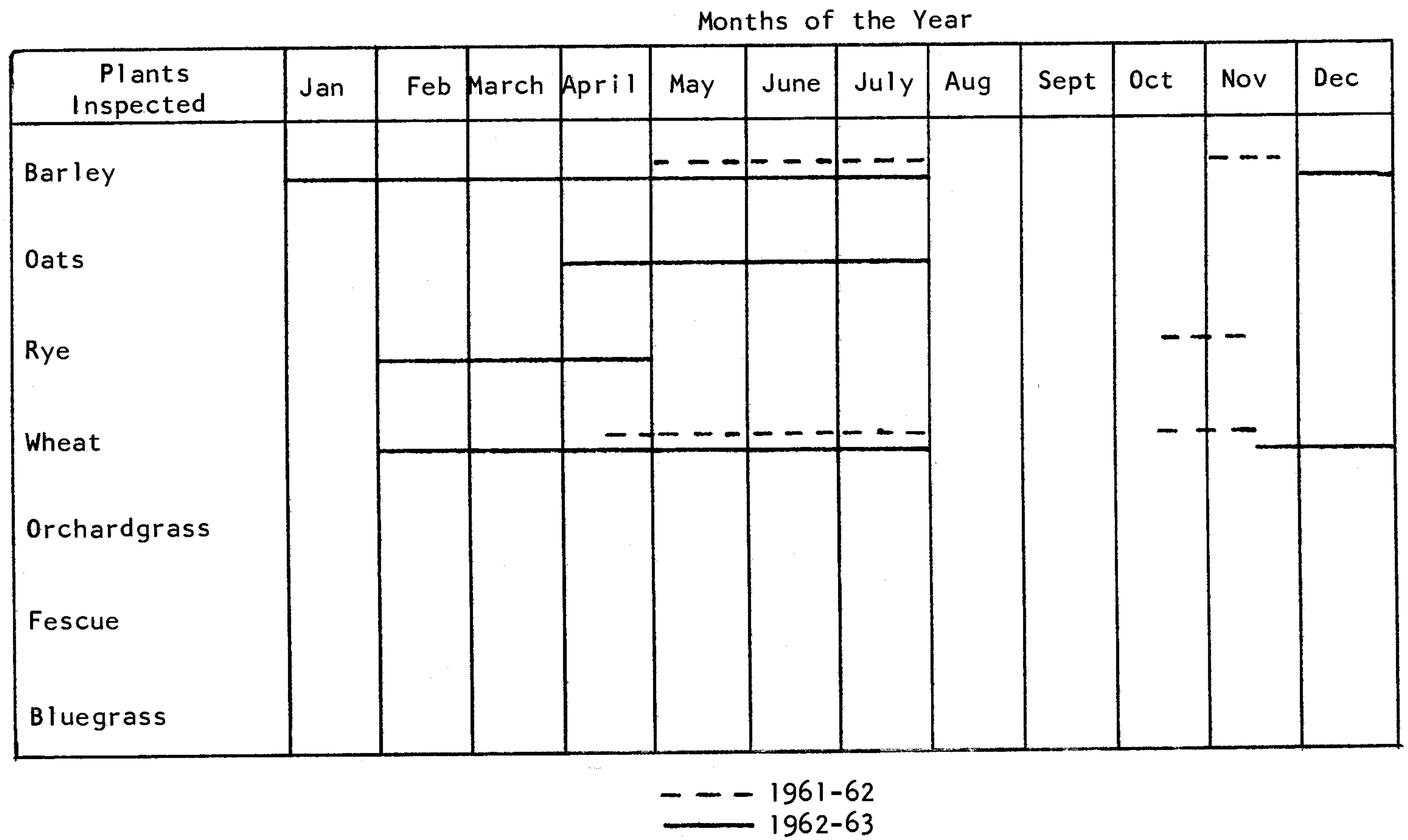


Figure 3. Two year summary of aphid observations on field plants showing the months of the year when Macrosiphum avenae was found on grain hosts near Corvallis, Oregon.

overwintering aphids were less than six inches tall until late February, and the April 16, 1962 observation of aphids (Figure 3) was on wheat plants that were 18 inches tall.

Acyrthosiphon dirhodum

The first observation of A. dirhodum in the field was April of 1962 in fields of orchardgrass and fescue, and later on barley (Figure 4). Specimens were observed in orchardgrass until July when the plants were harvested, however the populations declined after April. This species was observed again on orchardgrass during October of 1962 (Figure 4) after the burned stubble began to produce green shoots. Orchardgrass was the main overwintering host found for A. dirhodum and the largest populations (up to 10 per sweep of a sweepnet) were observed during April before the orchardgrass matured. Specimens were observed on other plants, but were less abundant.

During the second winter of study (Figure 4) rye, and barley were observed to support populations of A. dirhodum and peak numbers occurred on barley during February and March. The highest populations of aphids were observed on rye in January. Freezing temperatures and plant maturation corresponded with the disappearance of aphids on rye plantings after mid-January.

The long thin shape of A. dirhodum may be an adaptive

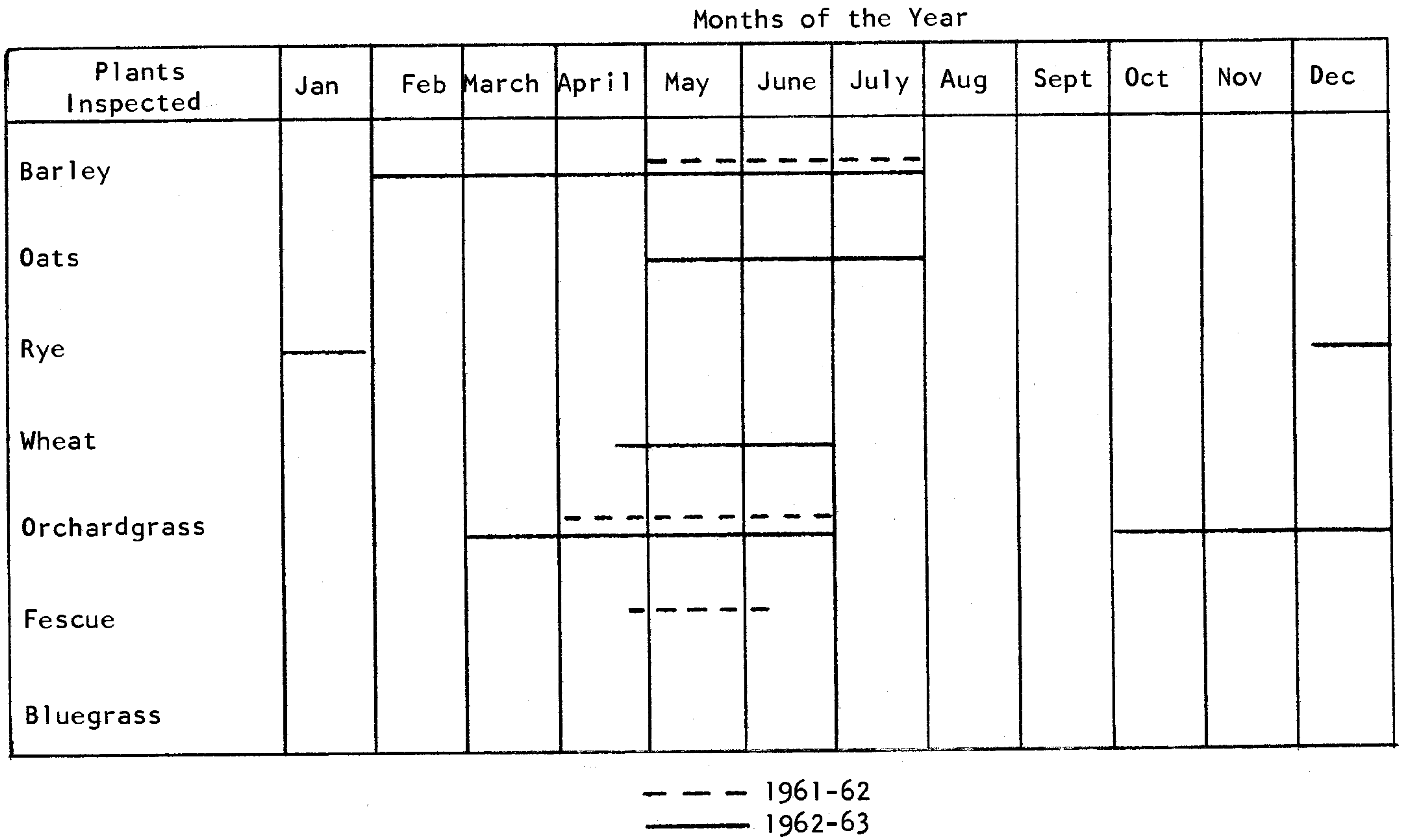


Figure 4. Two year summary of aphid observations on field plants showing the months of the year when Acyrthosiphon dirhodum was found on grain and grass hosts near Corvallis, Oregon.

characteristic for its existence on orchardgrass leaves. Orchardgrass leaves are "V" shaped in cross section with the dorsal surface forming a channel out from the midrib of the leaf. The aphids were observed in this groove with the stylets inserted into the midrib region, and nymphs of various ages in a row along the midrib. This phenomenon was also noticed to some extent on spring barley plants. The habit of lying in the "V" may contribute to the survival of this species by affording some protection from predators, leaf abrasion, or possibly affording a more desirable microclimate.

Mr. Hille Ris Lambers (personal communication) stated that _A. dirhodum_ would be found only on roses during the winter season. However, during the winter of 1963-64 one of the common winter hosts in western Oregon was orchardgrass.

Rhopalosiphum padi

R. padi was the most common grain aphid species observed during the 1961-62 overwintering host studies. The highest numbers of aphids per fescue plant were observed in early January, just prior to a sharp reduction in temperature from the 35°F. range to the 15°F. range.

During the second year of studies (Figure 5) _R. padi_ populations were observed in fields of barley, rye, and orchargrass. Rye and orchardgrass plants supported a continuous population

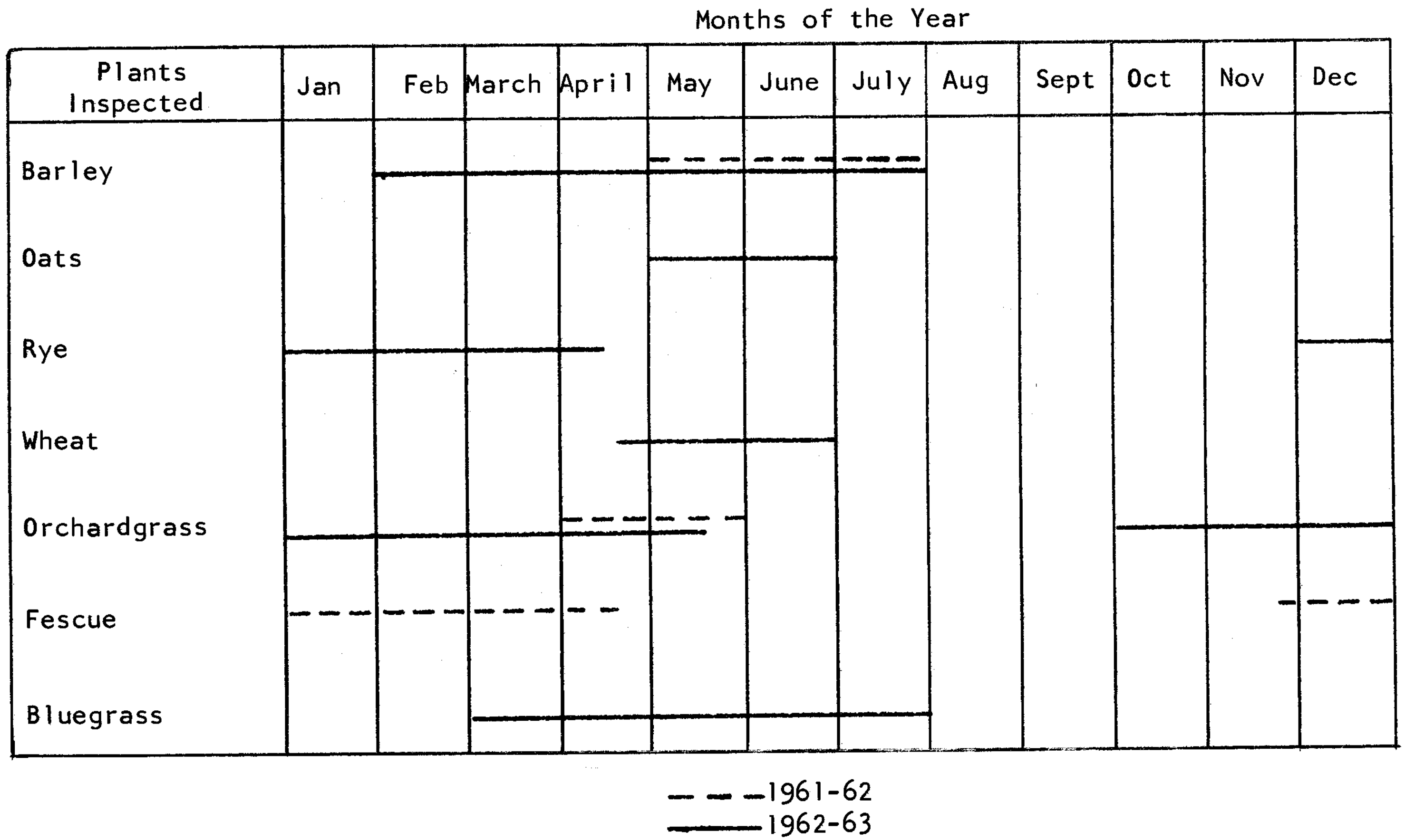


Figure 5. Two year summary of aphid observations on field plants showing the months of the year when Rhopalosiphum padi was found on grain and grass hosts near Corvallis, Oregon.

throughout the 1962-63 winter.

Snow covered the ground between the orchardgrass, rye, and barley rows on February 1, 1963 and R. padi were observed on the snow; many aphids were alive and crawling. Aphids were present on bluegrass during early spring in high enough numbers to damage the plants.

Populations of R. padi were highest during the cool mid-winter months in the Willamette Valley. Davis (16) reported winter occurrence of this species in the Missouri Valley and surrounding areas. This species was observed on rye and other plants more commonly on the dying leaves than on the green or growing leaves. This was interpreted as possibly an adaptation to feeding on leaves with low turgor pressure. However, plants in the greenhouse, or under cages in the field, appeared to be infested on all areas of the plant independent of leaf condition.

V. APHID FLIGHT

Information on aphid flight was of interest during this study because of the introduction of barley yellow dwarf virus into barley fields by winged aphids. The major objectives of the sticky trap studies were to determine the time of species migration into spring barley, and the seasonal occurrence of flights.

Trap Design

The following methods for sampling the flight of aphids have been employed: sticky coated screens (Rockwood, 75), revolving nets (Williams and Milne, 92), kites towing net funnels (Hardy and Milne, 29), sticky board traps (Hardy and Milne, 29), airplanes (Coad,12, Glick, 27, etc.), suction nets (Broadbent, 6 and Johnson, 38), wind vane traps (Davis and Landis, 15), turkish towels (Hottes 33), and water pan traps (Moericks, 64 and 65).

Sticky traps were chosen over other methods of aerial trapping because they are inexpensive, simple to operate and maintain, sample continuously, and have been used successfully by other workers.

Eastop (21) trapped 23 species of aphids and found that dicotyledon-feeding species were attracted to yellow traps, and grass and sedge feeding species were not attracted to yellow. Broadbent

(6) using black, white, and yellow trap colors, found traps painted yellow caught significantly more *Myzus persicae* (Sulzer) than black or white traps. Moericke (65), Kennedy (47), and others report yellow as being an aphid attracting color. Black and yellow were chosen as background colors for the sticky traps used in this study.

Seasonal Catches

Seasonal recoveries of grain aphids were summarized in Table 1 for the period from mid-April to mid-June during 1962 and Table 2 for the entire year during 1963. *Macrosiphum avenae* was the first species to be captured on the sticky traps during both years (Tables 1 and 2). During 1962, April 24 was the first date *M. avenae* were found on sticky traps, and the aphids appeared in low numbers until June when there was an increase in numbers. During 1963, the pattern was similar with the largest numbers being trapped during the first half of July, and none were captured between August 12 and October 8. Fall migrants from an unknown late summer host appeared during October and November.

The early 1963 catches and the peak numbers caught during July (Table 2) correspond to the activities observed during plant counts (Figure 7, Part A). During early field observations alatae were recorded, and first and second instars appeared May 25, indicating that winged aphids had to enter the field at an earlier date.

Table 1. Seasonal sticky trap catches of three species of aphids in western Oregon during 1962.

Date - 1962		Days Represented[a]	M. a.[b]	A. d.[c]	R. p.[d]	Total
April	17	0	0	0	0	0
	19	0	0	0	0	0
	24	5	7	0	0	7
	29	5	0	0	0	0
May	1	2	2	0	0	2
	4	3	1	0	0	1
	5	1	2	0	0	2
	7	2	1	0	0	1
	8	1	1	0	0	1
	10	2	2	1	0	3
	13	3	0	1	4	5
	15	2	0	3	1	4
	16	3	0	0	3	3
	18	2	3	15	2	20
	19	1	0	1	1	2
	23	4	4	7	2	13
	28	5	10	23	15	48
June	5	8	20	14	10	44
	14	21	22	5	373	400
	16	19	18	12	202	232
	18	21	19	10	150	179
Total			112	92	763	967

[a] The number refers to the days between checking traps. The period may be longer than reading dates indicate, because of the two replications.

[b] M. a. = *Macrosiphum avenae*

[c] A. d. = *Acyrthosiphon dirhodum*

[d] R. p. = *Rhopalosiphum padi*

Table 2. Seasonal sticky trap catches of three species of aphids in western Oregon during 1963.

		Days Represented[a]	Aphid Species M.a.[b]	A.d.[c]	R.p.[d]	Total Aphids
Jan.	8	8	0	0	0	0
	18	10	0	0	0	0
	25	7	0	0	0	0
Feb.	1	6	0	0	0	0
	8	8	0	0	0	0
	16	8	0	0	0	0
	22	6	0	0	0	0
March	3	9	1	0	0	1
	8	5	0	0	0	0
	21	13	0	0	1	1
	28	7	0	0	0	0
April	5	8	0	0	0	0
	11	6	1	0	0	1
	20	9	0	0	0	0
May	3	13	1	0	0	1
	11	8	5	0	0	5
	14	3	8	2	0	10
	18	4	19	0	4	23
	26	7	34	1	49	84
June	4	9	26	0	84	110
	10	6	12	0	137	149
	17	7	50	2	102	154
	24	7	75	0	92	167
July	2	8	47	10	92	149
	15	13	245	20	79	344
	30	15	31	2	0	33

(Continued)

[a] The number refers to the days between checking of the traps.
[b] M. a. = *Macrosiphum avenae*
[c] A. d. = *Acyrthosiphon dirhodum*
[d] R. p. = *Rhopalosiphum padi*

Table 2. (cont'd)

Date - 1963		Days Represented[a]	Aphid Species			Total Aphids
			M. a.[b]	A. d.[c]	R. p.[d]	
Aug.	12	13	3	0	0	3
	20	8	0	0	0	0
Sept.	5	16	0	0	0	0
	18	13	0	0	0	0
	23	5	0	0	0	0
Oct.	2	9	0	1	0	1
	8	6	1	0	5	6
	18	10	8	39	13	60
	30	12	3	2	5	10
Nov.	14	15	2	0	0	2
	30	16	6	0	0	0
Dec.	14	14	0	0	0	0
	31	17	0	0	0	0
Total			572	79	663	1,314

[a] The number refers to the days between checking of the traps.

[b] M. a. = *Macrosiphum avenae*

[c] A. d. = *Acyrthosiphon dirhodum*

[d] R. p. = *Rhopalosiphum padi*

Peak flight in mid-July (Table 2) occurred when the barley plants were drying, and the aphids were probably under stress due to an insufficient water supply. A large flight was expected in late July at the time aphids disappeared from the barley field (Figure 7, Part A), but Table 2 indicates the flight occurred before the aphid population decreased in late July.

Acyrthosiphon dirhodum alatae were first found on sticky traps in May (Tables 1 and 2), and the 1963 recoveries were low compared to the other two species. The A. dirhodum trap catches during the second week of May of both seasons were one week later than the first appearance of alatae on the barley plants (Figure 8, Part A). The higher trap catches during mid-July of 1963 corresponded with the population peak of this species on barley plants (Figure 8, Part A), and may have been migrants leaving the barley fields. The low number of A. dirhodum alatae caught during 1963, compared with M. avenae and R. padi recoveries, corresponds with the population levels of the three species observed on the barley plants (Figures 7, 8, and 9, Part A and Table 2).

Rhopalosiphum padi alatae were recorded in relatively high numbers compared to the other two species of grain aphids. During 1962 and 1963 this species was first observed during mid-May (Tables 1 and 2). Catches both years indicated a flight peak in early June, which corresponded with the peak field populations (Figure 9, Part A), and also with the heading of many known grass hosts present in western Oregon.

It is interesting that the late July termination of aphid catches coincides with the dry, warm summer period when most grass and herbaceous plants become dry. Aphids must have perished or left the fields because of the stress placed on the host plants for water. It was also mentioned in the discussion of Figures 3, 4, and 5 that none of the species was recovered in the field during this period. Small flights appeared after the fall rains began, and before cold weather inhibited flights in December. Compared to the spring flight, relatively few aphids were caught during the fall.

Trap Catches in Relation to Direction

The sticky traps were placed in the field facing the four cardinal directions, north, east, south, and west. It appears the aphids flew from north to south, because approximately one half of the catches were on the north face of the traps (Figure 6). This is the direction of the prevailing wind according to the weather station data recorded at the experimental farm.

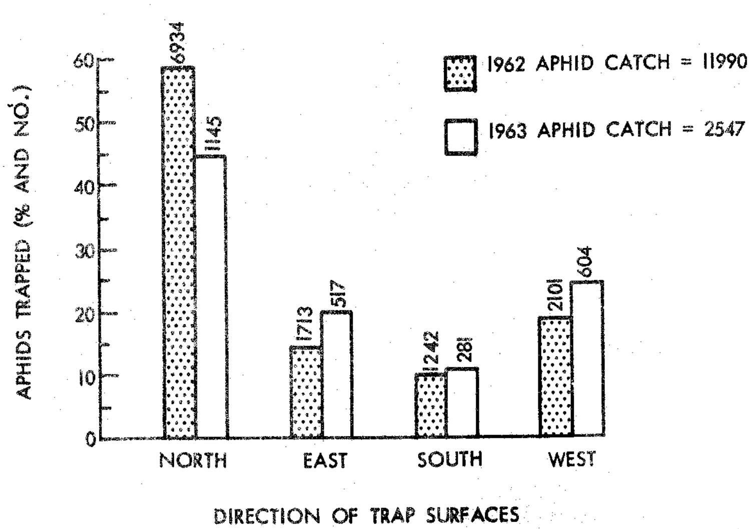


Figure 6. Number and percentage of aphids of all species caught on four directional faces of sticky traps during 1962 and 1963 near Corvallis, Oregon.

VII. SPRING BARLEY STUDIES

The objectives of the spring-seeded barley studies were to determine the identification of the aphid species associated with spring barley, the pattern of the aphid populations in the fields, the differences in aphid populations between barley fields planted in early April and those planted in May, and the biological factors which might aid in the understanding of the habits of grain aphids.

Plant Phenology

During the field studies of the aphid populations notes were taken concerning the development of the barley plants (Table 3).

The four barley fields differed in date of planting and the year grown. The three fields grown in 1962 were planted early, mid-way, and late in the barley planting season; whereas only a late season planting was possible during 1963. Plants in fields III (1962) and IV (1963) were quite similar in phenological development relative to calendar dates. A comparison of the two pairs of fields I and II, III (1962) and IV (1963) showed that plants in the first two fields matured or headed three weeks before the plants in the latter two fields. In each of the four fields, the plants dried and the kernels began to harden at approximately the same time in late July, regardless of when the field had been seeded. Thus, the

Table 3. Dates of observations in four spring barley fields relative to plant phenology.

1962			1963	Height of Plants	Phenological	
Field I	Field II	Field III	Field IV	in Inches	Plant Classes	
April 12	April 26	May 10	May 3	--	Seeding Date	
April 19	May 8	May 23	May 24	2	A[a]	1-leaf
April 24 & 29	May 13	May 31	--	3	B	2-leaf
May 1 & 4	May 16	June 5	June 3	4 to 5	C	3-leaf
May 7 & 11 & 15	May 21 & 26	June 9 & 14	June 10	6 to 8	D	4-leaf & stooling
May 18 & 30	June 6 & 9	June 21	June 20	10 to 12	E	4-leaf & boot forming
June 12	June 16	July 2	--	18	F	boot stage
June 20	June 22	July 14	July 16	24	G	heading
June 26	June 29	--	--	28[b]	H	heading & drying
July 8 & 16	July 9 & 20	July 24	--	28	I	av. 2.5 green leaves/stalk
July 25 & 31	July 23 & 30	July 31	July 30	28	J	only heads green, all leaves brown

[a] These letters are used on the abscissas in Figures 8, 9 and 10, Part B.

[b] Plants in fields II, III, and IV reached a height of approximately 28 inches, while the plants in field I were 36 inches tall.

time needed for plant growth was consistent, but the time between plant heading and grain maturity was longer for the plants seeded earlier in the season.

Seasonal Abundance

In general, the typical pattern for insect populations in annual crops is a small initial population which increases to a peak number and finally declines. This pattern, with some interesting deviations, was followed by grain aphids on barley in western Oregon.

Figures 7, 8, and 9 show the population patterns found for the three species of grain aphids during 1962 and 1963. These graphs are based on the numbers of aphids found on 200 plants. Figures from three dates (July 8, Field I; July 9, 20, Field II) had to be adjusted because fewer than 200 plants were observed. The statistical variance for the three adjusted counts may be greater than for counts when 200 plants were actually observed. Parts A and B of Figures 7, 8, and 9 are based on the same data for each species, but the abscissas differ. In Part A, the abscissa refers to calendar dates, the points being placed on the sampling dates. In Part B of each figure the abscissa represents the ten classes of plant phenology given in Table 3. The points of the lines occasionally differ vertically in the two figures because of combined sampling dates in Part B (two samples taken during one phenological class were added and divided by two for the vertical point of the line).

Macrosiphum avenae

Figure 7, Part A, shows the general increase and sharp decline in mid-July of *M. avenae* populations. In the fields planted early and in mid-season, plants were established before aphids appeared; in the fields seeded late in the season, populations of aphids were observed on the newly emerged leaves of the seedlings. Since aphids were found on late planted barley at the time the plants appeared, the only way to have counts free of aphids would have been to score bare soil. Kennedy, Booth, and Kershaw (53) indicated that aphids may be found on bare soil during aphid flight periods.

In each of the four fields (Figure 7, Part A), the early season increase in the *M. avenae* populations was interrupted by a slight drop in the number of aphids. This drop, as recorded for the 1962 fields, suggests that there may have been a generation effect: a phenomenon common with insects that have two or three generations a year (Thompson, 85). Part B of Figure 7 does not show this decline in fields I and II because sampling dates were combined. Following the drop in numbers, the populations

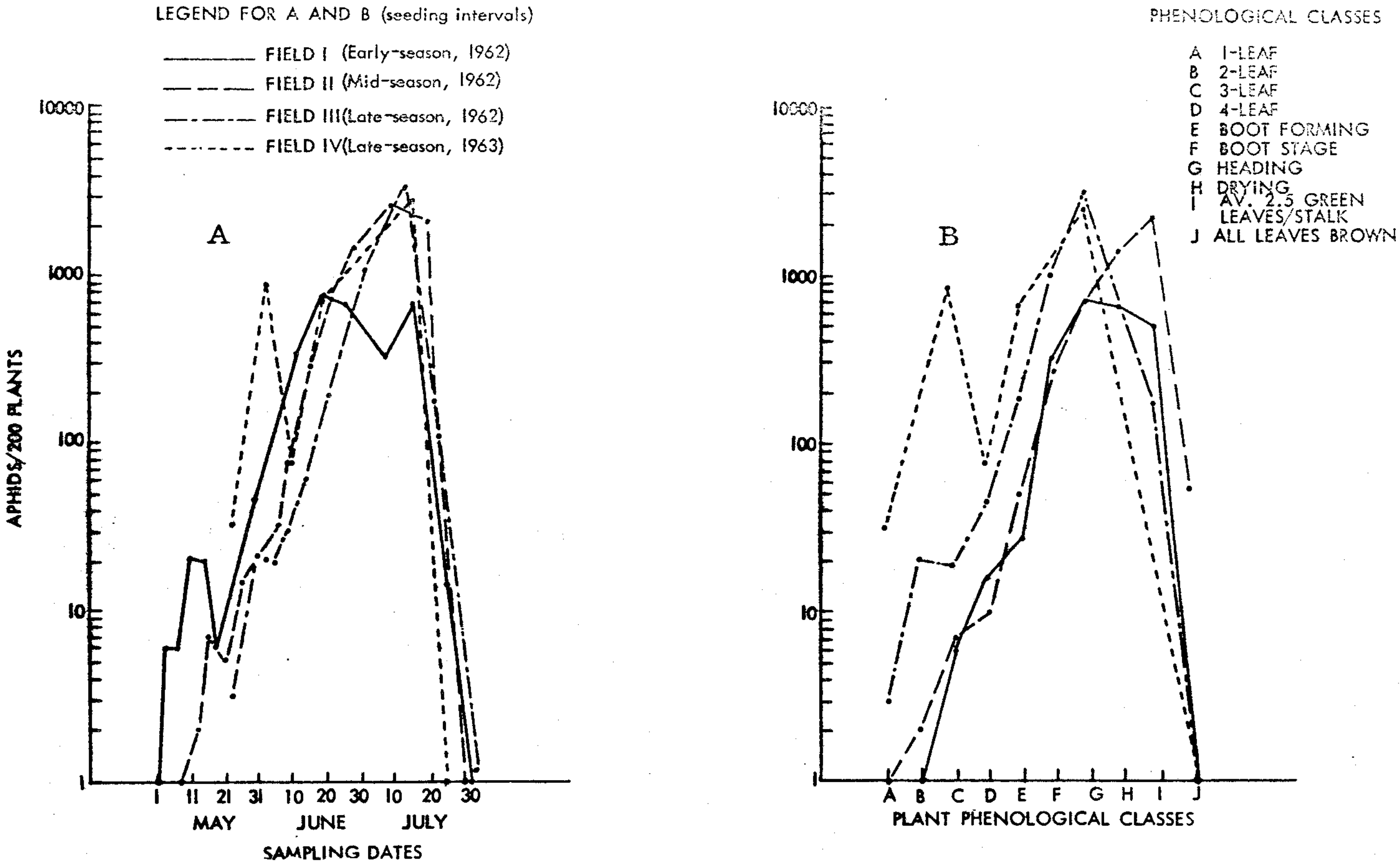


Figure 7. Seasonal abundance of Macrosiphum avenae on 200 randomly selected plants in four barley fields during 1962 and 1963. (A) Each point represents the total number of aphids observed at each sampling date cited in weekly intervals on the abscissas. (B) Each point represents the total number of aphids observed in relation to stages of plant growth cited on the abscissas, independent of calendar dates.

increased until mid-July, reaching a peak of three to fifteen aphids per plant. This peak population occurred at approximately the same calendar date in each of the four fields.

M. avenae disappeared from the headed barley plants by July 31 in all four experimental fields; a similar observation was made in commercial fields of barley during 1963. This rapid disappearance of aphids during the last two weeks of July was probably due to a combination of several factors. Plants were maturing and the leaves were turning brown so that the sap flow, and consequently the aphid food supply was reduced; temperatures rose above 90°F, and the relative humidity was below 30 percent. According to the literature and Hughes (personal communication) these three factors, reduced plant sap flow, increased temperature, and decreased relative humidity, may cause water deficiencies accounting for aphid disappearance.

Fields III (1962) and IV (1963) were both planted in early May, and the plants completed the phenological growth stages at about the same calendar dates (Table 3). Maximum populations occurred at an earlier phenological stage in these two fields than in fields I and II (Figure 7, Part B). This may have been the result of adverse climatic conditions during late July at which time the barley plants were mature in the fields planted in early and mid-season, but plants were still immature in the two late seeded fields.

Had the aphid populations continued to increase in the two late seeded fields until phenological class I, then the population peaks in the two late seeded fields would have been much higher.

Acyrthosiphon dirhodum

A. dirhodum was first found in spring barley fields at a later date in the spring than was M. avenae (Figures 7 and 8, Part A). In the early seeded field (field I, 1962), A. dirhodum reached a population peak approximating that of M. avenae. In the other three fields the peak numbers of A. dirhodum were much lower than the M. avenae peak numbers. The higher numbers of A. dirhodum per count fluctuated near the peak count level for nearly a month in each of the four fields. M. avenae populations (Figure 7, Part A) fluctuated in a similar manner in the early planted field, but reached definite population peaks in the other fields.

The sharp and consistent decline of populations of A. dirhodum in late July (Figure 8, Part A) was probably due to the same factors which caused the decline of M. avenae populations. It is interesting to note that A. dirhodum remained on the plants until a later phenological stage of plant growth in the early and mid-season planted fields than it did in the two late seeded fields. Late tillers produced by the plants during July in the early seeded field may have facilitated the extended peak aphid populations, but

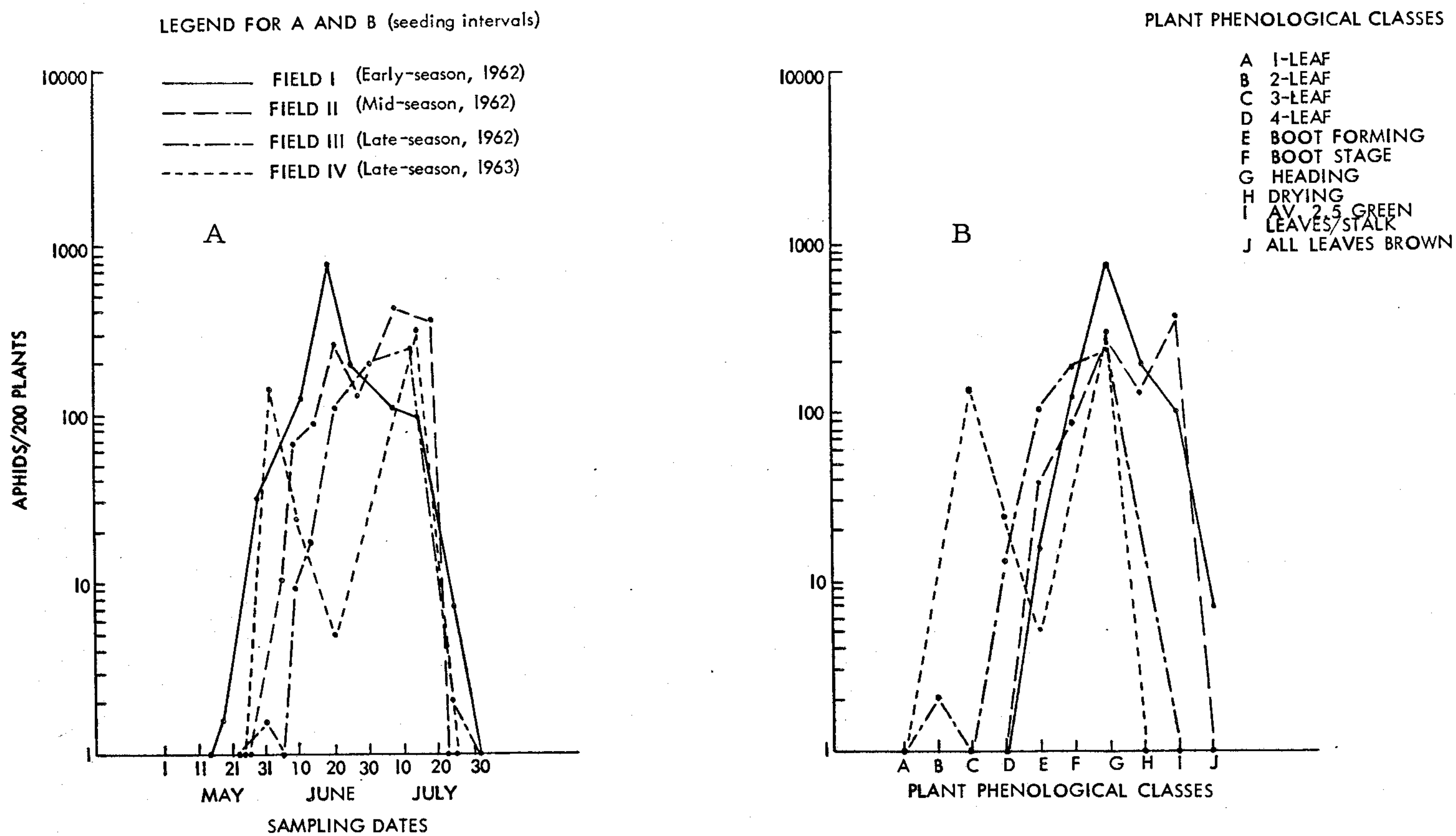


Figure 8. Seasonal abundance of Acyrthosiphon dirhodum on 200 randomly selected plants in four barley field during 1962 and 1963. (A) Each point represents the total number of aphids observed at each sampling date cited in weekly intervals on the abscissas. (B) Each point represents the total number of aphids observed in relation to stages of plant growth cited on the abscissas, independent of calendar dates.

no tillers were present in the field planted in mid-season. The leveling and extension of the A. dirhodum population peaks during June and July may have resulted from a combination of temperature and plant physiology. Plants maturing in early July supported peak aphid populations earlier in the season than plants maturing in mid-July and the peak numbers of aphids remained for an extended period of time (early and mid-season planted fields I and II). These flat population peaks occurred in fields III and IV where the plants reached maturity later in July because the plant maturity occurred along with high temperatures which desiccated the aphids resulting in the rapid population decrease (Figure 8, Part B).

Rhopalosiphum padi

During 1962 (Figure 9, Part A; fields I, II, and III) R. padi were found in relatively small numbers, 225 being the most observed on any one date, in contrast to the thousands of M. avenae recorded. However in the 1963 field, nearly 1,000 R. padi were found during one count. This high number resulted from observing the plant shoot below the soil surface, as well as the above ground plant parts. It is not known whether R. padi were also present below the soil surface in 1962, or whether observations to cover this habitat would have increased the number of aphids found. Plants retained from the 1962 fields did not show

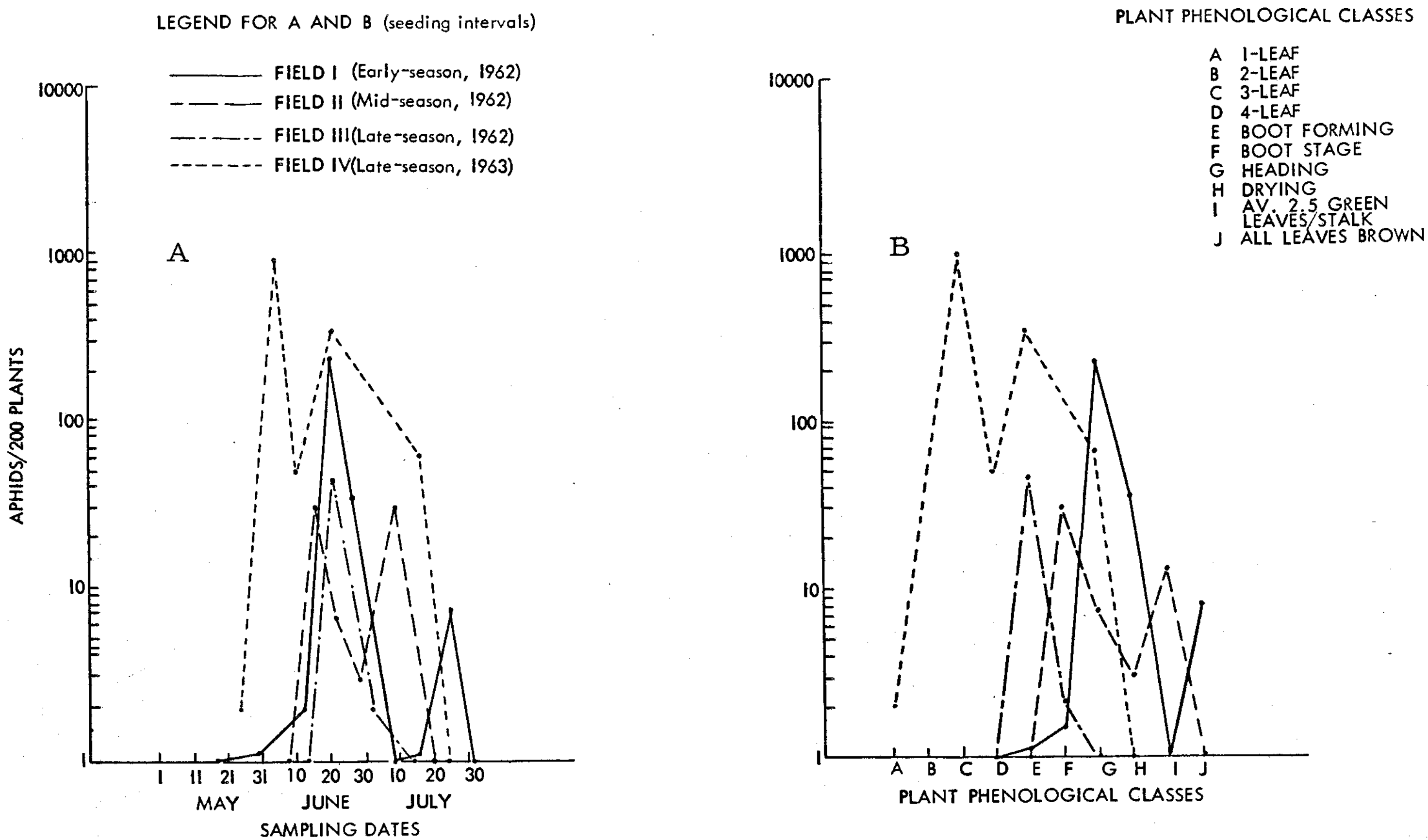


Figure 9. Seasonal abundance of Rhopalosiphum padi on 200 randomly selected plants in four barley fields during 1962 and 1963. (A) Each point represents the total number of aphids observed at each sampling date cited in weekly intervals on the abscissas. (B) Each point represents the total number of aphids observed in relation to stages of plant growth cited on the abscissas, independent of calendar dates.

feeding scars in this area, as did most 1963 plants.

R. padi first appeared in the fields at later dates than did the other two aphid species (Figures 7, 8, and 9, Part A). After the 1962 field work, I felt that this may have occurred because the plant condition became more favorable when the lower leaves began to senesce and lose their chlorophyll. However, the 1963 observations suggest that R padi may have been present on the plants below the soil surface during 1962, but remained unnoticed.

Peak numbers of R padi were observed in June instead of July, the peak month for the other two species. Population trends were not as evident for R, padi as for M. avenae, due to the distinct and erratic fluctuation in numbers of aphids observed. The numbers recorded were an accurate estimate of the R.padi present in the 200 plants observed, but, because of the high variation from plant to plant, may not have been representative of other barley fields in the area.

Figure 9, Part B shows that R. padi were present in high numbers in the late planted 1963 field during the early plant phenology stages, and again prior to heading. This timing may have been the result of weather and not the physiological condition of the plants. Richards (74) reported R. padi as a cool-adapted species. Temperature and humidity may therefore have limited a population increase of R. padi during July.

Proportions of Six Morphological Forms

The three species of aphids studied have six distinct and one intermediate morphological stages or forms. The six stages include four nymphal instars, wingless adults, or apterae, and the winged adults, or alatae. Individuals of an intermediate form, alatae with small nonfunctional wings, were recorded with the alate group.

The six morphological stages of M. avenae and A. dirhodum were observed and recorded during the observations in the four barley fields. The various nymphal stages of R. padi were very similar in size and each instar varied in size depending on the nutritional quality of the host plant, therefore valid instar records for this species could not be recorded.

The bars (F I, F II, F III and F IV) in Figures 10 and 11 represent field totals, and show the proportion of each of the six morphological stages of the two aphid species found in the four fields. The grand total bars (GT) include all specimens for each of the two species and indicate the overall population composition for the species. If totals from several years and fields were figured into a grand total, the estimated population composition would be similar to average rainfall and temperature estimates; in that it could be considered as a general picture of the average

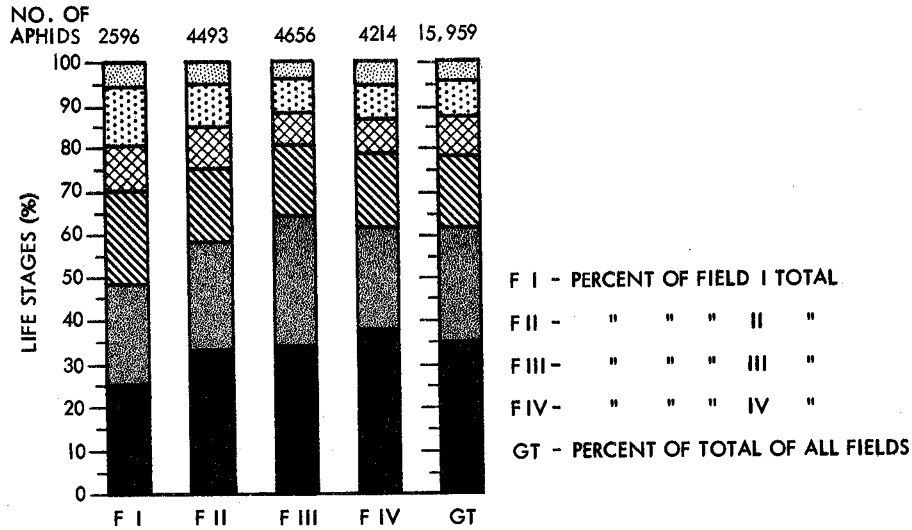


Figure 10. Relative percentages of six morphological stages of development of Macrosiphum avenae observed in four fields of barley during 1962 and 1963.

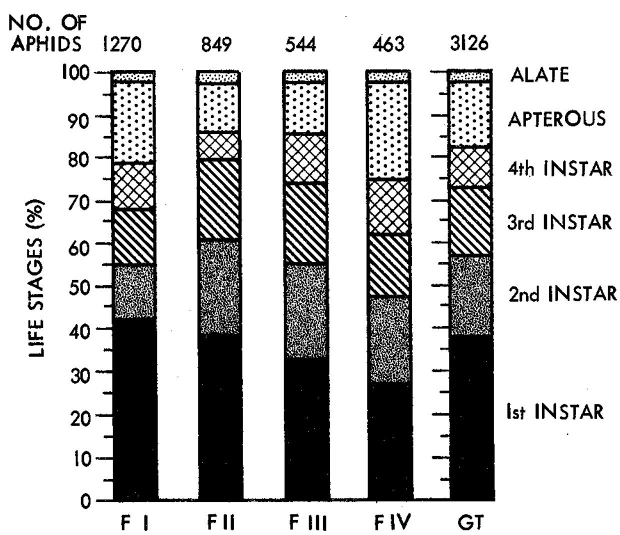


Figure 11. Relative percentages of six morphological stages of development of Acyrthosiphon dirhodum observed in four fields of barley during 1962 and 1963.

population composition expected for any one field or year.

The grand totals for the two species (GT, Figures 10 and 11) are similar in general proportions for each stage, with the first-instar nymphs and apterous forms making up a larger portion of A. dirhodum than of M. avenae, and with a correspondingly smaller portion of alatae and second-instar nymphs of A. dirhodum. The proportions of third- and fourth-instar nymphs are very similar for both species.

The proportion of alatae in the populations of A. dirhodum was smaller than the proportion of alatae recorded for M. avenae. Evidently a smaller proportion of the fourth-instar nymphs of A. dirhodum than M. avenae developed into alate individuals, and a larger portion of the last-instar nymphs of M. avenae than A. dirhodum produced alatae. The lower percentage of second-instar A. dirhodum than M. avenae may have resulted from errors in counting, since the first- and second-instar nymphs of A. dirhodum were more difficult to distinguish between than were the first- and second-instar nymphs of M. avenae. Sylvester (82), working with the green peach aphid [Myzus persicae (Sulzer)], pictured the nymphs, and showed less size difference between the first- and second-instar nymphs than between other instars. This was true for A. dirhodum in this study, but in the case of M. avenae all four instars were readily distinguishable.

Macrosiphum avenae

The proportions of M. avenae life stages for each of the field totals closely resemble the grand total proportions cited for this species in Figure 10. The early seeded field deviated from the grand total (Figure 10) by having a smaller proportion of first- and second-instar nymphs than the other three fields. In general, proportions of the aphid stages were similar in the late and mid-season seeded fields, which deviated little from the grand total proportions.

The percentage of alatae in each of the four fields and in the grand total was very close to five percent; and the fourth-instar nymphs contributed close to nine percent in all fields.

The grand total bars for M. avenae (Figure 10) indicate that there were progressively fewer aphids in each of the four immature stages, that more apterous than fourth-instar aphids were observed, and that alatae comprised the smallest category. The higher proportion of adults (apterous and alate) than fourth-instar nymphs may appear impossible, since all the adult aphids must come from fourth-instar individuals. The reason for the discrepancy lies in the duration of time required for the different life stages; the fourth-instar stage is of shorter duration than the adult stage.

During the first sampling dates in each of the fields, less than 100 total aphids were observed (Figures 12, 13, 14, and 15), and there was a larger proportion of first- and second-instar nymphs and adults than recorded on later sampling dates; this being particularly evident in the late and mid-season planted fields of 1962. The absence of late-instar nymphs and apterous adults early in the season substantiates the hypothesis that alatae are the first aphids to enter spring barley fields and are the progenitors of the ensuing aphid populations. Failure to find overwintering aphids at spring planting time supports this hypothesis. In all four fields, the last counting date showed a decrease from previous sampling dates in the proportion of first-instar nymphs.

In all four fields (Figures 12, 13, 14 and 15) when over 200 aphids were observed per sampling date there appeared to be two independent groups of the aphid stages; one group being the first- and second-instar nymphs, the other group consisting of the remaining morphological forms. When the proportion of the first-instar nymphs increased, the second-instar nymphs decreased, and vice versa. At the same time the other four forms tended to fluctuate, but each stage represented remained more stable than the first- and second-instar nymphal proportions.

The seasonal trend in the 1962 mid-season planted field (Figure 13) shows that during June the proportion of first-instar

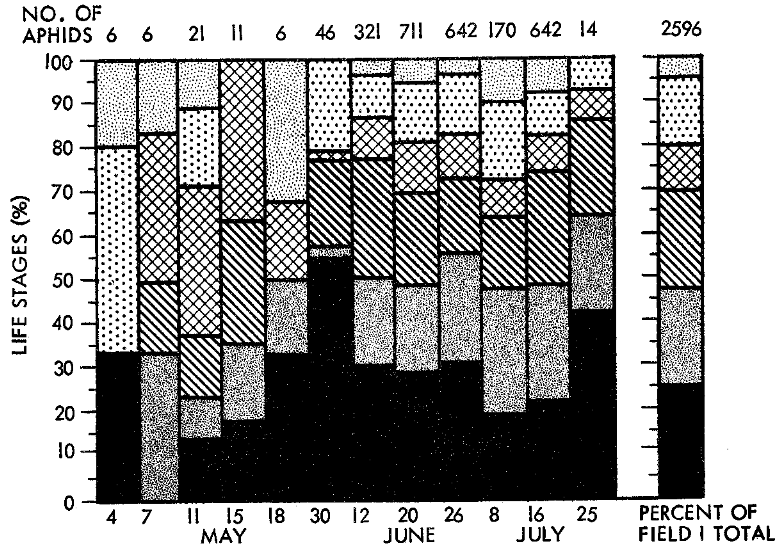


Figure 12. Relative percentages of six morphological stages of development of Macrosiphum avenae observed on 200 barley plants during each sampling date in the early season planted field I, 1962.

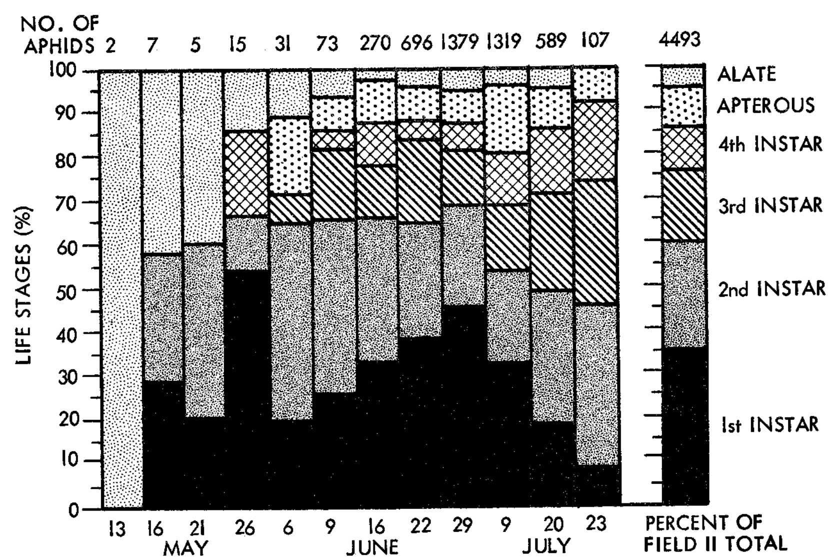


Figure 13. Relative percentages of six morphological stages of development of Macrosiphum avenae observed on 200 barley plants during each sampling date in the mid-season planted field II, 1962.

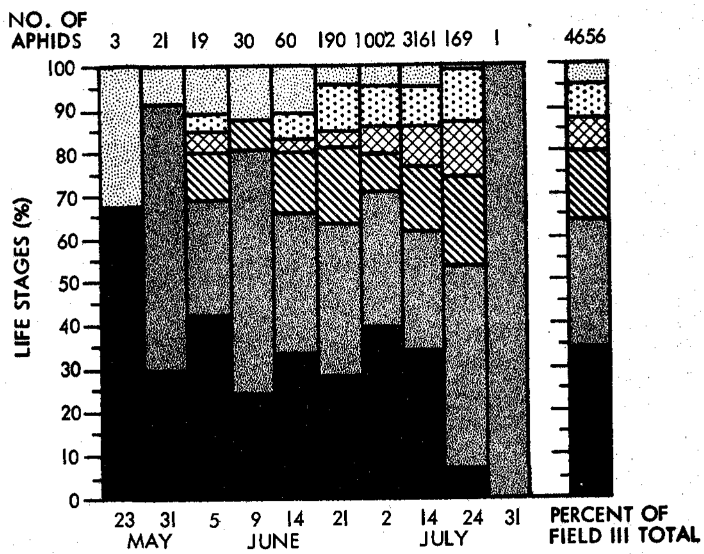


Figure 14. Relative percentages of six morphological stages of development of Macrosiphum avenae observed on 200 barley plants during each sampling date in the late season planted field III, 1962.

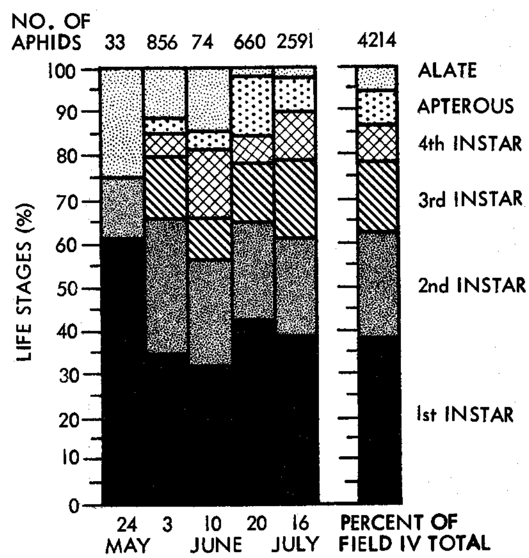


Figure 15. Relative percentages of six morphological stages of development of Macrosiphum avenae observed on 200 barley plants during each sampling date in the late season planted field IV, 1963.

nymphs progressively increased, accompanied by a decrease in the proportion of second-instar nymphs, but in July the reverse occurred, accompanied with an increase in the proportion of apterous adults. This seasonal pattern follows very closely the hypothesis put forth by Hughes (personal communication) that as the host plants mature and fail to meet the nutritional requirements of the aphids, fecundity decreases. The seasonal increase of first-instar nymphs during June correlates with the young growing barley plants as illustrated by the Phenological classes in Figure 7, Part B, and in the decrease during July correlates with the maturing and drying of the barley plants.

Acyrthosiphon dirhodum

There was considerably more variation of the morphological stages of A. dirhodum between fields than existed for M. avenae (Figures 10 and 11). Field totals and the grand total in Figure 11 show that the numbers of alatae found were nearly equal, although twice as many aphids were counted in the early planted fields as in the late planted field (Figure 11). The number of alatae did not seem to be related to the number of specimens observed, but were more constant from field to field, suggesting that the number of alatae in a field was unrelated to the apterous population level in that field.

Alatae were not found in the first few samples from the early and mid-season planted 1962 fields (Figures 16 and 17). The first aphid form to enter each of the fields can not be positively ascertained from these data, but alate migrants would be expected to establish the populations in newly sown barley fields.

The proportion of first-instar nymphs was higher for _A. dirhodum_ than for _M. avenae_ for most samples (Figures 12 through 19). The proportion of first-instar nymphs in the last sample in each field (Figures 16, 17, 18, and 19) was considerably lower than the field average for that nymphal stage, indicating that the first-instar nymphs may have disappeared from the population, or that the adult fecundity may have been reduced, resulting in the population decrease.

It is possible that some counts are of questionable validity for the proportions of the aphid stages, because of the low number of aphids present in the sample. Hughes (personal communication) using different methods of instar determination indicated that 400 aphids should be counted to gain a valid estimate of instar composition of the cabbage aphid.

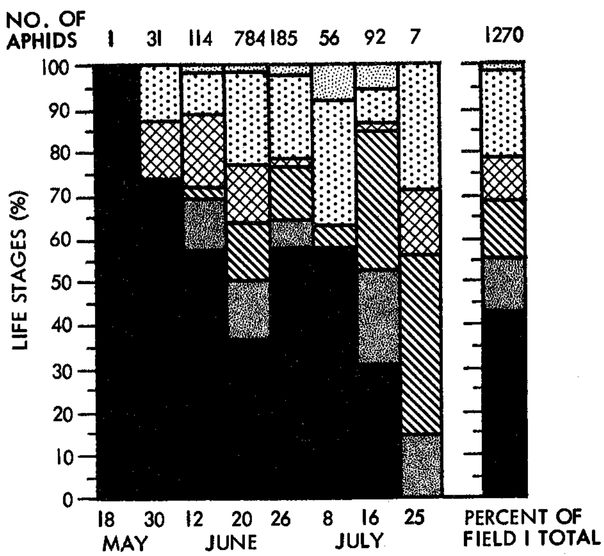


Figure 16. Relative percentages of six morphological stages of development of Acyrthosiphon dirhodum observed on 200 barley plants during each sampling date in the early season planted field I, 1962.

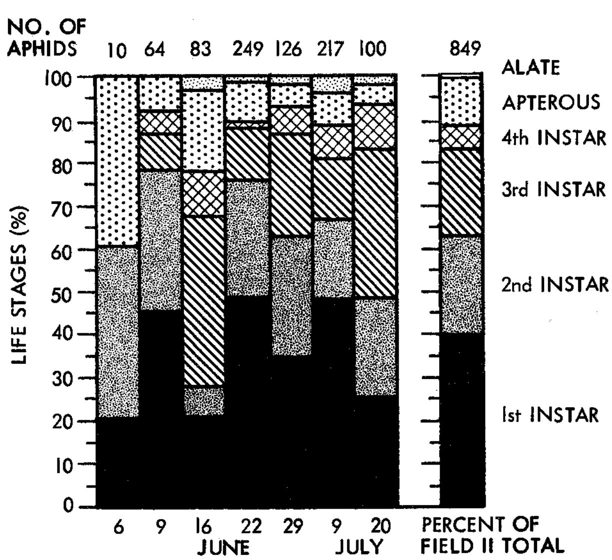


Figure 17. Relative percentages of six morphological stages of development of Acyrthosiphon dirhodum observed on 200 barley plants during each sampling date in the mid-season planted field II, 1962.

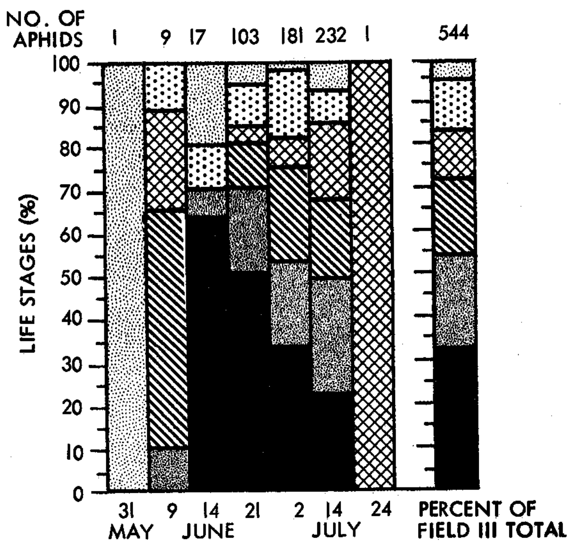


Figure 18. Relative percentages of six morphological stages of development of Acyrthosiphon dirhodum observed on 200 barley plants during each sampling date in the late season planted field III, 1962.

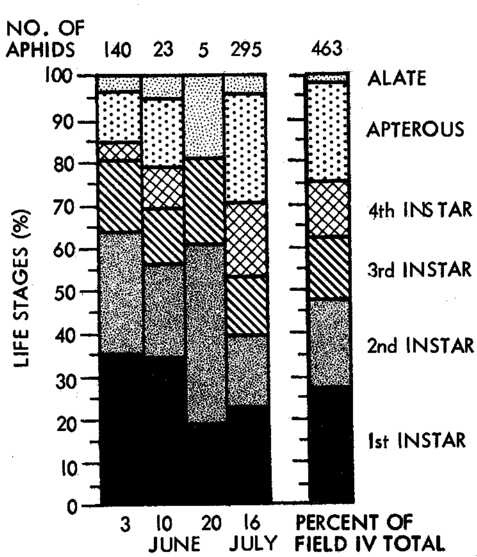


Figure 19. Relative percentages of six morphological stages of development of Acyrthosiphon dirhodum observed on 200 barley plants during each sampling date in the late season planted field IV, 1963.

Fecundity and Mortality Estimates for *M. avenae*

An attempt was made to calculate the reproductive rate of aphids under field conditions utilizing previously published data and field populations of *M. avenae* observed during 1962 and 1963.

Phillips (72) observed that 117 female *M. avenae* produced 2,333 young, for an average of approximately 20 young per adult, in an open air insectary in Indiana.

Ito (37) found that 21 young were produced per adult *M. avenae* on barley plants, and 41 per adult on wheat plants. These numbers of offspring actually occurred and survived in controlled environments, but the effect of natural mortality factors in the field on aphids living on undisturbed plants has not been determined.

Using Phillips' 1916 work, a formula was derived to estimate the fecundity of the aphid populations in the field. Phillips (72) reported an average 34.3 day life span for *M. avenae*, of which 12.6 days were spent as nymphs and 21.7 days as adults. By dividing the time spent as nymphs into the time spent as adults, a nymph to adult life factor of 1.7 was derived. This factor compensates for the proportion of nymphs produced per adult that have matured, and it is used in Table 4 to estimate the number of young produced by each adult. Since considerable variation is

Table 4. Number of *Macrosiphum avenae* immatures for each adult at weekly intervals in four fields of barley, and the estimated number of nymphs produced per adult.

Week	Field I, 1962			Field II, 1962			Field III, 1962			Field IV, 1963		
	Total Aphids	Nymphs/ Adults	X1.7[a]	Total Aphids	Nymphs/ Adults	X1.7[a]	Total Aphids	Nymphs/ Adults	X1.7[a]	Total Aphids	Nymphs/ Adults	X1.7[a]
May												
1-7	12	1.40	2.38	--	--	--	--	--	--	--	--	--
8-14	21	2.50	4.25	2	--	--	--	--	--	--	--	--
15-21	17	7.50	12.75	12	1.40	2.38	--	--	--	--	--	--
22-28	--	--	--	15	6.50	11.05	3	2.00	3.40	33	3.13	5.32
29-4	46	4.75	8.08	--	--	--	21	5.48	9.32	856	5.48	9.32
June												
5-11	--	--	--	104	4.47	7.60	49	6.00	10.20	74	4.29	7.29
12-18	321	8.17	13.89	290	6.71	11.47	60	4.45	7.57	--	--	--
19-25	711	4.78	8.13	696	7.39	12.56	190	4.94	8.40	660	5.23	8.89
26-2	642	4.49	7.63	1379	6.04	10.27	1002	5.19	8.82	--	--	--
July												
3-9	170	2.47	6.20	1319	4.17	7.09	--	--	--	--	--	--
10-16	642	5.06	8.60	--	--	--	3161	5.25	8.93	2591	7.15	12.16
17-23	--	--	--	589	5.93	10.80	--	--	--	--	--	--
24-31	14	13.00	22.10	107	9.70	16.49	170	6.39	10.86	--	--	--
Means		4.75	8.08		5.49	9.33		5.27	9.33		6.29	10.69
Modes		5.41	9.19		5.13	8.72		5.47	9.30		5.06	8.60

[a] The number of nymphs produced per adult was estimated by multiplying the number of nymphs per adult times 1.7 (the average life span of an adult divided by the average life span of a nymph).

apparent, I feel that the field means are probably the most reliable indication of what could be expected at any particular time.

In Table 4 the late and mid-season planted fields had means close to 5.50 and 5.25, while the early seeded field was 4.75, and the 1963 field had 6.29 young per adult. The mean estimates of young per adult was highest in the 1963 field, where the number of aphids increased the most rapidly.

The mode numbers of nymphs per adult were figured to see how much the total seasonal means deviated from the weekly figures (Table 4). In the fields seeded in late and mid-season during 1963, the means and modes were very similar, but in the early seeded 1962 and late seeded 1963 fields the means and modes differed by more than 0.5, indicating that in the latter two fields the mean was weighted by a few counts of high numbers of aphids.

When low numbers of aphids (less than 100) were observed (Table 4),the proportion of nymphs to adults was low. The early and mid-season planted fields of 1962 had high proportions of nymphs to adults during the last week of July. These two phenomena are related to population composition changes in the fields. The early counts were largely adults when the aphid populations first appeared in the fields. In the 1962 fields a rapid increase in the proportion of nymphs was recorded in the second or third week of May, probably the result of production of nymphs by immigrating adults, and the subsequent death of these adults before their offspring matured. This was not as apparent during 1963 (field IV) as in the three 1962 fields. The high numbers of immatures, compared to adults, in the last week of July may indicate a high rate of adult mortality or adult migration from the population, high reproductive rate, or slowed development during the immature stages. Of these three possibilities I would suspect the first and last to be most probable.

Estimates of immature mortality are calculated in Table 5. The total number of first-instar nymphs observed in the four fields multiplied by four (number of instars) estimates the total number of immatures possible had there been no mortality. The estimated number of nymphs, divided by the total number of adults observed is used to estimate the number of nymphs per adult. This figure multiplied by 1.7 (the age factor) resulted in an estimate of the total number of nymphs produced by each adult in the population. The resulting figure (14.9) is an estimate of the intrinsic rate of increase or adult fecundity in a field population. By contrast, the effective rates of increase (8.08 to 10.69 nymphs per adult) are the figures given in the third column for each field in Table 4.

An estimate of 75% of the potential nymphal production

Table 5. Estimations of adult fecundity, adult life span, and instar mortality based on field observations of *Macrosiphum avenae* populations during 1962 and 1963 in four fields of barley near Corvallis, Oregon

A.		Estimated Fecundity Under Field Conditions
	5,430	First-instar nymphs observed
X	4	Number of instars
	21,720	Total nymphs present had all first-instar nymphs matured
÷	21,720	Total nymphs estimated
	2,465	Total adults observed
	8.82	Nymphs/adult
	8.82	Nymphs/adult
X	1.7	Adult-nymph age ratio
	14.99	Estimated number of nymphs produced per adult
B.		Adult Life Span
÷	14.99	Nymphs produced per adult
	20.00	Number of nymphs/adult (Phillips 72)
75%		Percent of total nymphal production
	75%	Percent of total nymphal production
X	22	Average days of adult life (Phillips 72)
	16.5	Estimated life span of adults in days
C.		Estimated Immature Mortality
	15,959	Number of aphids observed in four fields
-	7,895	Number of adults and first-instar nymphs observed
	8,064	Number of second-, third-, and fourth-instar nymphs
	16,310	Number of second-, third-, and fourth-instar nymphs estimated
-	8,064	Number of second-, third-, and fourth-instar nymphs observed
	8,246	Number of second-, third-, and fourth-instar nymphal deaths (50%)

under field environments was estimated by comparing the number of nymphs estimated per adult to the number reported by Phillips (72). Assuming that 75% of the adult life was completed under field conditions, the average adult life span during this study was estimated to be 16.5 days. Further, when the number of second-, third-, and fourth-instar nymphs observed were subtracted from the estimated number, the mortality during these stages was approximately 50%.

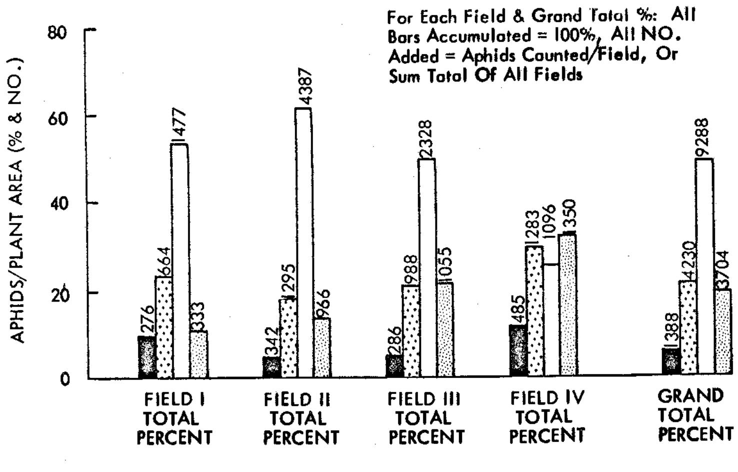
Portion of the Plants Inhabited

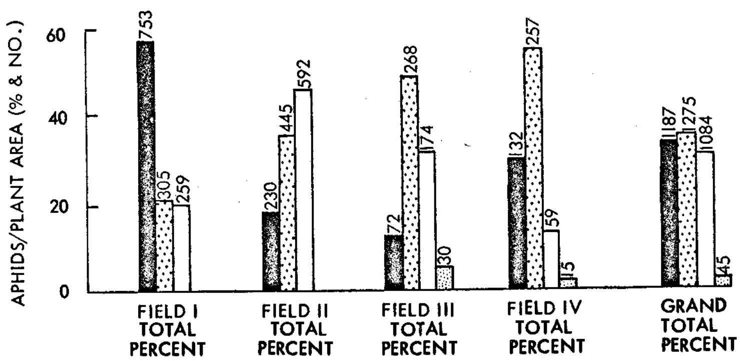
During 1962 and 1963 the numbers of aphids were recorded on areas of the plants being inhabited. Early in the growing season, barley plants were classified into lower and upper feeding areas. This is indicated in Figures 23 through 26, where only two plant areas are represented. Later in the season, plants were subdivided into three general feeding regions or areas; lower, mid, and upper. When the heads appeared, a fourth category (head) was added. This latter area included both the head and the upper leaf before the head extended from the leaf sheath, at which time the top leaf was considered to be a part of the upper portion of the plant. Division of the barley plants into feeding areas was prompted by the work of Kennedy (48), Kennedy and Booth (50), and Kennedy, Booth, and Kershaw (51,

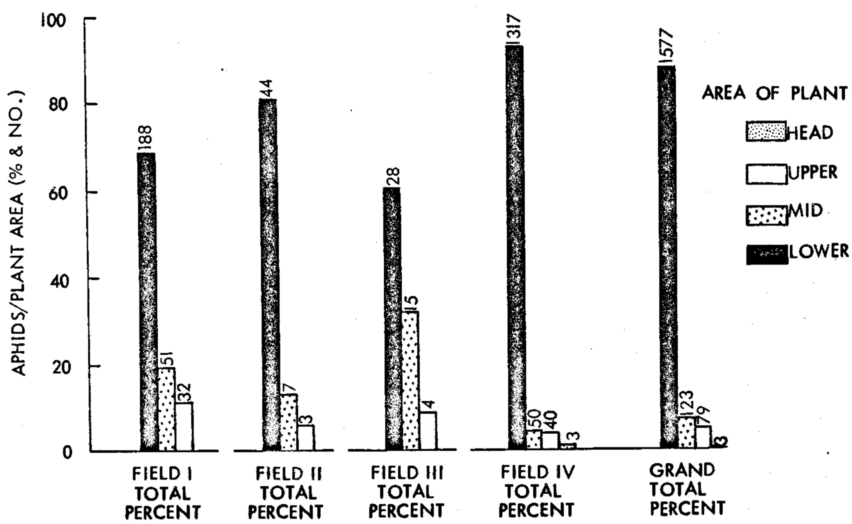
Figure 20. Plant areas occupied by *Macrosiphum avenae* calculated for each field total and the grand total of all four fields combined.

Figure 21. Plant areas occupied by *Acyrthosiphon dirhodum* calculated for each field total and the grand total of all four fields combined.

Figure 22. Plant areas occupied by *Rhopalosiphum padi* calculated for each field total and the grand total of all four fields combined.


For Each Field & Grand Total %: All Bars Accumulated = 100%, All NO. Added = Aphids Counted/Field, Or Sum Total Of All Fields
APHIDS/PLANT AREA (% & NO.)
0
20
40
60
80
276
664
1477
333
342
1295
4387
966
286
988
2328
1055
485
1283
1096
1350
1388
4230
9288
3704
FIELD I TOTAL PERCENT
FIELD II TOTAL PERCENT
FIELD III TOTAL PERCENT
FIELD IV TOTAL PERCENT
GRAND TOTAL PERCENT


APHIDS/PLANT AREA (% & NO.)
0
20
40
60
753
305
259
230
445
592
72
268
174
30
132
257
59
5
1187
1275
1084
45
FIELD I TOTAL PERCENT
FIELD II TOTAL PERCENT
FIELD III TOTAL PERCENT
FIELD IV TOTAL PERCENT
GRAND TOTAL PERCENT


APHIDS/PLANT AREA (% & NO.)
0
20
40
60
80
100
188
51
32
44
7
3
28
15
4
1317
50
40
13
1577
123
79
3
FIELD I TOTAL PERCENT
FIELD II TOTAL PERCENT
FIELD III TOTAL PERCENT
FIELD IV TOTAL PERCENT
GRAND TOTAL PERCENT
AREA OF PLANT
HEAD
UPPER
MID
LOWER

52, and 53), who divided plants into three leaf growth stages: young growing, mature, and senescening.

Developmental stages of aphid species were recorded with each entry in relation to their appearance on the different portions of the plant, but no pattern was apparent, so subdivisions are not included.

General trends of the plant area occupied on a seasonal basis by each of the three species are shown in Figures 20, 21, and 22. In each figure the grandtotal represents about 40 sampling dates, or approximately 8,000 plants. From a comparison of the grand totals for three species it is apparent that M. avenae was found predominately on the upper portion of the plants, A. dirhodum was recorded equally from three leaf areas, and R. padi occurred principally on the lower plant region.

Macrosiphum avenae

The populations of M. avenae on the plant areas during 1962 and 1963 differed in the proportions on the head and mid-regions (Figures 23, 24, 25, and 26). These two areas supported a larger proportion of the total aphids during 1963 than 1962, and the upper plant region supported a smaller proportion of aphids. The plant growth pattern for the two years may have influenced the relative populations on the three plant areas. The

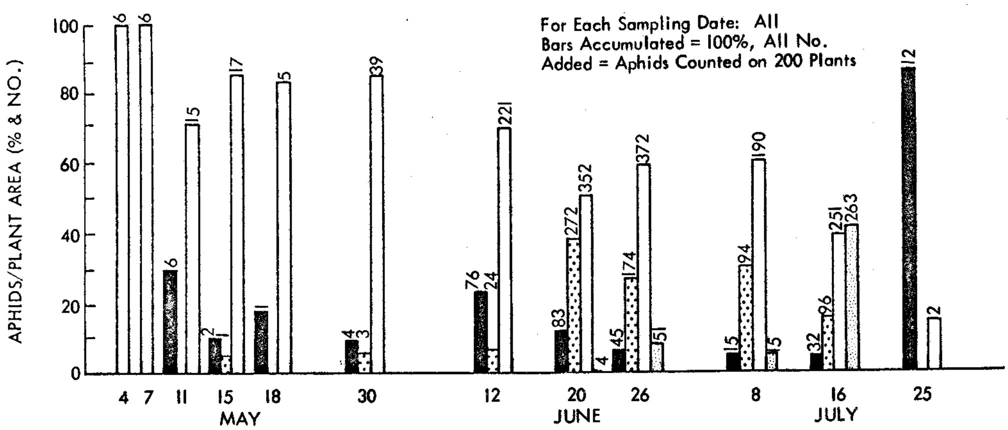


Figure 23. Percent and number of Macrosiphum avenae found at each counting date on the indicated areas of the plants during 1962 in field I.

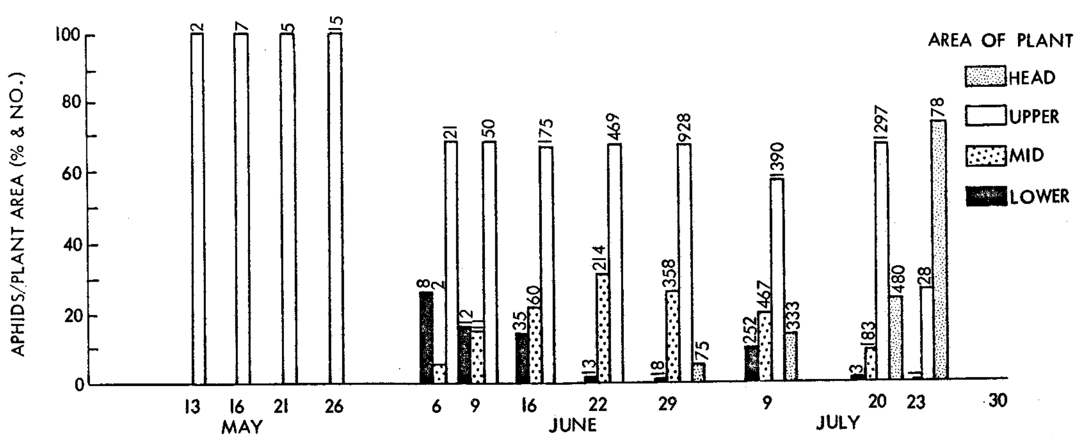


Figure 24. Percent and number of Macrosiphum avenae found at each counting date on the indicated areas of the plants during 1962 in field II.

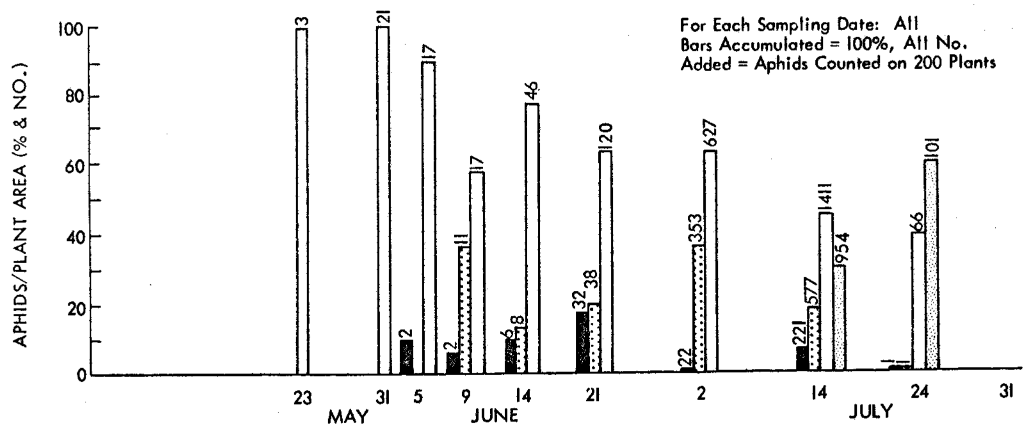


Figure 25. Percent and number of Macrosiphum avenae found at each counting date on the indicated areas of the plants during 1962 in field III.

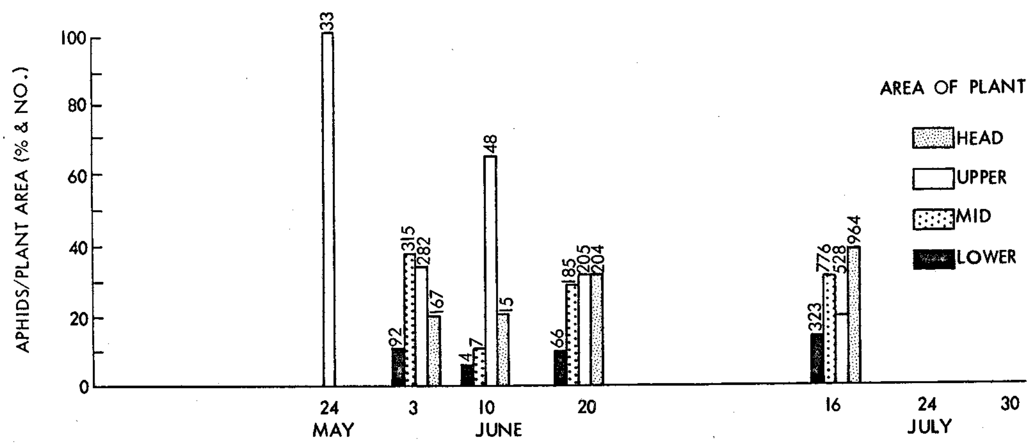


Figure 26. Percent and number of Macrosiphum avenae found at each counting date on the indicated areas of the plants during 1963 in field IV.

plant leaves remained green for a longer period during 1963 than 1962, thus giving M. avenae a longer period of time to develop on the middle plant area. The upper portion of the plants was succulent for a shorter length of time during 1963 than 1962; and the heads were occupied by aphids after the mid plant area began to dry during 1963.

M. avenae was most commonly found on the actively growing regions of the barley plants (upper area, Figures 23, 24, 25, and 26). The occurrence of M. avenae on green growing parts of the plant is made feasible by the movement of aphids to these plant parts. Once aphids reach the growing areas of the plant they may reproduce more rapidly than aphids on other plant areas. This hypothesis of increased reproduction is supported by the work of Ito (36). Possibly the increased supply or pressure of the plant sap in the growing tips was responsible for the M. avenae concentrating on that portion of the plants.

Acyrthosiphon dirhodum

Acyrthosiphon dirhodum was rather uniformly distributed on three areas of the plant, as shown by the grand total bar in Figure 21. This uniform distribution was a surprise, because A. dirhodum appeared to be most commonly found on the lower parts of the plant when making field readings. This uniformity in total distribution was probably skewed by the lack of populations on the lower area of the plants when the few late season counts were being made; thereby overshadowing the low numbers of aphids recorded on the lower plant areas during the majority of the counts when the majority of A. dirhodum were on the lower area.

The seasonal trends of the plant areas occupied by A. dirhodum (Figures 27, 28, 29, and 30) indicate that the first specimens were found on the lower plant areas during May, and the middle and upper areas were inhabited during June and July.

Nearly 60% of the total A. dirhodum found were on the lower area of the plants in the early planted field (Figure 27). During late June in that field, aphids were found to be abundant on leaf clumps formed on stooling barley plants. The plant heads had small infestations in the two late planted fields, and none in the early and mid-season seeded fields (Figures 27, 28, 29, and 30).

Yellowing plant leaves appeared to be preferred over green growing leaves by A. dirhodum. With minor exceptions the bars representing the largest aphid proportions in Figures 27, 28, 29, and 30 coincide with the plant areas where the leaves were turning yellow, particularly in the early and mid-season planted 1962 fields (see plant phenology classes by dates in Table 3 and Figure 8). The two late seeded fields (Figures 29

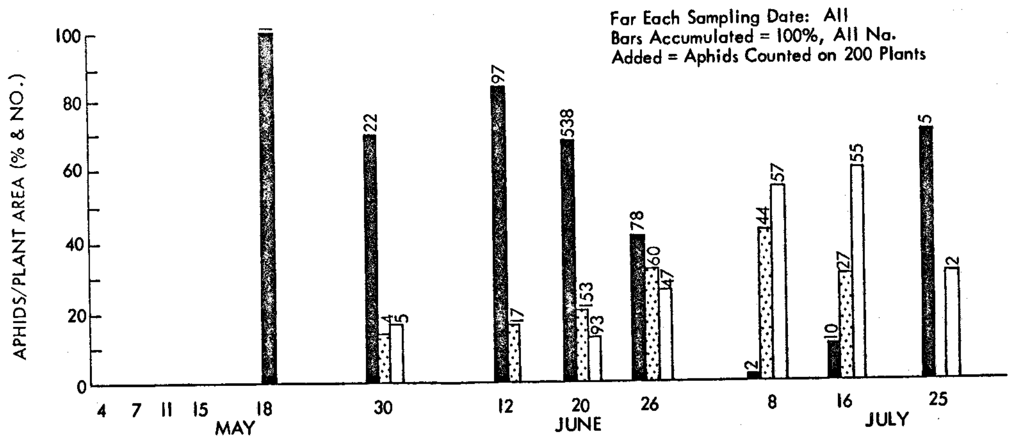


Figure 27. Percent and number of Acyrthosiphon dirhodum found at each counting date on the indicated areas of the plants during 1962 in field I.

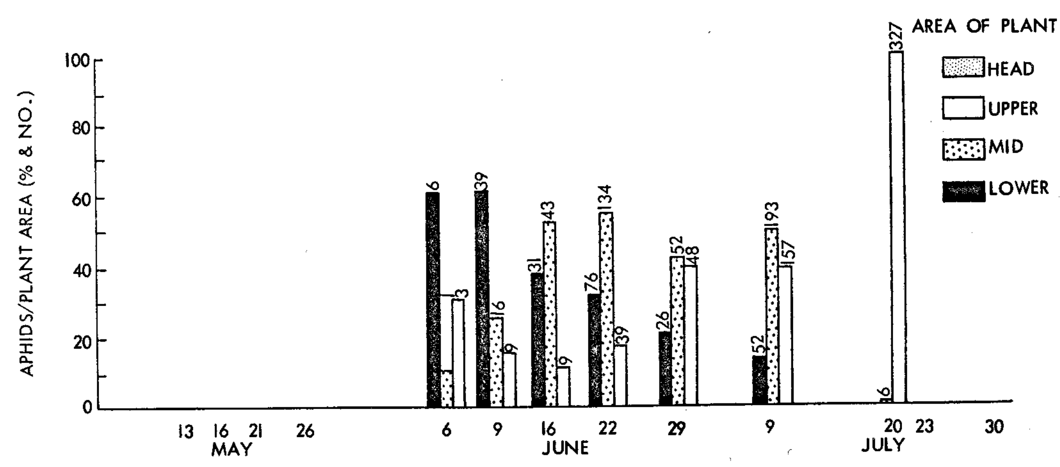


Figure 28. Percent and number of Acyrthosiphon dirhodum found at each counting date on the indicated areas of the plants during 1962 in field II.

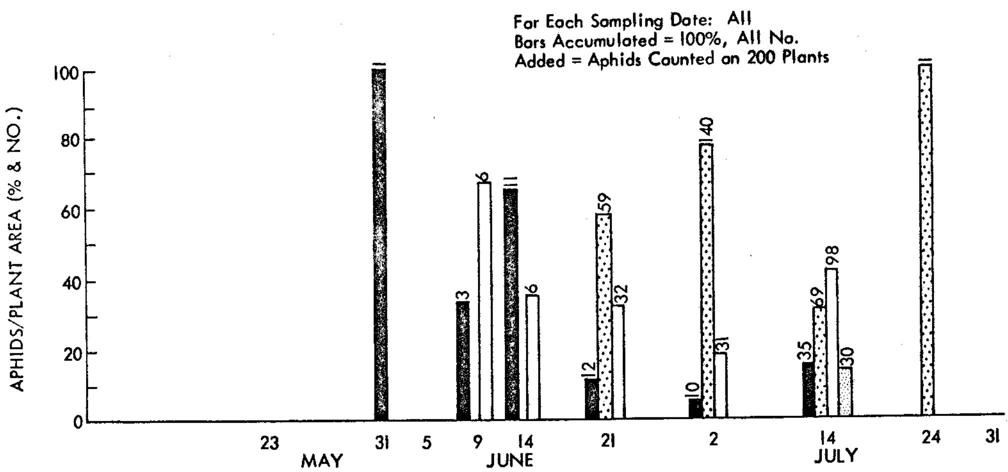


Figure 29. Percent and number of Acyrthosiphon dirhodum found at each counting date on the indicated areas of the plants during 1962 in field III.

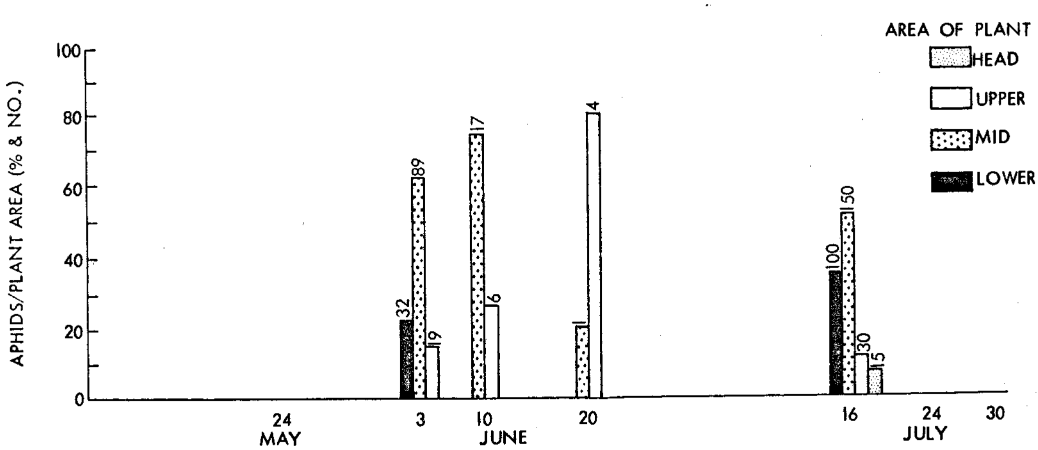


Figure 30. Percent and number of Acyrthosiphon dirhodum found at each counting date on the indicated areas of the plants during 1963 in field IV.

and 30) appear to show a pattern different from the early and mid-season planted fields, but if the dates with less than ten aphids are omitted, the majority of A. dirhodum in those two fields also occurred on the mature leaves. This species may survive best on barley leaves where the plant sap supply or pressure is reduced because of the mature condition of the leaves, or where the organic nitrogen compounds are reduced as suggested by Kennedy (46).

A. dirhodum appeared to occupy the plant area below the portion of the plants frequented by M. avenae (Figures 20 and 21). The occurrence of this species on mature or aging leaves may have been a reaction to sunlight. It was seldom found on the upper plant areas, the aphids were on leaves which had their upper surface turned down or facing the soil. On orchardgrass this species was usually found inside the grass clumps, rather than exposed to sunlight.

Rhopalosiphum padi

R. padi was found predominately on the lower portion of the plants during 1962, and at fewer sampling dates than the other two species (Figures 31, 32, 33, and 34). The lower areas of the plants was the optimum habitat for R. padi as indicated by each of the four field totals and the grand total (Figure 22). Only three R. padi were recorded from plant heads, those being three alatae observed July 16 in the 1963 field (Figure 34).

On the above-ground portions of the plants, this species was nearly always found on yellowing or dying leaves, or on areas of the plant under stress. When this was first observed, during 1962, it was felt there might be a symbiotic relationship between R. padi and barley yellow dwarf virus, in that infected plants may be better aphid hosts than non-infected plants. However, most plants have yellow or dead leaves, and during 1963 the species was observed on approximately 50% of the plants at a time when the incidence of barley yellow dwarf virus was extremely low.

There were few samples when R. padi were found predominantly on the upper and middle plant areas (Figures 31, 32, 33, and 34), and for these samples very few aphids were counted. The area of the plant occupied did not change from May to July as did the other two aphid species.

R. padi apparently feeds and survives on the plant where the sap pressure is very low, or possibly absent, such as on the lower yellow leaves. This species was observed to survive on barley leaves placed in a vial at room temperature (relative humidities near 30%) for seven days during three separate experiments. At the conclusion of the experiments the leaves were so dry and brittle they broke when handled. Under similar conditions, M. avenae survived only three days, and after the

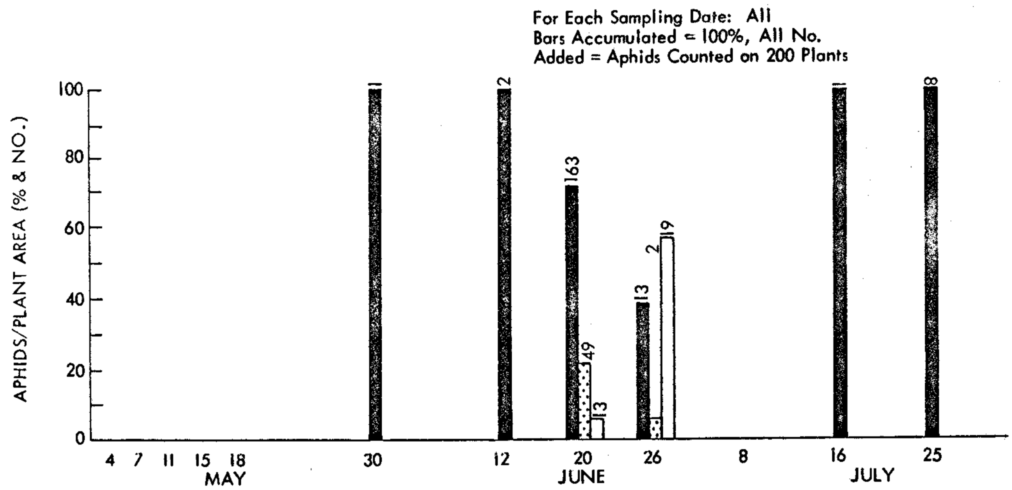


Figure 31. Percent and number of Rhopalosiphum padi found at each counting date on the indicated areas of the plants during 1962 in field I.

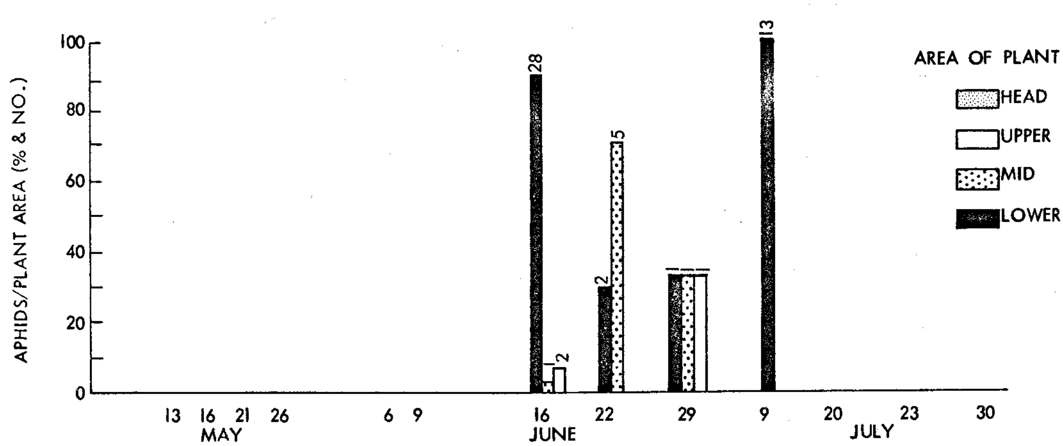


Figure 32. Percent and number of Rhopalosiphum padi found at each counting date on the indicated areas of the plants during 1962 in field II.

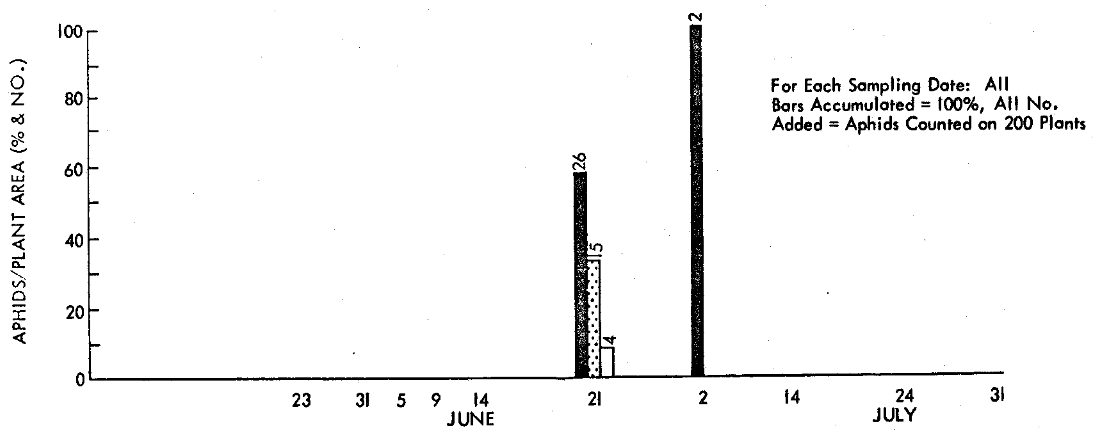


Figure 33. Percent and number of Rhopalosiphum padi found at each counting date on the indicated areas of the plants during 1962 in field III.

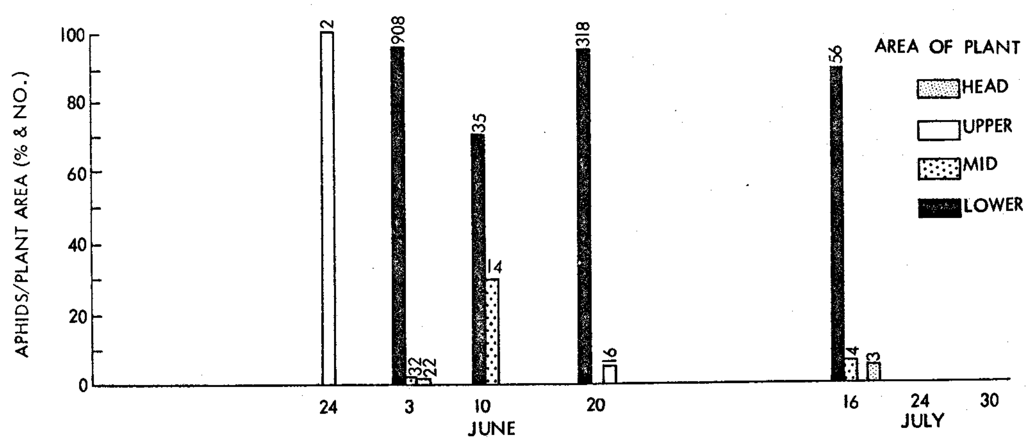


Figure 34. Percent and number of Rhopalosiphum padi found at each counting date on the indicated areas of the plants during 1963 in field IV.

leaves began to lose their turgidity the aphids were observed wandering around on the glass walls of the vial, as if searching for a suitable food supply. Baker and Turner (3) observed R. fitchii (probably R. padi) feeding on the lower surface of lower leaves, and stated that, "females could produce mature eggs only when fed a diet of old mature leaves."

Subterranean Habitat of Rhopalosiphum padi

R. padi was first discovered on the subterranean shoot area of barley plants during 1963. Colonies were observed on the shoots of barley plants that were pulled from the soil for barley yellow dwarf virus inspection (Figure 35). After this discovery, field counts were made by pulling plants from the soil and observing the number of aphids present on the shoot below the soil line.

The effect on the 1962 population counts of the exclusion of the subterranean plant area is unknown. However, as previously stated, plant samples retained from 1962 did not show the typical feeding scars.

Approximately 62% of the R. padi observed during 1963 were found below the soil surface with a range from 21% to 87% for individual sampling dates (Table 6). On June 3 and 20, the dates when the largest number of aphids were observed, the

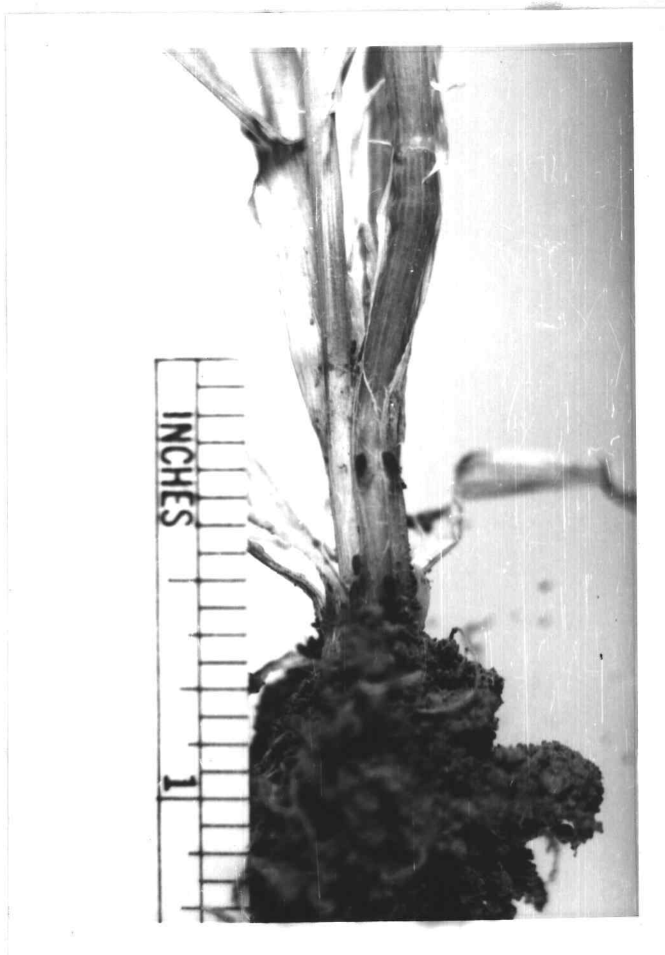


Figure 35. Position of Rhopalosiphum padi on the shoot of a barley plant below the soil surface. The end of the ruler near the middle of the picture corresponds to the soil surface.

Table 6. Seasonal occurrence of Rhopalosiphum padi on the subterranean area of 200 randomly selected barley plants during 1963.

Sample Date	Number of Aphids Subterranean	Total Aphids Observed	Percent Subterranean
May 24	0	2	0
June 3	557	962	58
June 10	13	49	27
June 20	291	334	87
July 16	13	63	21
Totals	874	1410	62

Table 7. Observations of Rhopalosiphum padi below the soil surface near Corvallis, Oregon.

Depth	June 11, 1963			June 1, 1964		
Below Soil Surface cm	No. of Plants	No. of Aphids	% of Aphids	No. of Plants	No. of Aphids	% of Aphids
0 to 1	1	1	1	12	27	13
1-2	10	86	69	103	177	85
2 +	5	38	30	1	3	2
Totals		125	100		207	100
Plants Sampled	25			200		

percentages of aphids found below the soil surface were largest.

Based on field observations, it appeared that R. padi was found to a greater extent below the soil surface as the season progressed. The avoidance of heat might be related to this occurrence since as the season progresses from May to July temperatures are increasing.

Richards (74) states that species of the genus Rhopalosiphum display a negative phototaxis. I suspect that light conditions were of little importance because light conditions would have changed very little from June 3 to July 16, yet the percentage of R. padi found on the subterranean plant region fluctuated considerably (Table 6).

An attempt was made to determine the occurrence of R. padi on plants at varying depths in the soil to learn what relation existed between the aphids and the soil air spaces. Table 7 shows that 69% and 85% of the R. padi were found between 1 and 2 cm below the surface of the soil in 1963 and 1964 respectively. The plant shoot from 0 to 1 cm below the soil surface was often surrounded with clods which permitted air circulation, and the 2 cm depth was the distance from the soil surface to the crown area of the plant (Figure 35). This area was not a uniform environment with all plants. Some plants were tightly surrounded by compact soil between the 1-2 cm depth, and some were completely exposed to the air, although the majority of the plants were in contact with compact dirt or clods in this area. The measurements in Table 7, and field observations, indicated that R. padi occurred where the soil was compact.

This information prompted additional field observations during the 1964 growing season. During early June, R. padi were more uniformly distributed through the field than during late June. In late June plant rows where the drill and tractor wheels had compacted the soil during planting were more likely to have R. padi colonies than plants growing in loose, cloddy soil indicating a pattern of abundance relative to soil compaction around the plant shoots. Also, in late June 1964 R. padi was often found on plant shoots surrounded by compact soil to depths of 2 cm.

VII. APHID DISTRIBUTION STUDIES

Number of Plants Infested

The number of plants infested with M. avenae increased from May until mid-July then decreased rapidly to zero by the end of July (Table 8). The later the seeding date during 1962, the later in June or July the number of infested plants surpassed 100 or 50%. The late seeded field of 1963 had 173 out of 200 plants infested on June 3 which was much earlier in the season than during 1962.

In general, the number of plants infested was related to the number of aphids per infested plant. This was particularly apparent as sampling dates progressed through the season, however there were some exceptions.

The number of M. avenae per plant increased in relation to the number of plants infested in the four fields (Table 8). The average number of aphids per infested plant was approximately two when the number of infested plants was below 100 or 50%. As the number of infested plants increased from 100 to 200 the number of aphids per infested plant increased from 4.52 to 15.80. For the 39 samples when aphids were observed, only four had more than ten aphids per infested plant. The largest average number of aphids per plant was 15.8 and for that count all plants observed were infested. The average number of aphids per infested plant was 2.33

Table 8. Number of plants infested with Macrosiphum avenae for each sampling date that aphids were found in each of the four fields. The number of aphids observed is divided by the number of plants infested.

Date	Number of Plants Infested	Number of M. avenae Observed	M. avenae per Infested Plant
	Field I (Early season seeded, 1962)		
May			
4	4	6	1.50
7	5	6	1.20
11	10	21	2.10
15	10	20	2.00
18	5	6	1.20
30	22	46	2.09
June			
12	62	321	5.18
20	104	711	6.84
26	132	642	4.86
July			
8[a]	46	170	3.69
16	142	642	4.52
25	6	14	2.33
	Field II (Mid-season seeded, 1962)		
May			
13	2	2	1.00
16	4	7	1.75
21	3	5	1.67
26	3	15	5.00
June			
6	17	31	1.82
9	37	73	1.97
16	62	270	4.35
22	103	696	6.76
29	145	1379	9.51

(Continued)

[a] The number of barley plants observed was 108 rather than 200.

Table 8. Cont.

Date	Number of Plants Infested	Number of *M. avenae* Observed	*M. avenae* per Infested Plant
July			
9[a]	97	1319	13.60
20[b]	47	589	12.53
23	49	107	2.18
	Field III (Late season seeded, 1962)		
May			
23	1	3	3.00
31	7	21	3.00
June			
5	11	19	1.73
9	13	30	2.31
14	33	60	1.82
21	80	190	2.38
July			
2	153	1002	6.55
14	200	3161	15.80
24	71	169	2.38
31	1	1	1.00
	Field IV (Late season seeded, 1963)		
May			
24	13	33	2.54
June			
3	173	856	4.95
10	48	74	1.54
20	111	660	5.95
July			
16	193	2591	13.42

[a] The number of barley plants observed was 108 rather than 200.

[b] The number of barley plants observed was 60 rather than 200.

or less for each of the last counts in July in the three 1962 fields (Table 8) indicating a uniform decrease in aphids from plant to plant.

The number of plants infested with A. dirhodum was low compared to the M. avenae figures (Tables 8 and 9); the maximum number of plants infested being 74 or 37%.

In the field seeded during mid-season, an average of 7.69 A. dirhodum was found on 13 plants in late July (Table 9). This suggested that some colonies remained on late maturing plants.

In general the number of plants with R. padi was very low compared to the other two species, with the exception of three counting dates (Table 10). However, the number of aphids per infested plant was higher for some of the counts than recorded for the other two species.

The greater abundance of R. padi in field IV (1963) than in the 1962 fields was influenced by finding and sampling the subterranean habitat of this species.

Plants Infested with Four Combinations of Three Aphid Species

The number of plants expected to have more than one species of aphids was calculated by comparing the number of plants expected to be infested with each of the three species (Table 11) to the number of plants found to be infested (Li 62). The expected

Table 9. Number of plants infested with Acyrthosiphon dirhodum for each sampling date that aphids were found in each of the four fields. The number of aphids observed is divided by the number of plants infested.

Date		Number of Plants Infested	Number of A. dirhodum Observed	A. dirhodum per Infested Plant
		Field I (Early season seeded, 1962)		
May	18	1	1	1.00
	30	9	31	3.44
June	12	18	114	6.33
	20	72	784	10.89
	26	41	185	4.51
July	8[a]	9	56	6.22
	16	24	92	3.83
	25	5	7	1.40
		Field II (Mid-season seeded, 1962)		
June	6	6	10	1.67
	9	21	64	3.05
	16	32	83	2.59
	22	43	249	5.79
	29	38	126	3.32
July	9[a]	37	217	5.86
	20[b]	13	100	7.69
		Field III (Late season seeded, 1962)		
May	31	1	1	1.00
June	9	8	9	1.12
	14	7	17	2.43
	21	36	103	2.86
July	2	43	181	4.21
	14	53	232	4.38
	24	1	1	1.00
		Field IV (Late season seeded, 1963)		
June	3	43	140	3.26
	10	15	23	1.53
	20	3	5	1.67
July	16	74	295	3.99

[a] The number of barley plants observed was 108 rather than 200.

[b] The number of barley plants observed was 60 rather than 200.

Table 10. Number of plants infested with Rhopalosiphum padi for each sampling date that aphids were found in each of the four fields. The number of aphids observed is divided by the number of plants infested.

Date	Number of Plants Infested	Number of R. padi Observed	R. padi per Infested Plant
	Field I (Early season seeded, 1962)		
May 30	1	1	1.00
June 12	2	2	1.00
20	64	225	3.52
26	19	34	1.79
July 8[a]	0	0	0.00
16	1	1	1.00
25	1	8	8.00
	Field II (Mid-season seeded, 1962)		
June 16	10	31	3.10
22	4	7	1.75
29	3	3	1.00
July 9[a]	1	7	7.00
	Field III (Late season seeded, 1962)		
June 21	15	45	3.00
July 2	1	2	2.00
24	1	1	1.00
	Field IV (Late Season seeded, 1963)		
May 24	2	2	1.00
June 3	160	962	6.01
10	6	49	8.17
20	52	334	6.42
July 16	24	63	2.63

[a] The number of barley plants observed was 108 rather than 200.

Table 11. The number of plants from the 200 plant samples expected and observed to be infested with four aphid species combinations.

Date		Number of Plants Expected with				Number of Plants Observed with			
		M.a. + *A.d.*	*M.a.* + *R.p.*	*A.d.* + *R.p.*	*M.a.* + *A.d.* + *R.p.*	*M.a.* + *A.d.*	*M.a.* + *R.p.*	*A.d.* + *R.p.*	*M.a.* + *A.d.* + *R.p.*
		Field I (Early season seeded, 1962)							
June	12	5.6	1.0	0.3	0.0	4	2	2	1
	20	37.4	33.2	23.0	12.0	40	34	24	12
	26	27.1	12.5	3.9	2.6	31	17	8	7
July	8	7.2	--	--	--	6	--	--	--
	16	17.0	1.4	0.2	0.0	22	2	1	1
	25	1.5	0.3	0.3	0.0	2	--	--	--
		Field II (Mid-season seeded, 1962)							
June	6	0.4	--	--	--	1	--	--	--
	9	3.9	--	--	--	2	--	--	--
	16	9.6	3.0	1.6	0.5	6	1	3	--
	22	23.0	2.3	0.9	0.5	24	2	2	--
	29	27.6	2.2	0.6	0.4	28	1	1	1
July	9	61.5	1.8	0.7	0.3	59	1	--	--
	20	9.2	--	--	--	10	--	--	--
		Field III (Late season seeded, 1962)							
June	9	0.5	--	--	--	3	--	--	--
	14	1.2	--	--	--	2	--	--	--
	21	14.8	6.2	0.3	1.1	23*	5	1	1
July	2	33.3	0.7	0.2	0.2	36	1	--	--
	14	53.0	1.0	0.3	0.3	53	1	1	1
	24	0.3	--	--	--	--	--	--	--

(Continued)

Table 11. Cont.

Date		Number of Plants Expected with				Number of Plants Observed with			
		M.a. + *A.d.*	*M.a.* + *R.p.*	*A.d.* + *R.p.*	*M.a.* + *A.d.* + *R.p.*	*M.a.* + *A.d.*	*M.a.* + *R.p.*	*A.d.* + *R.p.*	*M.a.* + *A.d.* + *R.p.*
					Field IV (Late season seeded, 1963)				
June	3	38.0	142.0	34.4	31.0	41	140	39	37
	10	3.6	1.4	0.4	0.1	4	1	--	--
	20	1.7	28.6	0.8	0.3	--	11*	2	--
July	16	71.8	23.3	8.8	8.6	72	23	10	10

*Samples where the expected and observed differ by more than five plants.

M.a. = *Macrosiphum avenae*   *A.d.* = *Acyrthosiphon dirhodum*   *R.p.* = *Rhopalosiphon padi* number of plants with two or more species of aphids was calculated for the four possible species combinations as follows:

E M.a. X A.d. = P M.a. X A.d.
E M.a. X R.p. = P M.a. X R.p.
E A.d. X R.p. = P A.d. X R.p.
E M.a. X A.d. X R.p. = P M.a. X A.d. X R.p.

In the equations E represents the proportion of plants expected to be infested with the species subfixed to E (such as E M.a. = the proportion of plants expected with M. avenae, E A.d. = the proportion with A. dirhodum, and E R.p. = the proportion with R. padi). The P stands for the number of plants observed with the species combinations listed with P.

The predicted and observed species combinations (the four expected and observed columns in Table 11) are very similar. In only two samples did the two combinations differ by more than five plants. Thus, it may be hypothesized, that the presence of any one species on a barley plant in no way influenced the presence of another species on the same plant. That is, the chances of any of the three species of aphids being present on a barley plant was at random, and was not influenced by the presence of any other species.

In discussing the segregation of the three species on the different plant areas (Figures 20, 21, and 22), my colleagues have suggested biological avoidance between species. However, I interpret the data in Table 11 as eliminating the possibility of any such relationships. If any degree of species avoidance were in operation, it would be improbable that the species would have established on the plants at random as the data indicates. In addition, the data in Table 11 indicate there was no attraction between species.

Contiguous Distribution

Sampling of the barley fields was done at random following a completely randomized design (Figure 2). Two adjacent plants (plants 1 and 2) were sampled at each location and designated as pairs, and each pair of plants was classed as follows: 0 = none of the two plants infested, 1= one of the two plants infested, or 2 = both plants infested.

The number of stations predicted and the number of stations observed in the three classes are shown in Tables 12 through 15. The number of aphids present are not considered because the data are based on the presence or absence of a species. The number of stations predicted to have 0, 1 or 2 plants infested are compared to the number of stations observed using the standard chi-square (X^2) formula.

No. of Infested Plants	Number of stations with the indicated number (0, 1, or 2) of infested plants						Chi Square
	Expected			Observed			
	0	1	2	0	1	2	
	$100q^2$	$100X^2qp$	$100p^2$				

q = "1 - p": the proportion of plants not infested.

p = "Proportion" of infested plants: the total number of infested plants divided by the number of plants observed.

$$X^2 = \frac{(O_0 - E_0)^2}{E_0} + \frac{(O_1 - E_1)^2}{E_1} + \frac{(O_2 - E_2)^2}{E_2}$$

E = "Expected" no. of locations with 0, 1, or 2 infested plants.

0 = "Observed" no. of locations with 0, 1, or 2 infested plants.

X^2 = Chi-square with 1 degree of freedom, and at the 5% level significance 3.841.

These calculations were made for all aphids regardless of species and for each of the three species when two or more of the 200 plants sampled were infested.

Contiguous Distribution of Aphids of All Three Species

The results of contiguous distribution studies considering aphids regardless of species are shown in Table 12. The expected number of plants infested with aphids of any of the three species differed significantly from the number observed for only three of the 37 observed samples (Table 12).

In field II for the June 16 sample (Table 12), the number of stations observed with no plants infested and both plants infested was smaller than expected; and the number of adjacent plants expected with only one plant infested was correspondingly larger than observed. This suggests a weak attraction of aphids to

Table 12. Chi-square values calculated by comparing the number of stations expected with 0, 1, or 2 plants infested to the number of stations observed with 0, 1, or 2 plants infested with aphids of three species.

Date		No. of Infested Plants	Number of Stations with the Indicated Number (0, 1, or 2) of Infested Plants: Expected 0[c]	Expected 1[d]	Expected 2[e]	Observed 0	Observed 1	Observed 2	Chi-Square
			Field I (Early season seeded, 1962)						
May	4	4	96.04	3.92	0.04	96	4	0	0.04
	7	5	95.06	4.88	0.06	95	5	0	0.06
	11	10	90.25	9.50	0.25	90	10	0	0.28
	15	10	90.25	9.50	0.25	90	10	0	0.28
	18	5	95.06	4.88	0.06	95	5	0	0.06
	30	34	68.89	28.22	2.89	68	30	2	0.40
June	12	78	37.21	47.58	15.21	36	50	14	0.26
	20	157	4.62	33.76	61.62	5	33	62	0.05
	26	146	7.29	39.42	53.29	10	34	56	1.90
July	8[a]	49	16.11	26.78	11.11	16	27	11	0.00
	16	143	8.12	40.76	51.12	9	39	52	0.19
	25	10	90.25	9.50	0.25	90	10	0	0.28
			Field II (Mid-season seeded, 1962)						
May	13	2	98.01	1.98	0.01	98	2	0	0.01
	16	4	96.04	3.92	0.04	96	4	0	0.04
	21	3	97.02	2.96	0.02	97	3	0	0.02
	26	3	97.02	2.96	0.02	97	3	0	0.02
June	6	22	79.21	19.58	1.21	78	22	0	1.53
	9	66	51.84	40.32	7.84	49	46	5	1.99
	16	92	29.16	49.68	21.16	23	62	15	6.15[f]
	22	126	13.69	46.62	39.69	17	40	43	2.02
	29	161	3.80	31.40	64.80	5	29	66	0.59
July	9[a]	103	0.11	4.77	49.12	0	5	49	0.12
	20[b]	48	1.20	9.60	19.20	1	10	19	0.05
	23	48	57.76	36.48	5.76	62	28	10	5.40[f]

(Continued)

a/ The number of barley plants observed was 108 rather than 200.
b/ The number of barley plants observed was 60 rather than 200.
c/ 0 equals none of the two plants at a station were infested.
d/ 1 equals one of the two plants at a station was infested.
e/ 2 equals both of the plants at a station were infested.
f/ Significant at the 95% level, X^2 value of 3.84 with 1 and 3 degrees of freedom.

Table 12. Cont.

Date		No. of Infested Plants	Number of Stations with the Indicated Number (0, 1, or 2) of Infested Plants: Expected 0[c]	Expected 1[d]	Expected 2[e]	Observed 0	Observed 1	Observed 2	Chi-Square
			Field III (Late season seeded, 1962)						
May	31	8	92.16	7.68	0.16	93	6	1	4.79[f]
June	5	11	89.30	10.40	0.30	90	9	1	1.83
	9	17	83.72	15.56	0.72	83	17	0	0.86
	14	38	65.61	30.78	3.61	65	32	3	0.16
	21	106	22.09	49.82	28.09	22	50	28	0.00
July	2	165	3.06	28.88	68.06	1	33	66	2.04
	14	200	0.00	0.00	100.00	0	0	100	0.00
	24	70	42.25	45.50	12.25	46	38	16	2.72
			Field IV (Late season seeded, 1963)						
May	24	15	85.56	13.88	0.56	85	15	0	0.65
June	3	191	0.20	8.60	91.20	0	9	91	0.22
	10	64	46.24	43.52	10.24	44	48	8	1.06
	20	153	5.52	35.96	58.52	6	32	62	0.69
July	16	196	0.04	3.92	96.04	0	4	96	0.04

a/ The number of barley plants observed was 108 rather than 200.

b/ The number of barley plants observed was 60 rather than 200.

c/ 0 equals none of the two plants at a station were infested.

d/ 1 equals one of the two plants at a station was infested.

e/ 2 equals both of the plants at a station were infested.

f/ Significant at the 95% level, X^2 value of 3.84 with 1 and 3 degrees of freedom.

establish on plants adjacent to plants already infested, and the July 23 sample suggests the opposite occurrence. The counts, indicating opposite distribution patterns for plant infestations, are undoubtedly variations of the normal distribution of aphids from plant to plant that existed in field II.

In field III the high X^2 value for May 31 resulted from the appearance of one station with both plants infested. This occurrence must be interpreted as of minor biological significance because the high X^2 value resulted from only one of the 100 stations deviating from the expected.

Thus, it can be concluded, based on the chi-square values in Table 12, that when considered collectively the three species of grain aphids appeared to be distributed at random in regard to the presence or absence of aphids on adjacent plants.

Macrosiphum avenae

The expected and observed number of stations in each of the three classes (Table 13) for this species was similar in all but five samples. These samples were in three of the four fields. Results indicate that the infestation of a plant at a station was at random when related to the presence or absence of *M. avenae* on the adjacent plant at that station.

Table 13. Chi-square values calculated by comparing the number of stations expected with 0, 1, or 2 plants infested to the number of stations observed with 0, 1, or 2 plants infested with Macrosiphum avenae.

Date	No. of Infested Plants	Number of Stations with the Indicated Number (0, 1, or 2) of Infested Plants: Expected 0[c]	Expected 1[d]	Expected 2[e]	Observed 0	Observed 1	Observed 2	Chi-Square
		Field I (Early season seeded, 1962)						
May 4	4	96.04	3.92	0.04	96	4	0	0.04
7	5	95.06	4.88	0.06	95	5	0	0.06
11	10	90.25	9.50	0.25	90	10	0	0.28
15	10	90.25	9.50	0.25	90	10	0	0.28
18	5	95.06	4.88	0.06	95	5	0	0.06
30	22	79.21	19.58	1.21	80	18	2	0.65
June 12	62	47.61	42.78	9.61	46	46	8	0.57
20	104	23.04	49.92	27.04	30	36	34	7.78[f]
26	132	11.56	44.88	43.56	15	38	47	2.35
July 8[a]	46	17.80	26.41	9.79	19	24	11	0.45
16	142	8.41	41.18	50.41	9	40	51	0.08
25	6	94.09	5.82	0.09	94	6	0	0.10
		Field II (Mid-season seeded, 1962)						
May 13	2	98.02	1.98	0.00	98	2	0	0.00
16	4	96.04	3.92	0.04	96	4	0	0.04
21	3	97.02	2.96	0.02	97	3	0	0.02
26	3	97.02	2.96	0.02	97	3	0	0.02
June 6	17	83.72	15.56	0.72	85	13	2	2.71
9	37	66.42	30.16	3.42	65	33	2	0.89
16	62	47.61	42.78	9.61	43	52	5	4.64[f]
22	103	23.52	49.95	26.52	24	49	27	0.04
29	145	7.56	39.87	52.56	5	45	50	1.65
July 9[a]	97	0.56	9.89	43.56	1	9	44	0.43
20[b]	47	1.40	10.20	18.40	1	11	18	0.20
23	49	57.00	36.99	6.01	62	27	11	7.30[f]

(Continued)

a/ The number of barley plants observed was 108 rather than 200.
b/ The number of barley plants observed was 60 rather than 200.
c/ 0 equals none of the two plants at a station were infested.
d/ 1 equals one of the two plants at a station were infested.
e/ 2 equals both of the plants at a station were infested.
f/ Significant at the 95% level, X^2 value of 3.84 with 1 and 3 degrees of freedom.

Table 13. Cont.

Date		No. of Infested Plants	Number of Stations with the Indicated Number (0, 1, or 2) of Infested Plants						Chi-Square
			Expected			Observed			
			0[c]	1[d]	2[e]	0	1	2	
			Field III (Late season seeded, 1962)						
May	31	7	93.12	6.76	0.12	93	7	0	0.13
June	5	11	89.30	10.40	0.30	90	9	1	1.83
	9	13	85.56	13.88	0.56	87	13	0	0.64
	14	33	69.72	27.56	2.72	70	27	3	0.04
	21	80	36.00	48.00	16.00	40	40	20	2.78
July	2	153	5.52	35.95	58.52	4	39	57	0.72
	14	200	0.00	0.00	100.00	0	0	100	0.00
	24	71	41.60	45.79	12.60	46	37	17	3.69
			Field IV (Late season seeded, 1963)						
May	24	13	85.56	13.88	0.56	87	13	0	0.64
June	3	173	1.82	23.35	74.82	3	21	76	1.02
	10	48	56.76	36.48	5.76	57	38	5	0.17
	20	111	19.80	49.39	30.80	33	23	44	28.55[f]
July	16	193	0.12	6.76	93.12	1	5	94	6.92[f]

[a] The number of barley plants observed was 108 rather than 200.

[b] The number of barley plants observed was 60 rather than 200.

[c] 0 equals none of the two plants at a station were infested.

[d] 1 equals one of the two plants at a station was infested.

[e] 2 equals both of the plants at a station were infested.

[f] Significant at the 95% level, X^2 value of 3.84 with 1 and 3 degrees of freedom.

Acyrthosiphon dirhodum

The chi-square values for *A. dirhodum* were non-significant for all samples, indicating that the establishment of *A. dirhodum* on the barley plants was at random (Table 14).

Rhopalosiphum padi

In fields I and II, *R. padi* was found randomly established on barley plants at the different stations. In fields III and IV, three samples had significant chi-square values where adjacent plants were predicted to be infested less often than was observed (Table 15). This suggests the aphid populations on one plant may have been influenced by the aphids on the adjacent plant.

The two X^2 values in field IV during June and July of 1963 were highly significant, showing considerable deviation between the expected and observed infestations. The subterranean habitat of *R. padi* investigated during 1963 possibly influenced this clumping of aphids on just one of the adjacent plants. A gathering of aphids in small areas in the field where aphids could survive was apparent during field observations.

Table 14. Chi-square values calculated by comparing the number of stations expected with 0, 1, or 2 plants infested to the number of stations observed with 0, 1, or 2 plants infested with *Acyrthosiphon dirhodum*.

Date		No. of Infested Plants	Number of Stations with the Indicated Number (0, 1, or 2) of Infested Plants: Expected 0[c]	Expected 1[d]	Expected 2[e]	Observed 0	Observed 1	Observed 2	Chi-Square
			Field I (Early season seeded, 1962)						
May	30	9	91.20	8.59	0.20	91	9	0	0.22
June	12	18	82.81	16.38	0.81	84	14	2	2.11
	20	71	41.60	45.79	12.60	44	41	15	1.10
	26	41	63.20	32.59	4.20	66	27	7	2.95
July	8[a]	9	45.38	8.24	0.37	46	7	1	3.44
	16	24	77.44	21.12	1.44	79	18	3	2.18
	25	5	95.06	4.88	0.06	95	5	0	0.06
			Field II (Mid-season seeded, 1962)						
June	6	6	94.09	5.82	0.09	94	6	0	0.10
	9	21	80.10	18.80	1.10	79	21	0	1.37
	16	32	70.56	26.88	2.56	71	26	3	0.11
	22	43	61.62	33.76	4.62	60	37	3	0.09
	29	38	65.61	30.78	3.61	66	30	4	0.06
July	9[a]	37	23.34	24.32	6.34	22	27	5	0.66
	20[b]	13	18.41	10.18	1.41	18	11	1	0.19
			Field III (Late season seeded, 1962)						
June	9	8	92.16	7.68	0.16	92	8	0	0.17
	14	7	93.12	6.76	0.12	93	7	0	0.13
	21	36	67.24	29.52	3.24	68	28	4	0.27
July	2	43	61.62	33.76	4.62	60	37	3	0.92
	14	53	54.02	38.96	7.02	54	39	7	0.00
			Field IV (Late season seeded, 1963)						
June	3	43	61.62	33.76	4.62	63	31	6	0.67
	10	15	85.56	13.88	0.56	86	13	1	0.40
	20	3	97.02	2.96	0.02	97	3	0	0.02
July	16	74	39.69	46.62	13.69	41	44	15	0.32

[a] The number of barley plants observed was 108 rather than 200.
[b] The number of barley plants observed was 60 rather than 200.
[c] 0 equals none of the two plants at a station were infested.
[d] 1 equals one of the two plants at a station was infested.
[e] 2 equals both of the plants at a station were infested.

Table 15. Chi-square values calculated by comparing the number of stations expected with 0, 1, or 2 plants infested to the number of stations observed with 0, 1, or 2 plants infested with Rhopalosiphum padi.

Date		No. of Infested Plants	Number of Stations with the Indicated Number (0, 1, or 2) of Infested Plants						Chi-Square
			Expected			Observed			
			0[b]	1[c]	2[d]	0	1	2	
			Field I (Early season seeded, 1962)						
June	12	2	98.02	1.98	0.00	98	2	0	0.00
	20	64	46.24	43.52	10.24	44	48	8	1.06
	26	19	81.90	17.20	0.90	81	19	0	1.10
			Field II (Mid-season seeded, 1962)						
June	16	10	90.25	9.50	0.25	90	10	0	0.28
	22	4	96.04	3.92	0.04	96	4	0	0.04
	29	3	97.02	2.96	0.02	97	3	0	0.02
July	9[a]	2	52.02	1.97	0.01	52	2	0	0.01
			Field III (Late season seeded, 1962)						
June	21	15	85.56	13.88	0.56	87	11	2	4.33[e]
			Field IV (Late season seeded, 1963)						
May	24	2	98.02	1.98	0.00	98	2	0	0.00
June	3	160	64.00	32.00	4.00	65	30	5	0.39
	10	6	94.09	5.82	0.09	94	6	0	0.10
	20	52	54.76	38.48	6.76	61	26	13	10.52[e]
July	16	24	77.44	21.12	1.44	82	12	6	18.65[e]

a/ The number of barley plants observed was 108 rather than 200.

b/ 0 equals none of the two plants at a station were infested.

c/ 1 equals one of the two plants at a station was infested.

d/ 2 equals both of the plants at a station were infested.

e/ Significant at the 95% level, X^2 value of 3.84 with 1 and 3 degrees of freedom.

Field Distribution of Aphids

Two types of field distribution were investigated. One concerned the field distribution of all specimens of a species observed on each sampling date. The second analysis compared the number of specimens on adjacent plants. The data were transformed using the square root transformation on each observation before the analyses were made (Li 62 p. 454-458).

Aphid Distribution Between Quadrants

The basic sampling plan shown in Figure 2 was divided into four equal quadrants to study the field distribution of aphids. Each quarter of the field contained 25 sampling locations, with two adjacent plants at each location. These quadrants of 50 plants each were in areas of the same size in the three 1962 fields, but in 1963 their size doubled because the barley field was twice the size of the 1962 fields.

The data after being transformed were set up for analysis of variance (Li 62 p. 162). Two hypotheses concerning field distributions were tested: one that the four quadrants were similar in the number of aphids present on the plants, and two, that the number of aphids at each of the 25 sampling stations within each of the four quadrants was similar.

Table 16 lists the mean squares (MS) and F-test values which were figured with the 1410 computer. Samples with fewer than 100 aphids were not used because they might have resulted in misleading conclusions on field distribution.

Macrosiphum avenae

Three samples in Table 16 have F-values indicating the quadrants differ significantly in the number of aphids present. These all occur in field IV, indicating a non-random distribution across that field, which differs markedly from the three 1962 fields where specimens of *M. avenae* appear to be randomly distributed from quadrant to quadrant. The 1963 field was twice the size of the 1962 fields, therefore there was twice the distance between samples, but this should not influence an estimation of field distribution. The date with the highest number of aphids, July 16, had next to the smallest F-value in field IV suggesting that as the number of *M. avenae* increased their distribution from quadrant to quadrant became more similar.

Acyrthosiphon dirhodum

The June 20 sample was the only one where the quadrants were significantly different in number of *A. dirhodum* present (Table 16). That sample yielded three times more aphids than any

Table 16. Comparison of the number of specimens of Macrosiphum avenae and Acyrthosiphon dirhodum between quadrants within quadrants for sampling dates when more than 100 specimens were recorded.

Date		Between Quadrant MS	Within Quadrant MS	Error MS	Between Quadrant F-value	Within Quadrant F-value
		MACROSIPHUM AVENAE				
		Field I (Early season seeded, 1962)				
June	12	9,5466	14.2225	15.8400	0.603	0.898
	20	14.4933	47.0291	53.8900	0.269	0.873
	26	3.2600	28.5145	24.9000	0.131	1.145
July	8	12.0600	5.6075	5.7300	2.105	0.979
	16	30.7400	20.7079	19.2900	1.594	1.074
		Field II (Mid-season seeded, 1962)				
June	16	11.0000	9.9612	11.4600	0.960	0.869
	22	30.9866	44.5725	47.2000	0.657	0.944
	29	164.8583	118.5325	86.5250	1.905	1.370
July	9	17.2050	133.9925	94.4850	0.182	1.418
	20		81.2087	46.9100		1.731*
	23	5.8800	10.0712	2.7400	2.146	3.676*
		Field III (Late season seeded, 1962)				
June	21	0.2983	3.6433	3.3750	0.088	1.080
July	2	35.9533	54.1783	27.8900	1.289	1.942*
	14	24.4850	237.7250	159.4950	0.154	1.490*
	24	2.1933	9.5929	3.6400	0.603	2.635*
		Field IV (Late season seeded, 1963)				
June	3	114.8133	37.4358	17.5700	6.535*	2.131*
	20	372.1916	22.5500	12.1250	30.696*	1.860*
July	16	423.9200	110.8783	88.4000	4.796*	1.254
		ACYRTHOSIPHON DIRHODUM				
		Field I (Late season seeded, 1962)				
June	12	15.4733	10.8187	5.9400	2.605	1.821*
	20	301.7650	69.2516	55.6050	5.427*	1.245
	26	2.8983	7.3995	6.2650	0.463	1.181
July	8	6.3333	7.4720	3.1000	1.992	2.350*
	16	5.2583	4.6091	2.9950	1.756	1.539*
		3 & 100 df	96 & 100 df		2.706	1.423

other sample in field I (Figure 16). The chi-square value of 5.427 indicated that the A. dirhodum in field I were clumped in some quadrants more than others. The quadrant means are not shown in Table 16, but one quadrant had a mean of 7.20 while the other three were similar to each other, 2.30, 2.28, and 2.28. The quadrant with the 7.20 mean value was located next to the orchardgrass field (Figure 1). This high mean value may have resulted from migration of A. dirhodum from the orchardgrass field into the barley field. The June 20 sample occurred about the same time the orchardgrass leaves were drying, possibly resulting in a major aphid migration across the grass roadway into the barley field. The rapid decline of A. dirhodum from the June 20 sample to the June 26 sample (784 to 185, Figure 16), and the change from the non-random distribution of June 20 to a random distribution from quadrant to quadrant on June 26, indicates that a larger proportion of A. dirhodum disappeared from the quadrant adjacent to the orchardgrass field.

Aphid Distribution Within Quadrants (Plant to Plant)

Macrosiphum avenae

The F-test values, shown in Table 16 in the column headed "within quadrants," are comparisons of the number of aphids on each of two adjacent plants. In a previous section, the distribution of aphids on the adjacent plants was considered, but those figures were sensitive to the presence or absence of aphids, and not sensitive to the number of aphids present on the plants.

The number of *M. avenae* were randomly distributed on the two adjacent plants for all samples in the early seeded field and during June in the field seeded in mid-season (Table 16). The distribution of aphids appears to have been non-random for most samples in the two late season planted fields, and in July for the field planted in mid-season, as indicated by the significant F-values. The differences between fields may have resulted from the total number of aphids per sample being lower in the early seeded field than in the other three fields. As the number of aphids per sample increased the number of plants with high numbers of aphids was greater. This would be expected, because once established on a plant aphids most frequently stay on that plant and increase in numbers, as indicated by Hafez (28) and Hughes (35) for other aphid species. When this occurred, one plant of a pair would be found to have 50 + aphids while the adjacent plant would have ten or less aphids.

Acyrthosiphon dirhodum

The numbers of *A. dirhodum* per plant were non-randomly distributed between plants for three of five counts (Table 16). It seems unusual that the distribution changed as it did. With the clumping of aphids on plants on June 12 and during July, I would expect the June 20 and 26 F-values to have been significant. The numbers of aphids observed on the June 20 and 26 samples are 784 and 185 respectively, while the other three counts had 114, 56 and 96 specimens. These numbers indicated that the numbers of A. dirhodum were evenly distributed from plant to plant as the population increased.

Aphid Form - Plant Area

The first statistical analysis discussed compares the number of aphids on the different areas of the plants. All samples of M. avenae that were analyzed had significantly more aphids on one plant area than on another (Table 17). The unequal numbers of aphids on the different plant areas (high F-values) were expected after looking at Figures 23, 24, 25, and 26.

The numbers of A. dirhodum in field I were more uniformly distributed on the plant areas than were M. avenae. One sample (July 8) was apparently uniformly distributed from area to area (Table 17). The F-values for the five A. dirhodum samples were smaller than for the M. avenae samples, indicating a more uniform distribution from plant area to area for A. dirhodum than for M. avenae. In addition, it was influenced by the lower counts of A.

Table 17. Statistical analyses of the number of aphids on four areas of 200 plants, number of aphids in the six morphological stages, and the interaction of these two aphid distributions for sampling dates when more than 100 specimens were observed.

Date		Area of Plant MS 1	Aphid Form MS 2	Area of Plant Aphid Form MS 3	Error MS	F-values Figured from Corresponding MS Values 1	2	3
				MACROSIPHUM AVENAE				
				Field I (Early season seeded, 1962)				
June	12	30.1119	4.2895	2.3196	.8876	33.925*	4.833*	2.613*
	20	52.2862	9.5183	2.1493	1.3633	38.353*	6.982*	1.577
	26	35.6688	12.2722	1.4850	1.0135	35.194*	12.109*	1.465
July	8	12.2329	1.1591	.7343	.7080	17.278*	1.637	1.037
	16	31.4077	8.5120	2.2332	.9499	33.064*	8.961*	2.351*
				Field II (Mid-season seeded, 1962)				
June	16	24.7128	5.3466	2.2965	.9406	26.278*	5.684*	2.442*
	22	77.2023	12.2260	3.7487	.9235	83.598*	13.239*	4.059*
	29	117.9169	27.5578	5.0250	1.1803	99.904*	23.348*	4.257*
July	9	52.0773	16.4662	1.9872	1.7333	30.045*	9.488*	1.146
	20	40.9750	3.6013	1.8184	2.6601	15.404*	1.354	0.684
	23	14.4928	2.4729	1.0528	.4986	29.067*	4.960*	2.112*
				Field III (Late season seeded, 1962)				
June	21	15.4972	3.3514	.9994	.4237	36.576*	7.910*	2.359*
July	2	115.6854	15.0959	5.8262	.6170	187.497*	24.467*	9.443*
	14	94.9013	53.5867	4.2553	1.0116	93.813*	52.972*	4.207*
	20	19.4595	3.8252	1.7415	.4374	44.489*	8.746	3.981*

(Continued)

Table 17. Cont.

Date	Area of Plant MS 1	Aphid Form MS 2	Area of Plant Aphid Form MS 3	Error MS	F-values Figured from Corresponding MS Values 1	2	3
			Field IV (Late season seeded, 1963)				
June 3	17.4954	21.3321	1.5134	.8062	21.701*	26.460*	1.877*
20	100.3849	4.7799	3.8973	2.0362	49.300*	2.347	1.914*
July 16	31.8682	64.5032	.9637	1.0168	31.342*	63.437*	0.948
			<u>ACYRTHOSIPHON</u> <u>DIRHODUM</u>				
			Field I (Early season seeded, 1962)				
June 12	8.0218	1.2406	.7688	.8085	9.922*	1.534	0.951
20	60.3653	9.0404	2.3920	3.4814	17.339*	2.597*	0.687
26	8.6140	8.2739	1.5148	.4446	19.375*	18.610*	3.407
July 8	1.3434	.8628	.4407	.5065	2.652	1.703	0.870
16	4.5654	1.1532	.6052	.6092	7.494*	1.893	0.993
Degrees of Freedom	3 & 72	5 & 72	15 & 72	F-value Critical Region	2.743	2.347	1.820

dirhodum than *M. avenae*.

The second statistical analysis consisted of comparing the six morphological stages of the aphids (F-value column 2, Table 17). *M. avenae* were unevenly distributed between the six morphological forms as indicated by the significant F-values. This result was suspected because each stadia from first instar to fourth had progressively fewer individuals at each count (Figures 12, 13, 14,and 15).

F-values for the comparison of the interaction of the six aphid stages on each of the four plant areas are shown in the F-value column 3 of Table 17. Several counts had similar numbers of aphids in each of the 24 classes (six aphid stages times four plant areas = 24 classes). The differences which probably existed were so minor they were insignificant after the square root transformation. The writer felt that all dates should have had significant values in the right hand column after comparing the proportions of aphids in each of the 6 morphological forms and the four plant areas (Figures 10 through 30). Counts for each sample date were subdivided, first into 200 individual plants, then each plant was subdivided by 24, which means 4800 aphids would have had to be present to produce an average of one aphid for each square root figure. None of the samples had that number of aphids of one species present. Even with the large number of subdivisions and small number of aphids present, the six forms of M. avenae were apparently normally distributed between plant areas for only 6 of 18 samples tested.

There were apparently no differences in plant area - aphid form distributions for A. dirhodum (Table 17).

Aphid Populations per Acre

During the winter of 1962 means and variances of the 1962 field samples were calculated in the process of determining which statistical methods would best fit the data. These calculations were used to estimate the number of aphids in an acre.

The number of plants per acre was estimated by counting the number of plants in three foot sections of row at ten locations in the 1962 barley plantings. The mean number of plants per section, and the variance between ten samples of three foot sections of row were calculated (Li, 62, page 65). The 95% confidence interval was estimated using the formula $K\bar{y} \pm 1.96 \frac{Ks}{\sqrt{n}}$ (Li, 62, p. 141-150) where K is the number of all possible samples in one acre, $\bar{y}$ is the mean number of plants per sample, s is the square root of the variance between samples, and n is the number of samples used when figuring the mean number of plants per sample and the variance between the ten samples. The estimated number of plants per acre, based on the ten samples of three foot of row, was 1,029,865 plus or minus 114,788. This estimate is for 95% of all the possible acre samples from the same area from which the ten samples were obtained. The estimated number of plants per foot or row was 13.9, which was larger than the 8.7 and 11.9 number of plants given by Dickason, et al. (17). The discrepancy between results may have resulted from different seeding rates or environmental conditions which vary from year to year.

The number of aphids expected on an acre of barley and the confidence limits were found by the same formulae (Li, 62, p. 141-150) used to estimate plants per acre. The standard deviations varied with each sampling date and are shown in Table 18. All sampling dates for field I are given, and two from field II and field IV. In all samples (except July 8 where n = 108) n = 200; K is 1,029,865 the estimated number of plants per acre; $\bar{y}$ is the mean number of aphids found per plant for each of the 200 plants; 1.96 is the 95% confidence level; and s is the standard deviation.

The confidence limits indicated that when the mean number of aphids was less than one per plant, the estimated mean number of aphids per acre was smaller than the distance between the confidence limits. In these cases the number of plants sampled should have been increased to give a more reliable estimate of the aphid populations present. Estimates of less than one aphid per plant in field I for May 4 and July 25 (Table 18) are correct statistically, but misleading biologically, because a group of plants cannot be infested by a minus

Table 18. Expected number of Macrosiphum avenae in an acre of barley and the confidence limits calculated using means and variances of the 200 plant samples.

Field and Date		One Sample of 200 Plants $y^{a/}$	$s^{b/}$	Mean No. of Aphids	One Acre Estimates Confidence Limits	Confidence Limit ÷ Mean[c/]
Field I, 1962						
May	4	0.03	0.24371	30,895	34,783	1.13
	7	0.03	0.18156	30,895	13,223	0.43
	11	0.10	0.62119	102,986	88,664	0.86
	15	0.05	0.24952	51.493	35.615	0.69
	18	0.03	0.07053	30.895	10.067	0.33
	30	0.23	0.88374	236.869	126,138	0.53
June	12	1.60	1.22328	1,647,784	174,602	0.11
	20	3.47	6.82952	3,563,632	974,791	0.27
	26	3.21	2.60029	3,305,866	371,146	0.11
July	8	1.57	2,40131	1,616,888	342,745	0.21
	16	3.21	4.48850	3,305,866	640,654	0.19
	25	0.07	0.55374	72,090	79,037	1.10
Field II, 1962						
June	22	3.48	6.75932	3,583,930	964,774	0.27
	29	6.84	10,15578	7,044,277	1,449,558	0.21
Field III, 1962						
July	2	5.01	6,36968	5,159,623	909,159	0.18
	14	15.75	14.17383	16,266,718	2,023,064	0.12

a/ y = the mean number of aphids per plant based on a 200 plant sample.

b/ s = the standard deviation of the aphids found on 200 plant sample, $s = \sqrt{s^2} = (y-\bar{y})^2$.

c/ This column is used as an index of the sample variation divided by the mean.

number of aphids.

The confidence limit divided by the means (Table 18, the right hand column) resulted in values below 0.30 when the $\bar{y}$ values were higher than one. Values above 0.30 resulted when $\bar{y}$ values (mean number of aphids per plant based on 200 plants) were less than one. Thus, if the confidence limit divided by the mean equals 0.30 or larger, the number of plants sampled should have been increased. The 0.30 figure is directly related to the variation in the sample taken, and values over 0.30 indicate a poor estimate was made of the mean number of aphids per plant.

In comparison to Herrick's (31) figure of 1.56^8 aphids from one stem mother, this study has produced an estimate of the actual number of aphids present on an acre of barley plants and the variation of these estimates. The mean number of aphids ranged from 30,895 to 16,266,718 aphids per acre, depending on the mean number of aphids found per plant. The confidence limits give an indication of the variation expected, and for the 16 million figure, the confidence limits were from 14, 243,654 to 18,289,782 which is a fairly narrow range for that high an estimate of field populations.

Dahms and Wood (14) estimated that 7,500,000 greenbugs would have to be present per acre from 13 to 29 days to reduce grain yields by one bushel. According to the estimates in Table 18 and the counts in Figure 7, the populations of _M. avenae_ were not above

7, 500, 000 aphids per acre long enough to reduce the yield of barley by one bushel. The presence of *M. avenae* on the heads, however, may have resulted in yield reductions greater than those predicted for the greenbug, and yields may have been reduced in field III when over 16 million aphids were estimated on July 14 (Table 18).

VIII. PREDATORS AND PARASITES

Field Samples of Aphid Predators

Field observations of predators and parasites were made in conjunction with sampling the 200 plants for aphids during 1962 and 1963. The data in Table 19 show the numbers of insects observed, but the data are based on field observations and are not sensitive to species. The number of specimens of each species identified in Table 20 represents the relative numbers collected during 1963 using a sweep net.

Adult lady beetles were observed during most sampling dates, and all fields yielded similar numbers of specimens (Table 19). Most samples yielded small numbers of adults because they flew or ran when approached by the observer. Well over three-fourths of the lady beetles observed in barley fields during 1963 were *Coccinella trifasciata subversa* LeConte and *Hippodamia sinuata spuria* LeConte (Table 20). Three specimens of the parasite, *Perilitus coccinellae* (Shrank), were found on the lady beetle *Coccinella trifasciata subversa* LeConte.

Adult syrphids were excluded from the field observations because of their fast flight habits. Eggs and larvae of Syrphidae were recorded during the random plant sampling (Table 19). The eggs and larvae were observed on the plant leaves, usually near an

Table 19. Parasites and predators observed while sampling the 200 barley plants on each counting date during 1962 and 1963.

Date		Coccinellidae[a]				Syrphidae[a]		Parasit-ized	Dead
		Adults	Pupae	Larvae	Eggs	Larvae	Eggs	Mummies	Aphids
		Field I (Early season planted, 1962)							
May	11	0	0	0	0	0	0	0	1
	15	2	0	0	0	0	0	0	0
	18	5	0	0	0	0	0	0	0
	30	3	0	0	0	0	0	0	1
June	12	5	0	0	0	0	0	0	4
	20	1	1	3	0	1	7	1	0
	26	0	0	6	0	2	3	1	5
July	8	1	0	0	0	0	0	7	0
	16	3	0	0	0	0	1	33	3
TOTALS		20	1	9	0	3	11	42	13
		Field II (Mid-season planted, 1962)							
June	6	6	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	1	2
	16	0	0	0	0	0	0	0	1
	22	2	0	3	0	2	5	0	0
	29	1	2	5	0	13	2	1	0
July	9	0	7	1	0	1	5	23	2
	20	1	0	0	0	1	0	45	3
	23	5	1	0	0	2	0	91	57
TOTALS		15	10	9	0	19	12	161	65

(Continued)

[a] Identifications of representative specimens are given in Table 20.

Table 19. Cont.

Date	Coccinellidae[a]				Syrphidae[a]		Parasit-ized	Dead
	Adults	Pupae	Larvae	Eggs	Larvae	Eggs	Mummies	Aphids
	Field III (Late season planted, 1962)							
May 31	3	0	0	0	0	0	0	0
June 9	1	0	0	0	0	0	0	0
14	2	0	0	0	0	0	0	0
21	2	0	0	0	0	0	1	1
July 2	2	1	1	0	1	3	1	0
14	0	10	0	0	6	5	74	3
24	7	0	0	0	1	1	64	40
TOTALS	17	11	1	0	8	9	142	44
	Field IV (Late season planted, 1963)							
June 3	2	9	6	24	0	1	6	37
10	1	0	2	0	0	1	1	0
20	1	2	5	3	1	0	0	18
July 16	14	9	6	3	3	5	317	231
TOTALS	18	20	19	30	4	7	324	286

[a] Identifications of representative specimens are given in Table 20.

Table 20. List of predator species identified from field collections made during 1962 and 1963 from barley and wheat plants.

Scientific Name	Relative Numbers[c]
Coccinellidae[a] (Lady beetles)	
Coccinella trifasciata subversa LeConte	15
Coccinella trifasciata perplexa Mulsant	1
Hippodamia sinuata spuria LeConte	9
Hippodamia convergens Guerin	5
Hippodamia quinquesignata ambigua LeConte	3
Psyllobora 20-maculata taedata LeConte	4
Mulsantina picta minor Casey	3
Cycloneda polita Casey	1
Chilocorus probably fraternus LeConte	1
Syrphidae[b] (Flower flies)	
Scaeva pyrastri (L.)	16
Platycheirus quadratus (Say)	5
Eupeodes volucris O.S.	4
Eristalis tenax (L.)	1
Sphaerophoria menthastri (L.)	1
Sphaerophoria melanosa Will. or sulphuripes (Thomson)?	1
Toxomerus occidentalis Curran	1
Syrphus opinator O.S.	1
Metasyrphus subsimus Fluke	1

[a] Specimens were examined by Dr. Kenneth S. Hagen, Division of Biological Control, University of California, Berkeley, California.

[b] Identifications were made by W. W. Wirth, Insect Identification and Parasite Introduction Research Branch ARS, USDA.

[c] The relative numbers represent the proportion of each species collected with an insect sweep net, and are not estimates of field abundance.

aphid colony. As with the lady beetle larvae the majority of the specimens in fields I and II were observed during June and in fields III and IV during July. During 1963 syrphid larvae were commonly noticed on the plant heads in association with *M. avenae* which was probably their major food source in the barley fields.

The influence of syrphid flies on the field populations of aphids was probably insignificant. This is based on the small number of plants that were occupied by larvae or eggs.

The syrphids were parasitized to a greater extent than were the coccinellids. In a group of approximately 100 syrphid larvae taken into the laboratory 15 parasites emerged from 43 specimens that pupated. The dominant parasite was *Diplazon laetatorius* (F.). Two specimens of *Homotropus decoratus* (cress.) and one of *Syrphoctonus flavolineatus* (Grav.) were found. Wasps similar to these three Ichneumonidae were observed in the field as commonly as were the Syrphidae.

Sticky Trap Catches of Aphid Predators

Aphid predators were collected on the sticky traps maintained in the field during 1963. Coccinellidae catches began in March and reached a peak in late-July and early-August (Table 21) during a period when lady beetles were observed in relatively large numbers in the field.

Chrysopidae catches (Table 21) followed a pattern similar to lady beetle catches, but neither adults nor larvae were observed in the barley fields, suggesting they were possibly developing in another area.

July seemed to be a period of large aphid migrations (Table 2) and the lady beetle and lacewing peak catches occurred approximately 15 days after the aphid peak populations during 1963 (Table 21).

The sticky traps were placed in the field facing the four cardinal directions, north, east, south and west. Figure 36 shows the percentage and number of predators caught on each trap face during 1963. The predators were caught quite uniformly on the four trap faces suggesting that the predators were influenced by wind direction much less than were the aphids (Figures 6 and 36).

Aphid Parasites

During the spring of 1963, 100 parasitized aphids were gathered from the barley field by collecting five mummies at each of 20 locations. The leaf to which the parasitized aphid adhered was cut to fit into a 2 dram glass vial. The vials containing mummies were plugged with cotton and maintained in a study room where the temperature fluctuated around 70°F.

It is evident (Table 22) that the parasites *Aphidius*

Table 21. Seasonal sticky trap catches of two families of aphid predators in western Oregon.

Date-1963		Days Repre-sented[a]	Aphid Predators Coccinellidae	Aphid Predators Chrysopidae	Date-1963		Days Repre-sented[a]	Aphid Predators Coccinellidae	Aphid Predators Chrysopidae
Jan.	8	8	0	0	July	2	8	5	7
	18	10	0	0		15	13	16	41
	25	7	0	0		30	15	68	68
Feb.	1	6	0	0	Aug.	12	13	94	36
	8	8	0	0		20	8	10	1
	16	8	0	0	Sept.	5	16	27	1
	22	6	0	2		18	13	7	1
March	3	9	0	0		23	5	7	1
	8	5	1	1	Oct.	2	9	1	0
	21	13	4	1		8	6	0	0
	28	7	0	0		18	10	5	0
April	5	8	4	0		30	12	4	0
	11	6	0	0	Nov.	14	15	0	0
	20	9	4	0		30	16	0	0
May	3	13	12	0	Dec.	14	14	0	0
	11	8	4	1		31	17	0	0
	14	3	8	0					
	18	4	17	4					
	26	7	22	5	TOTAL			396	182
June	4	9	20	3					
	10	6	3	1					
	17	7	21	4					
	24	7	32	4					

[a] The number refers to the days between checking of the traps.

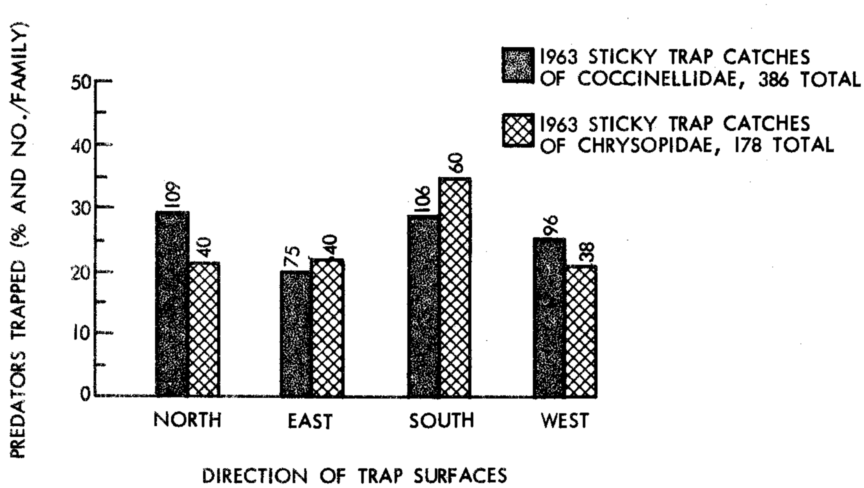


Figure 36. Number and percent of predators caught on four directional surfaces of sticky traps during 1963 near Corvallis, Oregon.

Table 22. Emergence data recorded for insect genera and species from 100 parasitized Macrosiphum avenae collected from barley plants July 12, 1963, at the Hyslop Agronomy Farm.

Scientific Name	Emergence Date (1963)	Sex & No. Emerged Female	Male	Undeterm.
PARASITES[a]				
Braconidae				
Aphidius obscuripes Ashmead	July 12-17	29	24	
Aphidius sp.	July 16	1		
HYPER-PARASITES[b]				
Proctotrupidae				
Lygocerus (prob.) niger Howard	July 20-24	3	7	
Pteromalidae				
Pachyneuron sp.	July 22-29			4
Cynipidae				
Charips sp. near victrix (Westwood)	July 17-23			12
Unidentified Hyper-parasites consisting of				
Asaphes sp., Pachyneuron sp., & Lygocerus (prob.) niger	July 21-23			7
Died during emergence[c]				5
Failed to emerge in one year				8
Total			100	

[a] All aphid parasites were identified by Dr. M.J.P. Mackauer of the Entomology Research Institute, Belleville, Ontario, Canada.

[b] Hyper-parasites were determined by Dr. Kenneth Hagen, Department of Entomology, Division of Biological Control, University of California, Berkeley, California.

[c] Caps were cut in mummies, but parasites or hyper-parasites failed to emerge.

obscuripes Ashmead, emerged soon after the mummified aphids were collected, but the hyper-parasites required a longer development time. This would be expected, because the development of the aphid parasite must take place before the hyper-parasite can complete development on the parasite. From the data in Table 22, it is apparent that A. obscuripes would be an efficient aphid parasite based on the length of its life cycle. Most emergence occurred within four days after collection, which would be about the time of appearance of adult reproductive aphids from the same aphid colonies. The parasite, therefore, requires about the same number of days for maturation as does M. avenae (Hafez 28).

Primary parasites emerged from slightly over one half of the collected mummified aphids (Table 22), and hyper-parasites emerged from 33% of the samples. This emergence data indicates that hyper-parasitism was high in the field. The number of mummified aphids not producing living insects was only 13%.

The actual effects of aphid parasites on the field populations of M. avenae (the host of A. obscuripes) were slight. The number of parasitized aphids observed before July was negligible (Table 19) and the parasite would have had to have been abundant earlier in the season.

An entomophagous fungus was observed to a very limited extent attacking Acyrthosiphon dirhodum on orchardgrass early in the spring when the temperature rose above 50°F. The effect of this biotic factor on the aphid populations during 1962 and 1963 was very limited.

SUMMARY AND CONCLUSIONS

Field biology studies of three grain aphids, Macrosiphum avenae (Fabr.), Acyrthosiphon dirhodum (Walker), and Rhopalosiphum padi (L.), were conducted near Corvallis, Oregon, from 1961 to 1964.

M. avenae is distributed throughout the grain growing areas of North America and has been reported from all continents of the world. A. dirhodum has been reported from the eastern and western United States and Europe on several species of grass and rose. R. padi has a wide host range of grasses and grains over the world. This species was found to feed on the subterranean areas of the barley plants, indicating that R. padi (L.) and R. fitchii (Sand.) are two taxons for the same biological species. Winter grain and grass hosts were found for all three aphid species.

M. avenae was found only on grain plants (barley, oats, rye and wheat) during the fall, winter, and spring. It was found more commonly on plants six inches or taller than on shorter plants. Population densities were low during the fall and winter on grain plants compared to the numbers found in spring seeded barley fields. Winter wheat supported the largest winter population of M. avenae until maturity and heading during May. This may be a major source of the alate M. avenae which populate the spring barley fields.

A. dirhodum was found on orchardgrass during the winter of 1962-63. Specimens were abundant on orchardgrass during April and May, and this host supported larger populations of A. dirhodum than any other winter host. Orchardgrass leaves form a "V" in cross-section, with the midrib at the base. This aphid species was commonly observed in the bottom of the "V," possibly protected from wind abrasion and predators.

R. padi had a broader host range than the other two species and was observed on barley, oats, rye, wheat, fescue, orchardgrass, and bluegrass. This species was most abundant during the mid-winter and is apparently adapted to temperatures below 60^{o}F. It survived temperatures below freezing when the temperatures dropped slowly over a period of weeks, but did not survive when the temperatures dropped abruptly.

Sticky traps caught migrating winged aphids from March 3 to August 12, and then from October 2 until November 14 during 1963. The major flights of M. avenae and A. dirhodum occurred during July, and the major flights of R. padi were during June. Aphids were caught predominantly on the north face of the traps.

The major part of this study was conducted in spring barley fields. This yielded information on seasonal abundance, aphid developmental stages, and areas of the plant occupied by each species.

The seasonal population fluctuations on barley plants were related to the planting date of the barley and growth stages of the plants during 1962 and 1963. The most common aphid species, M. avenae was first observed on barley plants during May and disappeared by July 30. There was a generation lag between entrance of alatae and their offspring, and the appearance of the third generation. From early June to mid-July the populations increased from 13 to 63 fold, depending on the field.

A very rapid decline in aphid numbers occurred during the last two weeks of July and was related to plant maturity. The peak aphid populations occurred at an earlier plant phenological stage in the early season planted barley than they did on plants in the late planted fields.

A. dirhodum was found in the barley fields about two weeks later than M. avenae; and reached less distinct population peaks. This species also left the barley fields in late July. In the two early planted fields of 1962, A. dirhodum remained abundant at later plant phenological stages than it did in the late planted fields. In one field, late tillers appeared during July, supporting A. dirhodum after the main stalk of the plants dried.

R. padi populations were the smallest of the three species. This species was observed on barley plant shoots below the soil surface during 1963. R. padi appeared on barley later in the spring than the other two species. They were most abundant during June and declined during late June and early July in contrast to the late July populations of the other species. A temperature, rather than a plant phenological, relationship appeared to cause this earlier population peak and decline.

Six life stages were recorded for M. avenae and A. dirhodum. For both species the total population composition progressively declined from the youngest to the oldest life stage, except for apterous adults which were more abundant than the fourth instar nymphs or the alate stage. The apterous individuals live longer than the fourth-instar individuals, thereby accounting for their relatively greater abundance.

The proportions of each M. avenae life stage for the four field totals were quite similar. Alatae constituted a larger proportion of the population during early counts than during later observation. The proportions of each stage varied in two groups, one composed of first- and second-instar nymphs, the other of the remaining forms. In one field the proportion of first instar nymphs increased until July, then decreased while the number of second-instar nymphs varied in a reverse fashion. During the population decline, the proportion of alatae did not increase, indicating that the aphids do not migrate to other plants.

The distribution of morphological forms of A. dirhodum varied considerably. The proportion of first-instars decreased in the last sample before the population disappeared in each of the four fields. The number of alatae observed appeared to be unrelated to the total number of aphids observed.

The reproductive rate of aphids under field conditions has not been reported previously. The average effective (living) young produced per M. avenae adult was estimated to be from 8.08 to 10.69, and the actual births per adult under field conditions was estimated to be 14.9. The estimated life span for adults in the field was 16.5 days, which is 75% of the time reported by Phillips (72) from insectary rearings. Fifty percent of the second-, third-, and fourth-instar nymphs were estimated to die under field conditions.

The three aphid species were found on different areas of the plant. In dividing the plant into four areas, M. avenae were found predominantly on the upper growing tips, A. dirhodum varied in location on the plant from lower to upper areas, and R. padi were found principally on the lower areas of the plant.

M. avenae was the only aphid of the three which moved to the plant heads late in the season. This aphid was found on winter plants by selecting the taller plants and searching the upper growing leaves. During the spring barley growing period, M. avenae were most abundant on the upper growing areas of the plant. The upper plant region supported a smaller proportion of aphids during 1963 than during 1962.

A. dirhodum was found about equally on the lower, middle, and upper areas of the plant, and the plant heads supported only 45 of the over 3,000 specimens observed. In the early planted barley fields, the lower plant area supported a majority of the specimens; although in the two late season planted fields, the middle, and upper plant parts supported the majority of specimens. This species seemed to be on the intermediate plant areas, those between the growing and the older senescent leaves where the plant sap pressure is reduced.

R. padi was found mostly on the lower plant parts at the time drying and yellowing of the leaves became apparent. This aphid species apparently survives where the plant sap pressure is low or absent. During 1963 a major part (62%) of the total R. padi population was subterranean on the plant shoot. The majority of the subterranean R. padi were found from 1 to 2 cm below the soil surface. R. padi was concentrated in areas of a field where the soil was compact during late June of 1964.

The number of grain aphids per infested plant was below five for most sample dates when less than 50% of the plants were infested. As the number of plants infested with M. avenae surpassed 100 (50%), the number of aphids per infested plant ranged from 4.52 to 15.81. The number of M. avenae per plant increased as the proportion of plants infested increased, and over 50% of the plants were infested on several counting dates, and 100% were infested on but one of forty counts.

The number of A. dirhodum per infested plant was lower than for M. avenae. The most plants found infested was 74 of 200.

The number of plants found infested with R. padi was lower than for A. dirhodum. During 1963 the number of aphids per infested plant was 6 to 8, this was higher than the number of aphids per plant during 1962 and was influenced by the observation of the subterranean habitat.

The presence or absence of two or three of the aphid species on the same plant was calculated for all species combinations, and no interactions were found.

By sampling two adjacent plants, and applying the chi-square test, it was shown that most barley plants were infested at random. For the majority of the samples, a random infestation of plants by M. avenae was indicated. The calculated number expected and the number of plant pairs found infested with A. dirhodum were similar, indicating that each plant was infested independently of the adjacent plant. R. padi was distributed at random in the 1962 early and mid-season planted fields, but in the late planted fields of 1962 and 1963 three of five samples produced significant chi-square values. These values resulted from more pairs of adjacent plants being infested than expected under random distribution conditions.

M. avenae was evenly distributed among four quadrants in the three 1962 barley fields, but was unevenly distributed during 1963 when over 100 aphids were observed per sample. They were evenly distributed within the quadrants in the early planted field, but were unevenly distributed within quadrants for several samples in the other three fields.

A. dirhodum was evenly distributed between quadrants in the early planted field except for one count during June. Specimens were unevenly distributed within the four quadrants, during three of five counts.

M. avenae was unequally distributed from one area of the plant to the next, and the number of specimens in each of the morphological forms was significantly different. The six morphological forms were non-randomly distributed on the four areas of the plant for several samples tested.

A. dirhodum was more uniformly distributed on the four plant areas than was M. avenae. Comparing the six stages of A. dirhodum on each of the four plant areas, the specimens were apparently uniformly distributed.

The number of aphids per acre of barley was estimated for M. avenae, and the expected variation of the estimates calculated. The number of aphids per acre of plants ranged from

30,895 to 16,266,718 when the mean number of aphids per plant was 0.03 to 15.75. The confidence limits indicated that when the mean number of aphids was less than one per plant, the estimated mean number of aphids per acre was smaller than the distance between the confidence limits. In these cases the number of plants sampled should have been increased to give a more reliable estimate of the aphid populations present.

The major predators observed in the field were of the families Coccinellidae and Syrphidae. Ciccinella trifasciata subversa LeConte and Hippodamia sinuata spuria LeConte were the most prevalent lady beetles found, and Scaeva pyrastri (L.) was the most common flower fly associated with aphids, primarily M. avenae. Several secondary parasites were identified from specimens of the two families of predators collected from barley fields. The dominant aphid parasite collected was Aphidius obscuripes Ashmead. From 100 parasitized aphid mummies collected, 54 live A. obscuripes emerged within six days. In addition, 33 hyperparasites emerged from the sample. Sticky traps caught Coccinellidae from late February to late October with major numbers caught from May to September, a peak number recovered in late July and early August. Catches of Chrysopidae followed a similar pattern. Trap directions were very similar in number of specimens of coccinellids and chrysopids caught.

An entomophagous fungus was observed to a very limited extent attacking *A. dirhodum* on orchardgrass early in the spring when the temperature rose above 50°F. The effect of this biotic factor on the aphid populations during 1962 and 1963 was very limited.

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