

DISPERSAL OF APHIDS
(HOMOPTERA: APHIDIDAE)
WITHIN AND BETWEEN CEREAL FIELDS

43

A Thesis
Submitted to the faculty
of
Graduate Studies
The University of Manitoba
by
Samuel Mishek Migui
In Partial Fulfilment of the
Requirements for the Degree
of
Master of Science
Department of Entomology

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Physical Oceanography	0415

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Nutrition	0570
Obstetrics and Gynecology	0380
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Ophthalmology	0381
Pathology	0571
Pharmacology	0419
Pharmacy	0572
Physical Therapy	0382
Public Health	0573
Radiology	0574
Recreation	0575

Speech Pathology	0460
Toxicology	0383
Home Economics	0386

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Physics	
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Atomic	0748
Electronics and Electricity	0607
Elementary Particles and High Energy	0798
Fluid and Plasma	0759
Molecular	0609
Nuclear	0610
Optics	0752
Radiation	0756
Solid State	0611
Statistics	0463
Applied Sciences	
Applied Mechanics	0346
Computer Science	0984

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General	0537
Aerospace	0538
Agricultural	0539
Automotive	0540
Biomedical	0541
Chemical	0542
Civil	0543
Electronics and Electrical	0544
Heat and Thermodynamics	0348
Hydraulic	0545
Industrial	0546
Marine	0547
Materials Science	0794
Mechanical	0548
Metallurgy	0743
Mining	0551
Nuclear	0552
Packaging	0549
Petroleum	0765
Sanitary and Municipal	0554
System Science	0790
Geotechnology	0428
Operations Research	0796
Plastics Technology	0795
Textile Technology	0994

PSYCHOLOGY

General	0621
Behavioral	0384
Clinical	0622
Developmental	0620
Experimental	0623
Industrial	0624
Personality	0625
Physiological	0989
Psychobiology	0349
Psychometrics	0632
Social	0451

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BY

SAMUEL MISHEK MIGUI

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba
in partial fulfillment of the requirements of the degree of

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permission.

Dedicated to
my wife Monicah
and our children

Mishek

Mary

and

Grace

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ABSTRACT

Populations of several species of aphids are usually present each year on grain fields in Manitoba. The species include, *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae*. Primary colonization of cereal fields and spread of infestations from one field to another are accomplished by flying aphids. Following initial colonization, aphid infestations are spread by movement of juveniles and adults between plants. The main focus of the present studies was to find out the relative dispersiveness of aphid species commonly found on cereal crops in Manitoba and assess the role of dispersal on the pest status of these species. A series of experiments on aphid biology, distribution and dispersal were carried out with a sequential shift from controlled laboratory conditions to field conditions.

Studies on aphid biology involved rearing aphids on leaf pieces of barley in petri-dishes in the laboratory and determining the time taken to reach various developmental stages, longevity, survivorship at each stage and daily and lifetime fecundity. The intrinsic rate of natural increase was also determined. Species differed in their developmental rates and reproductive strategies. Aphid distribution and dispersal was evaluated by rearing aphids on barley plants in pots, large flats, 1 X 1 m field cages

and in 20 X 20 m open field plots and recording their positions along the height of the plant and distances moved from the point of infestation after a predetermined time. The tendency to disperse by adults and juveniles was evaluated on leaf pieces of barley in petri-dishes. The potential for dispersal through flight by each species was investigated by crowding aphids in petri-dishes and on whole barley plants and noting the proportion of progeny developing into winged forms.

Regions of highest abundance for each species were, the central unopened leaf of immature plants for *R. maidis*, the lower leaf sheaths for *R. padi*, the underside of the proximal end of lower leaves for *Sc. graminum*, and the distal end of middle and upper leaves of immature plants and on the head of filling grain for *Si. avenae*. Non-winged adults of *R. padi* moved most frequently between plants leaving a batch of offspring per plant. Larvae exhibited movement behaviour after each molt. *R. padi* larvae had the highest dispersal with over 90% of individuals reaching adulthood in locations other than their natal site. All species responded to the crowding stimulus, with the proportion of wing production increasing as the crowding period was increased. *Si. avenae* was most sensitive to the crowding stimulus while *Sc. graminum* was least sensitive. Without crowding, *Si. avenae* produced winged and non-winged

forms in alternating generations.

Various fields of cereal crops in southern Manitoba were inspected throughout the growing season in 1994 to determine aphid species composition, abundance and their patterns of distribution. Aphid populations on different cereal crops fluctuated over the season, reaching peak population numbers in the middle of July. *Si. avenae* was the most abundant species and comprised 77.7% of the total aphids recorded.

FOREWARD

This thesis is organised in manuscript style. Chapter 1 gives a general introduction and outlines the purpose of this study. Chapter 2 provides a literature review of behavioural patterns of aphid dispersal in cereal fields. Chapter 3 explains the aphid rearing process. The manuscripts are contained in chapter 4 in five parts. In the first part, the role of aphid biology in the pest status of the four aphid species is evaluated by comparing their developmental rates, survival rates, fecundity schedules and intrinsic rate of natural increase. The second, third and fourth parts focus on the role of intraspecific behaviour of both adult and juvenile aphids in determining their vertical distribution within the host plant, short range dispersal between host plants and production of winged dispersers respectively. The fifth part reports on the occurrence and abundance of aphid pests on farmers grain fields in Manitoba in 1994.

TABLE OF CONTENTS

	PAGE
LIST OF TABLES	ix
LIST OF FIGURES	x
LIST OF APPENDICES	xviii
CHAPTER 1 GENERAL INTRODUCTION	1
CHAPTER 2 BEHAVIOURAL PATTERNS OF APHID DISPERSAL IN CEREAL FIELDS - A LITERATURE REVIEW	5
Introduction	5
Aphid development and population growth	5
Spatial and temporal variation in aphid populations	7
Microhabitat distribution	9
Aphid dispersal	10
Tiller to tiller dispersal	10
Production of winged dispersers	13
Dispersal by winged aphids	16
CHAPTER 3 INSECT REARING	20
CHAPTER 4 MANUSCRIPTS	22
PART I DEVELOPMENT AND POPULATION GROWTH OF APHIDS ON BARLEY	22
Abstract	22
Introduction	23
Materials and Methods	25
Results	28
Discussion	30

Conclusions	36
References	57
PART II DISTRIBUTION OF CEREAL APHIDS ON THEIR HOST PLANTS	59
Abstract	59
Introduction	60
Materials and Methods	62
Results	66
Discussion	69
Conclusions	76
References	104
PART III DISPERSAL OF JUVENILE AND NON-WINGED ADULT APHIDS ON CEREAL CROPS	107
Abstract	107
Introduction	107
Materials and Methods	109
Results	113
Discussion	116
Conclusions	123
References	141
PART IV WING PRODUCTION IN CEREAL APHIDS AND ITS SIGNIFICANCE TO DISPERSAL	143
Abstract	143
Introduction	144
Materials and Methods	146
Results	148
Discussion	150

Conclusions157
References169
PART V APHID PESTS OF CEREAL CROPS IN MANITOBA173
Abstract173
Introduction173
Materials and Methods175
Results176
Discussion177
Conclusions180
References194
CHAPTER 5 GENERAL DISCUSSION195
Summary and conclusions205
Future studies208
REFERENCES209

LIST OF TABLES

PAGE

CHAPTER 4

PART I

Table I-1. Mean developmental time (days) of cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^{\circ}$ C) 37

Table I-2. Mean (\pm s.e.) total fecundity and mean (\pm s.e.) fecundity in 12 days of adult life of cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^{\circ}$ C) 38

PART V

Table V-1. Aphid species found reproducing on cereal crops in Manitoba in 1994 181

LIST OF FIGURES

CHAPTER 4

Part I

	PAGE
<p>Fig. I-1. A controlled environment chamber with aphid cultures. Aphids were raised on leaf pieces of barley in petri-dishes containing nutrient solution solidified with 1% agar and maintained in the controlled environment chambers</p>	39
<p>Fig. I-2. Development of winged and non-winged forms by the progeny of cereal aphids which were isolated individually in rearing dishes at first instar and raised on leaf pieces of barley to adult stage. N = non-winged, W = winged</p>	41
<p>Fig. I-3. Mean (\pm s.e.) chronological age to adult stage, commencement of reproduction, termination of reproduction and death of cereal aphids raised on barley under constant conditions in the laboratory ($20 \pm 1^\circ$ C). Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. n = 38 for <i>R. maidis</i>, 50 for <i>R. padi</i>, 40 for <i>Sc. graminum</i>, 61 for <i>Si. avenae</i> N and 54 for <i>Si. avenae</i> W. N = non-winged, W = winged</p>	43
<p>Fig. I-4. Mean (\pm s.e.) developmental rate of cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^\circ$ C). Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. n = 38 for <i>R. maidis</i>, 50 for <i>R. padi</i>, 40 for <i>Sc. graminum</i>, 61 for <i>Si. avenae</i> N and 54 for <i>Si. avenae</i> W. N = non-winged, W = winged</p>	45

- Fig. I-5. Survivorship curves of non-winged cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^\circ \text{C}$). $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae*. l_x = proportion of original cohort surviving in each age class 47
- Fig. I-6. Mean fecundity schedules of cohorts of cereal aphids raised on barley at a constant temperature ($20 \pm 1^\circ \text{C}$). $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged 49
- Fig. I-7. The intrinsic rate of increase of cereal aphids raised on barley at a constant temperature ($20 \pm 1^\circ \text{C}$) calculated using Birch's (1948) method and Wyatt and White's (1977) method. Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged 51
- Fig. I-8. Cohort generation time of cereal aphids raised on barley at a constant temperature ($20 \pm 1^\circ \text{C}$) calculated using Birch's (1948) method and Wyatt and White's (1977) method. Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged 53
- Fig. 1-9. Relationship of intrinsic rate of increase (r_m) of aphids calculated using Birch's method and Wyatt & White's method. The 95% confidence interval lines are for an individual observation using the *Myzus persicae*

Part II

Fig. II-1. Caged seedlings of barley in 12 cm high, 15 cm diameter pots showing the nine plant arena; one plant at the centre and eight plants at the periphery used in studies of aphid distribution and dispersal 78

Fig. II-2. A barley plant at three leaf stage, from the nine plant arena showing plant parts and locations of highest abundance for each species. RM = *R. maidis*, RP = *R. padi*, SG = *Sc. graminum* and SA = *Si. avenae* 80

Fig. II-3. Barley seedlings in flats used in studies of aphid distribution and dispersal at the time of:
(a) infestation of the central plants; the transparent plastic cages were used to ensure settlement of infested aphid on that plant 82
(b) taking records, one week after infestation. This plant shows *R. maidis* aggregated on the release plant with the aphids on the stem being mainly third and fourth instars 82

Fig. II-4. Barley plants in 1 X 1 m field cages at:
(a) tillering stage when the central plants in each cage were infested with 4 non-winged aphids (one species per cage) 84
(b) earing stage when records of aphid distribution were taken 84

Fig. II-5. A barley plant at flowering stage, from the 1 X 1 m field cages showing plant parts and locations of highest abundance for each species 86

Fig. II-6. The position of flats for field augmentation of aphids and sampling stations in 20 X 20 m open plots 88

- Fig. II-7. Mean (\pm s.e.) number of cereal aphids per location on potted barley plants. Bars from the same species with the same letter are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 71 for *R. maidis*, 108 for *R. padi*, 63 for *Sc. graminum* and 87 for *Si. avenae* 90
- Fig. II-8. Mean (\pm s.e.) number of cereal aphids per location on barley plants in flats. Bars from the same species with the same letter are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 82 for *R. maidis*, 149 for *R. padi*, 68 for *Sc. graminum* and 81 for *Si. avenae* 92
- Fig. II-9. Mean (\pm s.e.) number of cereal aphids per location on barley plants in 1 X 1 m cage plots. Bars from the same species with the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 40 for *R. maidis*, 56 for *R. padi*, 56 for *Sc. graminum* and 40 for *Si. avenae* 94
- Fig. II-10. Mean (\pm s.e.) number of cereal aphids per location on barley plants in 20 X 20 m open plots. Bars with the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 19 for *R. maidis*, 108 for *R. padi*, 52 for *Sc. graminum* and 483 for *Si. avenae* 96
- Fig. II-11. A flag leaf of barley with a colony of *R. maidis* among which

most of the large larvae had wing buds and were destined to fly out of the open habitat 98

Fig. II-12. Mean (\pm s.e.) number of offspring from winged and non-winged mothers of *Si. avenae* per location on potted barley plants. Bars from the same maternal morph with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. Number of infested plants per maternal morph is 87 for *Si. avenae* N, and 84 for *Si. avenae* W. N = non-winged, W = winged 100

Fig. II-13. Mean (\pm s.e.) number of cereal aphids per tiller of barley in 20 X 20 m open plots in July 1994. n = 40 plants per sampling date 102

Part III

Fig. III-1. Experimental design for study of adult movements between leaf pieces of barley in petri-dishes; L = left leaf, M = middle leaf, R = right leaf 125

Fig. III-2. Experimental design for study of dispersal of larvae from their natal location on leaf pieces of barley in petri-dishes 127

Fig. III-3. Dispersal behaviour of adult aphids on leaf pieces of barley in petri-dishes
 (a) Mean number of adult movements in 12 days
 (b) Mean time spent by adults to produce each group
 (c) Mean number of larvae produced in one natal location.
 Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. Number of replicates contributing to each

	mean (n) = 33 petri-dishes per species129
Fig. III-4.	Cummulative percent dispersal of aphid larvae from their natal location. n = 33 larval groups per species131
Fig. III-5.	Mean (\pm s.e.) percent infestation of barley plants, seven days after the release of one aphid on: (a) potted plants (9 plant arena). n = 16 pots/species (b) plants in flats (170 plant arena). n = 10 flats/species. Bars with the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P > 0.05$133
Fig. III-6.	Mean proportion of cereal aphids at various distances from initial point of aphid release on barley plants in flats after seven days. n = 10 flats/species135
Fig. III-7.	Mean proportion of cereal aphids at different times and at various distances from initial point of aphid release on barley plants in 20 X 20 m open field plots. n = 4 transects/sampling date137
Fig. III-8.	Distances moved by <i>R. maidis</i> and <i>Sc. graminum</i> at different times from the point of augmentation in 20 X 20 m open field plots. n = 4 transects/sampling date139

Part IV

Fig. IV-1.	Design for the experiment testing the effect of artificially crowding adult aphids on production of winged forms159
Fig. IV-2.	Single barley plants in plastic cages in which different groups of adult aphids of a species were crowded for	

	24 hours to determine their response in production of winged progeny161
Fig. IV-3.	Mean (\pm s.e.) proportion of winged progeny produced by <i>R. maidis</i> , <i>R.</i> <i>padi</i> and <i>Sc. graminum</i> after groups of 10 non-winged adults of each species were separately crowded in petri-dishes for different time periods. Each test of 10 was replicated three times per crowding time163
Fig. IV-4.	Mean (\pm s.e.) proportion of winged progeny produced by <i>Si. avenae</i> after groups of 10 non-winged and 10 winged adults were separately crowded in petri-dishes for different time periods. Each test of 10 was replicated three times per crowding time165
Fig. IV-5.	Mean (\pm s.e.) proportion of winged progeny produced by cereal aphids after different groups of adults were crowded on single barley plants for 24 hours in plastic cages. n = 11 plants per crowded group per species167

Part V

Fig. V-1.	Numbers and the percent occurrence of each aphid species on cereal crops in Manitoba in 1994182
Fig. V-2.	Mean (\pm s.e.) number of <i>Si. avenae</i> per location on wheat, barley and oats in southern Manitoba in 1994. Number of plants contributing to each mean is 275 for wheat, 148 for barley and 113 for oats184
Fig. V-3.	Mean (\pm s.e.) number of <i>R. padi</i> per location on wheat, barley, oats and corn in southern Manitoba in 1994. Number of plants contributing to each mean is 84 for wheat, 56 for barley, 72 for oats and 15 for corn186

Fig. V-4.	Mean (\pm s.e.) number of <i>R. maidis</i> per location on barley and corn in southern Manitoba in 1994. Number of plants contributing to each mean is 42 for barley and 35 for corn188
Fig. V-5.	Mean (\pm s.e.) number of <i>Sc. graminum</i> per location on wheat and barley in southern Manitoba in 1994. Number of plants contributing to each mean is 18 for wheat and 13 for barley190
Fig. V-6.	Mean number of cereal aphids per tiller of wheat, barley and oats in southern Manitoba during summer, in 1994192

APPENDIX 3

Fig. 1.	Mean (\pm s.e.) proportion of winged progeny produced by <i>R. padi</i> clones after groups of 10 non-winged adults of each clone were separately crowded in petri-dishes for different time periods. Each test of 10 was replicated three times per crowding time236
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LIST OF APPENDICES

Appendix 1.	Cohort life tables of cereal aphids	220
Appendix 2.	Cohort fecundity schedules of cereal aphids	227
Appendix 3.	Effect of crowding on wing production by seven clones of <i>R. padi</i>	234

CHAPTER 1

GENERAL INTRODUCTION

The occurrence of aphids is common wherever cereal crops are grown. Often several species infest each field, their abundance and economic importance varying from one geographic location to another. The worldwide importance of cereal aphids as pests has been reviewed by Carter *et al.* (1980) and Dixon (1987a). In North America, the most important species reported to attack wheat and barley include corn leaf aphid, *Rhopalosiphum maidis* (Fitch); bird-cherry oat aphid, *R. padi* L.; greenbug, *Schizaphis graminum* (Rondani) (hereafter referred to as *Sc. graminum*); English grain aphid, *Sitobion avenae* (Fabricius) (hereafter referred to as *Si. avenae*); Russian wheat aphid, *Diuraphis noxia* (Mordvilko) and rose grain aphid *Metopolophium dirhodum* (Walker) (Robinson & Hsu, 1963; Ba-Angood & Stewart, 1980; Elliot & Kieckhefer, 1987; Schotzko & Smith, 1991). All these species, except *D. noxia*, have been reported to attack cereal crops in Manitoba (Robinson & Hsu, 1963). There is no evidence that cereal aphids can overwinter in the Canadian prairies or the northern plains of U.S.A. where winters are long and cold (Robinson & Hsu, 1963; Irwin & Thresh, 1988). Since large displacements of aphids have been recorded in North America (Bruehl, 1961; Johnson, 1969), the northern areas, such as Manitoba, are thought to be re-invaded annually by migrants from the south. Some of

the migrants are likely to be viruliferous (Irwin & Thresh, 1988).

Aphid feeding causes substantial yield loss by removal of plant nutrients (George, 1974; Kolbe & Linke, 1974), injection of toxic saliva that causes necrosis of plant tissue (Robinson & Hsu, 1963; Starks & Burton, 1977b), and reduction of photosynthetic area by contamination of plant surfaces with honeydew and associated sooty moulds (Wratten, 1975; Rabbinge *et al.*, 1981).

In 1948 and 1962 cereal aphids were present in Manitoba in unusually large numbers and crops had to be sprayed with insecticides to prevent further damage, while in 1955 thousands of acres of late seeded barley were destroyed by *R. maidis* in western Canada (Robinson & Hsu 1963). In 1916, *Sc. graminum* destroyed 2.1 million hectares of wheat and oats in Oklahoma (Kelly, 1917). In 1986, in Alberta and Saskatchewan, a heavy infestation of the greenbug covering one million hectares of wheat resulted in serious yield losses (Haber, 1990). Wratten, (1975) reported that in Europe, direct yield losses, caused by aphids during severe infestations in wheat and barley exceeded 30 percent and the main species implicated were *Si. avenae* and *M. dirhodum*. Grain aphids also affect the bread-making quality of wheat by reducing the amount of nitrogen in the grain (Wratten & Redhead, 1976).

Besides direct damage to crops, cereal aphids transmit viruses, especially barley yellow dwarf virus (BYDV) (Gildow, 1984). BYDV is the most widespread virus disease of cereals (Conti, 1990). In the middle of the 1980's, *Sitona avenae* was recognised as an important vector of BYDV in England (McGrath & Bale 1990). In western Canada, crop losses attributable to BYDV affect late sown spring barley and oats whereas in eastern Canada, BYDV infects all spring cereal crops (Haber, 1990).

Purpose of this study

The relative importance of aphid species that are pests of cereal crops in Manitoba is not clear. Their impact on cereal crops may be dependent upon, among other factors, their dispersal from distant locations into grain fields in the Canadian prairies, their ability to spread quickly within and between fields, their population dynamics and their specific feeding locations on their grain hosts. The importance as pests of the four commonly reported aphid pests in Manitoba was compared in laboratory and field experiments designed to address the following objectives:

- (1) To compare growth rates and reproductive potential of the four aphid species
- (2) To examine the pattern of distribution of each species on their host plants
- (3) To determine the role of adult and juvenile behaviour in

the dispersal of each species within grain fields

- (4) To investigate the role of aphid interactions in the initiation of alata production
- (5) To carry out a survey of aphid pests in Manitoba

The relevance of laboratory data obtained at controlled conditions to the situation in the field warrants attention. In pursuit of this, a series of experiments under objectives 2, 3 and 4 were carried out with a sequential shift from controlled laboratory conditions to field conditions. Barley was used as the host plant in all experiments to maintain consistency and comparability of results.

CHAPTER 2
BEHAVIOURAL PATTERNS OF APHID DISPERSAL
IN CEREAL FIELDS - A LITERATURE REVIEW

INTRODUCTION

Initial colonization of cereal fields is accomplished by flying aphids. After settlement on the crops, adults start reproducing. Two behavioural patterns are considered to contribute to the spread of aphid infestations within fields. These are local flights by winged aphids with deposition of small batches of offspring and tiller-tiller dispersal of non-winged adults and juveniles (Cannon, 1985).

To determine the impact of individual aphid species on grain production, it is necessary to understand their biology, dispersal capacity of both adults and juveniles, distribution patterns within host plants and within fields and their abundance each year. The following review provides background information on what is known about some of these characteristics.

APHID DEVELOPMENT AND POPULATION GROWTH

Cereal aphids reproduce parthenogenetically throughout the summer and pass through several generations on grass hosts. Larvae go through four instars before molting into adults. Temperature affects the rate of development with each species having a different relationship with

temperature (Dean, 1974a; Cannon, 1984). Studies by Vickerman & Wratten (1979) on some aspects of aphid biology using three aphid species subjected to variable temperatures indicated that *R. padi* has the fastest development, highest fecundity, and lowest longevity and that there is little difference between *Si. avenae* and *M. dirhodum* .

Other studies on the biology of cereal aphids have demonstrated that, in many species, the non-winged forms (apterae), are often larger, reach maturity faster and are consistently more fecund than the winged forms (alatae) (Vickerman & Wratten, 1979; Dixon, 1987a). Reproductive rates of aphids are strongly correlated with adult size, with large aphids being more fecund than small ones (Taylor, 1975; Dixon & Wratten, 1971; Wratten, 1977).

The rate of increase of an aphid population depends on the speed of development, survival and fecundity. Wyatt and White, (1977) reported that in many aphid species reproduction rises rapidly in the early stages of adult life and 95 percent of the contribution to the intrinsic rate of natural increase is usually achieved within the first few days of adult life, equivalent the period from birth to onset of reproduction. They reported that the rate of reproduction then falls gradually over a variable time dependent on characteristics of a species. Thus, they argued that the earliest progeny have the greatest influence

on population growth and therefore, overall fecundity may not be a useful measure of population dynamics. The small amount of information available on field survival of post-reproductive aphids (Dixon, 1987b) suggests that senile aphids, commonly observed under laboratory conditions are rarely found in the field.

The type and growth stage of host plant markedly affects the rate of increase of aphid populations (Leather & Dixon, 1981). Host quality varies seasonally and among species and cultivars of cereals. *Si. avenae*'s reproductive rate is almost three times higher, when it feeds on ears at the milk stage than when it feeds on leaves (Watt, 1979). In contrast *M. dirhodum* reproduces poorly on the ears and best on leaves (Cannon, 1986).

SPATIAL AND TEMPORAL VARIATION IN APHID POPULATIONS

Cereal aphids are present in Manitoba from approximately June until killed by frost (Robinson & Hsu, 1963). Initial colonization of spring cereal fields by flying aphids occurs in a random pattern but when the adults start reproducing, aggregations arise. Aggregation is a common feature in aphid populations but aphid species differ in cluster size and compactness (Cannon, 1985; Ekblom *et al.*, 1985). As the population density increases further, aphids disperse over the entire field and the distribution may tend towards Poisson (Southwood, 1978).

In Europe, Watt (1979) reported that before all the ears had emerged, 42 percent of the tillers in a local wheat field were infested with *Si. avenae* even though the average population density was low (two aphids/tiller). Watt (1979) measured the reproduction and survival of *Si. avenae* in clip cages in field wheat and observed that as the plants matured, reproduction decreased, both larval and adult mortality increased and there was a steady increase in the production of alatae three weeks before the aphid population declined. Thus, effects of aphid crowding and host quality are important in shaping the dynamics of *Si. avenae* on cereals.

Sites of aphid colonization may differ with species. In a survey of aphid pests on cereal crops in Wisconsin, Medler & Smith (1960) reported that greenbugs were more abundant in wind protected places, on lighter soils, along field margins where plants were widely spaced and of unthrifty growth and where fields had been planted late. In Europe, Dean (1973) found that *M. dirhodum* emigrants were widespread over the field, whereas *S. avenae* invaded areas sheltered by hedges and woodland. Consequently, aphid spread to the entire crop occurred after 2-5 weeks for *M. dirhodum* and 4-7 weeks for *S. avenae* (Dean, 1974b). However, in Germany, there was no consistent pattern in the distribution of *S. avenae* in different fields (Vickerman &

Wratten, 1979).

Aphid distribution patterns vary from one location to another and from one season to another. Knowledge of spatial dispersion patterns of aphids is used to develop sampling plans for monitoring populations and criteria for making management decisions. Several methods have been used to describe aphid population patterns and trends in the field (Southwood, 1978). Models and indices commonly used include; Taylor's power law (Taylor *et al.*, 1978), Lloyd's mean crowding index, (m^*) (Lloyd, 1967), dispersion parameter k for the negative binomial distribution (Southwood, 1978) and Iwao's regression index (Iwao, 1968). The model that best fits data collected in the field is used to make future prediction of aphid populations and assist in making decisions on aphid control.

MICROHABITAT DISTRIBUTION

There are distinct differences among the species in their feeding site preferences on the host plant. These are important in relation to the type and amount of damage caused by the aphids. On wheat, *Si. avenae* prefers the upper leaves and the ears, once these have emerged (Dean, 1974b; Wratten, 1975). On the ear, the aphid feeds mainly at the glume bases and on the rachis between the spikelets (Vickerman & Wratten, 1979). *M. dirhodum* is almost entirely a leaf feeder on all cereal species. As the lower leaves

senesce and the population increases, a substantial proportion feed on the upper leaves, including the flag leaf (Dean, 1974b). Dean (1974b) found that *R. padi* prefers to feed on the lower leaves of winter wheat especially near leaf bases and inside leaf sheaths. However, on oats, a large proportion of *R. padi* are found on the inflorescence (Vickerman & Wratten, 1979). Starks & Burton (1977a) found that more greenbugs *Sc. graminum* tend to be located on the lower half of the plant. *R. maidis*, a serious pest of corn, sorghum, barley and to a lesser extent, wheat (Liquido & Irwin, 1986), prefers feeding within the central whorls of growing plants.

APHID DISPERSAL

Tiller to tiller dispersal

Most species of aphids, at all stages of development, move about over the surface of their host plants and even between adjacent plants. These local movements result in slow diffusive dispersal. Movement of apterous adults between plants in the field is a common phenomenon in some aphid species (Hogson, 1991) and probably plays an important role in local spread of viruses within crops. Greenbugs, which prefer wheat to rye, move more frequently on rye than on wheat (Starks & Burton, 1977a). Over an 18-day period Starks & Burton (1977a) reported that the mean distance

travelled by apterae on susceptible plants was 19.2 cm. Dean (1973) found that infestations of wheat and barley fields by *R. padi*, *Si. avenae* and *M. dirhodum* are spread from the few invasion foci of the emigrant winged aphids by movement of older larvae and non-winged adults across leaf bridges between plants. Similarly, Holmes (1988) found that once populations of *Si. avenae* were established in the field, the infestation spread within the crop through movement of up to 2 m by apterous individuals.

BYDV transmission studies by McGrath & Bale (1990) also revealed that *Si. avenae* regularly moves from plant to plant. Dean (1974b) observed that alate *M. dirhodum* stay in one spot on a tiller for less time (1.8 days) than apterae (2.3 days), while both morphs of *S. avenae* are equally active (1.9 days). Cannon (1985) reported that the main dispersal stage for apterous *M. dirhodum* is the fourth instar. He found that because of this tendency to disperse, few colonies persist longer than a week.

Ribbands (1964) found that apterae of *Myzus persicae* (Sulzer) frequently move from plant to plant and are responsible for spread of yellows virus in sugarbeets. Hogson (1991) compared dispersal in three species of aphids, *M. persicae*, *Brevicoryne brassicae* L. and *Megoura viciae* Buckton on their respective host plants and reported that the main emigrants are fourth instars and pre-larviposition

adult apterae.

The studies of Johnson (1957) and MacKay & Downer (1979) emphasized the occurrence of a restless dispersive phase of teneral adults in several species of aphids. Two behavioral patterns are considered to contribute to the spread of aphid infestations within fields. These are alate (Winged aphids) flitting with deposition of small batches of offspring and tiller-tiller dispersal of apterae and nymphs (Cannon, 1985).

Major factors that initiate apterous dispersal include climatic effects, parasitoids, predators, food quality and intra and interspecific population interactions. Apterous may be dislodged from their hosts by strong winds and rain or may abandon an aging, overpopulated plant. Zuniga (1985) reported that under conditions of natural rainfall 45.6 percent of *R. padi*, *Si. avenae*, *M. dirhodum* and *Sc. graminum* leave their original host.

Aphid dispersal may also be influenced by predators such as Coccinellids, Syrphids and Chrysopids. When an aphid encounters a natural enemy, the aphid produces alarm pheromone that cause other aphids either to drop to the ground or to walk off the plant (Dixon, 1973). Apterous pea aphids, *Acyrtosiphon pisum* (Harris) and *M. dirhodum*, readily drop from plants when disturbed by natural enemies (Roitberg et al., 1979; Dewar & Dean, 1982). *M. dirhodum*

has a high sensitivity to the alarm pheromone E- β -farnesene (Dawson *et al.*, 1982), which is probably released in high amounts when high densities of aphids are disturbed. Holmes (1988) found that coccinellids cause *Si. avenae* to jump from the ear of wheat. However, *Si. avenae* is less sensitive than *M. dirhodum* when exposed to alarm pheromone (Dewar & Dean, 1982). Holmes (1988) reported that aphids dislodged from their feeding sites by climatic factors climb back on plants and infest new ears. Aphids mechanically dislodged from their hosts by wind and rain, exhibit phototaxis, and become oriented to the nearest vertical object (Phelan *et al.*, 1976). This behaviour increases their chance of locating hosts.

Production of winged dispersers

Aphids are minute insects and cannot walk for long distances. Field to field dispersal is performed by winged morphs. Factors implicated in development of winged forms include: crowding, host plant quality, temperature, photoperiod, and intrinsic factors (Kawada, 1987). The proportion of alatiform fourth instar larvae in the field has been used to estimate the production of alate emigrants (Lamb & MacKay, 1979; Watt & Dixon, 1981) as alatae are likely to leave the crop shortly after molting to the adult stage (Rabbinge *et al.*, 1979). Watt & Dixon (1981) and Cannon (1985) found that the proportion of alatiform larvae

of *Si. avenae* in the field was significantly correlated with aphid density. Lees (1967) confirmed that tactile stimulation occurring among crowded aphids led to production of alatae. He found that the fourth larval instar and adult of *M. viciae* has the highest alate production in response to crowding and that there is no response in first instars.

The period when the aphids are sensitive to a crowding stimulus, or group effect differs between species. Wing production may be dependent on prenatal and/or post natal crowding. Some species appear to "monitor" crowding continuously. A period of isolation following a period of crowding partly reverses the effects of crowding and intermediates develop (Dixon, 1973). In *R. padi* and *Si. avenae* (Dixon and Glen, 1971; Watt and Dixon, 1981), both mothers and offspring respond to crowding. The more intense the crowding, the higher the proportion of alatae that develop, especially if both mothers and offspring experience crowding (Dixon, 1985).

Noda (1959) reported that the most sensitive period to tactile stimulation in *R. padi* is in the middle of its larval period. He observed that production of alate forms by alate mothers of *R. padi* and *R. maidis* was less common than in *Si. avenae*. Alate offspring of *Si. avenae* that have not flown can be induced by crowding to give birth to a high proportion of alatae (Watt & Dixon, 1981). In *Si.*

avenae, the morph of the parent is important in determining the proportion of alatae produced, with apterous parents producing more alate offspring than alate parents (Watt & Dixon, 1981). Tests on production of alatae in the pine aphid, *Cinara pinea* (Mordv.) reveal that maternal experience of crowding does not have any effect on the nymphal response (Kidd & Tozzer, 1984). In the pea aphid, Roitberg *et al.* (1979) reported that the production of alatae in response to declining resource quality has a lag time of up to one generation.

The condition of the host plant also influences alata production in aphids. On a dying or wilting plant or if food deteriorates, aphids become more "restless", and are more likely to touch one another. *A. pisum*, when placed on mature bean leaves, develops winged forms (Sutherland, 1969), indicating that poor food in itself may also induce alate production. In *S. avenae*, winged forms develop in response to changes in the nutritional quality associated with the ripening of the seed (Dixon, 1985). Watt & Dixon (1981) found that when mothers reared on the ears of grasses at flowering are crowded in glass vials for short periods, they give birth to proportionally fewer winged offspring than mothers similarly treated but reared on mature ears. Branson & Simpson (1966) found that the percentage of alate *R. maidis* on nitrogen deficient sorghum plants is twice that

on plants that were not deficient.

Many morphs of species in several subfamilies show interclonal reproductive diversity. Some individuals have few ovarioles while others have many and this phenomenon may reflect the "urge" to disperse (Walters & Dixon, 1983). Even within the same species different clones or colour forms may vary in their response to alata producing stimuli. Investigations by Lowe (1980) and Watt & Dixon (1981) reveal that a green clone of *Si. avenae* readily gives birth to alatae but a brown clone treated in the same way gives birth to very few alatae. Colour forms in other aphids are associated with differences in production of alatae, different reproductive strategies and differences in survival and reproduction at different temperatures (Sutherland, 1969).

Dispersal by winged aphids

Aphid flight is complex and involves behavioral responses such as readiness to fly, to maintain flight and to land in response to suitable visual and olfactory stimuli (Robert, 1987). In black bean aphids, *Aphis fabae* (Scopoli), Shaw (1973) reported that there is great variation in readiness to fly in alate forms and this is correlated with the degree of crowding experienced. Walters & Dixon (1982) found an inverse relationship between the degree of crowding experienced by alatiform nymphs and the

time of take off, with the crowded alatae leaving sooner than the isolated ones. Flight activity is related to crop phenology (Kieckhefer *et al.*, 1974, Kieckhefer & Lytle, 1976). Walters and Dixon (1982) observed that alate adults of *Si. avenae* do not reproduce before migration when crowded, or on poor quality hosts, but do when isolated or on good quality hosts. This flight strategy enables *Si. avenae* to colonise a sequence of ephemeral high quality habitats and to take advantage of any changes in host quality. Physical factors also affect take off. Aphids are more likely to take flight at high light intensities and high temperatures, and low wind speeds (Dixon, 1985).

Aphids are weak fliers and cannot progress against a headwind of about 2 km/h or greater (Johnson, 1954; Heathcote, 1970). Nonetheless, aphids have been observed to fly for several hours in tethered flight (Liquido & Irwin, 1986), fly at high altitudes (Berry & Taylor, 1968) and can be carried for long distances by wind (Rose *et al.*, 1975; Wallin & Loonan, 1971). The fact that live aphids have been caught at 300-1200 m is indicative that long-distance migrants can arrive at their destination in sound condition and are able to reproduce (Taylor, 1960) and establish new colonies. Several modes of atmospheric transport of aphids have been suggested, and these include; stratiform drift, boundary layer movements, dispersive transport by convection

currents and low level jet-streams (Loxdale *et al.* 1993). Low level jet streams are persistent, horizontal air streams at altitudes between 300 and 1000 m. In the central U.S.A. and Manitoba, low level jet-streams are considered to be responsible for long distance movement of aphids (Rose *et al.*, 1975).

Aphid dispersal is a one way move and there is no return journey for any individual. Moreover, there is no evidence of a return movement of a later generation, suggesting that areas such as Canada and the northern U.S.A. are a "sink" for aphids and may have no impact on the genetic makeup of the population. Evidence for local movement of aphids has been derived from direct observations, sampling using sticky traps and suction traps, and by sampling using markers such as enzyme electrophoresis, virus transmission, radioactive labels and insecticide resistant strains (Loxdale *et al.*, 1993). The distribution of insecticide resistant strains of *M. persicae* suggests that short range movement is more common than long distance migration. (Loxdale *et al.*, 1993). Smith (1987) used photoperiodic response of pea aphids, *Acyrtosiphon pisum* to map out their migration from more southerly populations into southern Manitoba.

Winged aphids seek out and colonise plants. If the migrant aphid lands on an unfavourable host plant it quickly

takes off again (Wiktelius, 1982), but if the plant is favourable it settles and reproduces (Kennedy & Booth, 1963). The readiness to probe and settle increases with the flight duration (Loxdale *et al.*, 1993). Cockbain *et al.* (1963) found that *A. fabae* if flown to exhaustion will settle permanently on a poor host.

Wiktelius (1982) investigated the settling behaviour of *R. padi* and reported that the aphid usually landed on the upper half of a leaf, moved towards the base of the plant and finally settled and larviposited on the leaf sheath. Brown (1972) reported that winged forms of *Sc. graminum* settle on wheat when provided with wheat, rye and oats. When provided with young and mature wheat plants the aphids do not show any preference, but are more likely to depart from mature plants. However, landing in aphids is indiscriminate and host selection depends on the differential rate of take-off (Robert, 1987).

Alate aphids do not remain flight active throughout adult life. Shortly after settling their flight muscles undergo autolysis (Johnson, 1953), which reduces their chance of dispersal and much of their energy is possibly dedicated to reproduction. This phenomenon enables aphids to seek out host plants effectively, colonize them and ensure aphid survival.

CHAPTER 3

INSECT REARING

Throughout the experimental work a continuous supply of aphids and barley seedlings was required. Barley cv. 'Argyle' was planted each week on flats measuring 52 cm long, 26 cm wide and 6 cm deep. The soil medium used was Metro-mix® which is composed of vermiculite, water, bark and related material, spagnum peat moss, quartz, gypsum perlite and calcium carbonate. The plants were watered using nutrient solution which contained the following compounds (weight/1000 l of solution): the macronutrients, 202.22 g KNO_3 , 272.18 g KH_2PO_4 , 708.48 g $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, 493.00 g $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 36.71 g FeEDTA, and the micronutrients, 5.00 g H_3BO_3 , 3.00 g $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$, 0.20 g ZnCl_2 , 0.10 g $\text{CuCl}_2 \cdot 2\text{H}_2\text{O}$ and 0.10 g MoO_3 . In addition to room lighting in the laboratory, the plants were provided with fluorescent lighting to give a photoperiod of 16 h light and 8 h dark. Temperature in the laboratory varied between 18-22° C. Approximately 10 days after planting, the first leaves were fully opened and ready for use in aphid stock cultures and experiments. Other subsequent leaves were not used and the plants were discarded after the first leaves were used up.

One clone of each of aphid species *R. padi* (RP06), *Sc. graminum* (SG01) and *Si. avenae* (SA01), was established from cultures maintained for several years in the laboratory of

Dr. P.A. MacKay, Department of Entomology, University of Manitoba. A clone of *R. maidis* (RM01) collected from a barley field in southern Manitoba in 1994 was also cultured. Aphids were maintained on two, 4 cm pieces of barley leaf placed in 60 X 15 mm plastic petri-dishes containing nutrient solution solidified with 1% agar (rearing dishes). This medium kept the leaf pieces fresh and green for 3-5 days.

The stock cultures were raised in controlled environment chambers maintained at constant temperature ($20 \pm 1^{\circ}$ C) and photoperiod (20 hours light, 4 hours dark). This photoperiod was chosen to ensure that aphids remained parthenogenetic and were not exposed to conditions that might trigger development of sexual forms. Each aphid species was reared in separate dishes and placed on separate racks to avoid the risk of cross contamination. The clones were perpetuated as uncrowded colonies by regular transfer of aphids onto fresh barley leaves in fresh rearing dishes. Rearing densities were five to eight for first and second instars; in the third instar, aphids were individually raised in fresh rearing dishes where they developed to the adult stage. From the stock cultures, a reliable supply of standard aphids of uniform age, maternal age, morph and size was obtained each week.

CHAPTER 4 MANUSCRIPTS

PART I

DEVELOPMENT AND POPULATION GROWTH OF APHIDS ON BARLEY

ABSTRACT

A study of the biology of four aphid species, *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae*, which are usually present each year in cereal crop fields in Manitoba, was conducted in the laboratory. First instar aphids of each species were reared until death on leaf pieces of barley. The time taken to reach various developmental stages, their fecundity and longevity were noted. Results indicated that the species differed in their developmental rates and reproductive strategies. Larvae from non-winged mothers of *R. maidis*, *R. padi* and *Sc. graminum* developed into non-winged adults, but with *Si. avenae*, the progeny of non-winged mothers and winged mothers predominantly developed into winged and non-winged forms respectively. In the laboratory, aphid survivorship was high with mortality being concentrated at the end of the maximum lifespan, giving a type I response curve. *R. padi* had the highest rate of development, highest fecundity at 12 days of adult life, and highest intrinsic rate of increase, while the winged morph of *Si. avenae* had the lowest values for these parameters. Aphid reproduction in the first 12 days of adult life appeared to be the most

important in determining the contribution of an individual to the population dynamics of cereal aphids.

INTRODUCTION

Aphids can cause substantial losses by the direct effects of their feeding or as vectors of several plant viruses (George, 1974; Kolbe & Linke, 1974; Haber, 1990). Populations of several species of aphids are usually present each year in fields of wheat and barley in Manitoba. These species include, the corn leaf aphid *Rhopalosiphum maidis* Fitch, bird-cherry oat aphid *R. padi* L., greenbug *Schizaphis graminum* Rondani (hereafter referred to as *Sc. graminum*) and English grain aphid *Sitobion avenae* Fabricius (hereafter referred to as *Si. avenae*) (Robinson & Hsu, 1963). The relative importance of these species as pests of cereal crops in Manitoba is not clear.

To determine the relative performance of the aphid species on cereal crops, it is essential to obtain detailed information on their biology and reproductive capacity. The intrinsic rate of increase (Birch, 1948) is a simple statistic that tells how fast a population multiplies and is often used to compare the population growth rate of organisms subjected to different sets of conditions. It is derived from the survival rates and reproductive performance of a cohort of females.

$$\sum e^{-r_m x} l_x m_x = 1$$

$$T_c = \frac{\text{Log}_e \sum l_x m_x}{r_m}$$

Where r_m = intrinsic rate of increase

x = age

l_x = proportion of original cohort surviving to the beginning of age class x

m_x = number of larvae produced per surviving individual in each stage

T_c = cohort generation time

The Birch method requires compilation of detailed life tables and lengthy computations. Working on three species of aphids, *Brevicoryne brassicae* L., *Myzus persicae* (Sulz.), and *Hyadaphis pseudobrassicae* Davis at seven temperatures, DeLoach (1974) reported that the time required to contribute 95% to the r_m was shorter when development was more rapid. Examination of his graphs by Wyatt and White (1977) revealed that the reproductive time required to contribute 95% to the r_m corresponded closely in value to the pre-reproductive period. They further reported that the young produced in

the first few days of reproduction contribute most to the value of r_m , the proportional contribution falling rapidly for later progeny. Using this information, they formulated a simplified equation for calculation of r_m and cohort generation time.

$$r_m = 0.738 (\log_e M_d) / d$$

$$T_c = 4d/3$$

where r_m = intrinsic rate of increase

d = pre-reproductive time i.e. the period from birth to first reproduction

M_d = number of progeny produced in an equal time to d

T_c = cohort generation time

In this study both methods were used to determine the rate of increase of four cereal aphid species, *R. maidis*, *R. padi*, *Sc. graminum* and *Si. avenae*, and their results were compared to evaluate the validity and generality of Wyatt & White's method.

MATERIALS AND METHODS

Non-winged aphids from one clone of each of the four species were reared on two, 4 cm pieces of barley leaf on

agar in 60 X 15 mm petri-dishes (rearing dishes) (see Chapter 3 for details). Both winged and non-winged forms of *Si. avenae* were included in experiments, because it became evident from the performance in stock culture that this species produced a mixture of winged and non-winged offspring in each generation. Winged adults of *Si. avenae* produced mostly non-winged progeny, and non-winged adults produced mostly winged progeny. Low proportions of the progeny of *R. maidis* also developed into winged forms. To obtain an adequate number of experimental aphids, recently molted adults from stock cultures were placed individually on fresh foliage overnight. The following day, first instar aphids were collected and individually placed in fresh rearing dishes, which were placed in controlled environment chambers (Fig. I-1) maintained at $20 \pm 1^{\circ}$ C and a photoperiod of 20 h light, 4 h dark. In order to obtain sufficient replicates per treatment, a large number of first instar aphids were isolated in petri-dishes. The initial numbers of first instars obtained from non-winged adults of *R. maidis*, *R. padi*, *Sc. graminum* and *Si. avenae* were 40, 50, 40 and 60 respectively and 60 from winged adults of *Si. avenae*. Larvae of all species except *Si. avenae* that developed into winged morphs were discarded. All the progeny of *Si. avenae* were saved for use in experiments irrespective of the morph of parent. Individuals in each

cohort that survived to the adult stage were used in studies on reproductive performance. The eventual numbers of adult aphids used were 38 for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for non-winged *Si. avenae* and 54 for winged *Si. avenae*. Observations were made daily. Change from one developmental stage to another was monitored by noting when aphids shed their exuviae. After commencement of reproduction, the progeny were counted and carefully removed each day. Adults were regularly transferred to fresh rearing dishes to avoid fungal growth and deterioration of foliage. Data collection continued until all adults died naturally. Records taken included, time taken to reach each developmental stage, survivorship at each stage, longevity and daily and lifetime fecundity.

Developmental rate for each aphid species was calculated using the formula:

$$\textit{Developmental rate} = 1 / D$$

where D = time in days from birth to adult moult.

The intrinsic rate of natural increase was computed for each cohort of aphids using the formulae by Birch (1948) and Wyatt & White (1977). Results were subjected to analysis of variance and where significant results were obtained ($P < 0.05$), Tukey's test was used to separate the means.

RESULTS

Larvae from non-winged mothers of *R. maidis*, *R. padi* and *Sc. graminum* developed into non-winged adults but with *Si. avenae*, the progeny of non-winged mothers and winged mothers predominantly developed into winged and non-winged forms respectively (Fig. I-2). The time taken by aphids to reach various developmental stages during their life cycle is given in Table I-1 and Fig. I-3. Developmental period from birth to adult stage was shortest (7 days) for *R. maidis* and *R. padi*, longest (9.5 days) for winged *Si. avenae* and intermediate (8.4 days) for *Sc. graminum* and non-winged *Si. avenae*. Developmental rate was highest for *R. padi* and *R. maidis* followed by *Sc. graminum* and non-winged *Si. avenae* and least for winged *Si. avenae* (Fig. I-4). However, there was no significant difference ($P>0.5$) between *R. padi* and *R. maidis* and between *Sc. graminum* and non-winged *Si. avenae*. *R. padi* took the shortest time to commencement of reproduction, termination of reproduction and death, while winged *Si. avenae* took the longest time to reach each developmental stage.

All species experienced high survivorship in the prevailing laboratory conditions, with mortality being concentrated at the end of the maximum lifespan. This gave a type 1 response curve for all species (Fig. I-5) (Begon *et al.*, 1990). Aphid species that lived longest were *Sc.*

graminum and *Si. avenae* (about 52 days).

There was no significant difference in mean total lifetime fecundity (about 80 offspring per individual) between non-winged mothers of all species (Table I-2). However, winged *Si. avenae* produced significantly ($P < 0.5$) fewer total number of offspring than the other treatments. The mean cumulative fecundity at 12 days of adult life was significantly different among all treatments, which, ranked in order of the highest number of offspring to the lowest, are, *R. padi*, *R. maidis*, *Sc. graminum*, non-winged *Si. avenae* and winged *Si. avenae* (Table I-2). Comparison of fecundity at 12 days of adult life was chosen because at this age, one of the species (*R. padi*) had produced 99% of its total fecundity (Table I-2) and for all species, the earliest born progeny would have been reproductive. Fig. I-6 shows the mean fecundity schedules of the aphids. The reproductive performance of similarly aged aphids was highest for *R. padi* and lowest for winged *Si. avenae*. In the early stages of adult life, fecundity schedules of *Sc. graminum* and *Si. avenae* were similar, but differed by the age of 12 days after birth.

Life tables (Appendix 1) and fecundity schedules (Appendix 2) were constructed for use in calculation of intrinsic rate of increase. Fig. I-7 shows the estimates of intrinsic rate of increase, calculated using the iterative

method of Birch (1948) and the Wyatt & White (1977) formula. All species were significantly different from one another ($P < 0.05$). *R. padi* had the shortest cohort generation time, while winged *Si. avenae* had the longest (Fig. I-8). Values for r_m and T_c computed using both methods produced similar relationships among species with Wyatt & White's estimates being consistently lower than Birch's estimates. A comparison between r_m values calculated using Birch's method and Wyatt & White's method show that the linear regression line for *Myzus persicae* data obtained under various combinations of environmental conditions (Wyatt & White, 1977) has a 45° slope and passes through the origin (Fig. I-9). All the r_m values obtained in the present study are within or touch the 95% confidence limits for an individual observation, constructed using the *Myzus persicae* data.

DISCUSSION

The pest status of many aphid species is partly due to their remarkable rate of increase. During the growing season, grain aphids reproduce parthenogenetically and can quickly reach damaging population sizes when conditions are favourable. Growth and reproduction are separate processes that together determine the size of aphid populations. Species that have a high rate of development and a high rate of reproduction are likely to be important pests in regions where they occur.

The four species that are commonly reported to occur in Manitoba, were found to differ in their developmental rates and reproductive strategies. Non-winged mothers of *R. maidis*, *R. padi* and *Sc. graminum* produced offspring that developed into non-winged adults. Non-winged aphids have often been observed to be larger, to reach maturity faster and to be consistently more fecund than winged forms in many species (Vickerman & Wratten, 1979; Dixon, 1987a). Furthermore, reproductive rates of aphids are reported to be strongly correlated with adult size, with large aphids being more fecund than small ones (Taylor, 1975; Dixon & Wratten, 1971; Wratten, 1977). On one hand, aphid species that consistently produce non-winged progeny would, under favourable conditions, rapidly increase in numbers, and depending on their dispersal ability, may cause heavy local damage. On the other hand, aphid species capable of producing both winged and non-winged progeny are capable of spreading to adjacent and distant crops. *Si. avenae* innately produced winged and non-winged progeny in alternating generations. The winged forms are better able to locate suitable distant habitats than non-winged aphids. In summer, this strategy by *Si. avenae* enables it to seek out and colonize flowering grasses, its preferred feeding stage (Walters & Dixon, 1982).

Aphid survivorship was high in the laboratory with a

type 1 response curve (Fig. I-5) (Begon *et al.*, 1990), possibly because they were provided with nearly ideal conditions. The majority of aphids died due to old age, long after they had stopped reproduction. In the laboratory, it was observed that two weeks after commencement of reproduction, the mothers showed signs of aging such as sluggishness, they were easily dislodged from their feeding positions and their colour changed to become very dark. This phenomenon is not likely to be observed in the field, as aphid survival would be affected by frequent changes in weather, climate, host conditions and natural enemies. The little information available on field survival of aphids into post-reproductive life (Dixon, 1987b) suggests that senile aphids commonly observed under laboratory conditions are rarely found in the field. Weak aphids that become dislodged from their host plants are not likely to relocate their feeding sites. Aphids of all ages, particularly young larvae, would be expected to suffer high mortality due to desiccation in dry weather and drowning in very wet weather. Nonetheless, aphid survival through harsh environments is made possible by their ability to exist in several polymorphic forms. Both larvae and adults exhibit polymorphism, and as many as five or more distinct adult female phenotypes are known (Miyazaki, 1987). In the middle of summer when temperatures are high and humidities are low

and unfavourable for soft bodied insects, such as aphids, some species produce "summer dwarfs" (Hille Ris Lambers, 1966) which are tolerant to the hot dry conditions. Among cereal aphids, aestivating forms are reported in *Sc. graminum* and *Si. avenae* (Daniels, 1960; Miyazaki, 1987). In the middle of summer, in Manitoba, *R. padi* was found beneath the lower leaf sheaths of barley (Part II).

Plant density appears to influence the rate of population increase in some grain aphids. Dixon (1987) reported that *M. dirhodum* and *R. padi* did better on dense stands and *Si. avenae* in sparse stands. He suggested that temperature is lower in dense stands and was probably suitable for *M. dirhodum* while in sparse stands, the higher temperature was suitable for *Si. avenae*. Under low temperatures development of crops is slowed down more than aphid population growth (Dixon, 1987). Therefore, in a cool season the crop will remain at an optimal stage and available to aphids for a longer time than in hot seasons. This implies that high peak aphid numbers are more likely in cooler than in hot years.

The short developmental periods, high fecundity in the first 12 days of adult life and high intrinsic rate of increase by *R. padi* and *R. maidis* clearly suggests that these species, under favourable field conditions, can rapidly increase in numbers and cause serious plant damage

through their feeding. *Sc. graminum* and apterous *Si. avenae* had similar developmental periods but *Sc. graminum* produced significantly ($P < 0.05$) more offspring in the first 12 days of adult life than *Si. avenae*. The first 12 days of adult life appear to be the most important in determining individual contribution to the population dynamics of each aphid species.

In addition to plant damage caused by removal of plant nutrients through feeding, *Sc. graminum* causes necrosis of plant tissue by injection of toxic saliva (Robinson & Hsu, 1963; Starks & Burton, 1977). Among the four species, *Sc. graminum* possibly causes the heaviest local damage. Therefore, assessment of aphid impact on cereal crops based on aphid numbers alone may not give a clear view of the actual situation.

The similarity of relationships among species of the values of r_m and T_c obtained using the methods of both Birch (1948) and Wyatt & White (1977) suggests that either method is useful in comparing species. The T_c values were obtained from independent sources in each method. Computation of T_c using Birch's method is dependent on the reproductive performance of individual aphids while T_c obtained from Wyatt & White's method is dependent on the prereproductive period, or time from birth to the onset of reproduction. Since Wyatt & White's method is simple and does not involve

many measurements, it appears to be a useful method for comparing aphid species and obviates the need for lengthy measurements. However, Wyatt & White's method always underestimates both r_m and T_c and its use may have serious implications for management decisions and ecological conclusions. An underestimation of r_m may lead to a decision not to control, where in fact, control was required while an underestimation of T_c may lead to a control decision where control was not required. Wyatt & White's method appears good for general comparisons but may not always be useful in determination of specific insect management programs. Birch's method may be preferable for making insect control decisions. The estimates of r_m for *Myzus persicae* under various combinations of environmental conditions by Wyatt & White (1977) appear to match Birch's estimates better than the estimates in this study. All points from this study lie above the linear regression line, which suggests that there may be some consistent deviation from the line predicted from *M. persicae*. This is possibly because unlike the *M. persicae* study, the present study involved different aphid species examined under one set of condition and species differed in prereproductive period. One assumption made by Wyatt & White (1977) in formulating the simplified r_m equation is that aphid patterns of reproduction are similar. However, the fact that all

estimates in this study lie within the 95% confidence limits for an individual observation suggests that the Wyatt & White method may be useful in comparing the performance of many species at one set of conditions.

CONCLUSIONS

Among the four aphid species that are commonly reported to occur on cereal crops in Manitoba, *R. padi* has the highest potential for population growth and development. *R. maidis* ranks close behind *R. padi* and is likely to reach damaging populations in favourable weather and host conditions. In addition to the reproductive potential of *Sc. graminum*, its damage to plants through feeding and necrosis of plant tissue accounts for its pest status. The production of winged and non-winged progeny in alternate generations by *Si. avenae* give an indication of the dispersive potential of this species, and probably relates to its importance as a pest of cereal crops. Overall, the first two weeks of adult life are the most important in determining individual contribution to population dynamics of cereal aphids.

Table I-1. Mean developmental time (days) of cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^\circ \text{C}$).

Aphid species or morph	Sample size	First molt	Second molt	Third molt	Fourth molt
<i>R. maidis</i>	38	2.1a	4.0a	5.3a	7.1a
<i>R. padi</i>	50	2.4b	3.8a	5.3a	7.0a
<i>Sc. graminum</i>	40	2.9c	4.4b	6.3bc	8.4b
<i>Si. avenae</i> N	61	2.8c	4.4b	6.1b	8.4b
<i>Si. avenae</i> W	54	2.6c	4.3b	6.4c	9.5c

Form of *Sitobion avenae*: N = Non-winged, W = Winged

Means in the same column followed by the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P > 0.05$.

Table I-2. Mean (\pm s.e.) total fecundity and mean (\pm s.e.) fecundity in 12 days of adult life of cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^\circ$ C).

Aphid species or morph	Sample size	Total fecundity	Fecundity 12 days	% of total fecundity in 12 days
<i>R. maidis</i>	38	79.7 (0.8)a	75.9 (0.6)a	95
<i>R. padi</i>	50	82.3 (1.0)a	81.8 (0.9)b	99
<i>Sc. graminum</i>	40	81.7 (1.0)a	69.6 (0.9)c	85
<i>Si. avenae</i> N	61	79.3 (1.0)a	49.8 (0.7)d	63
<i>Si. avenae</i> W	54	67.2 (0.8)b	33.9 (0.5)e	50

Form of *Sitobion avenae*: N = Non-winged, W = Winged

Numbers in parentheses are standard errors of the mean.

Means in the same column followed by the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P > 0.05$.

Fig. I-1. A controlled environment chamber with aphid cultures. Aphids were raised on leaf pieces of barley in petri-dishes containing nutrient solution solidified with 1% agar and maintained in the controlled environment chambers.



Fig. I-2. Development of winged and non-winged forms by the progeny of cereal aphids which were isolated individually in rearing dishes at first instar and raised on leaf pieces of barley to adult stage.
N = non-winged, W = winged

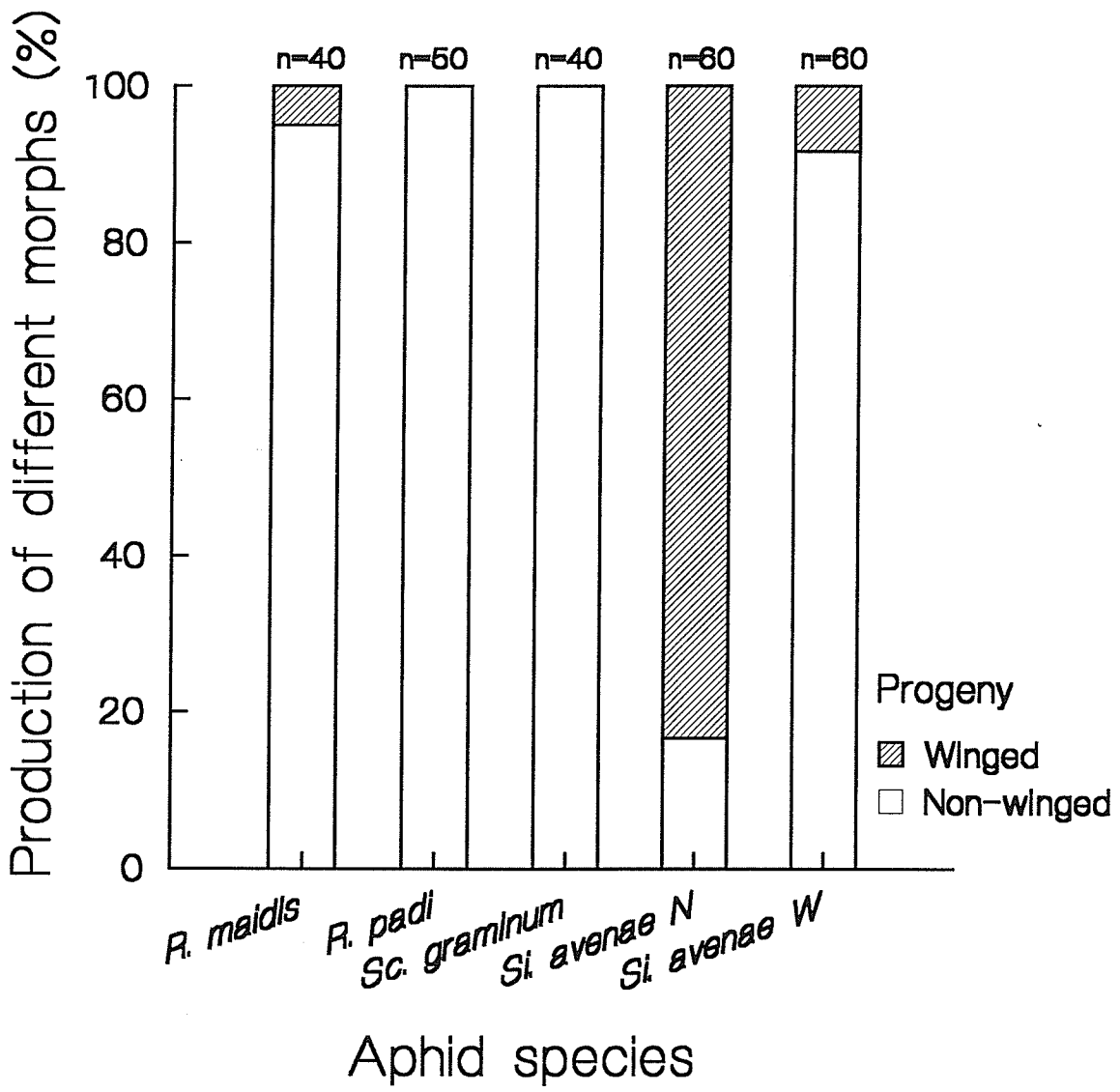


Fig. I-3. Mean (\pm s.e.) chronological age to adult stage, commencement of reproduction, termination of reproduction and death of cereal aphids raised on barley under constant conditions in the laboratory ($20 \pm 1^{\circ}$ C). Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged

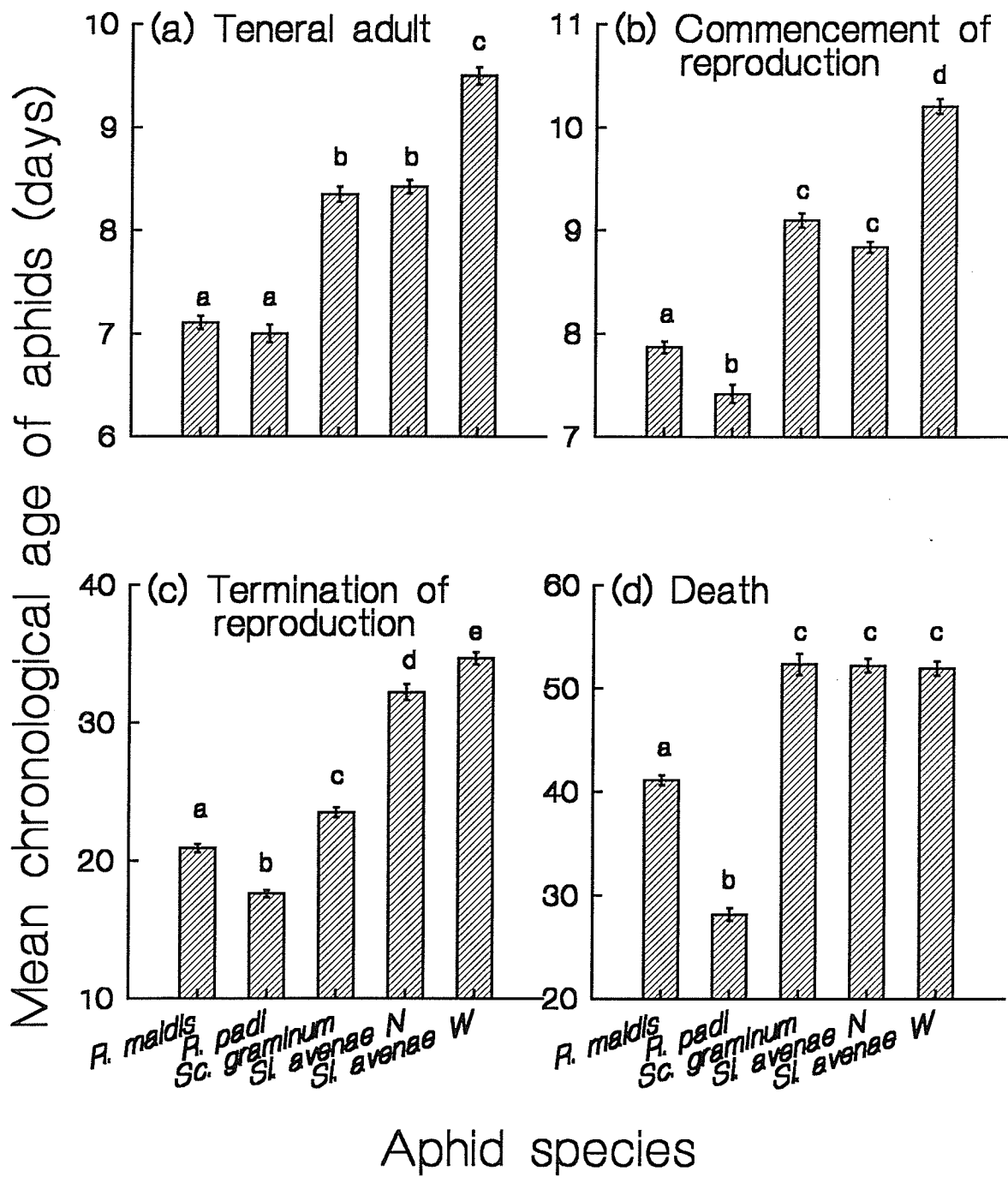


Fig. I-4. Mean (\pm s.e.) developmental rate of cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^\circ$ C). Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged

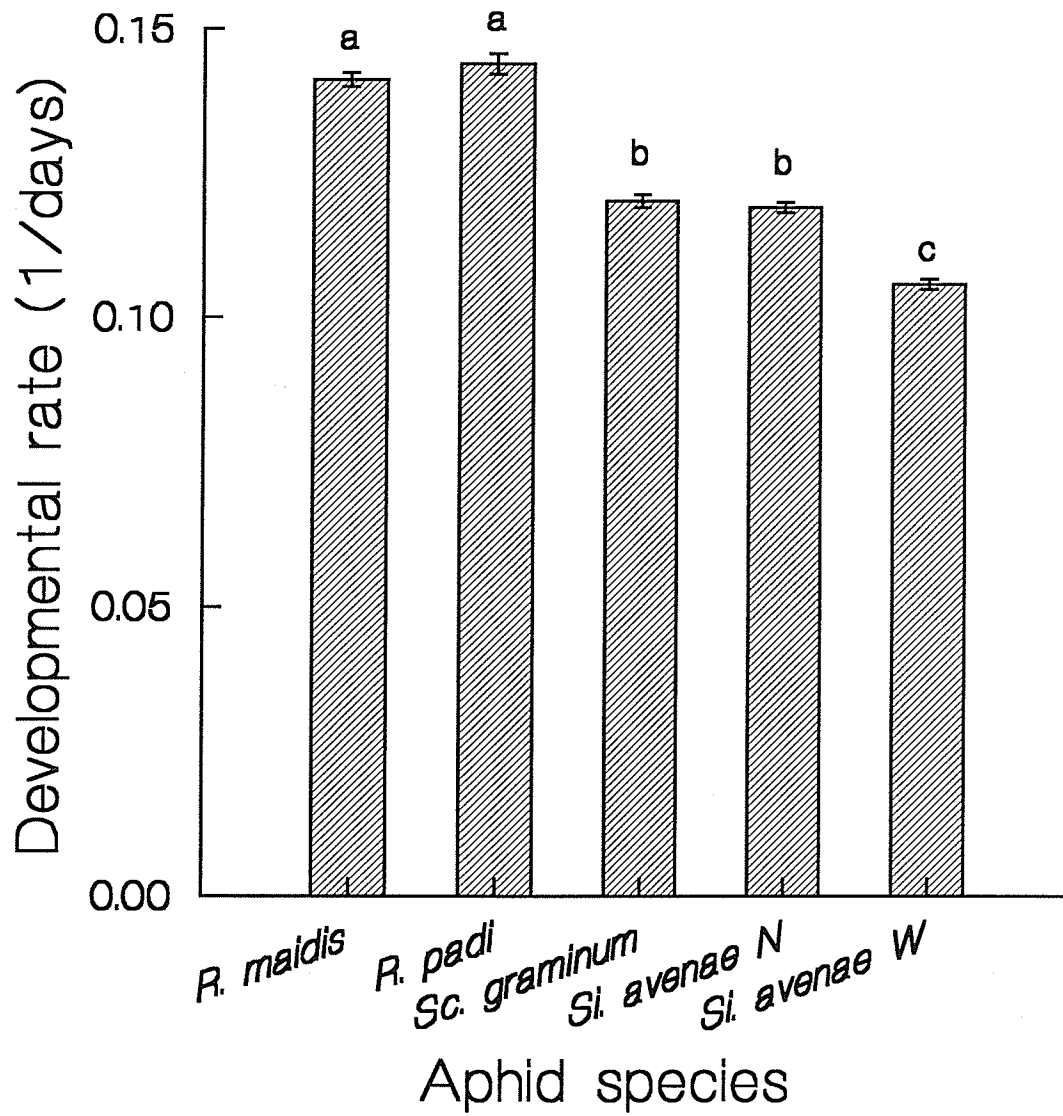


Fig. I-5. Survivorship curves of non-winged cereal aphids raised on barley in the laboratory at a constant temperature ($20 \pm 1^{\circ}$ C). $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae*. l_x = proportion of original cohort surviving in each age class.

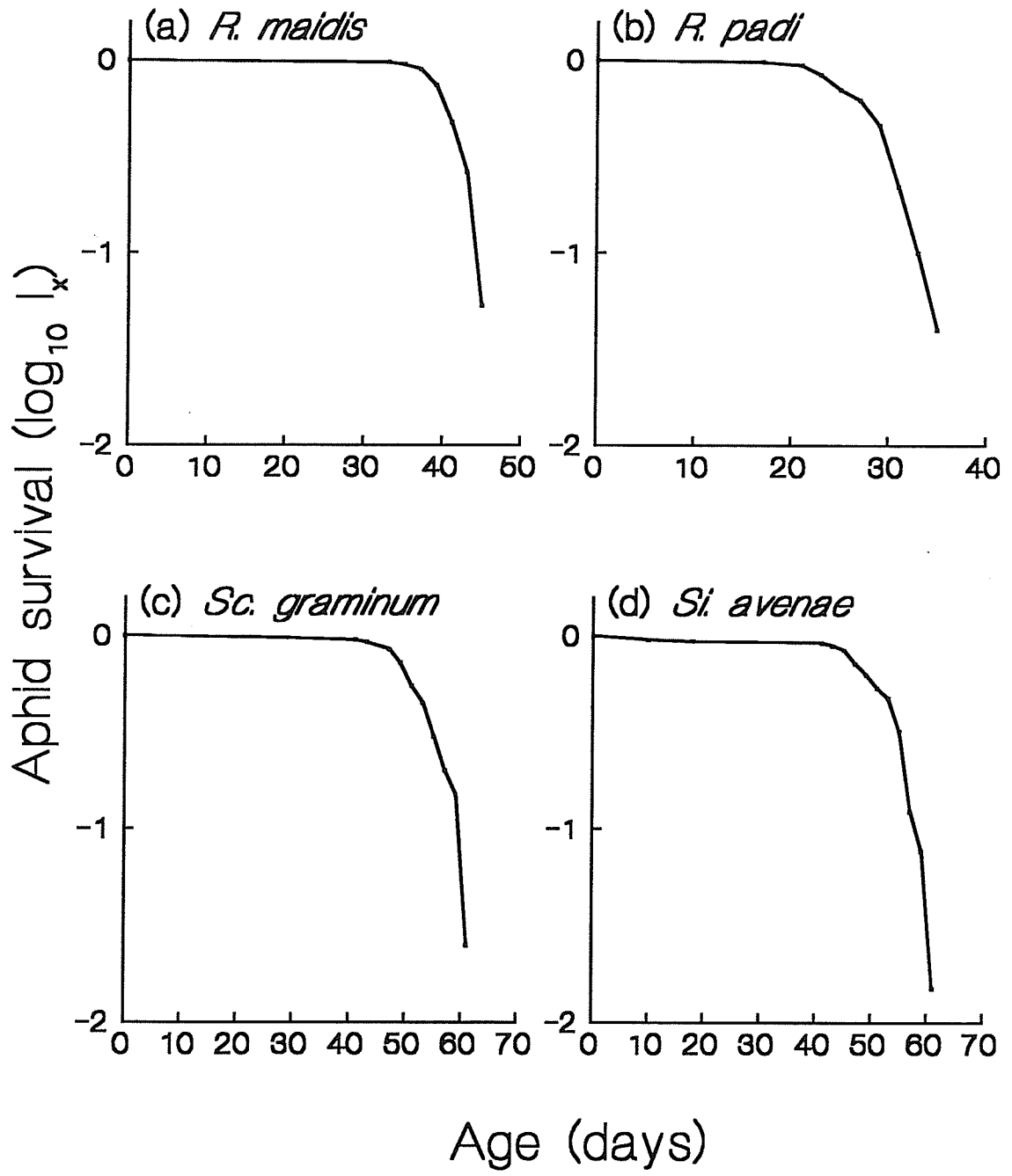


Fig. I-6. Mean fecundity schedules of cohorts of cereal aphids raised on barley at a constant temperature ($20 \pm 1^\circ \text{C}$). $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged

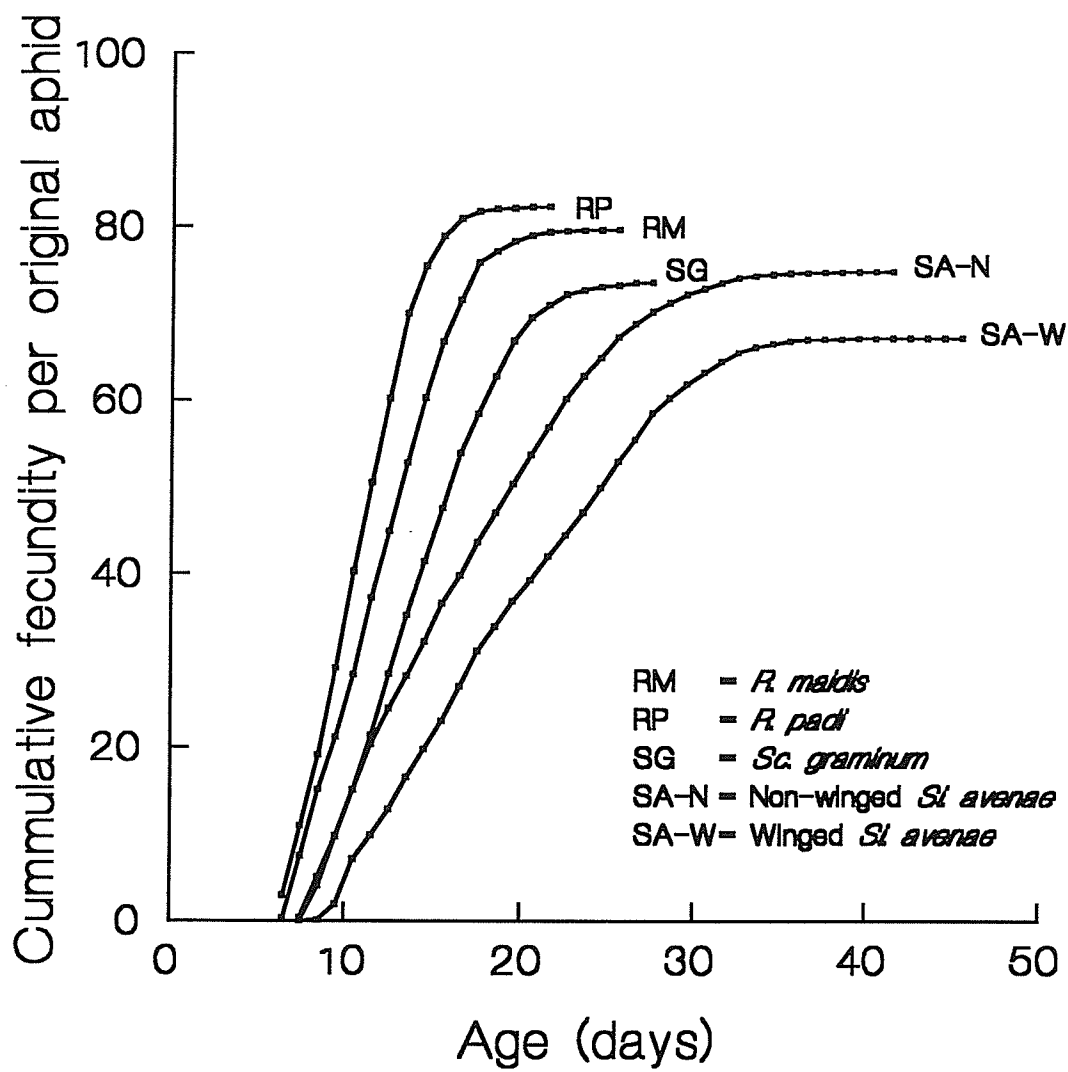


Fig. I-7. The intrinsic rate of increase of cereal aphids raised on barley at a constant temperature ($20 \pm 1^\circ \text{C}$) calculated using Birch's (1948) method and Wyatt and White's (1977) method. Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged

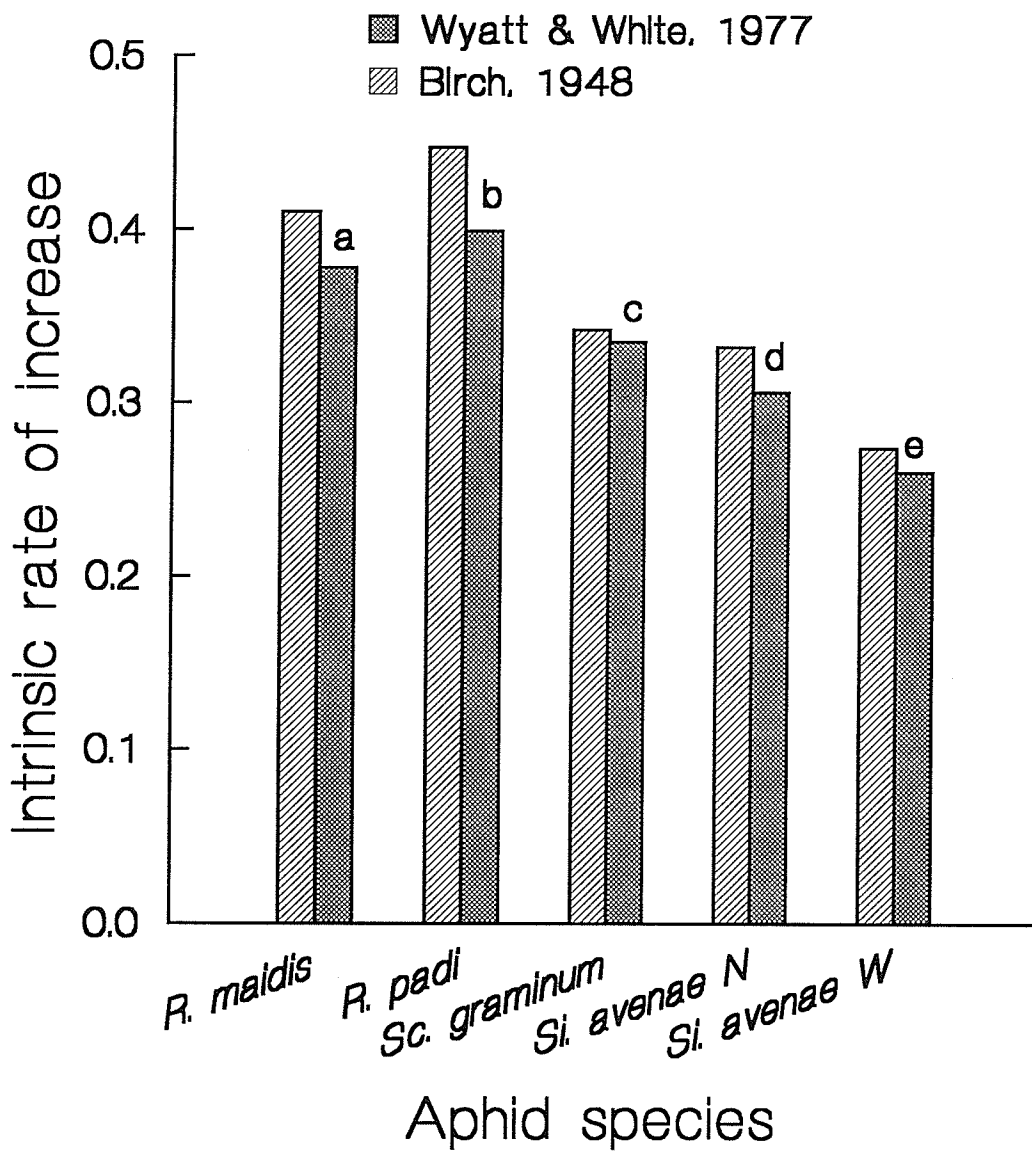


Fig. I-8. Cohort generation time of cereal aphids raised on barley at a constant temperature ($20 \pm 1^\circ \text{C}$) calculated using Birch's (1948) method and Wyatt and White's (1977) method. Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. $n = 38$ for *R. maidis*, 50 for *R. padi*, 40 for *Sc. graminum*, 61 for *Si. avenae* N and 54 for *Si. avenae* W. N = non-winged, W = winged

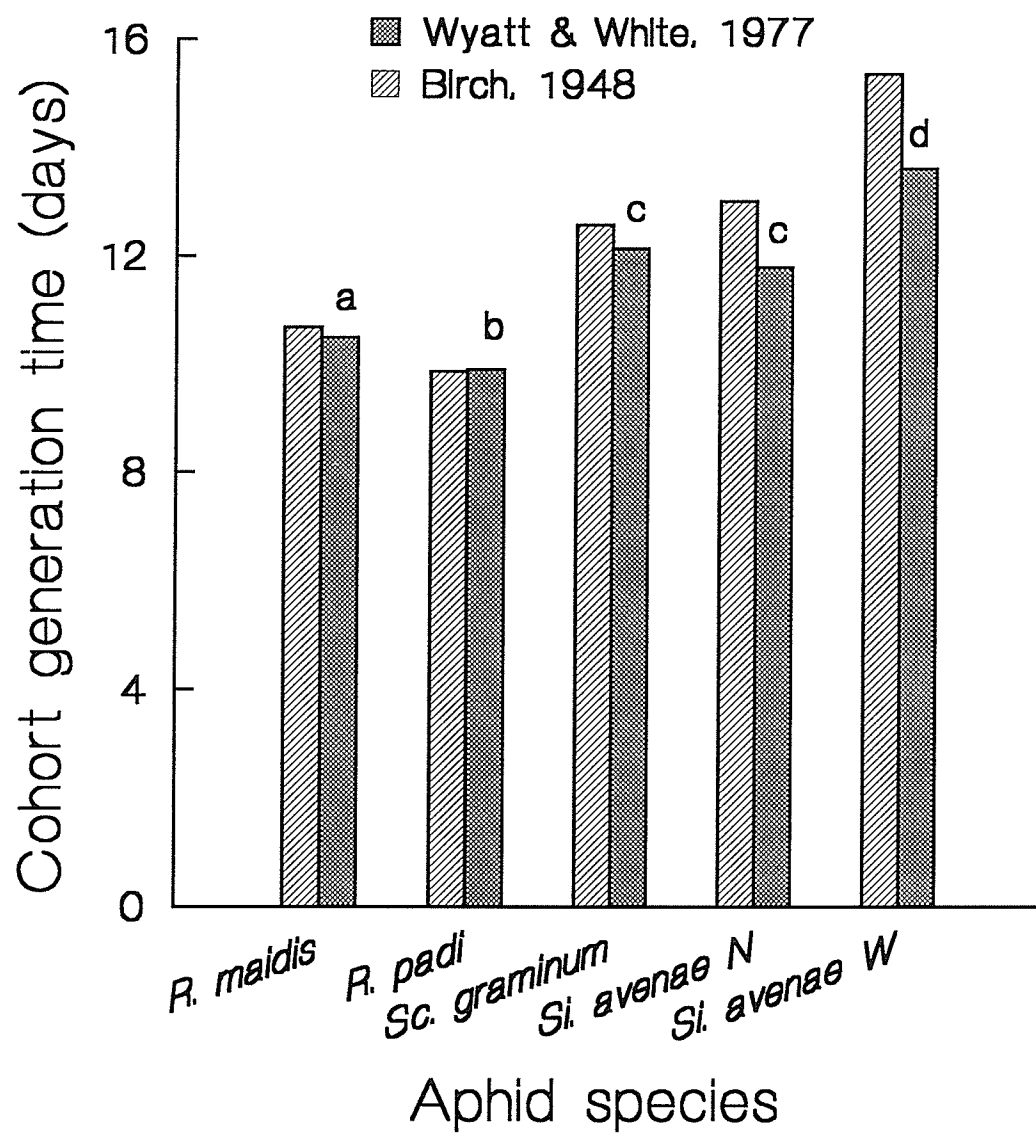
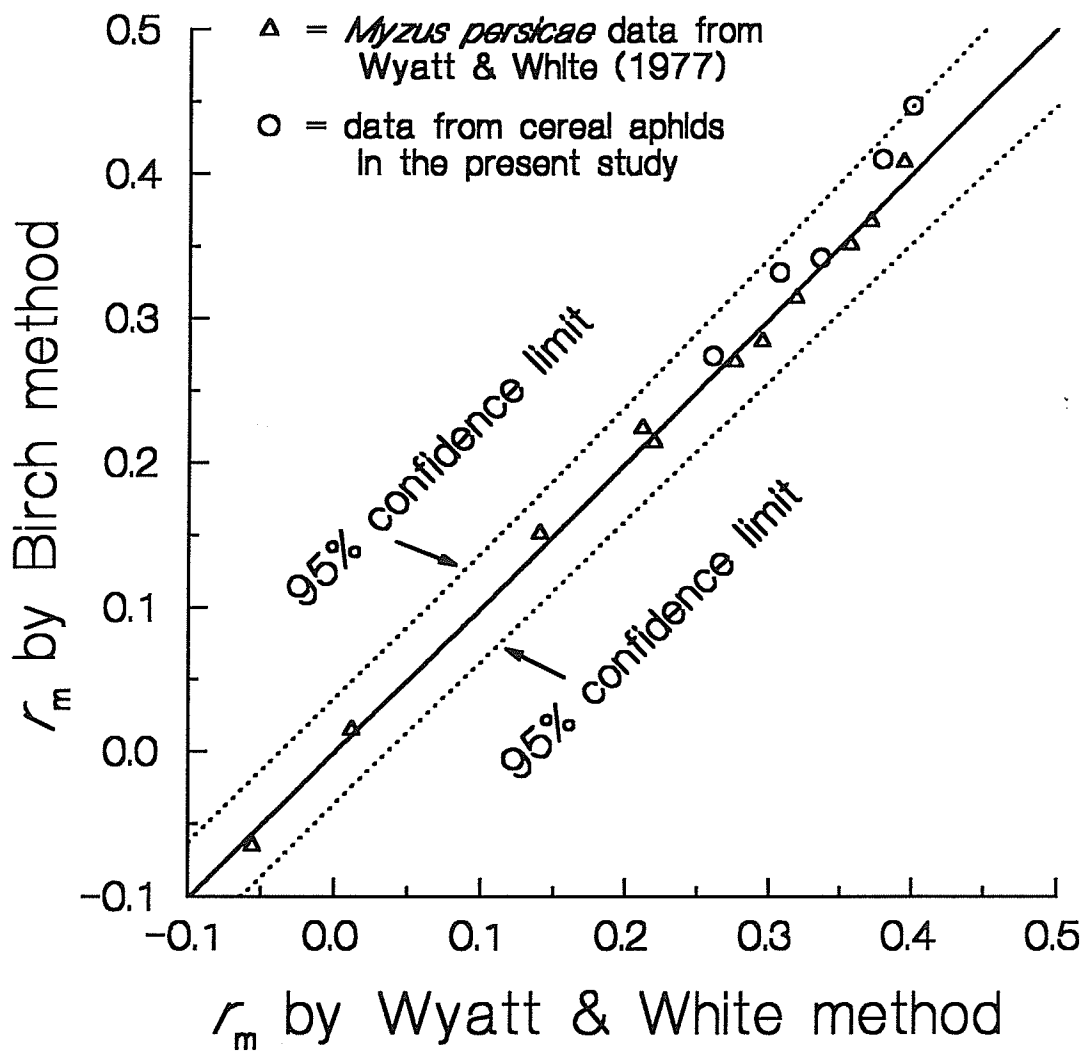


Fig. 1-9. Relationship of intrinsic rate of increase (r_m) of aphids calculated using Birch's method and Wyatt & White's method. The 95% confidence interval lines are for an individual observation using the *Myzus persicae* data.



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PART II

DISTRIBUTION OF CEREAL APHIDS ON THEIR HOST PLANTS

ABSTRACT

Studies of the distribution of four aphid species were conducted on barley planted in pots and in flats in the laboratory and in 1 X 1 m caged plots and 20 X 20 m open field plots. *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae* were tested individually in these experiments except in the 20 X 20 m open plots where all species occurred together. Each aphid species appeared to prefer a specific feeding location where reproduction also occurred. Regions of highest abundance for each species were, the central unopened leaf of immature plants for *R. maidis*, the lower leaf sheaths for *R. padi*, the underside of the proximal end of lower leaves for *Sc. graminum*, and the distal end of middle and upper leaves of immature plants and on the head of filling grain for *Si. avenae*. Colony structure was small and loosely aggregated for *R. padi* and *Si. avenae* and large and tightly aggregated for *R. maidis* and *Sc. graminum*. The pattern of distribution within the field varied among the four aphid species. *Si. avenae* was the most abundant species and was widely distributed. The population of the other three species was very low and their distribution within the field was patchy.

INTRODUCTION

Cereal crops in North America are commonly colonized by aphids, which include, corn leaf aphid, *Rhopalosiphum maidis* (Fitch); bird-cherry oat aphid, *R. padi* L.; greenbug, *Schizaphis graminum* (Rondani) (hereafter referred to as *Sc. graminum*); English grain aphid, *Sitobion avenae* (Fabricius) (hereafter referred to as *Si. avenae*); Russian wheat aphid, *Diuraphis noxia* (Mordvilko) and rose grain aphid, *Metopolophium dirhodum* (Walker) (Robinson & Hsu, 1963; Ba-Angood & Stewart, 1980; Elliott & Kieckhefer, 1987; Schotzko & Smith, 1991). Although *D. noxia* is reported to be a pest of wheat and barley in the western United States and southwestern Canada (Schotzko & Smith, 1991), it has not been reported on grain crops in Manitoba.

Although these species can attack a wide range of cereal crops, they have preferred host plants and feeding locations within the host. On spring wheat, *Si. avenae* prefers to feed on the upper leaves and when the head emerges, a large proportion are found on the spike (Dean, 1974; Wratten, 1975). On the spike, the aphid feeds mainly on the glume bases and on the rachis between the spikelets (Vickerman & Wratten, 1979). On spring barley, most *Si. avenae* are found on leaves with only a few individuals on the spike (George, 1974). *M. dirhodum* is almost entirely a leaf feeder on all cereal species. As the lower leaves

senesce and the population increases, a substantial proportion move to feed on the upper leaves, including the flag leaf (Dean, 1974). *R. padi* prefers to feed on the lower leaves of winter wheat especially near leaf bases and behind leaf sheaths (Kolbe, 1969; Dean & Luuring, 1970; Dean, 1974). However, on oats, a large proportion of *R. padi* are found on the inflorescence (Vickerman & Wratten, 1979). *R. maidis* is a serious pest of corn, sorghum, barley and to a lesser extent, wheat (Liquido & Irwin, 1986), and prefers feeding within the central whorls of growing plants. *Sc. graminum* is a major pest of wheat and is a leaf feeder. Starks & Burton (1977) found that greenbugs tend to be more frequent on the lower half of the plant.

The site of preference on the host plant for each species is related to the type and amount of damage these aphids cause on their hosts. Most of the studies cited above did not include all aphid pest species occurring in the regions of investigation. It is important to look at all pest species because more than one species usually occur together in the field. The purpose of the present study, therefore, was to determine how the four commonly reported aphid species in Manitoba, viz. *R. maidis*, *R. padi*, *Sc. graminum* and *Si. avenae* are distributed within cereal crops.

MATERIALS AND METHODS

A series of experiments on distribution of the four species of cereal aphids, was carried out with a sequential shift from controlled laboratory conditions to field conditions. Barley var. "Argyle" was used as the host plant in all experiments.

Aphid distribution under laboratory conditions

In the laboratory, barley was planted in pots, measuring 12 cm high and 15 cm in diameter, using Metro-mix[®] soil medium and watered using nutrient solution (see chapter 3 for details). After emergence plants were thinned to nine plants, one in the middle and eight near the edge of the pot (Fig. II-1). At the two leaf stage, GS 12 (Tottman & Makepeace, 1979); one late fourth instar was placed on the central plant in each pot. To ensure that the introduced aphid settled on the central plant, a small cage was placed over that plant for 24 hours, after which the small cage was removed and replaced with a large cage that enclosed all plants within the pot. Sixteen replicates per species were set up (two per week). The experiments were conducted on the laboratory bench at room temperature which varied from 18 to 22° C. Overhead fluorescent lights were used to supplement room lighting and provide a photoperiod of 16 hours light and 8 hours dark. Seven days after infestation, the cages were dismantled and records were taken on vertical

distribution of aphids on the plants which were then at the three leaf growth stage, GS 13 (Tottman & Makepeace, 1979) (Fig. II-2) . Records of aphid movement among the plants were also taken and these are described in Part III.

Similar experiments were conducted in a larger arena consisting of flats, 52 cm long, 26 cm wide and 6 cm deep, placed in growth rooms with controlled conditions (temperature: $20 \pm 1^{\circ}$ C). A population of 170 plants per flat was established. Aphid infestation was done at a slightly younger growth stage in flats than in pots to avoid interference of vertical growth of plants because the cages for the flats were 15 cm high. After the first leaf had emerged, GS 11 on all plants (Tottman & Makepeace, 1979), a central plant in each tray was marked by inserting a wooden toothpick in the soil near it and it was infested with one pre-reproductive adult. A small cage was placed over the central plant for 24 hours to ensure settlement of the aphid on that plant (see Fig. II-3), after which it was replaced with a large aphid proof cage that enclosed all plants in a flat. Each tray received one species and each species was replicated 10 times. Seven days after infestation, the cages were dismantled and records of distribution of aphids within and among plants were taken. Records on aphid movements among plants in flats are described in Part III.

Aphid distribution under field conditions

Field experiments were conducted at the University of Manitoba Field Station, Glenlea, 25 km South of the Fort Garry Campus. Barley var. 'Argyle' was planted in two 50 X 50 m plots, one on 14 May and the other on 2 June, 1994. After emergence, 24, 1 X 1 m cage plots and 4, 20 X 20 m open plots were marked out. The 1 X 1 m cage plots were enclosed with aphid proof cages made of fine terylene cloth anchored with four metal bars at each corner (Fig. II-4). At tillering stage, plants in the centre of each cage were infested with four apterous fourth instar aphids. Each cage received one species and each species was replicated six times in each 50 X 50 m plot. At ear emergence, GS 65 (Tottman & Makepeace, 1979) (Fig. II-5), the cages were dismantled and records on vertical distribution and abundance of aphids were taken on 20 randomly selected plants from each cage plot.

To ensure that all aphid species examined in the laboratory and in the cage plots were present for sampling in the 20 X 20 m open plots, aphids of each species were raised in the laboratory on barley planted in flats (see Fig. II-3) (one species per flat), for the purpose of field augmentation. When barley plants in the flats were at the two leaf stage, GS 12 (Tottman & Makepeace, 1979), they were infested with 20 pre-reproductive adults per species,

covered with ventilated aphid-proof lids and allowed to multiply in the laboratory. After 10 days, field populations of aphids in the 20 X 20 m open plots were augmented by placing four flats (containing each of the four species), in the centre of each replicate (see Fig. II-6). The lids on the flats were removed to enable released aphids to spread naturally. At the time of field augmentation barley plants in the 20 X 20 m open plots, were at tillering stage, GS 24 (Tottman & Makepeace, 1979). To avoid aphid disturbance, sampling tracks were marked prior to aphid augmentation. Each 20 X 20 m plot was sub-divided into four sampling quarters (Fig. II-6). Four line transects of radius 10 m projecting from the centre, equally spaced within a sampling quarter were marked. Records were taken from a new sampling quarter in each replicate each sampling week. Each week, a different quarter from each 20 X 20 m plot was sampled, so that each week was represented by a quarter from each of the four compass points. In each sampling quarter, records were taken from four line transects at 10 stations (spaced 1 m apart) per transect. A string with 1 m graduated markings was laid out along each transect and the nearest tiller to each station was selected for sampling. On 7, 12, 22 and 27 July, records were taken, and included the number of aphids of each species at each station, and their height on the plant.

RESULTS

The four aphid species were found on different feeding sites. Fig. II-7, and Fig. II-8 show the preferred feeding sites of each aphid species on young barley in pots and flats respectively. Aphids infested in flats were pre-productive adults, so they started reproducing soon after settlement and their populations at the time of taking records were higher than aphid populations in pots. Both experiments exhibited similar distribution patterns despite their differences in plant growth stage and aphid population numbers. Results from field experiments indicated similar trends even though, in the 20 X 20 m plots, more than one species was present (Fig. II-9 and Fig. II-10). There was little overlap in choice of feeding location among the four species.

R. maidis preferred to feed on the inside of the central leaf of young plants (Fig. II-7 and Fig. II-8). In the laboratory 59% of the population of this species occurred within the central leaf. Sometimes it was difficult to know whether a plant was infested until the central leaf was slit open. However, the presence of exuviae at the mouth of the central leaf served as an indicator of infestation by this species. Close observations of plants in the 1 X 1 m cage experiments revealed that *R. maidis* continued to occupy the central leaf

up to ear emergence. At the time when field records in 1 X 1 m cage experiments were taken, 52% of the population of this species were found on the flag leaf (Fig. II-11) and out of a total of 683 large larvae recorded on the flag leaf, 87.4% had wing buds. Some of the tillers in cages previously infested with *R. maidis* appeared shorter than other plants although plant height measurements were not taken. Close observation in a few of these cages revealed that some of the side tillers had a dead central shoot and appeared to have ceased growing suggesting previous feeding and damage by the aphids.

R. padi preferred to feed on the stem region of young plants (Fig. II-7 and Fig II-8). Ninety percent of individuals of this species occurred on the stem region of plants in pots and flats. In the flat experiment (Fig. II-8), an infested plant usually had an adult at the base of the stem with a batch of 8-12 young ones, or a batch of small larvae but no adult on the stem, or a few large larvae on the stem and leaves. In the field, 91% of the population of this species occurred on the lower leaves and stems of barley. As the host plant matured and the weather became hot and dry, *R. padi* were found located under leaf sheaths near the base of the plant. Colony sizes of 2-5 individuals were common and only loosely aggregated.

Sc. graminum settled on the lower leaves of barley

(Fig. II-7, Fig. II-8 and Fig. II-9). The frequency of this species on the lower leaves and stem regions of the barley plant was 93% and 70% for the laboratory and field populations respectively. This species occurred in large aggregated colonies on the underside of the proximal end of leaves. A number of reproducing adults and large and small larvae were often found in the same colony. As many as 150 aphids of this species occurred on the same colony and many individuals appeared to touch one another. Adults were non-winged and the large larvae did not appear to have wing buds, and were, therefore, destined to be non-winged as well. Necrotic symptoms due to feeding by this species were clearly visible from the top side of an infested leaf. This symptom gave a visible indication that the lower side of the leaf was infested by *Sc. graminum*.

A large proportion of *Si. avenae* preferred to feed on the distal end of middle and upper leaves of immature plants (Fig. II-7 and Fig. II-8). Experiments started from winged and non-winged mothers produced similar patterns of distribution (Fig. II-12). In the field population, 90% of *Si. avenae* were found on leaves within and above the middle region of the plant. On leaves, the species occurred on both upper and lower surfaces and did not exhibit any preference for surfaces. Aphid colony structure was loose, with small aggregates of 2-5 individuals and with very

little contact between individuals. On the ear, aphids of this species were found feeding on the soft awns of recently emerged heads, on the glumes of filling grain and on the rachis between spikelets (Fig. II-9 and Fig. II-10).

Laboratory and field observations revealed that adults of all species were almost always found in specific locations on the host plant where the highest abundance of each species was recorded. Aphids recorded in other locations were mainly large larvae.

Si. avenae was the most abundant species in the 20 X 20 m open plots, where aphid numbers were enhanced (Fig. II-13). The other three species were in very low population numbers. Out of the total population of aphids sampled, 80% were *Si. avenae*, 10.5% *Sc. graminum*, 8.5% *R. padi* and 1% *R. maidis*. Except for *Sc. graminum*, the population of the species exhibited an increasing trend with time, reached a peak on 22 July and then started declining by 27 July, 1994.

DISCUSSION

The occurrence of different species of cereal aphids at different feeding sites may reduce interspecific competition. The four cereal aphid species in this study were all found to occupy different feeding sites within the barley plant. The feeding habits of each species is related to the type and amount of damage done to the host plant.

R. maidis prefers feeding within the youngest unfolding

leaf near the growing point of immature plants, thereby depriving the growing region of essential nutrients required for growth. Inside the folded leaves, the pest is provided with a suitable environment with moderate fluctuations in temperature and humidity. Furthermore, individuals in this microenvironment are protected from many natural enemies and environmental hazards. At ear emergence, all leaves are fully open eliminating that habitat and the population of *R. maidis* breaks down. This was confirmed by the fact that most of the large larvae recorded on the flag leaf had wing buds, and after molting into adults would fly out in search of other favourable habitats. Large colonies were found in infested tillers suggesting that *R. maidis* has a tendency to aggregate. This behaviour, combined with favourable environmental conditions that promote a high rate of reproduction, such as warm dry weather (Wanjama, 1979), would result in intense feeding and cause stunting of infested tillers and lead to a reduction in the number of grains per ear. A heavy infestation by this species may also lead to a reduction in the number of tillers per plant as some infested tillers die before maturity.

R. padi preferred to feed on the stems of young barley plants which are probably the most nutritious region of the plant at this stage in development. As the plant grows, this species continues to feed on the stem and lower leaves.

Leather & Dixon (1981) tested the effect of cereal growth stage and aphid feeding site on the reproductive potential of *R. padi* using three host plants, wheat, barley and oats. On earing plants, they found that aphids had a higher rate of potential increase on stems. Among the three host plants they reported that *R. padi* was most fecund while feeding on the stems of barley, suggesting that barley is probably the most suitable cereal crop host for *R. padi*. Among the four aphid species studied, *R. padi* occupies the lowest stratum of the habitat. The occurrence of this species under leaf sheaths near the ground level during mid-summer is probably a survival mechanism adapted to the hot and dry conditions.

The pest status of *R. padi* is related to its high capacity for increase and it may quickly reach damaging population size when conditions are suitable. Moreover, the frequent movement of adults between plants leaving a batch of offspring at each natal site is suggestive of a high local dispersal capacity of this pest (Part III). This species is reported to occur frequently in Northern European countries and Southern Australia and often achieves outbreak levels (Rautapaa, 1976; De Barro, 1992). In Britain, *R. padi* is a very abundant species in trap catches yet it is rare in British cereals (Dean, 1974). In Manitoba, studies indicate that, among the common species that occur on cereal crops, *R. padi* has the highest intrinsic rate of natural

increase (Part I). Although serious outbreaks of this pest have not been reported recently in Manitoba, its occurrence every year poses a potential threat to grain production.

Sc. graminum feeds on leaves of the lower half of the plant. This species occurs in tightly packed colonies on the underside of leaves. This species causes severe injury to crops by sap removal and injection of a toxic saliva (Starks & Burton, 1977b). Due to the compact pattern of distribution and the direct and side effects of feeding by *Sc. graminum*, low pest populations are likely to cause severe local damage, and pest outbreaks are likely to cause devastating losses. Damage is particularly serious during prolonged dry weather (Wanjama, 1979) and even light infestations may kill young plants (Muthangya et al., 1990).

The host plant and its stage of development are important in determining the feeding position of *Si. avenae* and in regulating its population dynamics. On immature plants, this species prefers to feed on the middle and upper leaves, but at flowering stage, *Si. avenae* rapidly colonizes the ears (Dean, 1973). There occurs a marked increase in the reproductive potential of this species on the ears of cereal crops compared to the leaves. Watt (1979), found the species to have its highest reproductive rate when feeding on ears of wheat and oats at milk stage when it was almost three times as fecund as when feeding on leaves. The

reproductive rate then rapidly declines as the grain ripens (Walters & Dixon, 1982). Judging by the aphids' developmental and reproductive rates, grasses in the early stages of flowering provide *Si. avenae* with a high quality habitat. Moreover, on the ears, the aphids probably suffer less mortality from rain (Dhalival & Singh, 1975).

Since grain weight is related to photosynthesis mainly from the flag leaf and ear (Thorne, 1965), aphids that feed on these plant parts are most likely to cause a reduction in grain yield. While feeding on the ears of filling grain, *Si. avenae* deprives the grain of essential nutrients and directly reduces the amount and quality of harvestable product. *M. dirhodum* is almost entirely a leaf feeder and as the lower leaves senesce and the population increases, a substantial proportion feed on the upper leaves, including the flag leaf (Dean, 1974b). Wratten, (1975) examined the effects of *Si. avenae* and *M. dirhodum* on the growth of wheat and found that they reduced grain weight by 14 percent and 7 percent respectively. The percentage grain protein was also significantly reduced by both aphids. Relative effects of the two aphids apparently resulted from the degree of nutrient drain imposed at a particular feeding site and reduction in leaf area of the flag leaf. The amount of damage to wheat caused by the two species was directly proportional to the number of aphids on or above the flag

leaf. Wratten (1975) suggested that the relative impact of these aphids was determined by the numbers of aphids at each feeding site after anthesis and not due to differences in their feeding or physiology.

In all aphid species examined, most adults settled on their preferred locations on the host plant where feeding and reproduction took place. The morph of the reproducing adult does not influence the distribution of aphids within the host plant. This is supported by the fact that experiments started from winged and non-winged mothers of *Si. avenae* resulted in similar patterns of distribution (Fig. II-12). For all aphid species examined, aphids recorded outside their most common microhabitat were large larvae, suggesting that adults actively search for their preferred habitat before larvipositing and are probably more selective with respect to feeding location than larvae. As larvae disperse from their natal groups, colonies become smaller and colony structure becomes looser. This movement behaviour by both adults and larvae enables aphid infestations to spread to other host plants within cereal fields. Distances moved by each species within the field is dependent upon their intrinsic tendency to disperse (see Part III). Colony structure in the field was small and loosely aggregated for *R. padi* and *Si. avenae* and large and compact for *R. maidis* and *Sc. graminum*. This observation

suggests that *R. padi* and *Si. avenae* have a higher tendency to disperse locally than *R. maidis* and *Sc. graminum*. For these reasons, assessment of aphid effects on field crops based on numbers per plant alone may not give a clear picture of their damage. Kieckhefer & Kantak, (1986) reported that *Sc. graminum* and *R. padi* caused more yield losses than *Si. avenae* and *R. maidis* at similar population densities.

Si. avenae was the most abundant aphid species and was widely distributed within the 20 X 20 m open plots. It was clear from observations in nearby fields that the wild population of *Si. avenae* was high and this may have masked the effects of augmentation of this species. The populations of the other three species were very low and patchily distributed within the field. It is not clear why these aphid populations were very low. The main reason may be that the wild populations in the 20 X 20 m open plots were very low or non-existent, and the only aphids present were the result of the augmentation. The prevailing conditions in Manitoba during summer are probably most suitable for the growth and development of *Si. avenae* population. Since the growing season in Manitoba is short, it would be of considerable advantage to an aphid species to be able to multiply and spread while the host plant is still in a suitable condition. Such a species would be more

likely to be a pest of economic importance. The high rate of reproduction of *Si. avenae* on the ear (Watt, 1979), combined with its high dispersal ability (Part III & Part IV), largely accounts for its pest status in Manitoba. Severe outbreaks of *Si. avenae* in Britain and in some other European countries often results in widespread application of insecticides (Vickerman & Wratten, 1979).

CONCLUSIONS

The occurrence of different species of aphids at different locations on the host plant indicates that cereal aphids do not compete for feeding sites. Adults of each species are more selective than juveniles in determining suitable locations for settlement, feeding and reproduction. *R. maidis* prefers to feed within the central leaf of immature plants and no longer becomes an important pest after head emergence. *R. padi* feeds on the stems and lower leaves of barley. This species moves beneath the lower leaf sheaths near ground surface during hot and dry conditions in mid-summer. *Sc. graminum* prefers to feed on the underside of the proximal end of lower leaves of grain crops. Its occurrence in large and compact colonies, and the toxic effects of its saliva, suggests that this species is likely to cause serious local damage even when the aphid population is small, but during a pest outbreak, devastating losses may occur. *Si. avenae* prefers to feed within the middle and

upper leaves of immature crops and on the ears after the heads have emerged.

Colonies were small and loosely aggregated for *R. padi* and *Si. avenae* and large and tightly aggregated for *R. maidis* and *Sc. graminum*. *Si. avenae* was the most abundant species in the field and was widely distributed. The populations of the other three species were very low and their distribution within the field was patchy.

Fig. II-1. Caged seedlings of barley in 12 cm high, 15 cm diameter pots showing the nine plant arena; one plant at the centre and eight plants at the periphery used in studies of aphid distribution and dispersal.

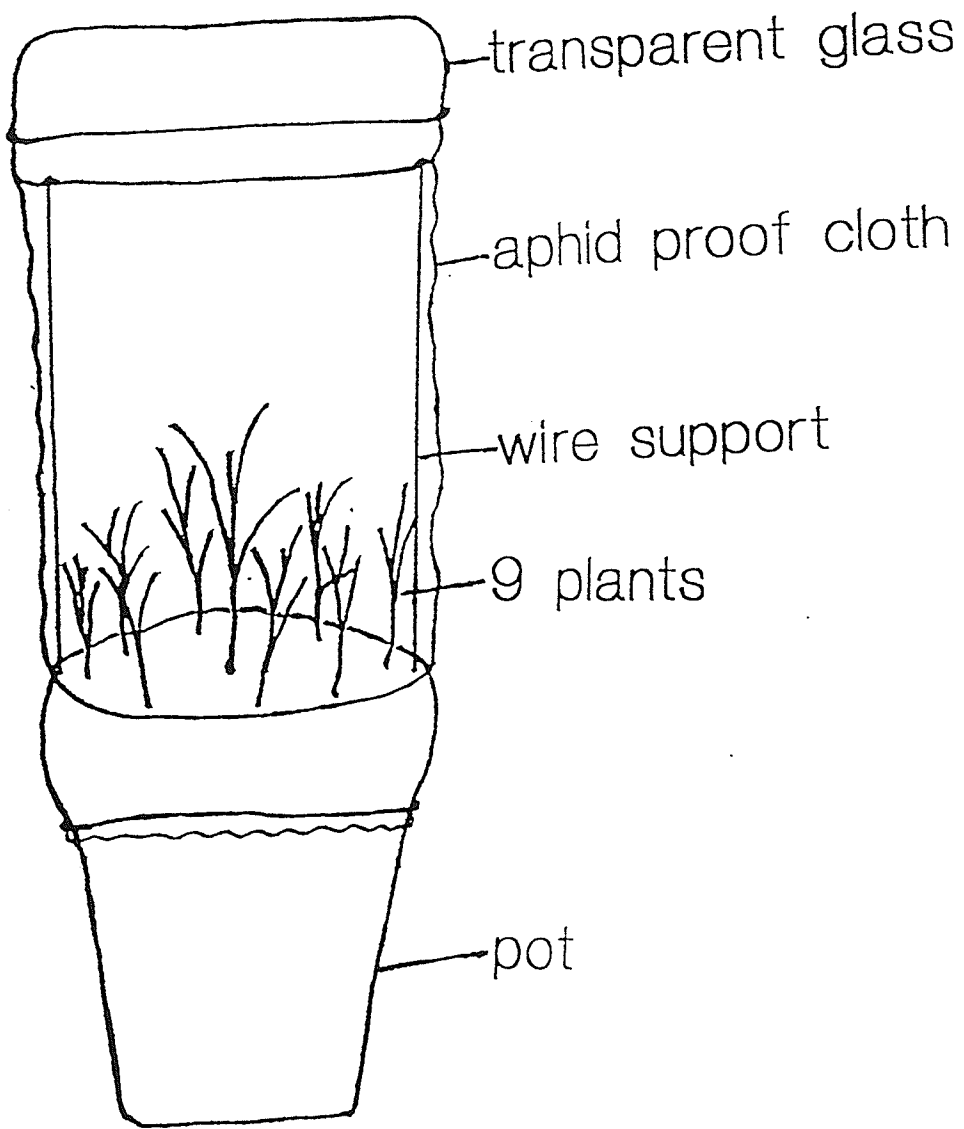
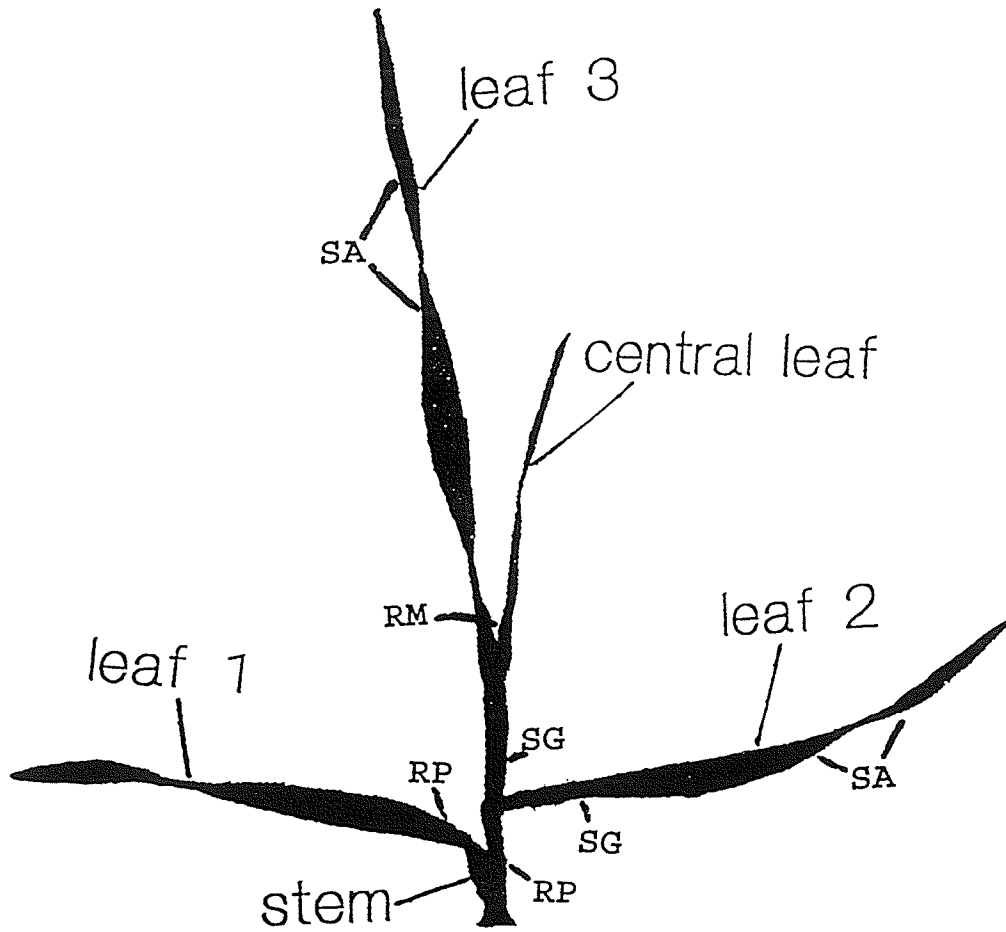
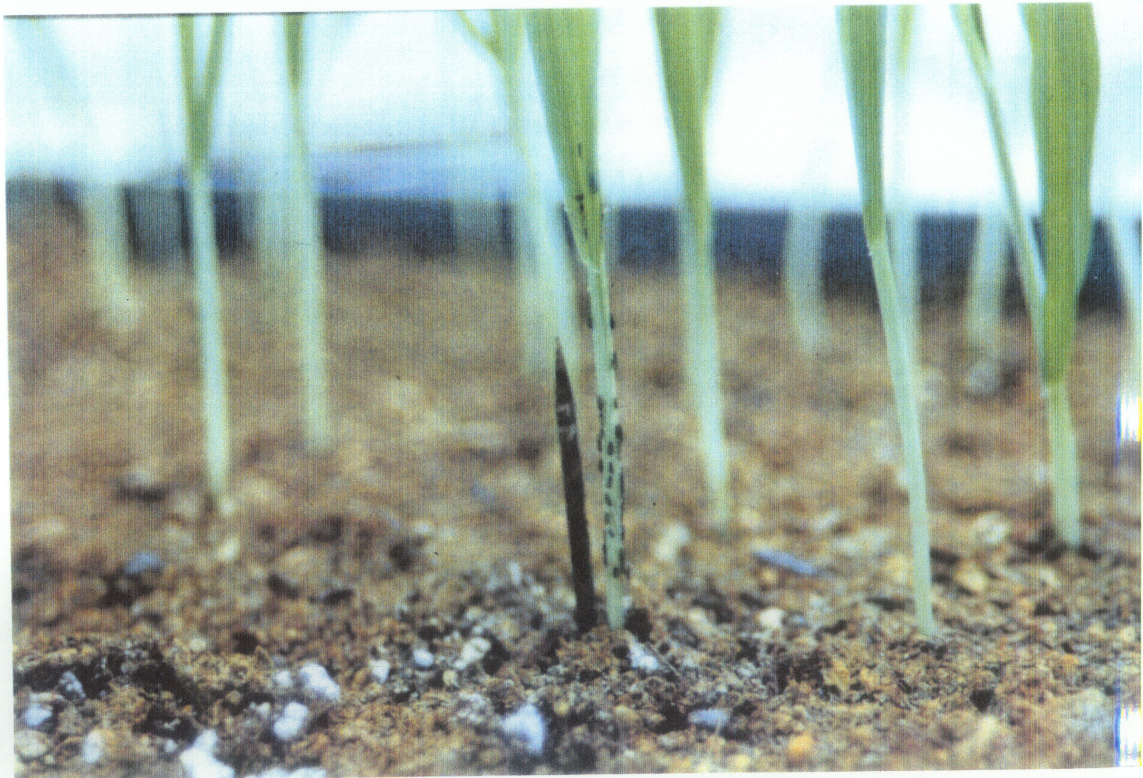
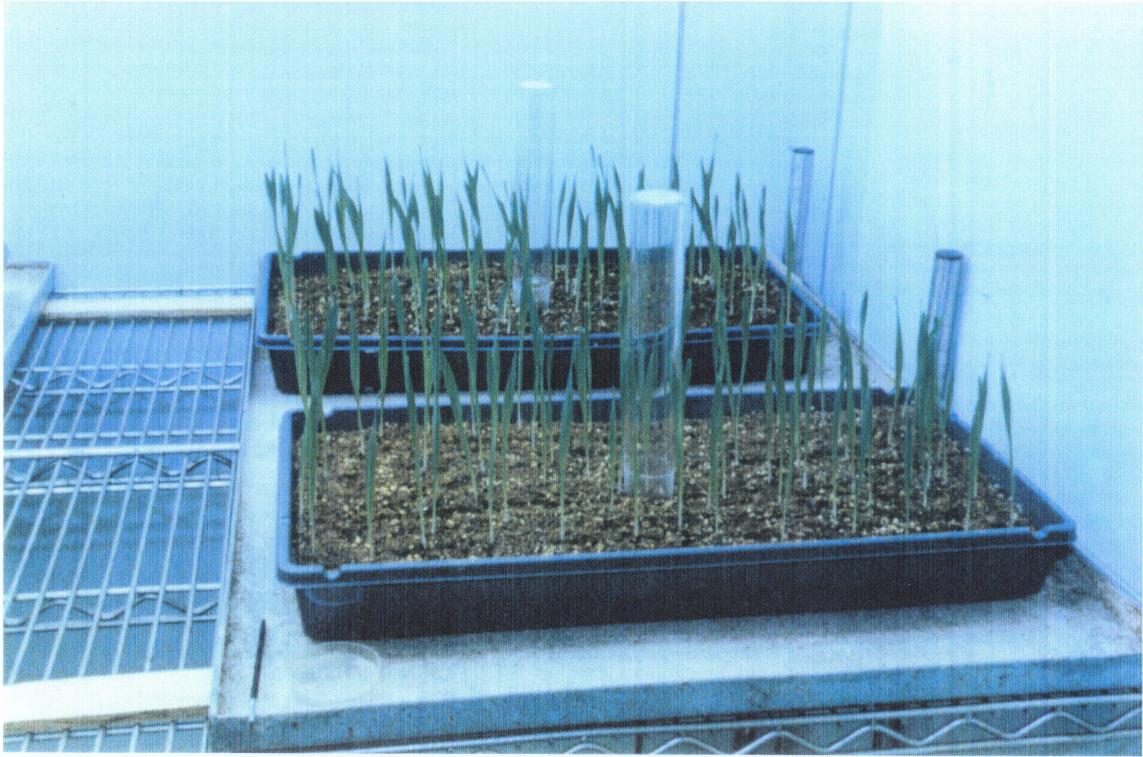


Fig. II-2. A barley plant at three leaf stage, from the nine plant arena showing plant parts and locations of highest abundance for each species. RM = *R. maidis*, RP = *R. padi*, SG = *Sc. graminum* and SA = *Si. avenae*.



- Fig. II-3. Barley seedlings in flats used in studies of aphid distribution and dispersal at the time of:
- (a) infestation of the central plants; the transparent plastic cages were used to ensure settlement of infested aphid on that plant.
 - (b) taking records, one week after infestation. This plant shows *R. maidis* aggregated on the release plant with the aphids on the stem being mainly third and fourth instars.



- Fig. II-4. Barley plants in 1 X 1 m field cages at:
- (a) tillering stage when the central plants in each cage were infested with 4 non-winged aphids (one species per cage).
 - (b) earing stage when records of aphid distribution were taken.



Fig. II-5. A barley plant at flowering stage, from the 1 X 1 m field cages showing plant parts and locations of highest abundance for each species.

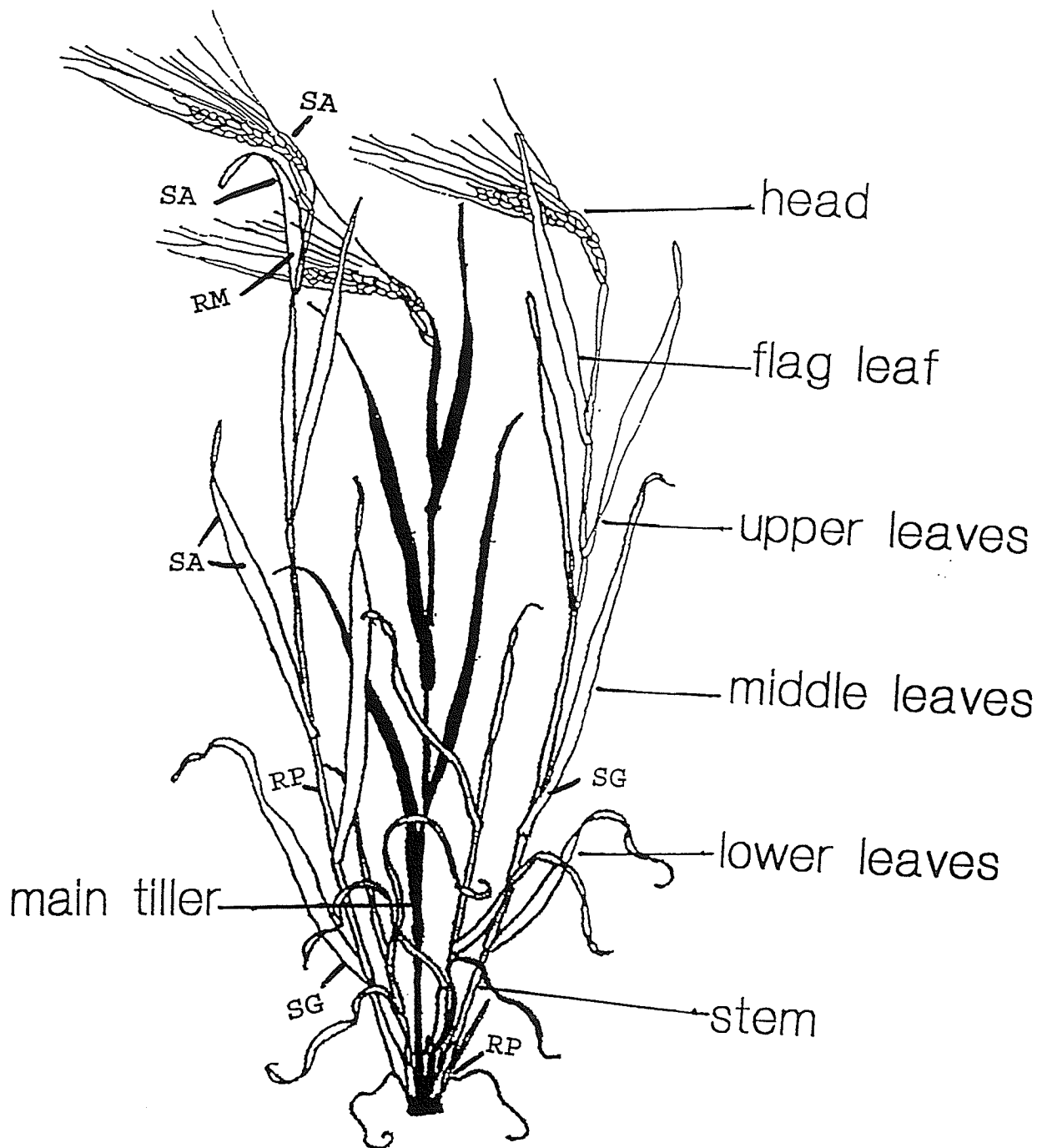


Fig. II-6. The position of flats for field augmentation of aphids and sampling stations in 20 X 20 m open plots.

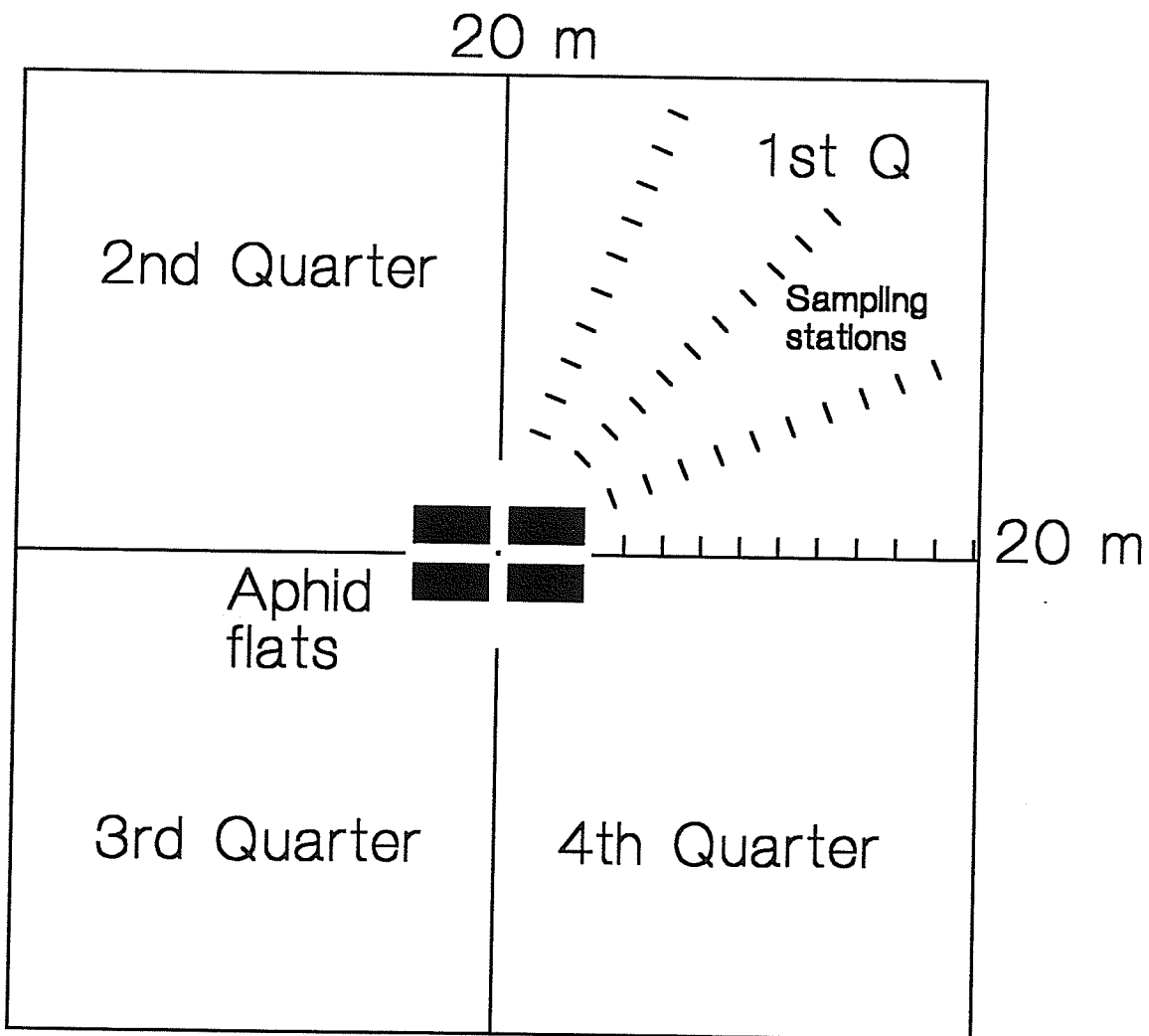


Fig. II-7. Mean (\pm s.e.) number of cereal aphids per location on potted barley plants. Bars from the same species with the same letter are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 71 for *R. maidis*, 108 for *R. padi*, 63 for *Sc. graminum* and 87 for *Si. avenae*.

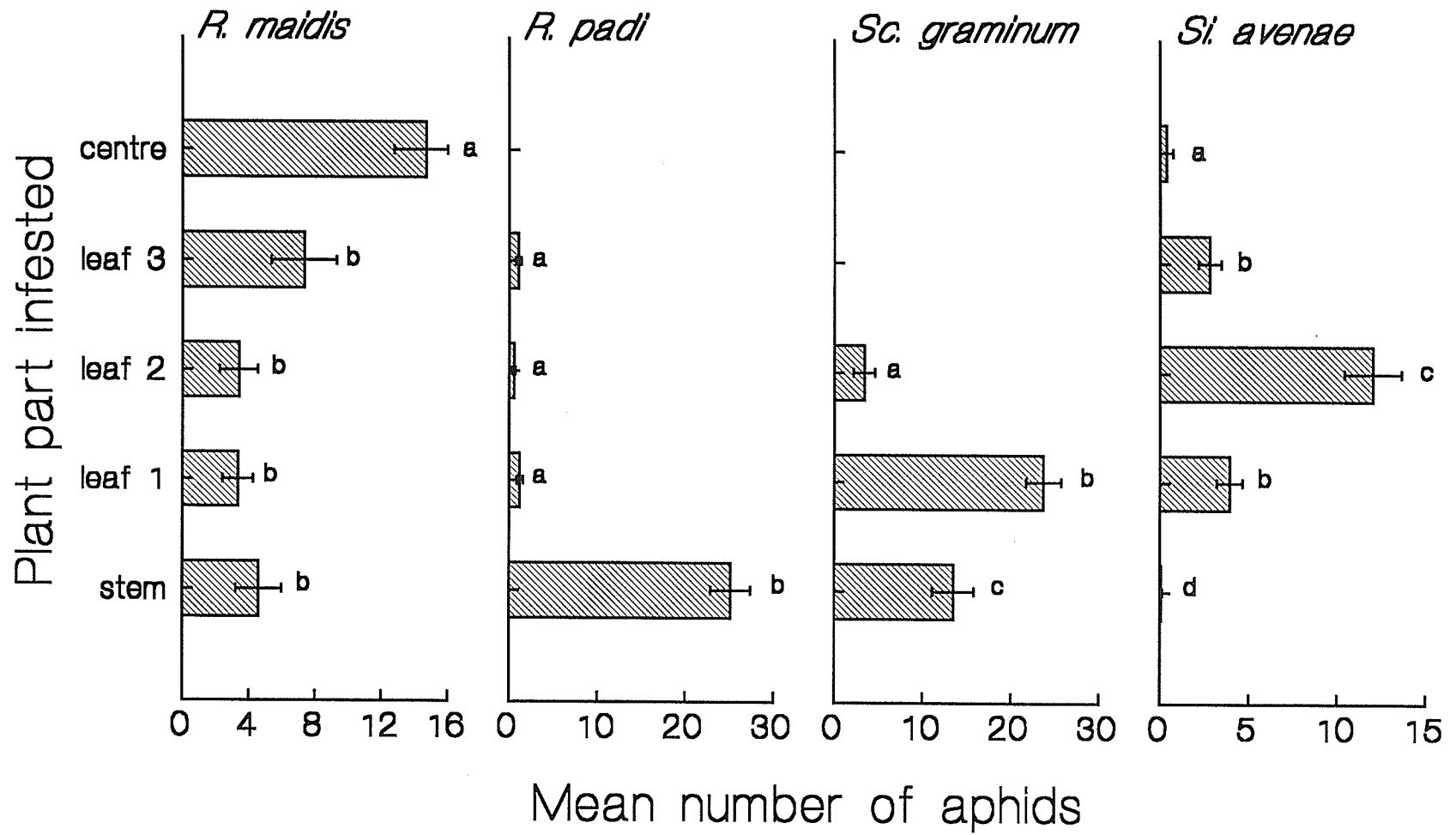


Fig. II-8. Mean (\pm s.e.) number of cereal aphids per location on barley plants in flats. Bars from the same species with the same letter are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 82 for *R. maidis*, 149 for *R. padi*, 68 for *Sc. graminum* and 81 for *Si. avenae*.

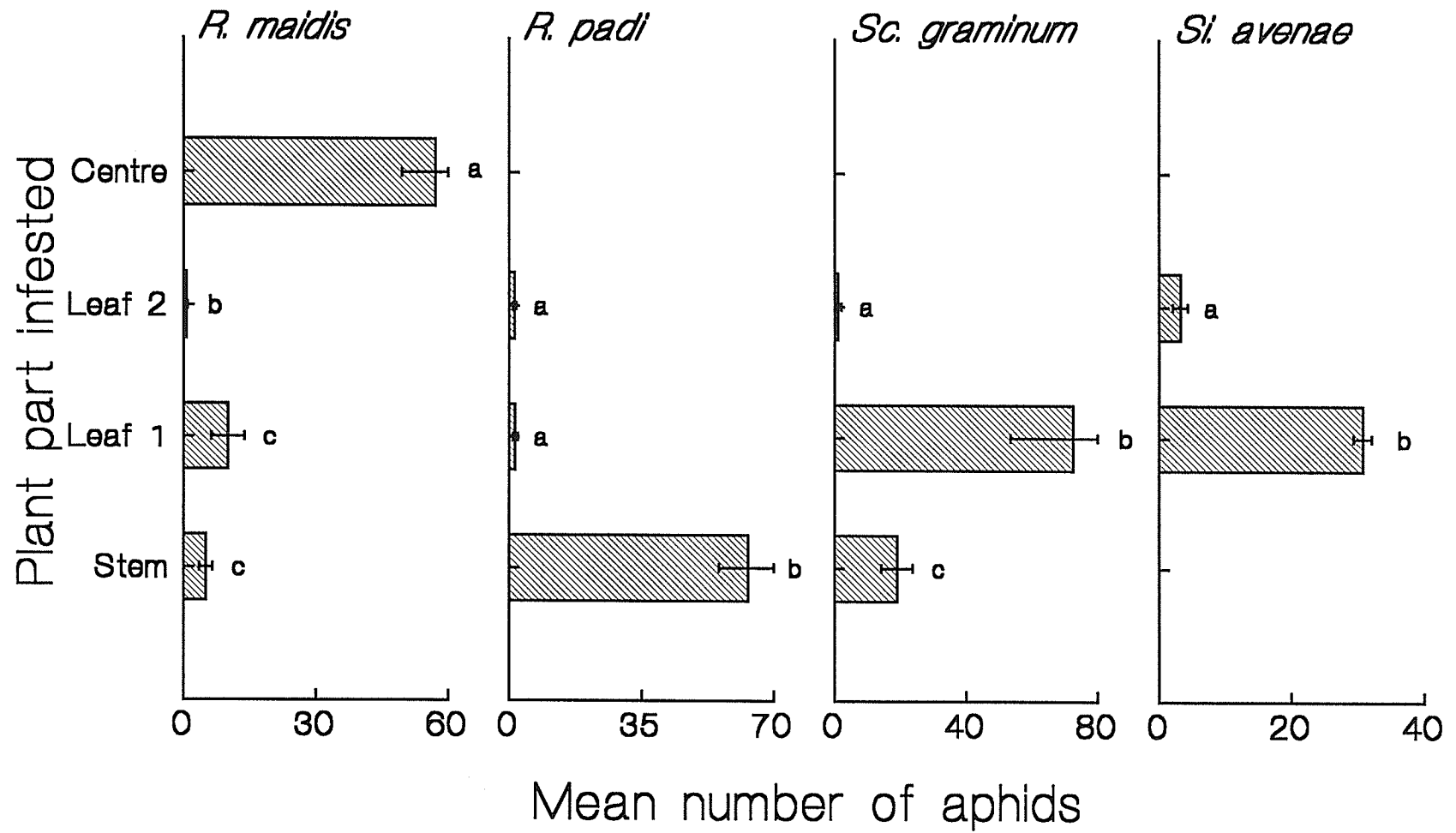


Fig. II-9. Mean (\pm s.e.) number of cereal aphids per location on barley plants in 1 X 1 m cage plots. Bars from the same species with the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 40 for *R. maidis*, 56 for *R. padi*, 56 for *Sc. graminum* and 40 for *Si. avenae*.

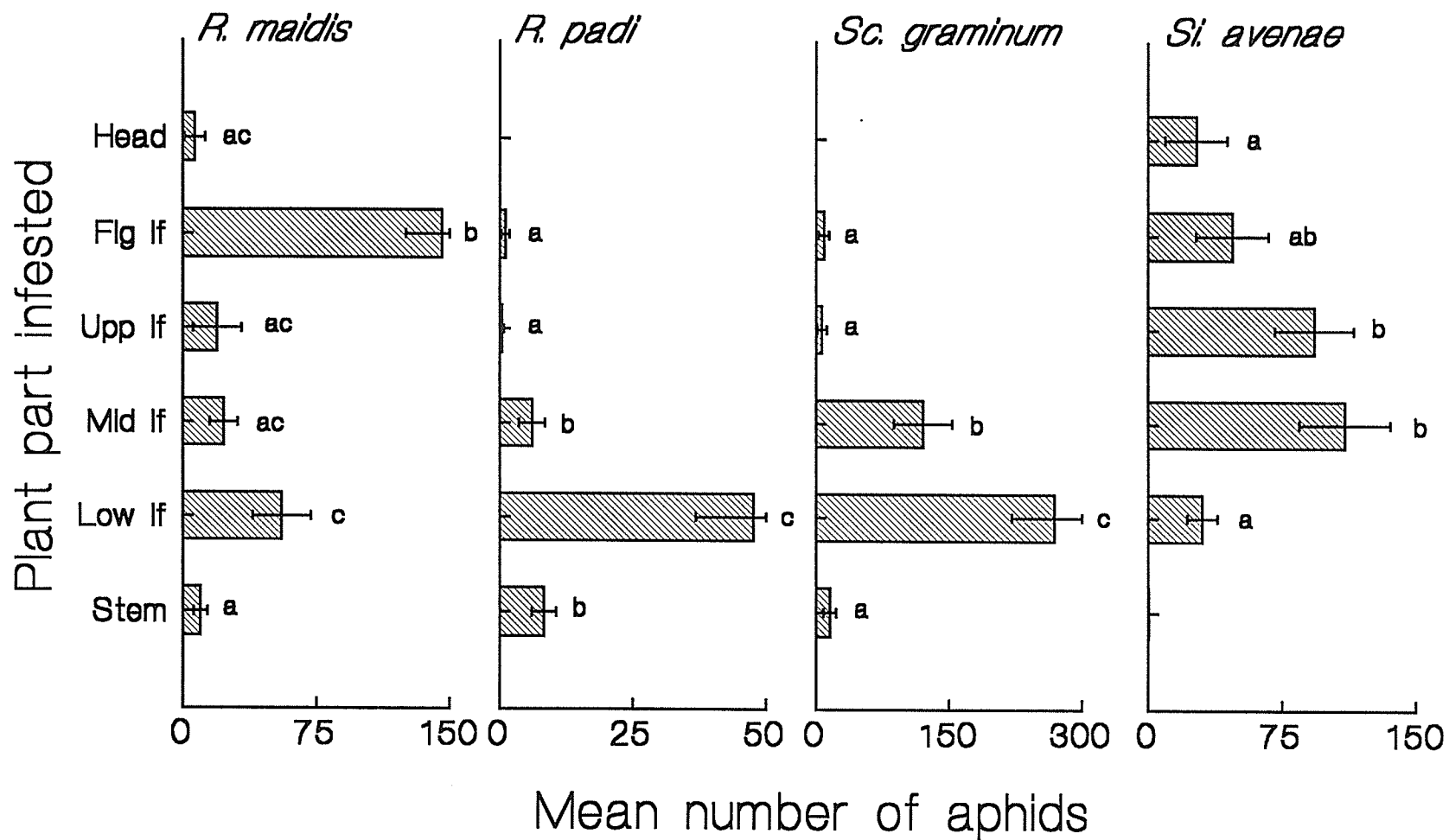


Fig. II-10. Mean (\pm s.e.) number of cereal aphids per location on barley plants in 20 X 20 m open plots. Bars with the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P>0.05$. Number of infested plants per species is 19 for *R. maidis*, 108 for *R. padi*, 52 for *Sc. graminum* and 483 for *Si. avenae*.

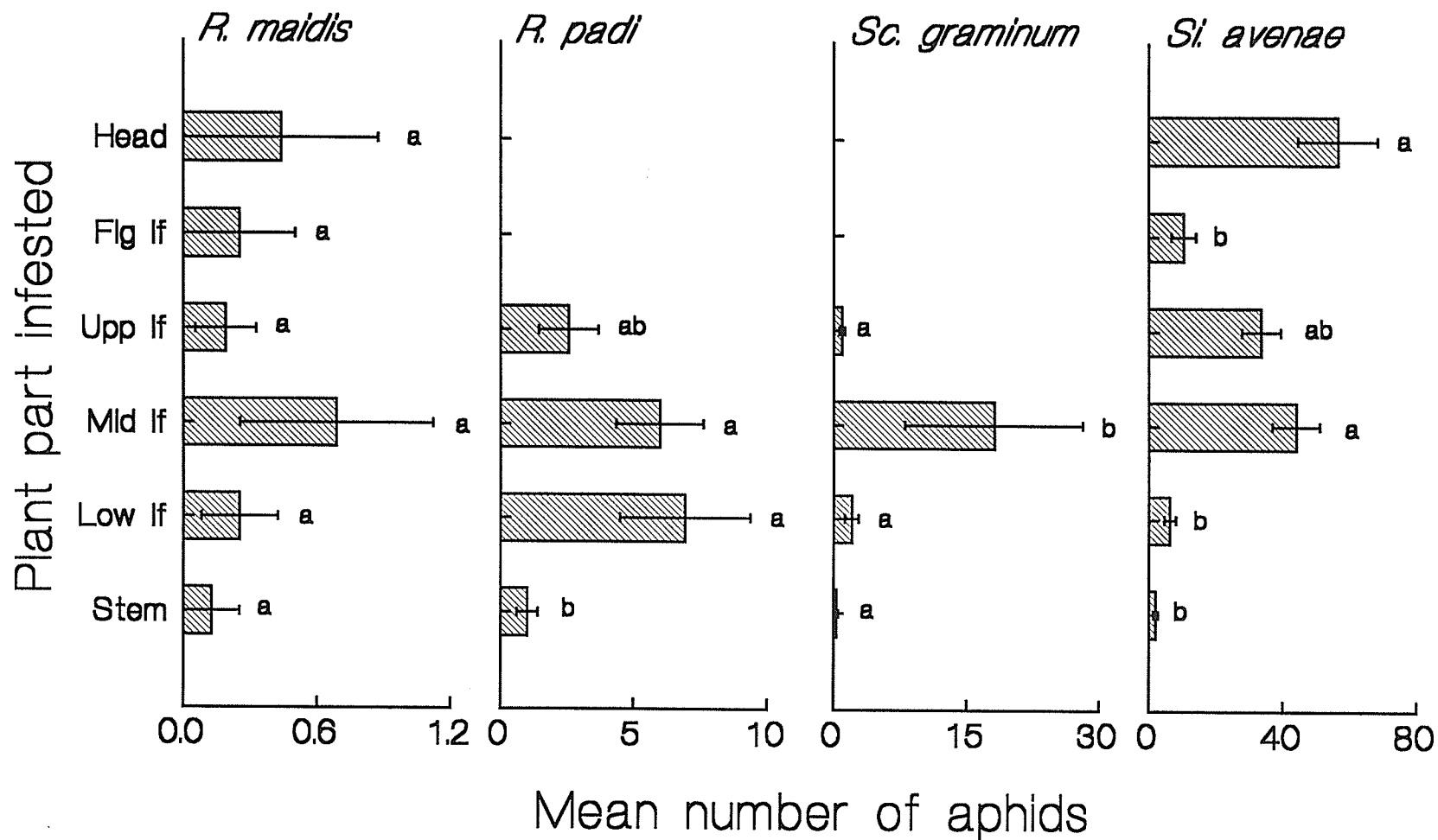


Fig. II-11. A flag leaf of barley with a colony of *R. maidis* among which most of the large larvae had wing buds and were destined to fly out of the open habitat.



Fig. II-12. Mean (\pm s.e.) number of offspring from winged and non-winged mothers of *Si. avenae* per location on potted barley plants. Bars from the same maternal morph with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. Number of infested plants per maternal morph is 87 for *Si. avenae* N, and 84 for *Si. avenae* W. N = non-winged, W = winged.

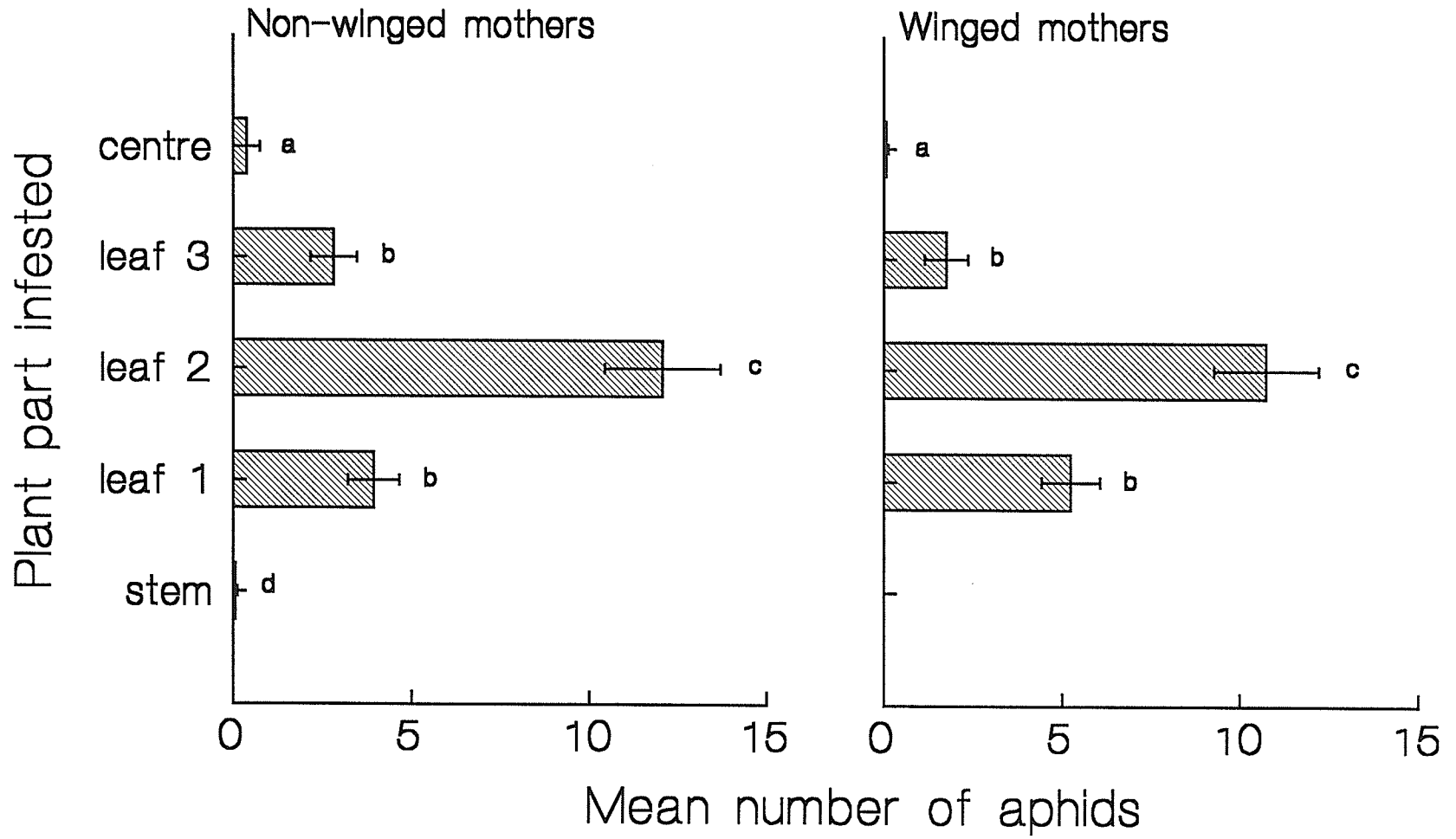
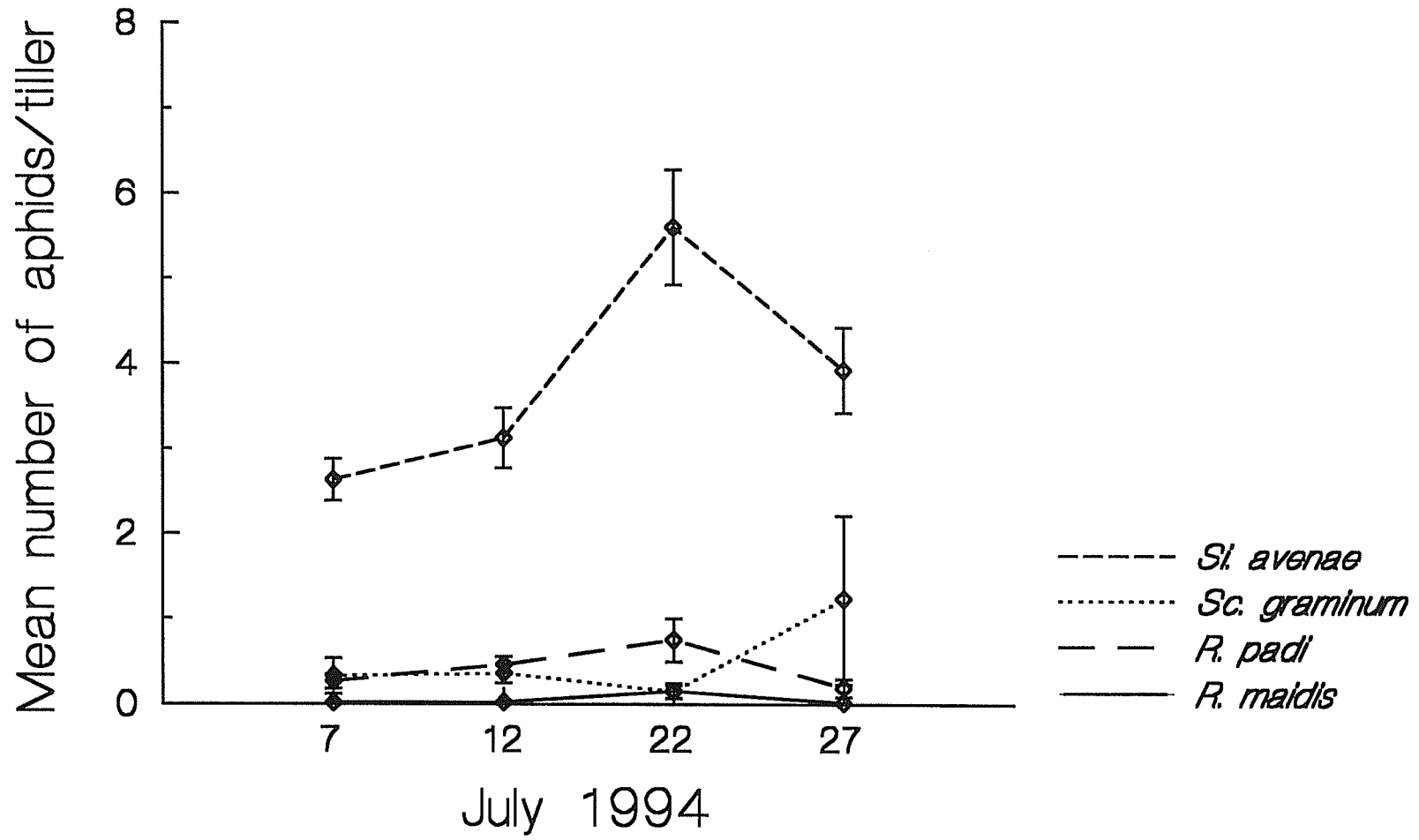


Fig. II-13. Mean (\pm s.e.) number of cereal aphids per tiller of barley in 20 X 20 m open plots in July 1994. n = 40 plants per sampling date.



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PART III

DISPERSAL OF JUVENILE AND NON-WINGED APHIDS ON CEREAL CROPS

ABSTRACT

Dispersal of four cereal aphids, *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae* was monitored on barley under laboratory and field conditions. In the laboratory, studies were done on adult and juvenile movements between leaf pieces of barley in petri-dishes and between barley plants established in pots and flats. Adults of *R. padi* moved most frequently between leaf pieces in petri-dishes and between plants leaving a batch of offspring per plant. Different aphid species deposited different group sizes of offspring per natal location. Small larval group sizes were associated with a high rate of dispersal, while large group sizes were associated with less dispersive species. Larvae exhibited movement behaviour after each molt. *R. maidis* and *Sc. graminum* were least dispersive. Because of their high dispersal capacity, *R. padi* and *Si. avenae* had widespread distribution within cereal fields.

INTRODUCTION

Much information is available concerning dispersal by winged aphids (Berry and Taylor, 1968; Johnson, 1969; Wallin and Loonan, 1971; Wiktelius, 1982), but little is known about dispersal by non-winged forms. Dean (1973a) reported

that after primary colonization of wheat and barley fields by winged *Rhopalosiphum padi* L., *Sitobion avenae* Fabricius (hereafter referred to as *Si. avenae*) and *Metopolophium dirhodum* (Walker), the infestation is spread by movement of older larvae and apterous adults across leaf bridges between plants. In a field study of *Si. avenae*, Holmes (1988), observed that all apterous aphids move from the natal ear before reproducing, and over 50% stay on one ear for less than 24 hours. Cannon (1985) reported that the main dispersal stage for apterous *M. dirhodum* is the fourth instar. He found that because of this tendency to disperse, few colonies persist longer than a week. Hodgson (1991), compared the dispersal of three aphid species *Megoura viciae* Buckton, *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* L., on their respective host plants, *Vicia faba*, *Brassica rapa* and *Brassica oleracea*, and reported that in each situation, the main emigrants are fourth instars and prelarviposition non-winged adults.

Major factors that initiate dispersal by non-winged forms include climatic effects, parasitoids, predators, food quality and intra and interspecific population interactions (Dixon, 1973; Roitberg *et al.*, 1979; Dewar & Dean, 1982; Zuniga, 1985; Holmes, 1988). Aphids mechanically dislodged from their hosts by wind or rain exhibit phototaxis (Phelan *et al.*, 1976), and orientation to the nearest vertical

object increases their chance of locating hosts.

It is apparent that movement of non-winged adults and juvenile aphids between plants in the field is a common phenomenon and probably plays an important role in spread of aphid populations and their viruses within crops. Colony size in the field was small and loosely aggregated for *R. padi* and *Si. avenae* and large and compact for *R. maidis* and *Sc. graminum* (Part II) suggesting that *R. padi* and *Si. avenae* have a higher tendency to disperse locally than *R. maidis* and *Sc. graminum*. This paper presents the results of comparative studies on movement behaviour of non-winged adults and juveniles of four aphid species, *R. maidis* Fitch, *R. padi*, *Schizaphis graminum* Rondani (hereafter referred to as *Sc. graminum*) and *Si. avenae* on barley. The main objectives were to determine the relative dispersiveness among the species and assess the role of wingless forms on local spread of aphid infestations in cereal fields. To accomplish this, a series of experiments on aphid movement were conducted with a sequential shift from controlled laboratory conditions to field conditions.

MATERIALS AND METHODS

Aphid cultures of each of the four species were established and maintained in controlled environment chambers at a constant temperature ($20 \pm 1^{\circ}$ C and photoperiod 20L:4D) (see Chapter 3 for details).

Experimental and stock cultures were run at similar conditions. Barley var. "Argyle" was used as the host plant in both laboratory and field experiments.

Adult movement in petri-dishes

Three 2 cm pieces of the first fully opened leaf of barley were placed in a rearing dish. The leaf pieces did not touch one another and the distance between them was longer than the length of a mature aphid (Fig. III-1). This was to ensure that dispersing aphids had to walk across agar medium to get to another leaf. Thirty (replicates) late fourth instars without wing buds (destined to be non-winged adults) of each species were individually placed in the rearing dishes and kept in growth chambers. After they molted to the adult stage, close observations were taken to note the position of the adult and its offspring by recording whether they were on the left leaf, middle leaf, right leaf or not on a leaf (off-leaf). Approximately 12 days after commencement of reproduction, one of the species, *R. padi*, produces over about 99% of its total fecundity (Part I). Records were taken twice per day, for 12 days. During each observation, leaf pieces not inhabited by the adult were discarded and replaced with fresh ones. Off-leaf larvae were also discarded, but off-leaf adults were left undisturbed. During record taking, great care was taken not

to disturb the aphid or influence its movement. The transparent nature of the agar medium enabled aphids underneath leaves to be counted without having to turn the leaf pieces over.

Larval movement in petri-dishes

For each species, 40-50 recently molted adults were individually placed on single 2 cm pieces of barley leaf in rearing dishes. The adults were carefully removed when they had produced 10-15 new-borne aphids. In most cases, these were in a single compact group. However, larvae on top and on the underside of leaves were considered as one group. For each species, 30 progeny groups of appropriate size were selected and two more pieces of leaf were added in each dish, leaving the aphid infested leaf at the centre (Fig. III-2). Observations on larval dispersal from the centre leaf to the other two leaves were taken twice per day. Records taken included the number of larvae that moved from the centre leaf, their instar and morph. At each observation, the two leaves on either side of the centre leaf and any larvae on them were discarded and replaced with fresh leaves. Off-leaf aphids were also discarded. Records continued to be taken until all larvae on the central leaf had dispersed or when an aphid on the central leaf molted into an adult.

Adult and larval movement on potted plants and on plants in flats

Records of adult and larval movements on potted plants and on plants in flats were taken from the same experimental setups that were used for studies on aphid distribution under laboratory conditions (see Part II for details). In the potted plant experiment, records taken 7 days after infestation include, the number and stage of development of aphids on each plant, and the total number of plants infested in each pot. Records of aphid movement in the experiment on flats were also taken 7 days after infestation and these include, distance of infested plants from aphid release point, number of aphids per plant and the total number of plants infested. Information on aphid distribution is described in Part II.

Aphid movement in 20 X 20 m field plots

Information on aphid movement in the field was derived from records collected in 20 X 20 m open field plots (see Part II for details). Data that were considered useful for determination of aphid dispersal were distance of each sampled station from the aphid release point and the total number of aphids per species per station.

RESULTS

In petri-dishes, both adults and larvae of all species moved between leaves during the experimental period. Adult aphids in petri-dishes deposited a batch of offspring on one piece of leaf and then moved to another piece where the next batch was deposited. As adults moved between leaves, *R. padi* deposited the highest number of batches of offspring over a 12 day period, which was about twice the number of batches deposited by either *Sc. graminum* or *Si. avenae* (Fig. III-3a). The time spent by adults in each natal location was shortest for *R. padi* (1.5 days) and longest for *Sc. graminum* (3 days) (Fig III-3b). It was apparent that adults of each species produced a certain batch size of offspring (as evidenced by the small size of standard error bars) and then moved to another location where feeding and reproduction took place. Adults of *R. padi* and *Si. avenae* produced the lowest number of offspring per natal location while *Sc. graminum* produced the highest (about 19 individuals) (Fig. III-3c).

Fig. III-4 shows the pattern of dispersal by juveniles of each species from their natal location. There were little or no movement by first instar larvae of any species. However, after the first molt, all species exhibited movement behaviour. *R. padi* larvae had the highest dispersal with over 90% of individuals reaching adulthood in

locations other than their natal site. Larvae of *Si. avenae* and *Sc. graminum* appeared to have similar patterns of movement with about 60% of individuals reaching adulthood outside their natal location.

Aphids on barley plants in pots and in flats had similar patterns of infestation one week after their release (Fig.

III-5). In both experimental arenas, *R. padi* infested the highest number of plants. Close observations indicated that movement by both adults and large larvae (third and fourth instars) contributed to the spread of infestation from one plant to another. First and second instar larvae of all species occurred in groups, usually in their natal locations where the abundance of each species per host plant was highest. These preferred feeding locations are the central unopened leaf for *R. maidis*, the lower leaf sheaths for *R. padi*, the underside of lower leaves for *Sc. graminum*, and the middle and upper leaves for *S. avenae* (Part II).

It was apparent from experiments in flats, that adults of *R. padi* frequently moved between plants leaving one batch of first instar larvae per stem. As the larvae developed to third and fourth instars, the group sizes broke down as individuals spread out to other locations and adjacent plants. Third and fourth instars were found in loose colonies of one to three individuals. Some uninfested

plants in all treatments had aphid exuviae, an indication that they had previously been infested but after molting, the individuals moved to other plants.

Distances moved one week after aphids were released on barley plants in flats varied among species (Fig. III-6). *R. padi* and *Si. avenae* moved furthest, were evenly distributed among plants in each flat and had 21 and 26% of their population on the release plants respectively. *R. maidis* and *Sc. graminum* had a more aggregated distribution with 75% and 60% of their population on the release plants respectively. Adults of *R. maidis* were found on the same host plant one week after their release and 71% of individuals recorded on other plants were fourth instars.

Results of aphid movement studies done in the field are shown in Fig. III-7. *Si. avenae* was the most abundant species and almost all plants sampled were infested with this species. The other three species occurred in low population numbers with *R. maidis* being the least abundant. Populations of *R. padi* and *Si. avenae* were widely distributed within the field. Except for *Sc. graminum*, the overall population numbers increased from the initial records on 7 July, 1994, reached a peak on 22 July and started falling by 27 July. The populations of *R. maidis* and *Sc. graminum* appeared to show some pattern of dispersal from the aphid release location (Fig. III-8). Both *R.*

maidis and *Sc. graminum* had an aggregated distribution, in that aphids were found on a small number of plants. This aggregation phenomenon was particularly clear for *Sc. graminum*, which had a mean record of as many as 160 individuals, 3 m away from infestation point on 27 July while more than half of the other sampled locations had no aphids at all (Fig. III-7).

DISCUSSION

Whereas there is much information regarding dispersal by winged forms, there is less information on dispersal by non-winged aphids. However, there is increasing evidence that non-winged aphids readily leave their host plants and probably play an important role in spread of infestations within fields (Dean, 1973a; Holmes, 1988; Hogson, 1991). Movements by non-winged adults and juveniles over the surface of their host plants and between adjacent plants results in slow diffusive dispersal. Ribbands (1964) found that non-winged forms of *Myzus persicae* (Sulzer) frequently move from plant to plant and are responsible for spread of yellows virus in sugarbeets. Dispersal by non-winged aphids is reported to be initiated by the presence of factors such as rainfall, predators and deterioration of host quality (Roitberg *et al.*, 1979; Zuniga, 1985; Hogson, 1991). The present studies provide further evidence of the role of intraspecific population interactions in dispersal of non-

winged aphids on barley.

Aphid movement studies done in petri-dishes suggest that in the absence of other disturbing factors, adults produce offspring of a certain batch size characteristic of each species before moving to another natal location (Fig. III-3c). The length of time taken by adults of each species in one natal location may be related to their sensitivity to the presence of other individuals. Among the four aphid species, *R. padi* may have the highest response to tactile stimulation resulting in frequent moves between plants. In a similar study, involving five species of cereal aphids, *R. padi*, *R. maidis*, *M. dirhodum*, *Hysteroneura setariae* (Thomas) and *Sitobion* nr. *fragariae*, MacKay & Lamb (in press) reported that *R. padi* dispersed most rapidly on excised barley leaves in petri-dishes and on potted barley plants. Winged *M. dirhodum* stay in one spot on a tiller for less time (1.8 days) than non-winged adults (2.3 days), while both morphs of *Si. avenae* are equally active (1.9 days) (Dean, 1974). As the adult moves, it leaves offspring in each location, leading to spread of infestation. The large and compact group sizes of larvae deposited by *Sc. graminum* at a natal location implies that this species possibly has low sensitivity to tactile stimulation. The longer an adult spends in one location, the slower the spread of infestation.

During molting, aphids stop feeding for a while and there is increased opportunity for contacts between individuals as feeding resumes. This is probably the reason for the observed increase in larval dispersal after each molt. The fourth instar is reported to be the main larval dispersal stage in some aphid species (Cannon, 1985; Hogson, 1991). The studies of Johnson (1957) and MacKay & Downer (1979) emphasized the occurrence of a restless dispersive phase of teneral adults in several species of aphids. Findings from the present study suggest that larval dispersal is an important component in the spread of aphid infestations on cereal crops and for some species such as *R. padi*, larval movements soon after the first molt enhance the spread of infestations. Both adults and larvae of each species probably have the same innate tendency to disperse as their patterns of dispersal appear similar (Fig. III-3a and Fig. III-4).

Results of the laboratory study of adult and larval movements on leaf pieces of barley (Fig. III-3 and Fig. III-4) suggest that *R. maidis* is second to *R. padi* in dispersal potential and that there is little or no difference in dispersal potential between *Sc. graminum* and *Si. avenae*. However, studies of aphid movement on whole plants under laboratory and field conditions indicate that *R. padi* and

Si. avenae have a high dispersal ability with *R. maidis* and *Sc. graminum* having low dispersal ability (Fig. III-6 and Fig. III-7). On immature plants, *R. maidis* occurs in aggregated colonies within the central leaf, however, the studies of aphid movement using cut leaf pieces provided an open habitat. *R. maidis* may have become restless on the open leaves and become prone to disperse and this possibly overestimated the actual dispersiveness of this species. *Si. avenae* was often found off-leaf in the petri-dishes, suggesting that records of leaf to leaf movements were probably an underestimate of their actual dispersiveness. Therefore, studies done in the laboratory using whole plants give a clearer picture of what happens in the field situation than use of leaf sections.

Results obtained from experiments with nine plants in pots and a larger number of plants in flats showed similar infestation patterns, confirming that *R. padi* is the most dispersive among the cereal aphids. Since both adults and larvae of the same species appear to have closely similar tendencies to disperse, the combined dispersal behaviour would lead to a more uniform and widespread distribution for highly dispersive aphids and a more aggregated distribution for less dispersive aphids. The occurrence of *R. padi* and *Si. avenae* in loose colonies, and their widespread distribution within barley plants in flats and in field

plots are indicative of the high dispersal capacity of these two species. Holmes (1988) found that once populations of *Si. avenae* are established in the field, infestation spreads within the crop through movement of up to 2 m by wingless individuals.

Due to the high tendency to disperse by *R. padi* and *Si. avenae* among cereal crops, density-dependent population reduction mechanisms such as reduced fecundity, are unlikely to set in. The aphids are likely to be large and have a high reproductive performance as they spread to more nutritious habitats. Large aphids are reported to be often more fecund than small ones (Dixon & Wratten, 1971; Taylor, 1975). For species like *R. maidis* and *Sc. graminum*, with low levels of local dispersal, aggregations build up and two density dependent mechanisms begin to operate; reduced fecundity, mediated through deterioration of the host plant and increased wing production, mediated either through the host plant or crowding. Thus, if other factors are constant, local population growth for these two species may be low and the frequency of achieving pest status is lower than for *R. padi* or *Si. avenae*. However, the growth of aphid populations and dispersal in the field may be dependent upon other factors such as type and growth stage of host plant and environmental conditions (Acreman & Dixon, 1989; Dean, 1973b), so, we cannot accurately predict the

likelihood of a pest outbreak based on aphid dispersiveness alone.

Aphid population numbers in the field differed between species, making it difficult to associate spatial distribution patterns directly with dispersal capacity. However, aphid movement studies in the laboratory, using the same initial population of aphids on barley in flats suggests that *R. padi* is more dispersive than *Si. avenae*, in that the former species had a higher number of plants infested than the latter. Among the two less dispersive species, it could be concluded that *Sc. graminum* has a higher dispersal tendency than *R. maidis* because *Sc. graminum* had a more widespread distribution on barley in flats (Fig. III-8) than *R. maidis*.

The aggregation behaviour of *R. maidis* and *Sc. graminum* produces local pockets of heavy infestation and may lead to severe losses on individual infested plants. During pest outbreaks, attacks by *Sc. graminum* may lead to heavy feeding damage and this, combined with the toxic effects of its saliva can result in devastating crop losses. In 1986, in Alberta and Saskatchewan, a heavy infestation of *Sc. graminum* covering one million hectares of wheat resulted in serious yield losses (Haber, 1990).

Augmentation of the field populations with laboratory reared aphids can be associated with the observed counts of

some aphid species. *Si. avenae* was present in high numbers and its widespread distribution over the sampling distance during the entire sampling period shows that the wild population masked any relationships in aphid counts of this species that could be associated with the point of augmentation. Although the population of *R. padi* was low, its occurrence at all distances sampled throughout the sampling period made it difficult to associate aphid records with augmentation. However, its widespread distribution despite the low population size, is suggestive of a high dispersal capacity. Aphid counts of *R. maidis* and *Sc. graminum* at each location and sampling day showed increasing movement trends with time that could be associated with their dispersal from the point of aphid release (Fig. III-8). Both species appear to have closely similar progression of infestations. Greenbugs, which prefer wheat to rye, move more frequently on rye than on wheat (Starks & Burton, 1977). Over an 18-day period, Starks & Burton (1977) reported that the mean distance travelled by apterae on susceptible plants was 19.2 cm. Despite the observed slight progression of infestation by *R. maidis* and *Sc. graminum*, their horizontal distribution was patchy, an indication of the clustered nature of their populations.

Notwithstanding the fact that laboratory and field experiments on aphid movement were done under totally

different environmental conditions and experimental designs, the closeness of the results are suggestive of the intrinsic nature of the dispersal behaviour of each species. In the laboratory, experiments were run at constant conditions and aphid species were not mixed and so their interactions were at the intraspecific level. However, in the field, environmental conditions fluctuated and aphid interactions were interspecific as well as intraspecific. Other factors that could have influenced aphid dispersal in the field include natural enemies such as predators and parasitoids, rain, wind and host plant conditions.

CONCLUSIONS

Dispersal by non-winged adults and juvenile aphids between cereal plants is a common phenomenon and plays an important role in spread of infestations. Third and fourth instars are the main larval dispersal stage but for some species such as *R. padi*, larval movements commence soon after the first molt. Adults contribute to spread of infestations by their movements between plants, and by leaving their offspring on the different plants they visit. Different aphid species produce different sizes of groups of offspring in each natal location. Small larval group sizes are associated with species with a higher rate of dispersal, while large group sizes are associated with less dispersive species. The order of dispersal capacity of the four

species studied from the highest to lowest are, *R. padi*, *Si. avenae*, *Sc. graminum* and *R. maidis*. Because of their high dispersal capacity, *R. padi* and *Si. avenae* have widespread distribution within fields. This, in addition to the high abundance of *Si. avenae* in the field make this species an important pest in Manitoba.

Fig. III-1. Experimental design for study of adult movements between leaf pieces of barley in petri-dishes; L = left leaf, M = middle leaf, R = right leaf.

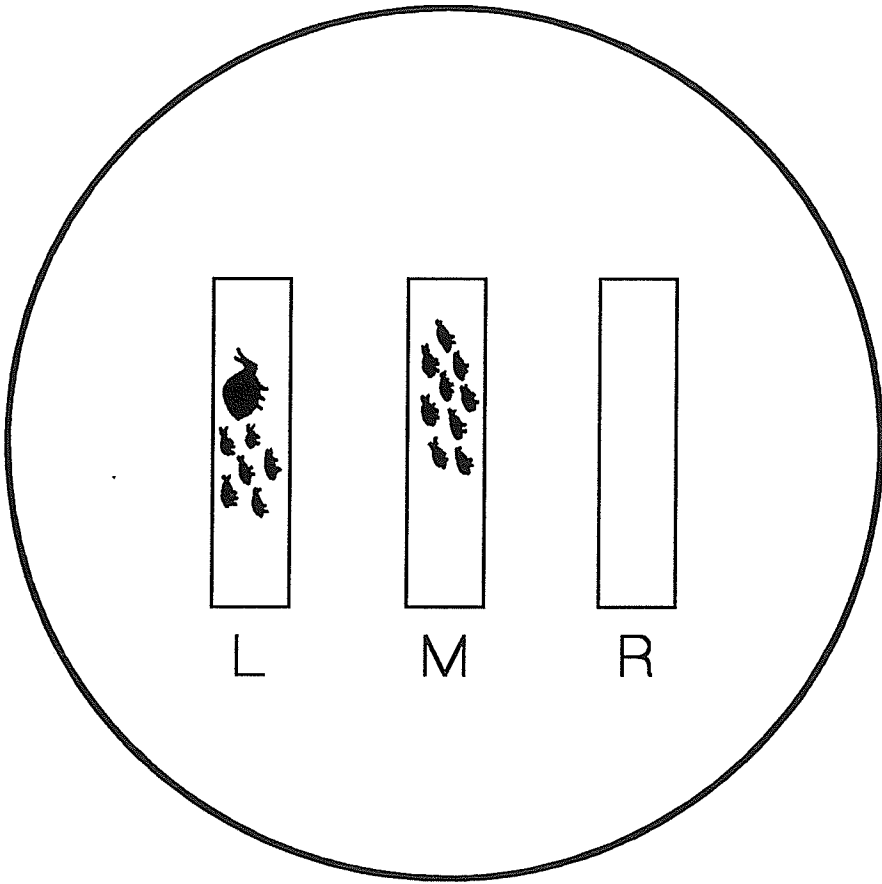


Fig. III-2. Experimental design for study of dispersal of larvae from their natal location on leaf pieces of barley in petri-dishes.

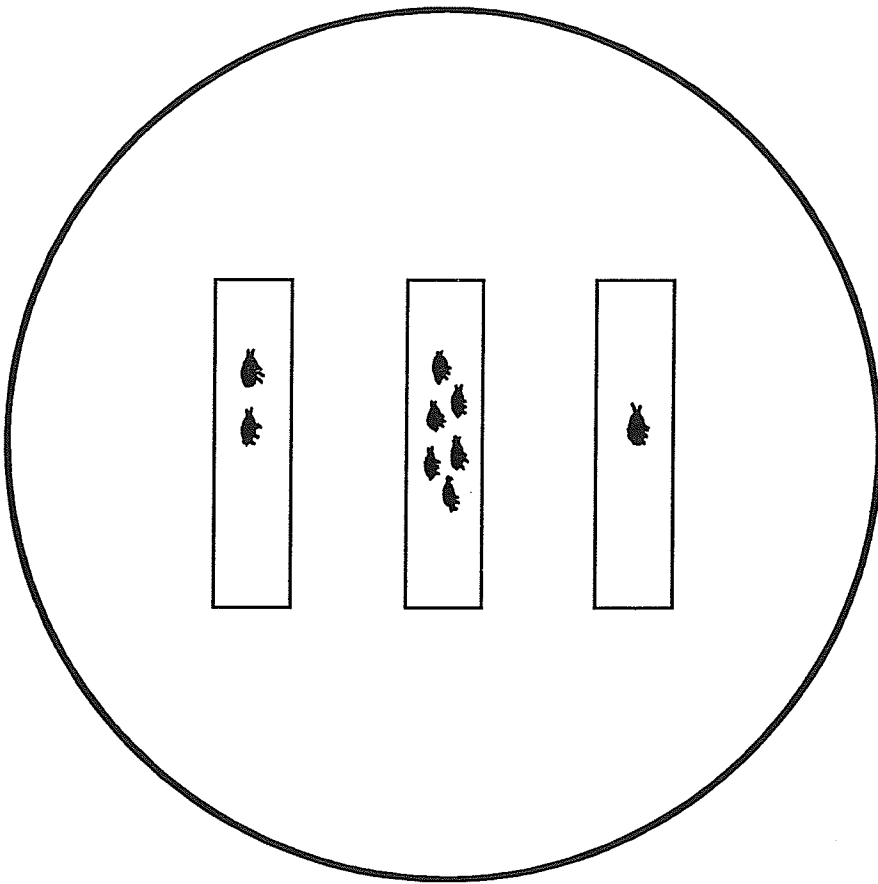


Fig. III-3. Dispersal behaviour of adult aphids on leaf pieces of barley in petri-dishes

- (a) Mean number of adult movements in 12 days
- (b) Mean time spent by adults to produce each group
- (c) Mean number of larvae produced in one natal location.

Bars with the same letter are not significantly different from one another using Tukey's studentized range test, $P > 0.05$. Number of replicates contributing to each mean (n) = 30 petri-dishes per species.

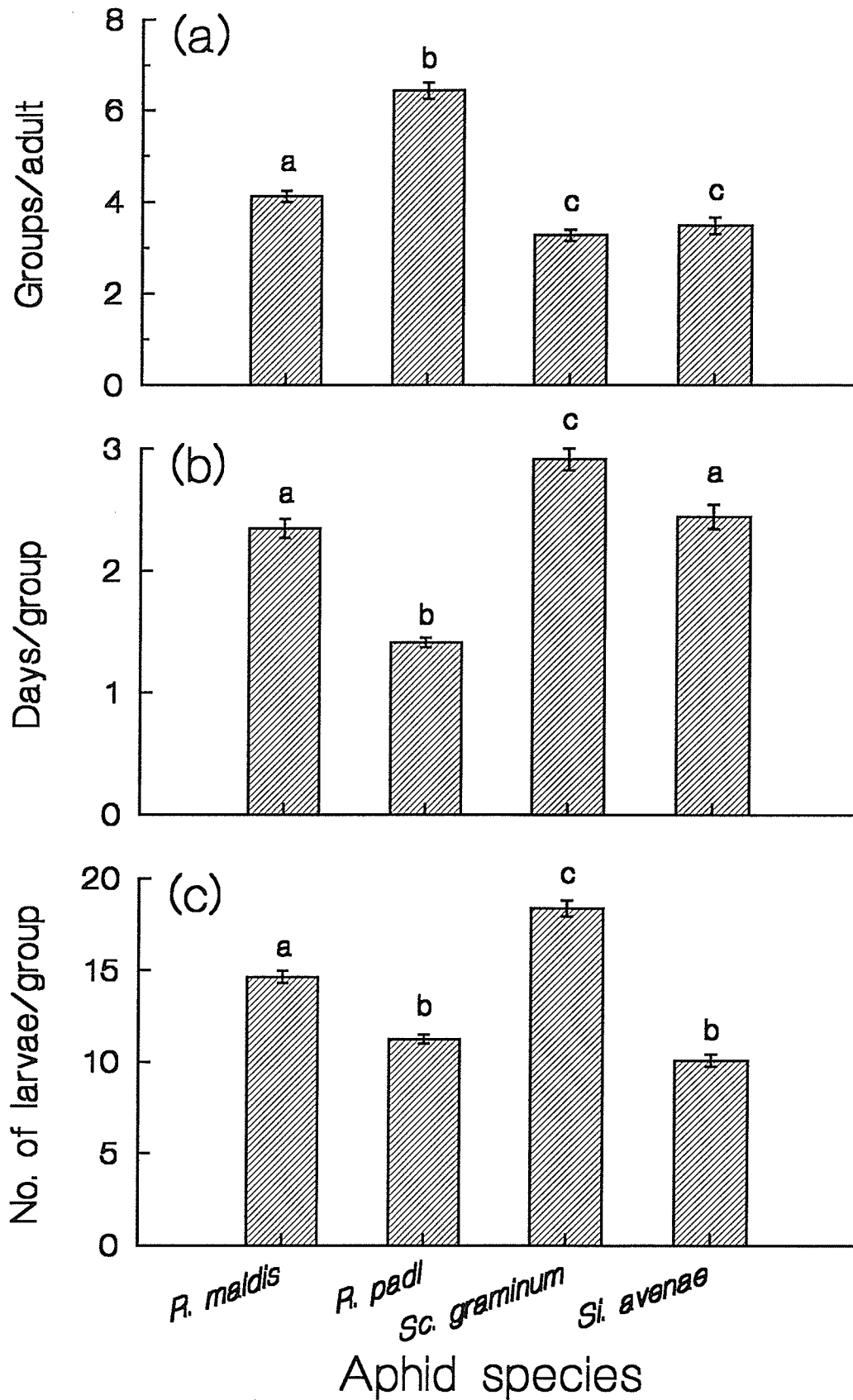


Fig. III-4. Cumulative percent dispersal of aphid larvae from their natal location. n = 33 larval groups per species.

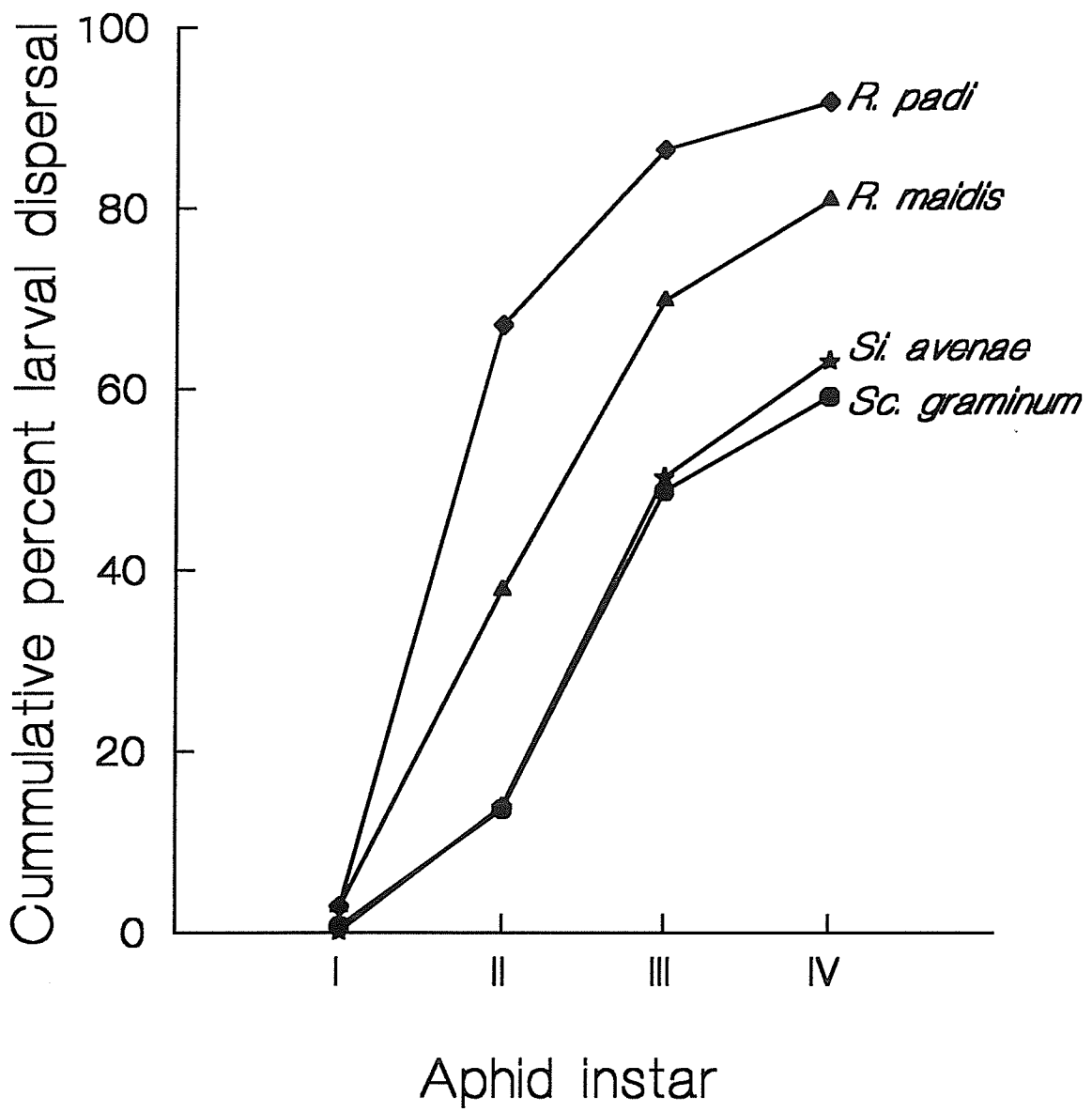
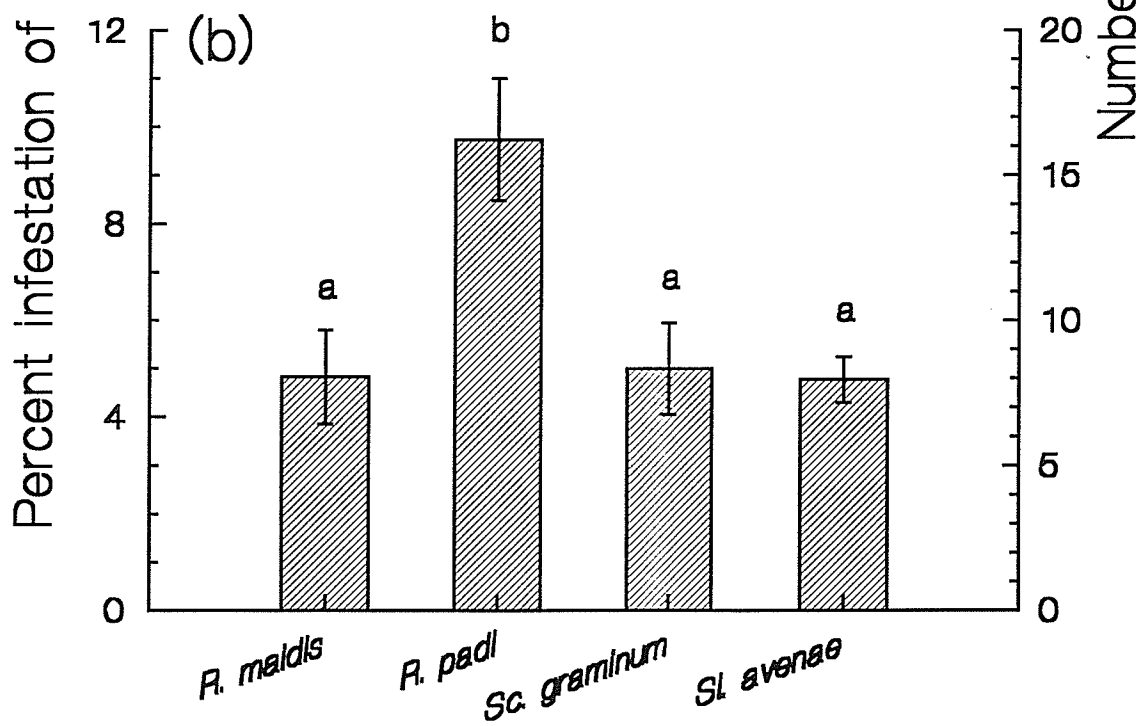
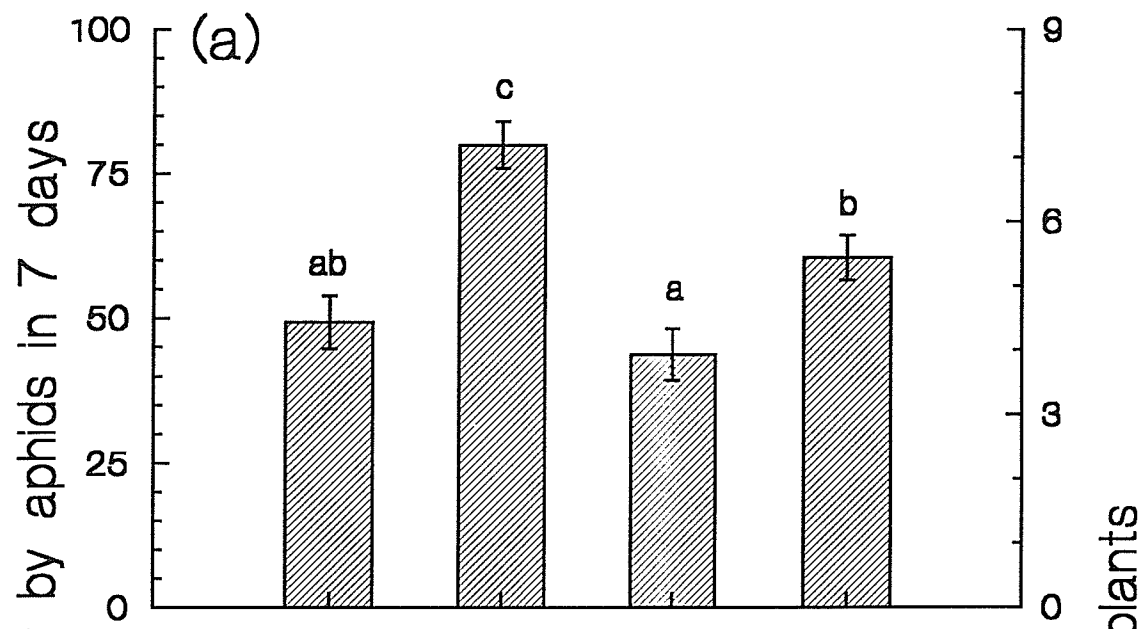


Fig. III-5. Mean (\pm s.e.) percent infestation of barley plants, seven days after the release of one aphid on:
(a) potted plants (9 plant arena). n = 16 pots/species
(b) plants in flats (170 plant arena). n = 10 flats/species.

Bars with the same letter(s) are not significantly different from one another using Tukey's studentized range test, $P > 0.05$.



Aphid species

Fig. III-6. Mean proportion of cereal aphids at various distances from initial point of aphid release on barley plants in flats after seven days. n = 10 flats/species.

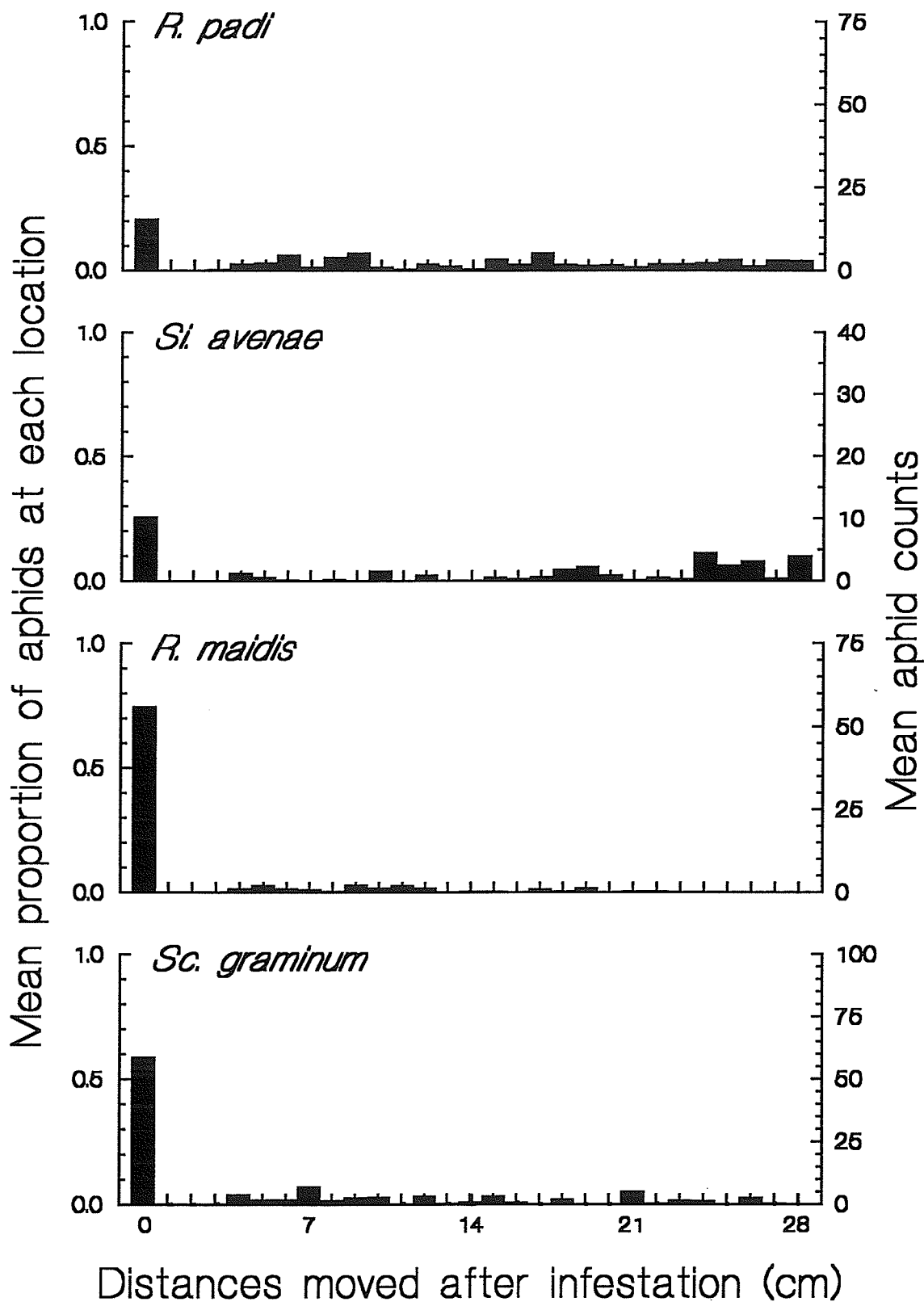


Fig. III-7. Mean proportion of cereal aphids at different times and at various distances from initial point of aphid release on barley plants in 20 X 20 m open field plots. n = 4 transects/sampling date.

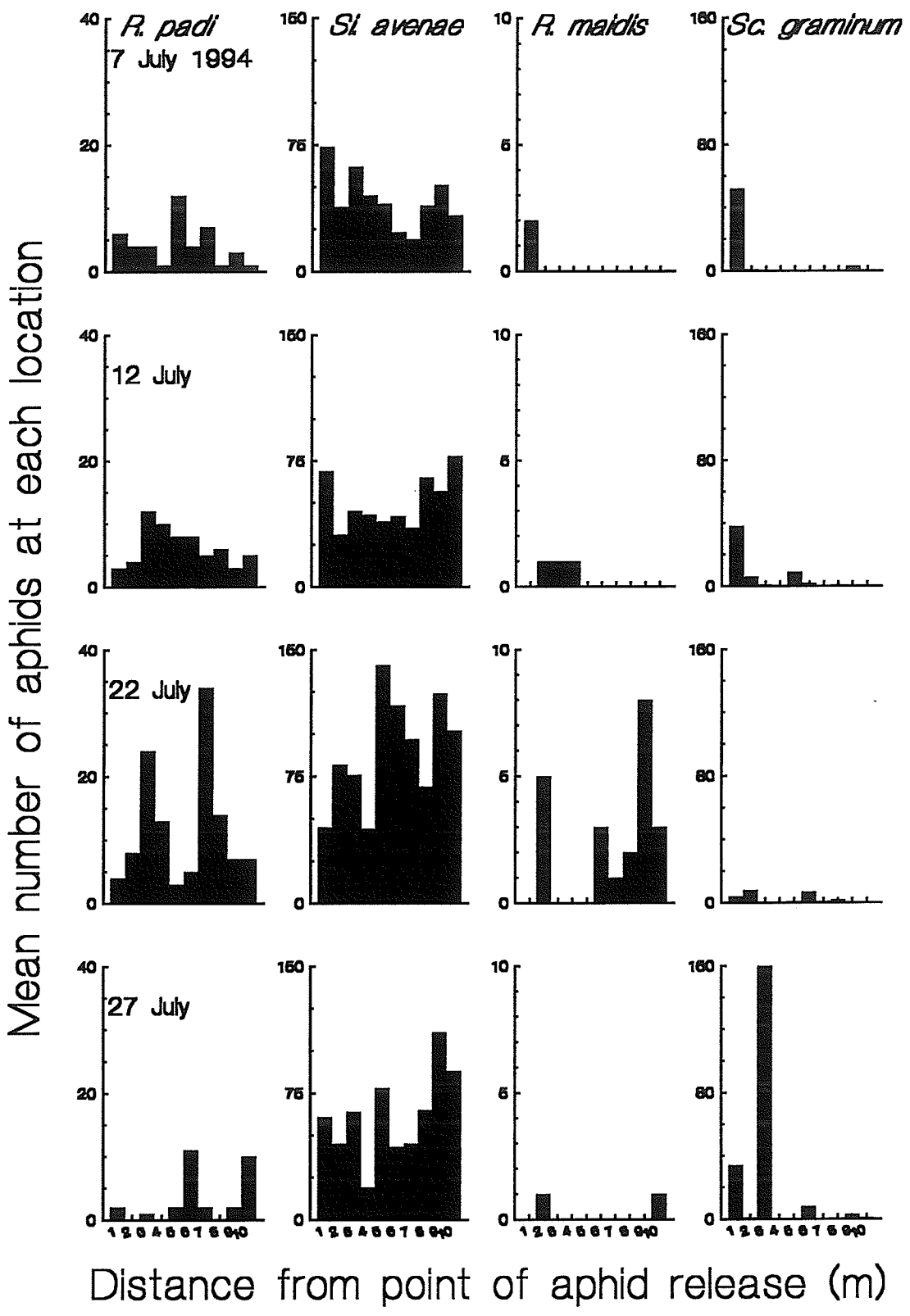
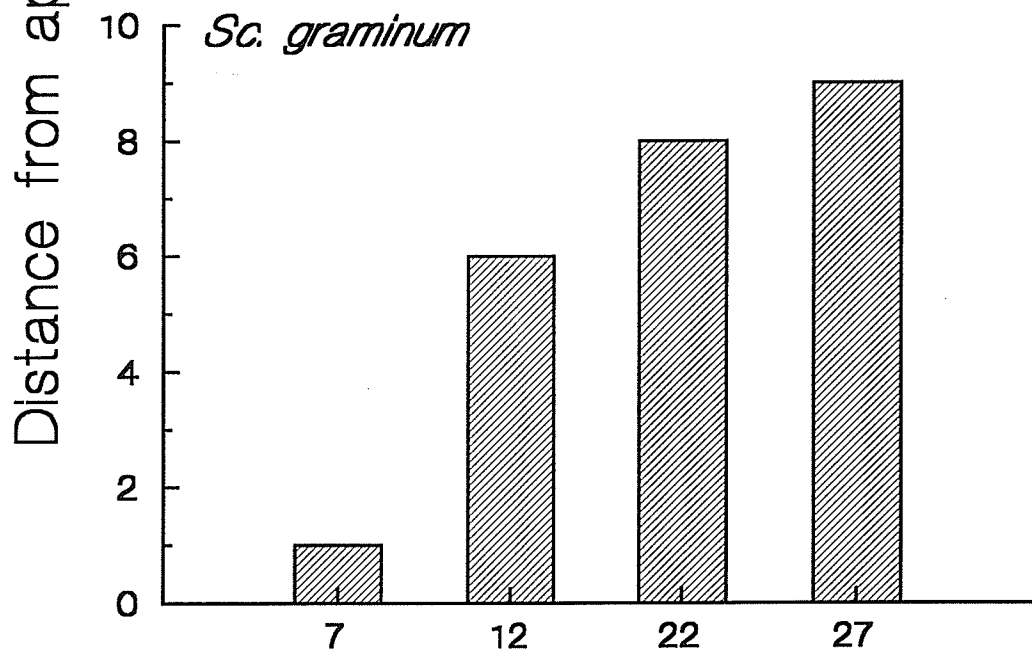
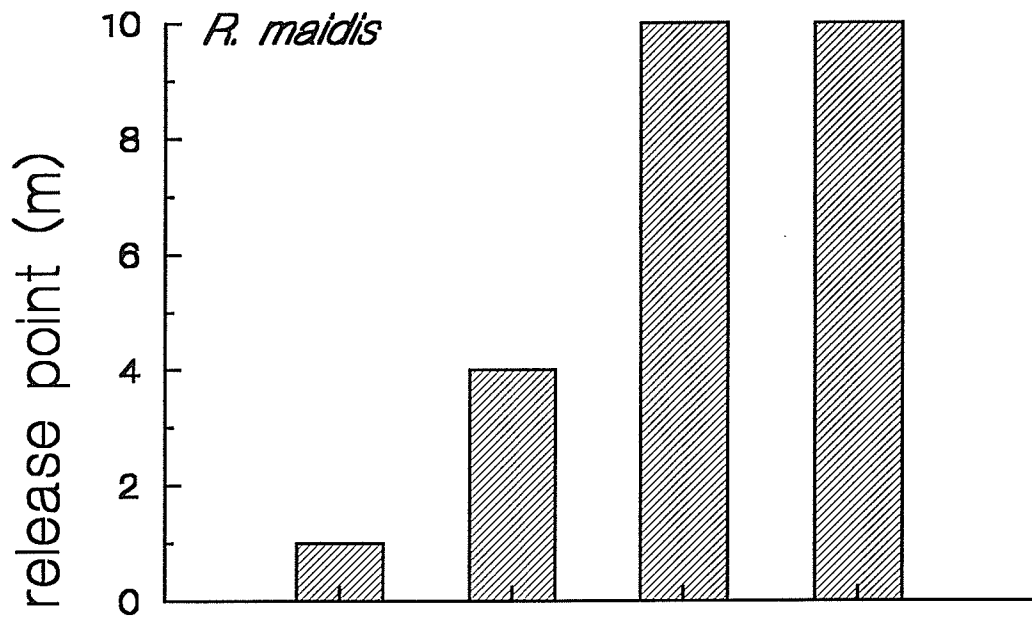


Fig. III-8. Distances moved by *R. maidis* and *Sc. graminum* at different times from the point of augmentation in 20 X 20 m open field plots. n = 4 transects/sampling date.



Date (July 1994)

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PART IV

WING PRODUCTION IN CEREAL APHIDS AND ITS SIGNIFICANCE TO DISPERSAL

ABSTRACT

The capacity for wing production by aphid species commonly found on cereal crops in Manitoba, *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae*, was evaluated by crowding aphids artificially in petri-dishes and more naturally on whole barley plants. In petri-dishes, groups of 10 adults of the same species were crowded for different time periods, while on whole barley plants different group sizes of adults were crowded. All aphid species responded to the crowding stimulus in petri-dishes by producing winged forms, but their degree of response differed. The proportion of winged forms increased as the crowding period was increased. Without crowding, *Si. avenae* produced winged and non-winged forms in alternating generations. On whole barley plants, the proportion of winged forms increased as crowding group size was increased except for *Sc. graminum*, which did not produce any winged progeny on whole plants. Differences in the ability to produce winged forms can be used to explain the distribution patterns in the fields. Wing production appears to play a major role in collapse of aphid populations at plant maturity.

INTRODUCTION

Aphids are important pests of cereal crops in North America (Apablaza & Robinson, 1967; Ba-Angood & Stewart, 1980; Johnson & Bishop, 1987; Feng & Nowierski, 1992). Aphid species reported to occur on cereal crops in Manitoba include, greenbug *Schizaphis graminum* Rondani (hereafter referred to as *Sc. graminum*), bird cherry oat aphid *Rhopalosiphum padi* L., corn leaf aphid *R. maidis* Fitch, English grain aphid *Sitobion avenae* Fabricius (hereafter referred to as *Si. avenae*) and rose grain aphid *Metopolophium dirhodum* Walker (Robinson & Hsu, 1963). There is no evidence that these species can overwinter in Manitoba or the northern plains of U.S.A. where winters are long and cold (Robinson & Hsu, 1963; Irwin & Thresh, 1988). Since large displacements of aphids have been recorded in North America (Bruehl, 1961; Johnson, 1969), the northern areas are thought to be re-invaded annually by migrants from the south (Kieckhefer & Kantak, 1986; Irwin & Thresh, 1988). Aphids are weak fliers and rely on wind currents to disperse widely (Kieckhefer & Lytle, 1976; Loxdale *et al.*, 1993).

Aphids are minute insects and cannot walk for long distances. Primary colonization of cereal fields is accomplished by flying aphids. Wing production in aphids is regulated by changes in density (Johnson, 1965; Lees, 1967) and/or food supply (Walters & Dixon, 1982; Howard & Dixon,

1992). Other factors implicated in production of winged forms include, temperature, photoperiod, and intrinsic factors (Kawada, 1987).

The proportion of fourth instar nymphs with wing buds in the field has been used to estimate the production of winged emigrants (Lamb & MacKay, 1979; Watt & Dixon, 1981) as winged forms are likely to leave the crop shortly after molting to the adult stage (Rabbinge *et al.*, 1979). Watt & Dixon (1981) and Cannon (1985) reported that the proportion of *Si. avenae* larvae that had wing buds in the field is significantly correlated with aphid density. Lees (1967) demonstrated that tactile stimulation occurring among groups of crowded aphids leads to production of winged forms.

Since aphid infestations in Manitoba are thought to originate from the south each year, an understanding of their ability to produce migrants and spread from one crop field to another is important in determining their pest status. This paper reports the results of comparative studies on production of winged dispersers by four aphid species that are commonly found on cereal crops in Manitoba. Wing production was evaluated by crowding non-winged adults on an artificial situation and on whole barley plants and their response in production of winged progeny was noted.

MATERIALS AND METHODS

Aphid cultures of *R. maidis*, *R. padi*, *Sc. graminum* and *Si. avenae* were established and maintained as uncrowded colonies on cut pieces of barley leaf placed in 60 X 15 mm petri-dishes (rearing dishes). Both stock and experimental cultures for pre-natal crowding were maintained at a constant temperature, $20 \pm 1^{\circ}\text{C}$ and photoperiod 20 h L: 4 h D in controlled environment chambers (see chapter 3 for details).

Crowding in petri-dishes

Thirty-fourty first instar larvae of each species were isolated individually in rearing dishes and raised to the adult stage. Except for *Si. avenae*, only non-winged aphids were used for crowding experiments. Since *Si. avenae* was observed to produce winged and non-winged forms in alternating generations (Part I), both morphs were subjected to crowding to determine their response in wing production. To obtain the required number of experimental insects per morph from *Si. avenae*, 40-50 first instar larvae, from each of winged and non-winged mothers were isolated individually in rearing dishes and raised to the adult stage. The progeny from winged and non-winged mothers developed into mainly non-winged and winged forms respectively. The progeny from the other three species developed into mainly non-winged forms.

From these, 20 pre-reproductive adults of each species or morph were selected for use in the crowding experiment. They were put individually in rearing dishes containing two pieces of barley leaf and placed in growth chambers to produce offspring. After 24 hours, the adults were subdivided into two batches of 10, one to undergo crowding and the other to serve as control (Fig. IV-1). Aphids from the crowding group of the same species were placed in a 60 X 15 mm petri dish with moistened filter paper for a predetermined time period (4, 8, 16 or 24 hours), after which the adults were individually transferred into new rearing dishes. At the same time aphids from the control batch were transferred into fresh dishes. Aphids in both batches were allowed to produce offspring for 48 hours and then transferred to a new set of rearing dishes for another 48 hours after which the adults were discarded. All aphid offspring obtained before and after crowding were raised to fourth instar, when records of wing production could be taken without difficulty. Experiments on each crowding period were replicated three times for each species or morph.

Crowding on whole barley plants

Single barley plants were established in cone shaped plastic tubes measuring 21cm long, 4cm in diameter at the

wide end and 1cm in diameter at the narrow end. The soil medium used was Metro-mix® and watered using nutrient solution (See Chapter 3 for details). The tubes were placed in a rack, designed to hold 98 tubes. Experiments were conducted on the laboratory bench, at room temperature which varied from 18-22° C. Overhead fluorescent lights were used to supplement room lighting and provide a photoperiod of 16 hours light and 8 hours dark. At the one leaf stage, G. S. 11 (Tottman and Makepeace, 1979), the plants were infested with pre-reproductive non-winged adult aphids at the rates of one, two or five aphids per plant per species. Clear plastic tubes, with fine mesh at the top, and measuring 23 cm long and 4 cm in diameter, were used as aphid proof cages (Fig. IV-2). The winged morph of *Si. avenae* was not used in this experiment because it never settled on the plant but always flew within the cage and stayed on the roof of the cage. After 24 hours all adults were removed and their offspring were raised in the cages until they developed to fourth instar when their morphs were determined.

RESULTS

All aphid species responded to the crowding stimulus by production of winged forms. Seven clones of *R. padi* were also subjected to the crowding stimulus. The results are presented in Appendix 3. Fig. IV-3 shows the response to crowding by *R. maidis*, *R. padi* and *Sc. graminum*, and Fig.

IV-4 shows wing development by progeny of crowded winged and non-winged mothers of *Si. avenae*. For all species, the proportion of wing production increased as the the crowding period was increased. Control treatments of *R. maidis* and *Si. avenae* produced winged progeny although they did not experience crowding. Over 80% of the progeny of *R. padi* and *R. maidis* developed into winged forms after 16 and 24 hours of crowding respectively. There was no difference ($P>0.05$) in wing production by *R. padi* between 16 and 24 hours of crowding. *Sc. graminum* had very little or no response to 0, 4, and 8 hours of crowding, but with 16 and 24 hours of crowding, over 50% of the progeny developed into winged forms.

Si. avenae was observed to produce winged and non-winged forms in alternating generations. Without crowding, non-winged adults produced over 80% winged offspring, while winged adults produced over 90% non-winged offspring. Both adult morphs of this species responded to crowding by producing a higher proportion of winged offspring.

Fig. IV-5 shows the effect of crowding non-winged adult aphids on whole barley plants, on development of their progeny into winged forms. Wing production by *R. maidis*, *R. padi* and *Si. avenae* increased as the number of adults in a crowding group are increased. With a crowding group of five adults, the proportions of progeny that developed into

winged forms were 53%, 85.5% and 96.6% for *R. maidis*, *R. padi* and *Si. avenae* respectively.

Sc. graminum did not produce any winged offspring in response to the crowding groups chosen. In the treatments that had a crowding group size of five adults, the offspring of *Sc. graminum* had almost killed the plant by the time records were taken about 6 days after infestation; plants were drooping and wilting at this time. However, plants infested by the other three aphid species were still green and upright and did not show any symptoms of impending death.

DISCUSSION

It is clear from the results that crowding aphids leads to development of winged forms. In the field situation, an increase in aphid density per host plant increases the frequency of aphid contacts and this brings about crowding. The similarity of wing production trends by aphids crowded in petri-dishes and on whole barley plants appears to validate the the petri-dish crowding technique. The results indicate marked differences between the species in their response to crowding. The order of response to wing production from the highest to the least is *Si. avenae*, *R. padi*, *R. maidis* and *Sc. graminum*. In a similar study, involving five species of cereal aphids, *R. padi*, *R. maidis*, *M. dirhodum*, *Hysteroneura setariae* (Thomas) and *Sitobion* nr.

fragariae, MacKay & Lamb (in press) reported that *R. padi* produced significantly ($P < 0.05$) more winged offspring at 4 and 16 hours of crowding than *R. maidis* and *M. dirhodum* and that there was no significant difference in wing production between the latter two species. Among all the species examined, they ranked *R. padi* as first in the tendency to disperse.

The differences in the ability of different aphid species to produce winged forms may be related to the availability of suitable feeding sites on host plants and the behaviour of individual aphids in the presence of other individuals. In Britain, Watt (1979) reported that before all the ears had emerged, 42% of the tillers in a local wheat field were infested with *Si. avenae* even though the average population density was low (2 aphids/tiller). Grasses in the early stages of earing provide *Si. avenae* with a high quality habitat (Walters & Dixon, 1982). Such a habitat remains suitable for a relatively short period of time sufficient only for the aphid to produce one or two generations. Since it takes approximately 13 days for this species to complete development under field conditions (Watt & Dixon, 1981), it appears to be of considerable advantage that both non-winged and winged adults are able to produce winged progeny, which fly off and colonize other favourable habitats. The high rate of wing production by *Si. avenae*

may be an adaptation to the very ephemeral nature of its preferred feeding habitat, flowering grasses.

Non-winged adults and juveniles of *R. padi* make frequent movements between plants (Part III) probably to avoid the occurrence of crowded situations. This type of behaviour leads to rapid spread of infestations. In my experiments aphids were restricted in their movements to the crowding arenas and the frequency of individual contacts was high, especially for the long crowding periods. If all other factors in the field are constant, aphid colonies of similar sizes to those tested in the laboratory would be expected to provide a low stimulus for wing production because the aphids would have more space in which to move. However, the conditions in the field are not constant and involve a complex of variable factors that interact within a framework of species-specific behaviour to determine the actual degree of wing production. For example, wing production by aphids is not only triggered through crowding but also through the condition of the host plant (Sutherland, 1969).

In *Si. avenae*, the morph of the parent appears to be important in determining the proportion of winged forms produced, with non-winged parents producing more winged offspring than winged parents. In many species, winged aphids produce winged progeny rarely if at all (Noda, 1959;

Shaw, 1970; MacKay, 1977). It is quite clear that this species produces winged and non-winged forms in alternating generations. This polymorphism strategy combines the benefits of the fast developmental rate and high fecundity of non-winged forms (Vickerman & Wratten, 1979; Dixon, 1987) with the high dispersal capacity of the winged forms. Fig. III-4b demonstrates that crowding winged mothers results in production of a high proportion of winged dispersers. Results from this study are in agreement with the findings of Watt & Dixon (1981), that unflown winged offspring of *Si. avenae* can be induced by crowding to give birth to a high proportion of winged forms. Noda (1959) reported that production of winged forms by winged mothers of *R. padi* and *R. maidis* is less common than in *Si. avenae*. Wanjama (1986) reported that winged mothers of *Sc. graminum* produce winged progeny when crowded as fourth instars and soon after the final molt.

Both mothers and offspring of *R. padi* and *Si. avenae*, respond to crowding (Dixon & Glen, 1971; Watt & Dixon, 1981). The more intense the crowding, the higher the proportion of development of winged forms, especially if both mothers and offspring experience crowding (Dixon, 1985). In this study, both mothers and offspring experienced crowding on barley plants. In the dishes, mothers and offspring also experienced crowding to a certain

extent in that the adult and its offspring remained in the same dish for 48 hours.

The period when aphids are sensitive to crowding stimulus or group effect differs among species. Noda (1959) reported that *R. padi* is most sensitive to tactile stimulation in the middle of its larval period. Presumably, this would still be pre-natal stimulus since it would be too late to affect the wing buds. Some species appear to continuously monitor crowding and a period of isolation following a period of crowding partly reverses the effects of crowding and intermediates develop (Dixon, 1973, Wanjama, 1986). In other species, crowding mothers alone may not result in production of winged progeny. Tests on wing production in the pine aphid, *Cinara pinea* (Mordv.) revealed that maternal experience of crowding did not have any effect on the larval response (Kidd & Tozzer, 1984).

R. maidis occurs in aggregated colonies within the central leaf of immature plants (Part II). The production of some winged progeny by this species even in the absence of crowding suggests that the winged forms play a role in the dispersal of this species from one plant to another. *M. dirhodum* is also reported to produce winged forms without crowding (MacKay & Lamb, in press). *Sc. graminum* is a leaf feeder and also occurs in aggregated colonies. In a growing season, the plants remain in a suitable condition for

infestation by *Sc. graminum* for a long time. Therefore, this species does not have to move for long distances in search of suitable habitats unless the host quality deteriorates with age. Based on its tendency to aggregate, it may be safe to assume that *Sc. graminum* is less sensitive to tactile stimulation from the presence of other individuals within a colony. This possibly explains the reason for the low sensitivity of this species to 0, 4, and 8 hours of crowding. Unlike *R. maidis* and *R. padi* which appear to monitor population density by producing more winged progeny as the period of crowding is increased, the non-responsiveness of *Sc. graminum* at 0, 4, and 8 hours of crowding and the strong response at 16 and 24 hours of crowding suggest a threshold limit above which the development of winged progeny is triggered. If the threshold theory for *Sc. graminum* is correct, then aphids crowded on whole barley plants probably did not receive a sufficient stimulus to trigger development of winged progeny.

Apart from causing necrotic lesions on host plants through feeding, *Sc. graminum* also affects plant growth form (Part V). In a field of wheat at milk stage in Manitoba, it was found that flag leaves were rolled and bent over and inside each of the rolled leaves was a colony of *Sc. graminum*. There is probably a minimum group size necessary

to cause this microhabitat and make a gall-like microhabitat.

Interactions between different species in the field may also play an important role in aphid dispersal. Lamb & MacKay (1987) investigated the role of interspecific interactions between the pea aphid, *Acyrtosiphon pisum* (Harris) and the blue green aphid, *A. kondoi* Shinji in Australian alfalfa fields on production of winged forms, and reported a positive correlation between percentage of larvae with wing buds and total aphid density. They reported that the pea aphids respond in the same way as with intraspecific contacts. Since cereal aphid species commonly occur on crops together, it is likely that physical contacts between them similarly stimulate production of winged forms.

The condition of the host plant also influences wing production in aphids. On a dying or wilting plant or if food deteriorates, aphids become more "restless", and are more likely to touch one another. *A. pisum*, when placed on mature bean leaves develop winged forms (Sutherland, 1969), indicating that poor food in itself may induce wing production. In *Si. avenae*, winged forms develop in response to changes in the nutritional quality associated with the ripening of the seed (Dixon, 1985). Watt & Dixon (1981) found that when mothers reared on the ears of grasses at flowering are crowded in glass vials for short periods, they

give birth to proportionally fewer winged offspring than when mothers are similarly treated but reared on mature ears. Branson & Simpson (1966) found that the percentage of alate *R. maidis* on nitrogen deficient sorghum plants was twice that on plants that were not deficient. It follows that the stimulus that triggers production of winged forms in aphids is brought about by increased interaction between individuals as a result of an increase in aphid density or "restlessness" of aphids on a poor quality plant.

Watt (1979) observed a steady increase in production of winged forms in *Si. avenae* three weeks before the aphid population declined. At ear emergence of barley, 87.4% of large larvae of *R. maidis* on the flag leaf had wing buds (Part II). Therefore, migration of aphids through flight may be a major factor responsible for collapse of aphid populations at plant maturity.

CONCLUSIONS

An increase in aphid density leads to crowding and the consequent frequent contacts between individuals produce a stimulus that causes production of winged forms. All four aphid species examined respond to maternal experience in crowding by production of winged forms. An interaction between crowding and species specific behaviour determines the actual degree of wing production as a response to a crowding stimulus.

Si. avenae has the highest capacity for production of winged dispersers. For this species, the morph of the parent is important in determining production of winged forms: non-winged parents produce a high proportion of winged offspring and winged parents produce a high proportion of non-winged offspring. Without crowding, this species produces winged and non-winged forms in alternating generations. *R. padi* ranked second in production of winged forms in response to crowding. Without crowding, this species produces virtually all non-winged forms. *R. maidis* continuously produces low proportions of winged progeny without the influence of crowding but when crowded situations occur, this species produces winged forms in proportion to the level of crowding. *Sc. graminum* has the least capacity for production of winged forms when subjected to crowded situations. This species is non-responsive to low levels of crowding but after a certain crowding threshold is reached, there occurs an abrupt switch to production of winged forms.

Fig. IV-1. Design for the experiment testing the effect of artificially crowding adult aphids on production of winged forms.

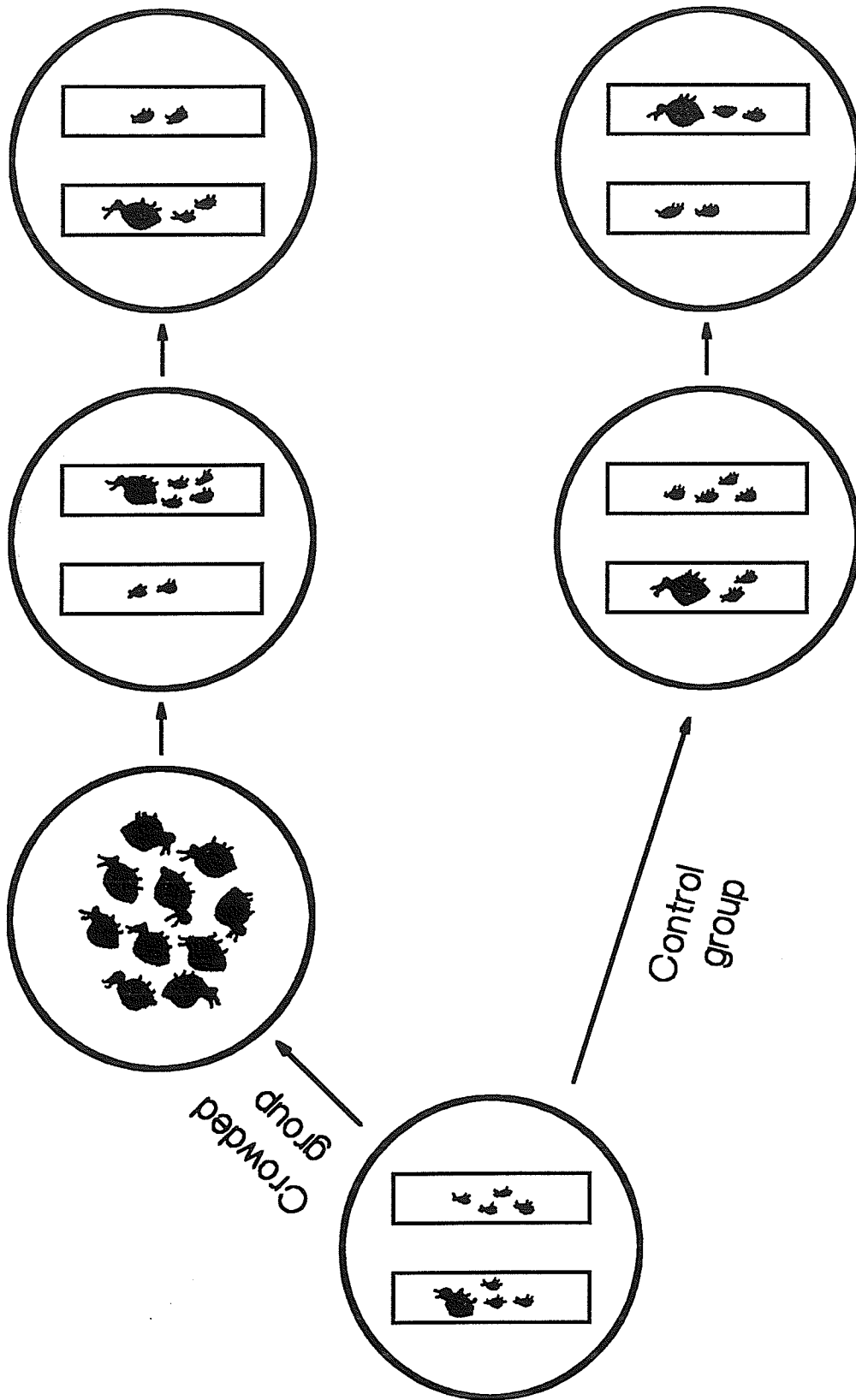


Fig. IV-2. Single barley plants in plastic cages in which different groups of adult aphids of a species were crowded for 24 hours to determine their response in production of winged progeny.

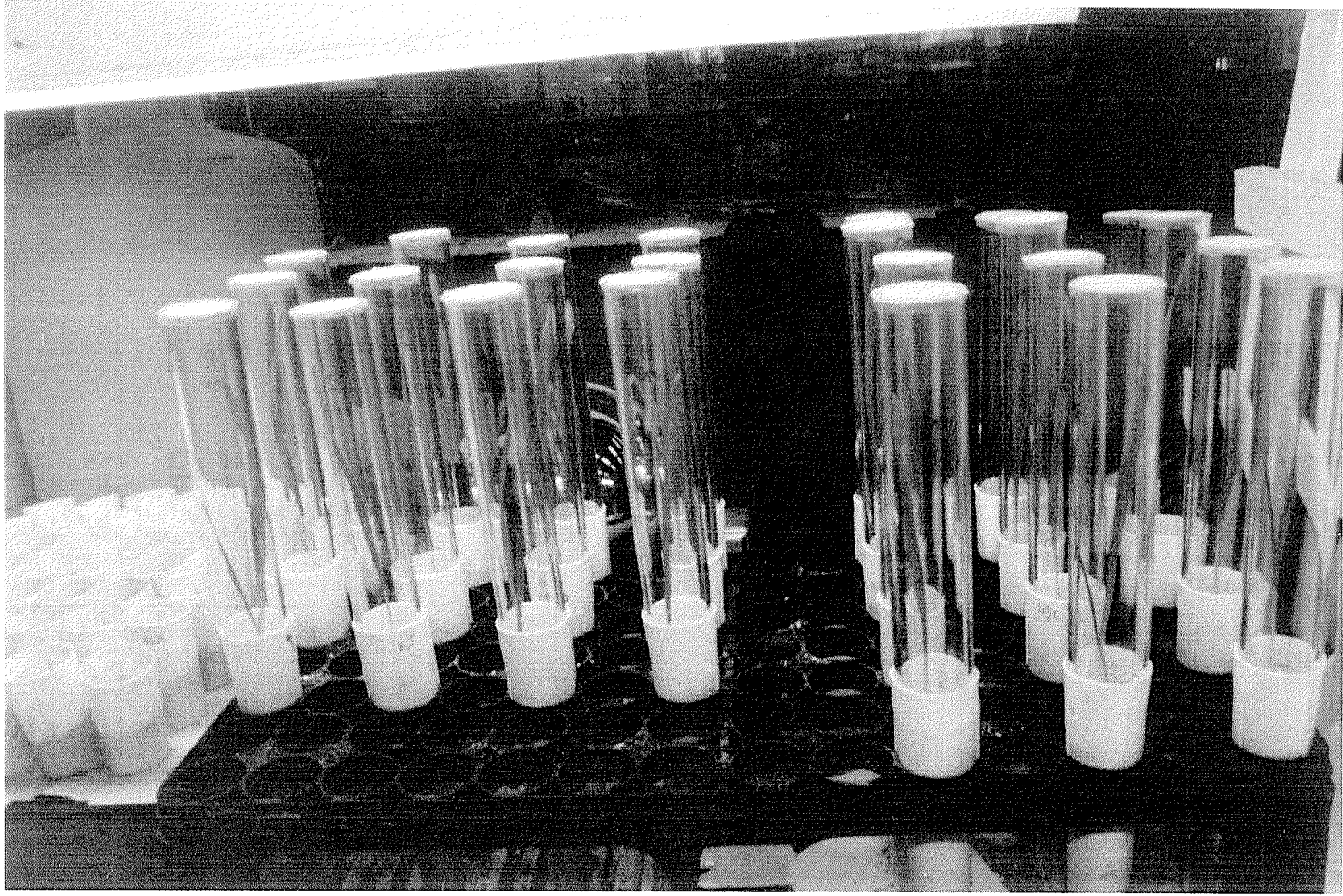


Fig. IV-3. Mean (\pm s.e.) proportion of winged progeny produced by *R. maidis*, *R. padi* and *Sc. graminum* after groups of 10 non-winged adults of each species were separately crowded in petri-dishes for different time periods. Each test of 10 was replicated three times per crowding time.

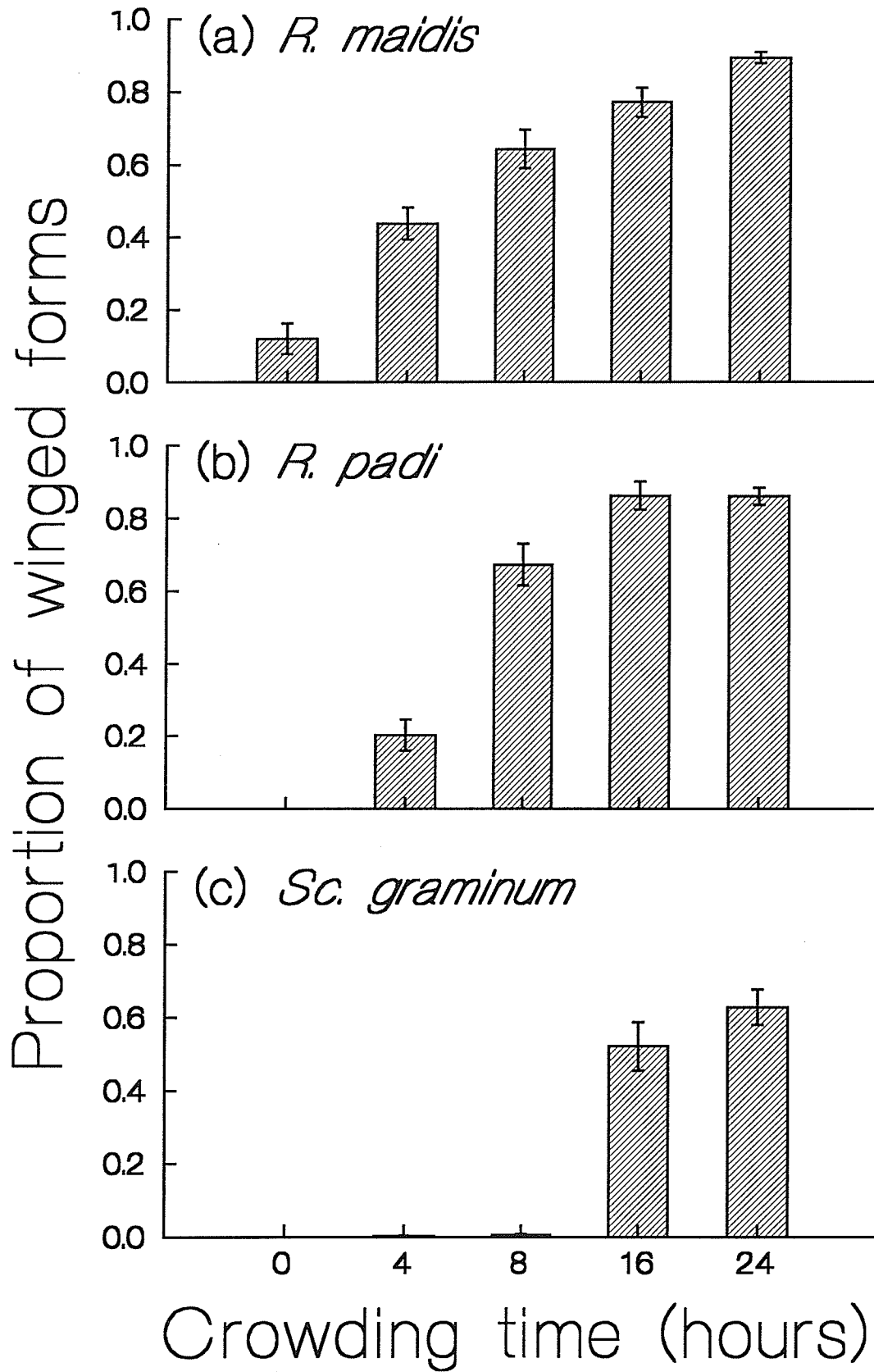
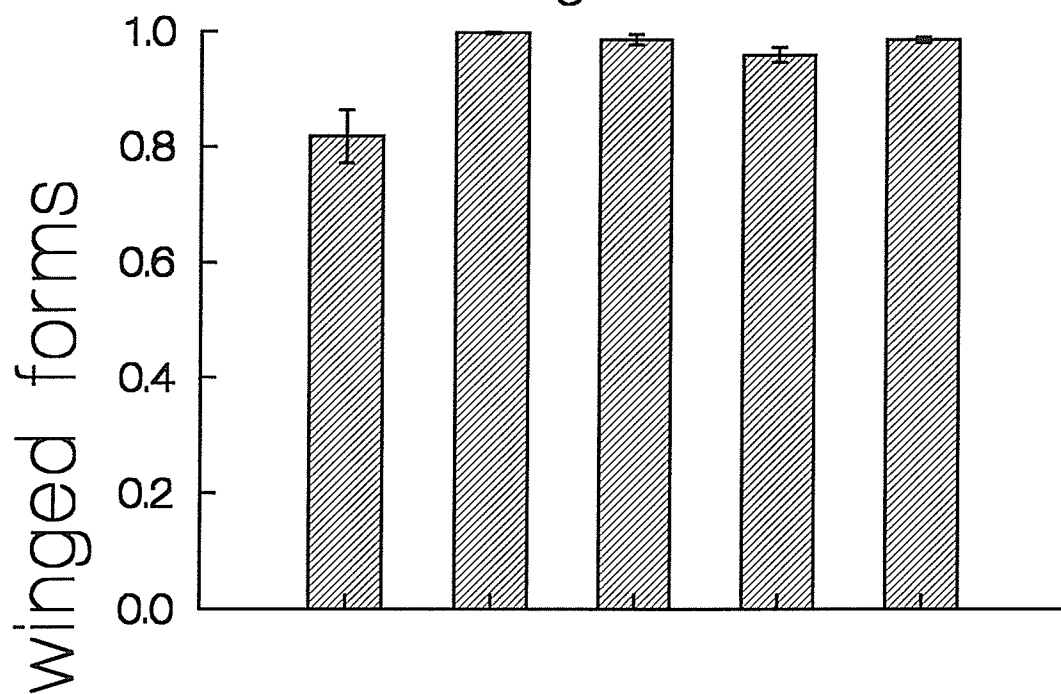


Fig. IV-4. Mean (\pm s.e.) proportion of winged progeny produced by *Si. avenae* after groups of 10 non-winged and 10 winged adults were separately crowded in petri-dishes for different time periods. Each test of 10 was replicated three times per crowding time.

(a) Non-winged mothers



(b) Winged mothers

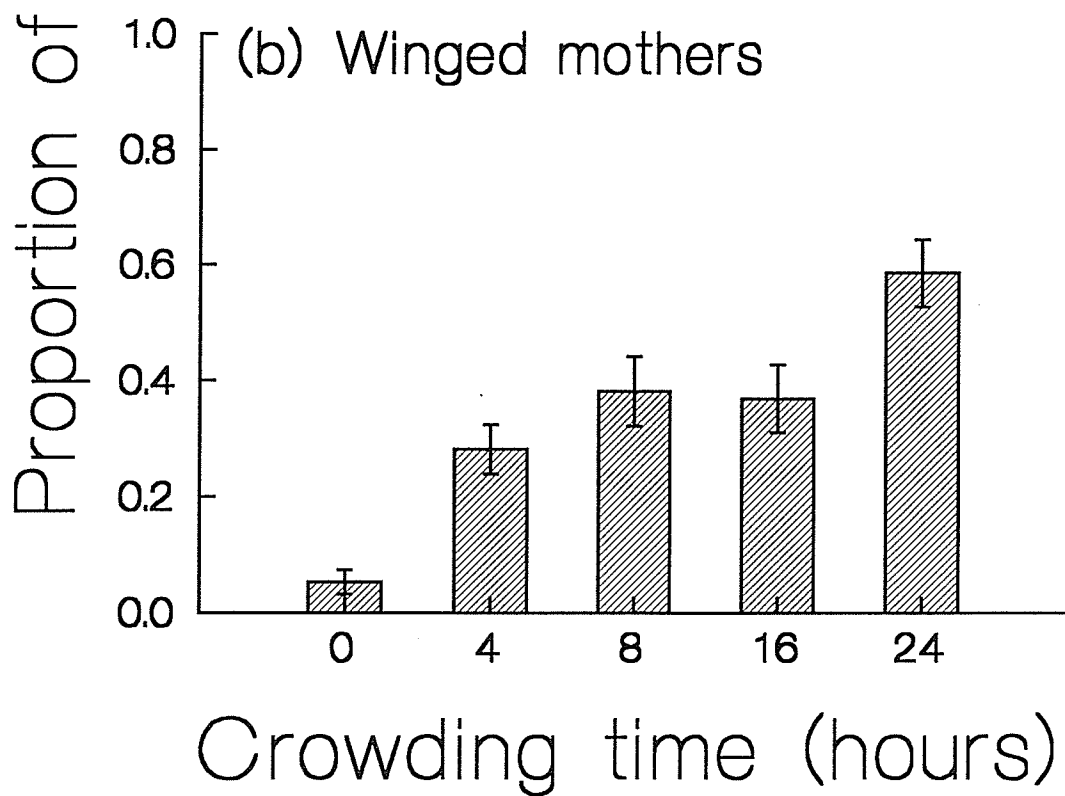
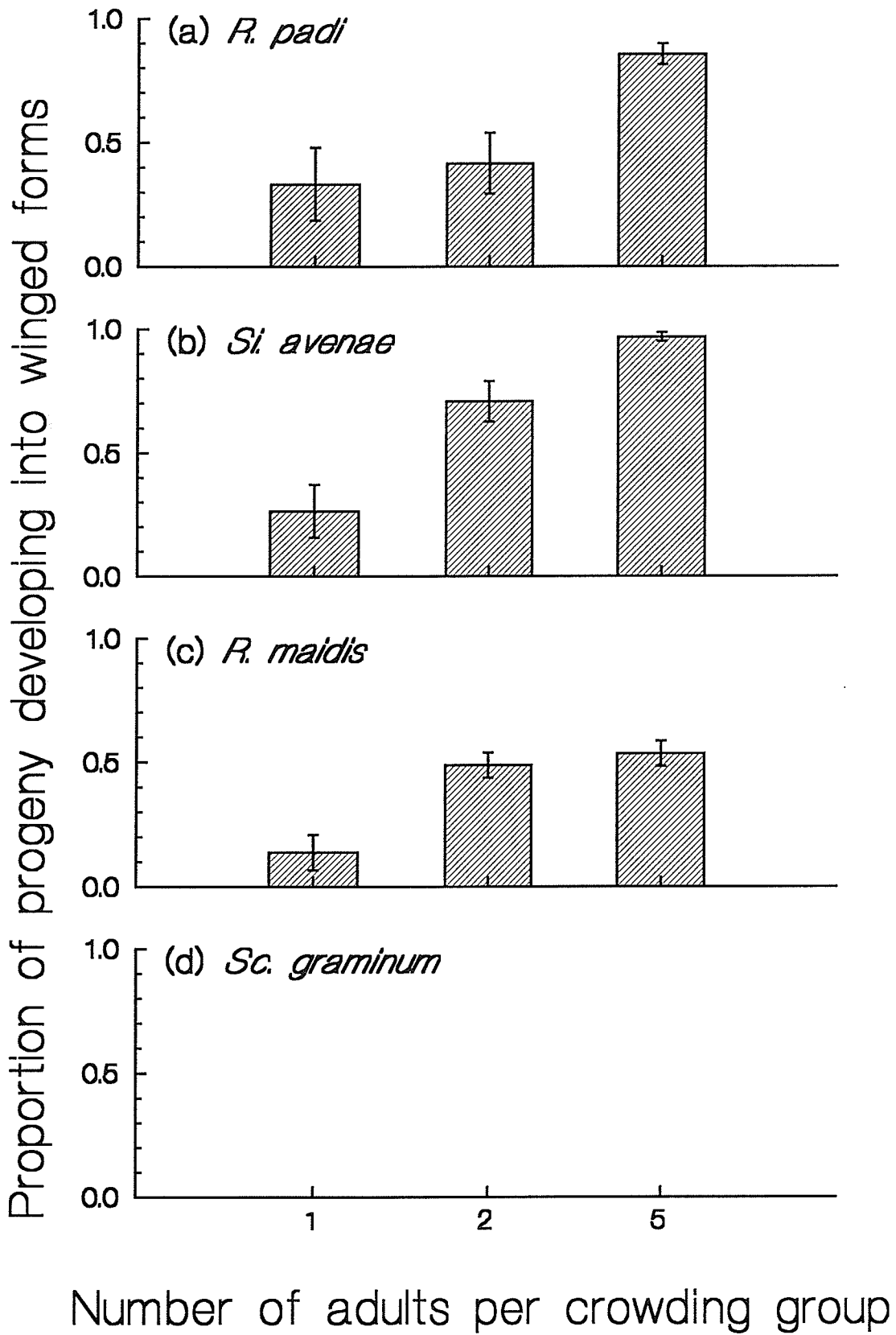


Fig. IV-5. Mean (\pm s.e.) proportion of winged progeny produced by cereal aphids after different groups of adults were crowded on single barley plants for 24 hours in plastic cages. $n = 11$ plants per crowded group per species.



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PART V

APHID PESTS OF CEREAL CROPS IN MANITOBA

ABSTRACT

A field survey of aphid pests attacking cereal crops in Manitoba was done at intervals of 8-9 days during the cropping season of 1994 in Manitoba. In each field, aphid records were taken from a total of 50 stations (1 tiller per station). The major species collected included *Rhopalosiphum maidis*, *R. padi*, *Schizaphis graminum* and *Sitobion avenae*. Vertical distribution of aphids varied with crop type and growth stage. Aphid populations on different crops fluctuated over the season, reaching peak populations in July. *Si. avenae* was the most abundant species and comprised 77.7% of the total aphids recorded. The appearance of *Si. avenae* early in the cropping season, its high abundance and rapid colonization of earing grain makes it a potentially serious pest of cereal crops in Manitoba.

INTRODUCTION

Wheat and barley are the major grain crops grown in the prairie regions of southern Manitoba. The crops are usually planted in late April and early May and develop to maturity in August. During the growing season, these crops are attacked by aphids, which are a threat to grain production.

The major species involved include the greenbug, *Schizaphis graminum* (Rondani) (hereafter referred to as *Sc. graminum*); bird-cherry oat aphid, *Rhopalosiphum padi* L.; corn leaf aphid, *R. maidis* (Fitch) and English grain aphid, *Sitobion avenae* (Fabricius) (hereafter referred to as *Si. avenae*) (Robinson & Hsu, 1963). These aphids are not known to survive the long and cold winters of Manitoba and are thought to migrate from the South during the growing season (Kieckhefer & Kantak, 1986; Irwin & Thresh, 1988). In Manitoba, cereal aphids are present from approximately June until they are killed by frost (Robinson & Hsu, 1963).

Serious crop losses caused by cereal aphids have been reported in the prairie provinces of Canada. In 1955, thousands of acres of late seeded barley were destroyed by *R. maidis* between June 21 and July 21 in western Canada (Robinson & Hsu, 1963). In 1986, in Alberta and Saskatchewan, a heavy infestation of *Sc. graminum* covering one million hectares of wheat resulted in serious yield losses (Haber, 1990). Studies by Kieckhefer & Kantak (1986), concluded that *Sc. graminum* and *R. padi* are the main aphid species most likely to threaten grain production in spring planted barley in the Northern Plains of the U.S.A. In 1994, a field study at the University of Manitoba experimental station, Glenlea (Parts II-III) established that *Si. avenae* was the most predominant species throughout

the growing season. Although it is recognised that the four aphid species are of economic importance in western Canada, their relative pest status is not known.

This paper describes the results of a survey done in 1994 in cereal fields in southern Manitoba in an attempt to document the major aphid pests, their relative abundance and patterns of distribution on their host plants.

MATERIALS AND METHODS

Field surveys of cereal crops in southern Manitoba were conducted at 8-9 day intervals from 16 June to 19 August, 1994. Each day, 5-7 fields spaced 5-10 km apart were sampled for aphids. In each field, aphid records were taken from a total of 50 stations spaced 10 m apart across two line transects starting from the same point on the field margin running to the interior at $\approx 90^\circ$ from one another and $\approx 45^\circ$ from the field margin. At each station, data were collected by randomly choosing one tiller and recording, crop type, aphid species and numbers on each feeding location along the height of the host plant (head, flag leaf, upper leaves, middle leaves, lower leaves, or stem). The importance of different aphid species as pests of cereal crops in Manitoba was ranked on the basis of their relative abundance.

RESULTS

All the major aphid species reported by Robinson & Hsu (1963) were found feeding on cereal crops. Table V-1 shows six species which were found reproducing on wheat, barley, oats or corn and their relative abundance. *Si. avenae* was by far the most abundant species and comprised 77.7% of the total aphids recorded. In all the small grain crops, this species was the most abundant while *R. maidis* was the most abundant on corn (Fig. V-1).

Vertical distribution of aphids varied with crop type and aphid species. Figures V-2 to V-5 show the distribution of each aphid species on the respective host plants during flowering-milk stage of wheat, barley and oats and immature stage of corn. *Si. avenae* mainly fed upon the head and flag leaf of the three small grain cereals (Fig. V-2). Colonies of *Si. avenae* and *R. padi* were loosely spread on the leaves. On the head of wheat and barley, *Si. avenae* and *R. padi* were found feeding on the glumes and on the rachis between spikelets. Higher numbers of both aphid species were found on the heads of wheat than on the heads of barley. On the head of oats, aphid colonies, with as many as 20 individuals per colony, occurred on the branches of the panicle especially at glume bases. *R. padi* was most abundant on the flag leaf of oats (Fig. V-3). On corn, *R. padi* occurred on the leaf sheaths near the base of the plant.

R. maidis was found in aggregated colonies within the inner surface of the central leaf of corn (Fig. V-4). On flowering barley, this species was most abundant on the flag leaf and almost all large larvae recorded had wing buds. *Schizaphis graminum* was found in very low numbers on the middle and lower leaves of wheat and barley (Fig. V-5).

Aphid abundance on different crops fluctuated over the entire season (Fig. V-6). *Si. avenae* was the only species recorded on wheat on the first sampling date, 16 June. This species remained the most abundant species throughout the season. On wheat, all aphid populations showed an increasing trend as the plants approached maturity. *Si. avenae* reached a peak on 22 July with over 1000 aphids/50 tillers while the population of other species appeared to be increasing by the last day of records on wheat crop on 10 August. On barley, three aphid species, *Si. avenae*, *R. padi* and *R. maidis* reached peak population numbers on 13 July, while *Schizaphis graminum* reached a peak on 1 August. Populations of the two species recorded on oats, *Si. avenae* and *R. padi* continued to rise early in the season, reached a peak on 22 July and then started falling.

DISCUSSION

The occurrence of aphids on cereal crops in Manitoba early in the cropping season and the increase in their populations as the crops approach maturity is suggestive of

their potential damage to these crops. The high abundance of *Si. avenae* throughout the season indicates that this pest is well adapted to the prevailing conditions in southern Manitoba and appears to be the most important cereal aphid in this region. On wheat, peak numbers of this species were recorded at milk stage, on 22 July, with most individuals feeding directly on the filling grain. Population levels of this species on the three small grain crops, wheat, barley and oats, exceeded the economic threshold of 12.5 aphids per tiller (Elliott et al. 1990). The mean *Si. avenae* numbers per tiller were 50.3 on wheat on 22 July, 18.3 on barley on 13 July and 18.4 on oats on 22 July. Aphid population levels particularly on wheat possibly caused economic yield losses. The feeding behaviour of *Si. avenae* combined with its high reproductive capacity (Watt, 1979) and rapid colonization of ears (Dean, 1973) largely accounts for its pest status.

It is apparent that aphids locate themselves on the most nutritious parts of the host plant. The occurrence of *R. padi* on the heads of the small grain cereals and on the flag leaf of oats enables it to derive nutrients destined for the filling grain. This feeding behaviour was quite noticeable on the oat crop where aphids aggregated at the glume bases. In a field of wheat population size of *R. padi* on the heads was 15.3 aphids per tiller which was above the

economic threshold (Elliott et al., 1990). This suggests that this species possibly causes economic yield losses. Findings from this study also show that *R. padi* and *Si. avenae* prefer to feed on the heads of wheat than on barley, possibly because as the grain matures the surrounding paleae of barley become hard and difficult to penetrate. George (1974) reported that, on barley, peak numbers of *Si. avenae* occur on the leaves with only a few individuals on the ear.

Despite the close proximity of corn fields to wheat fields, barley fields and oat fields, the occurrence of only two aphid species on corn, *R. maidis* and *R. padi* indicate that aphid species are selective in their choice of host plants. *R. maidis* is the most important aphid species on corn. Among the small cereal crops, this species apparently prefers barley to wheat and oats because this species was only recorded on barley. Late seeded barley has been reported to suffer heavy yield losses from infestation by *R. maidis* (Robinson & Hsu, 1963). Its restriction of feeding to the inner surfaces of the central leaf masks its detection and accurate estimation of numbers (Kieckhefer & Kantack, 1986). Its impact may therefore be underestimated. On flowering barley, the open leaves are no longer a suitable habitat for this species and the aphids develop into winged forms that fly off in search of host plants suitable for colonization.

Sc. graminum was present in very low numbers suggesting that either the conditions were not suitable for growth and reproduction of this species or there may not have been sufficient or timely migrations from the south to be able to develop significant infestations. This species is implicated as one of the most important economic pests of cereal crops in the U.S.A. (Kring and Gilstrap, 1983) and it may also be a threat to grain production in Manitoba. As aphid infestations on cereal crops in Manitoba appear to result from long range migrations on wind currents from the south, the timing of arrival of initial colonizers may be a major factor determining their effect on cereal crops.

CONCLUSIONS

On the basis of aphid abundance and feeding behaviour, it can be concluded that *Si. avenae* was the greatest threat to grain production in Manitoba in 1994. Its appearance on cereal crops early in the season combined with its fast colonization of earing grain enables rapid spread of infestations. *R. padi* was the second most important species in Manitoba in 1994. Its feeding on the head during grain filling directly reduces grain yields. *R. maidis* and *Sc. graminum* did not occur in sufficient numbers to cause a threat to grain production in 1994. However, depending on arrival periods of these species, they are also a potential threat to grain production especially on late seeded crops.

Table V-1. Aphid species found reproducing on cereal crops in
Manitoba in 1994.

<u>Scientific name</u>	<u>Common name</u>	<u>Host plants</u>
<i>Sitobion avenae</i>	English grain aphid	W, B, O
<i>Rhopalosiphum padi</i>	Bird cherry-oat aphid	W, B, O, C
<i>Rhopalosiphum maidis</i>	Corn leaf aphid	B, C
<i>Schizaphis graminum</i>	Greenbug	W, B
<i>Sipha agropyrella</i>	Quakegrass aphid	B
<u><i>Myzus persicae</i></u>	<u>Green peach aphid</u>	<u>W</u>

Host plants: W = wheat, B = barley, O = oats, C = corn

Fig. V-1. Numbers and the percent occurrence of each aphid species on cereal crops in Manitoba in 1994.

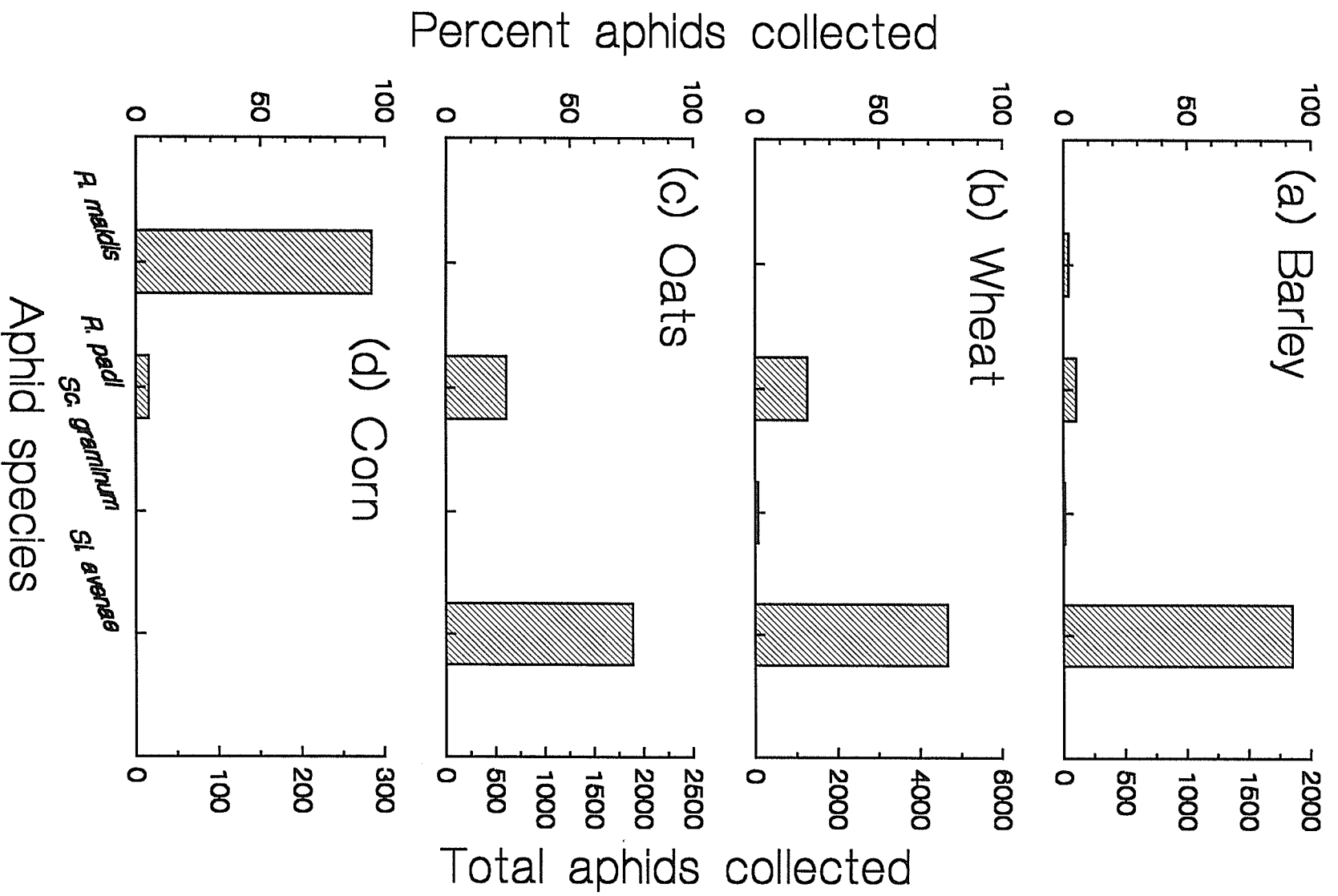


Fig. V-2. Mean (\pm s.e.) number of *Si. avenae* per location on wheat, barley and oats in southern Manitoba in 1994. Number of plants contributing to each mean is 275 for wheat, 148 for barley and 113 for oats.

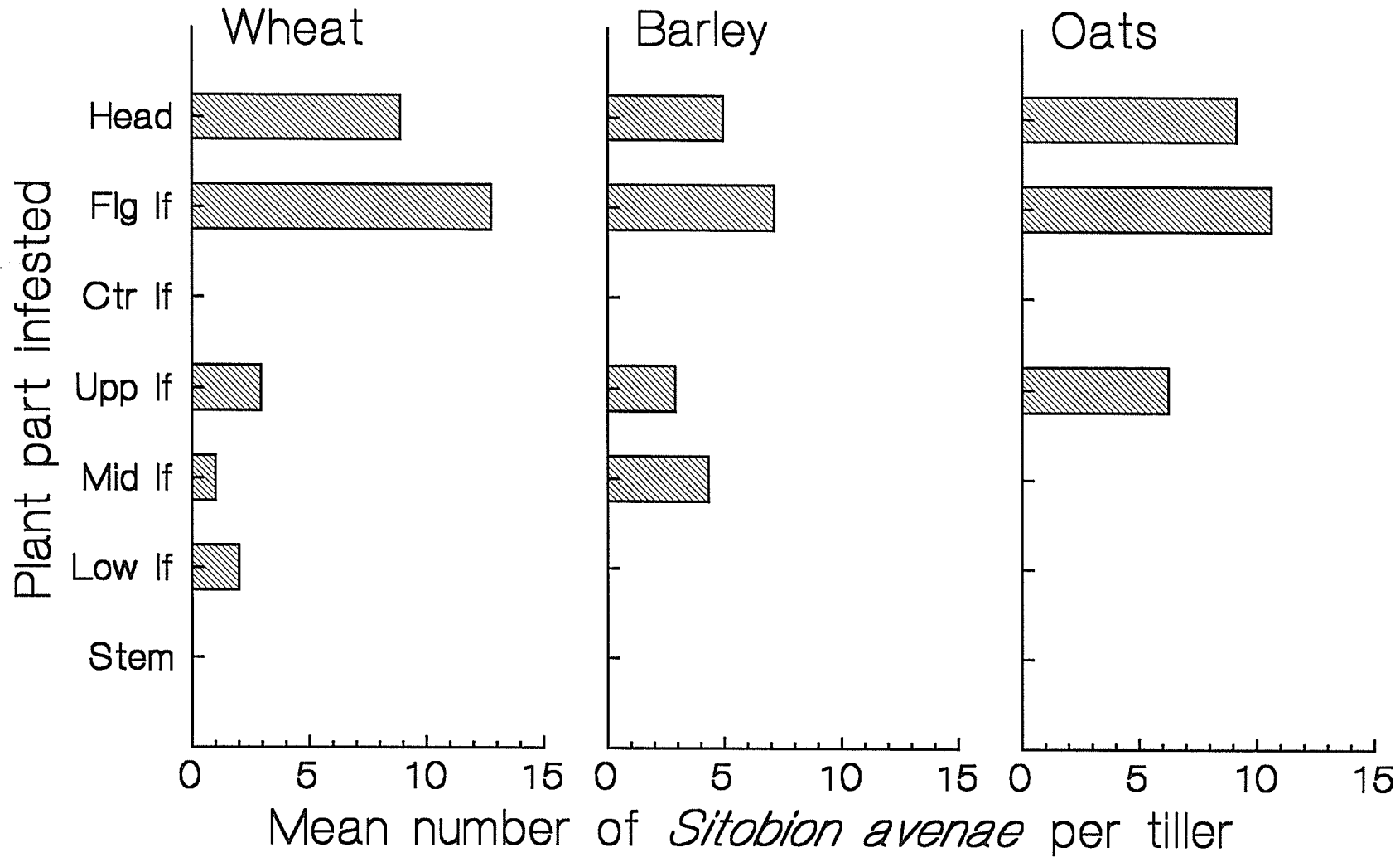


Fig. V-3. Mean (\pm s.e.) number of *R. padi* per location on wheat, barley, oats and corn in southern Manitoba in 1994. Number of plants contributing to each mean is 84 for wheat, 56 for barley, 72 for oats and 15 for corn.

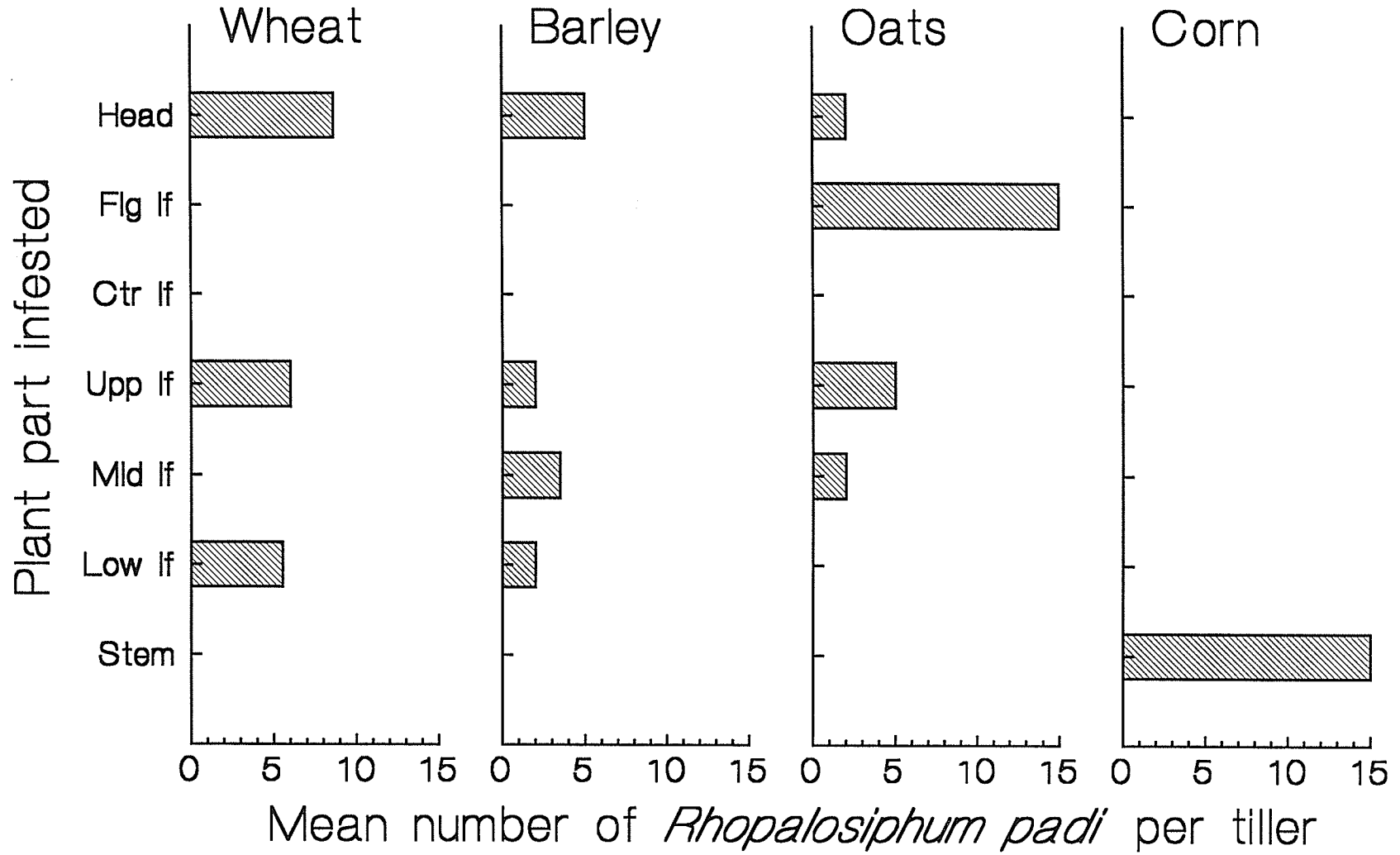


Fig. V-4. Mean (\pm s.e.) number of *R. maidis* per location on barley and corn in southern Manitoba in 1994. Number of plants contributing to each mean is 42 for barley and 35 for corn.

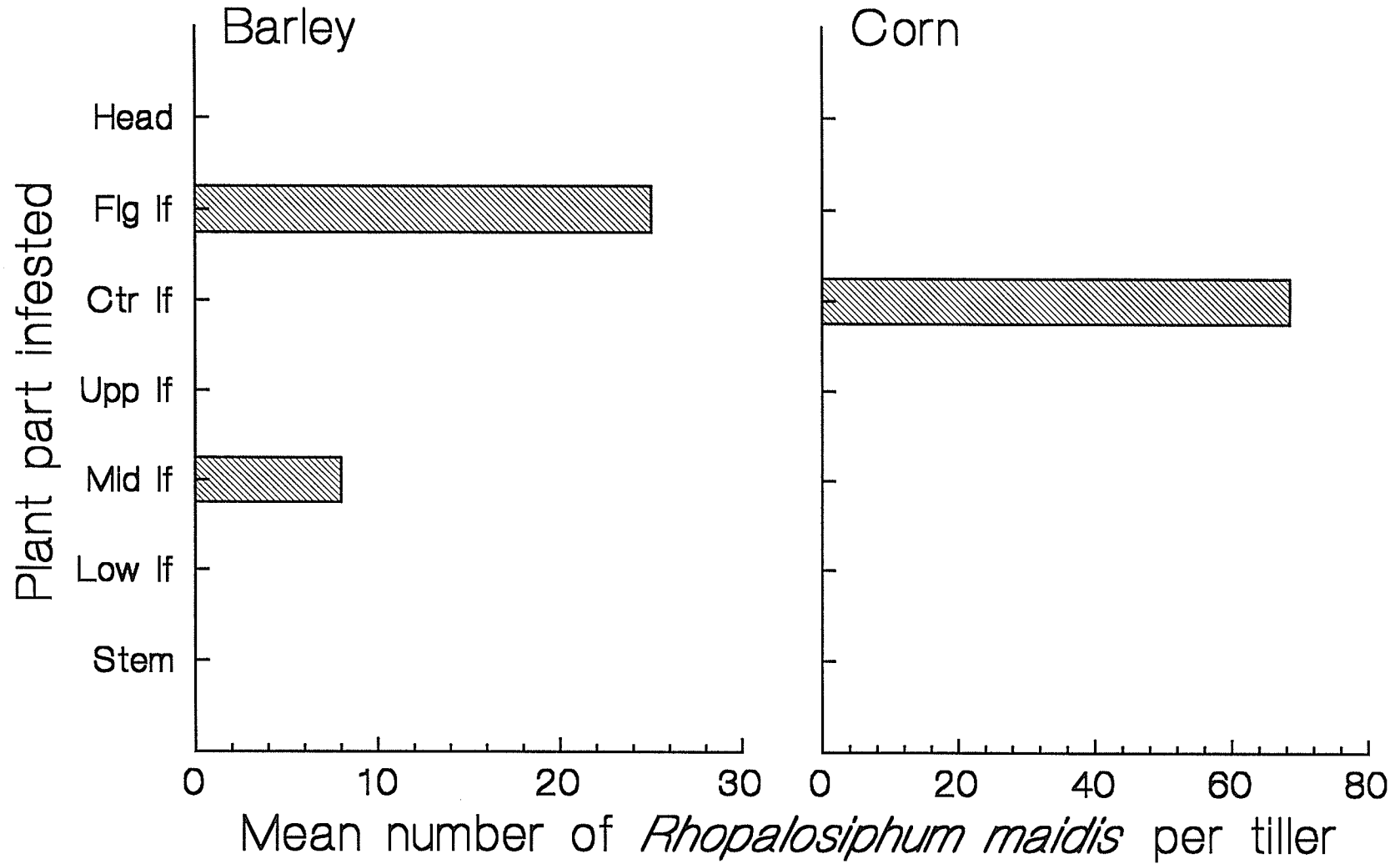


Fig. V-5. Mean (\pm s.e.) number of *Sc. graminum* per location on wheat and barley in southern Manitoba in 1994. Number of plants contributing to each mean is 18 for wheat and 13 for barley.

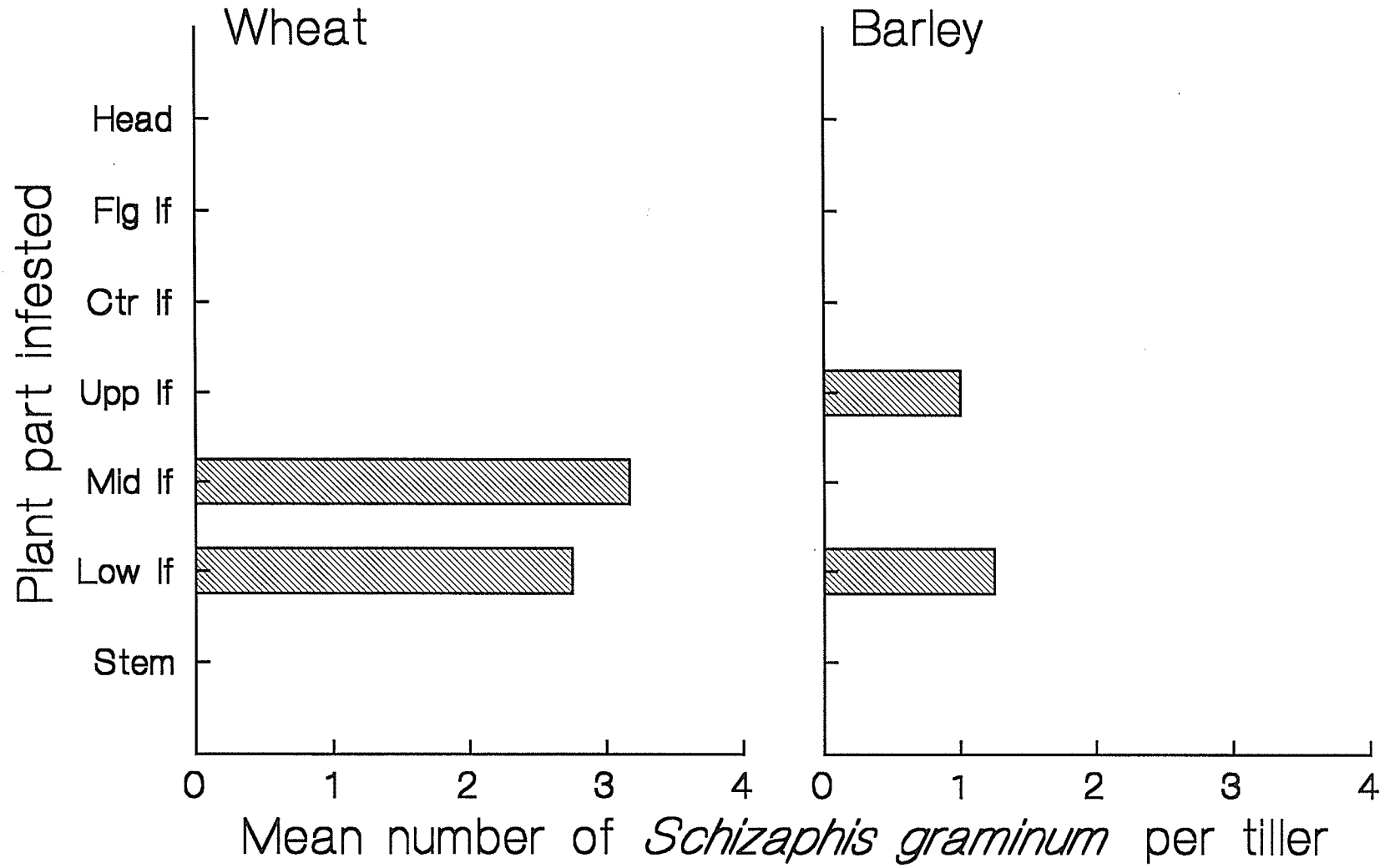
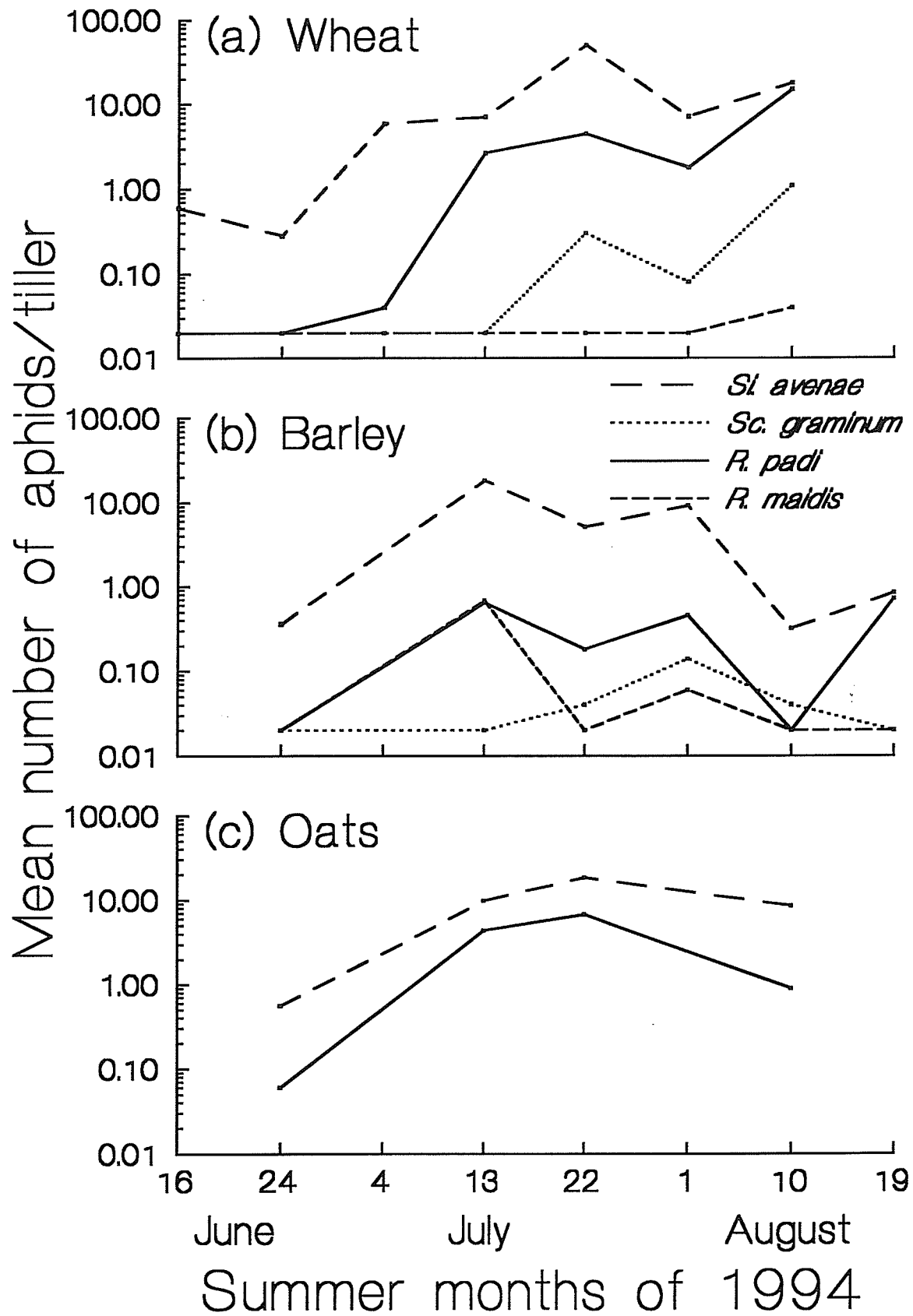


Fig. V-6. Mean number of cereal aphids per tiller of wheat, barley and oats in southern Manitoba during summer, in 1994.



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GENERAL DISCUSSION

Variations in annual abundance of cereal aphids in the prairies is not well understood. The sudden appearance of aphids in Manitoba and surrounding areas which are far beyond their northern overwintering range is suggestive of migration. Through back-track analysis of synoptic weather systems, the flight track for insects travelling between the earth's surface and ca. 1500 m has been estimated (Rose *et al.*, 1975). Southerly winds (Bruehl, 1961) and low level jet-wind systems (Wallin & Loonan, 1971) are thought to be the main systems that transport aphids from the Southern Plains of U.S.A. to the Northern Plains and Canada. Sources of the aphids still remain speculative (Smith & MacKay, 1989).

Primary colonization of cereal fields is accomplished by flying aphids. Therefore, an understanding of the ability of different species to spread from one crop field to another is important in determining their pest status. Wing production in aphids is regulated by changes in density, food supply, temperature, photoperiod and intrinsic factors (Johnson, 1965; Lees, 1967; Walters & Dixon, 1982; Kawada, 1987; Howard & Dixon, 1992). Lees (1967) demonstrated that tactile stimulation occurring among crowded aphids leads to production of winged forms. The results of experiments reported here, (Part IV) in which

aphids were crowded in petri-dishes and on whole barley plants produced marked differences between the species in their response to crowding. The order of response to wing production from the highest to the least is *Si. avenae*, *R. padi*, *R. maidis* and *Sc. graminum*.

In *Si. avenae*, the morph of the parent is important in determining the proportion of winged forms produced, with non-winged parents producing more winged offspring than winged parents. It is quite clear that this species produces winged and non-winged forms in alternating generations. This polymorphism strategy enables the benefits of the fast developmental rate and high fecundity of non-winged forms (Vickerman & Wratten, 1979; Dixon, 1987a) to be combined with the high dispersal capacity of the winged forms. Crowding winged mothers of *Si. avenae* gave rise to a high proportion of winged offspring. Watt & Dixon (1981) reported that unflown winged offspring of *Si. avenae* can be induced by crowding to give birth to a high proportion of winged forms. Production of winged forms by winged mothers of *R. padi* and *R. maidis* is less common than in *Si. avenae* (Noda 1959).

Both mothers and offspring of *R. padi* and *Si. avenae*, respond to crowding (Dixon & Glen, 1971; Watt & Dixon, 1981). The more intense the crowding, the higher the proportion of development of winged forms, especially if

both mothers and offspring experience crowding (Dixon, 1985). In these studies, both mothers and offspring experienced crowding on barley plants (Part IV).

The production of some winged progeny by *R. maidis* even in the absence of crowding suggests that the winged forms play a role in the dispersal of this species from one plant to another. Unlike *R. maidis* and *R. padi* which appear to "monitor" crowding by producing more winged progeny as the period of crowding is increased, the non-responsiveness of *Sc. graminum* at 0, 4, and 8 hours of crowding followed by an abrupt change to respond at 16 and 24 hours of crowding suggest a threshold limit above which the development of winged progeny is triggered.

Interactions between different species in the field may also play an important role in aphid dispersal. Lamb & MacKay (1987) investigated the role of interspecific interactions between the pea aphid, *Acyrtosiphom pisum* (Harris) and *A. kondoi* Shinji in Australian alfalfa fields, on production of winged forms and reported a positive correlation between percentage of larvae with wing buds and total aphid density. They reported that the pea aphids responded in the same way as with intraspecific contacts. Since cereal aphid species commonly occur on crops together, it is likely that physical contacts between them similarly stimulate production of winged forms.

The condition of the host plant also influences wing production in aphids. On a dying or wilting plant or if food deteriorates, aphids become more "restless", and are more likely to touch one another. *A. pisum* when placed on mature bean leaves develops winged forms (Sutherland, 1969), indicating that poor food in itself may also induce wing production. In *Si. avenae*, winged forms develop in response to changes in the nutritional quality associated with the ripening of the seed (Dixon, 1985). Watt (1979) observed a steady increase in production of winged forms in *Si. avenae* three weeks before the aphid population declined. Cannon (1985) found that the maximum levels of wing production of *M. dirhodum* are achieved shortly before population crashes. At ear emergence of barley, 87.4% of large larvae of *R. maidis* on the flag leaf had wing buds (Part II). Such observations suggest that migration of aphids through flight may be a major factor responsible for collapse of aphid populations with plant maturity.

The distribution of aphids among fields may be quite irregular and it is not clear whether the variability is due to differences in attractiveness of the crop to settling migrants (Vickerman & Wratten, 1979) or factors operating after invasion. Interplant movement of aphids appears to be a common event and is probably a strategy aphids use to ensure full utilization of their immediate environment.

Non-winged aphids are not capable of dispersing far because they can only walk, and their movements over the surface of their host plants and between adjacent plants results in slow diffusive dispersal. There is increasing evidence that non-winged aphids readily leave their host plants and probably play an important role in spread of infestations within fields. Ribbands (1964) found that non-winged forms of *Myzus persicae* (Sulzer) frequently move from plant to plant and are responsible for the spread of yellows virus in sugarbeets. After primary colonization of wheat and barley fields by *R. padi*, *Si. avenae* and *M. dirhodum*, infestation is spread by movement of old larvae and non-winged adults across leaf bridges between plants (Dean, 1973). In a field study of *Si. avenae*, Holmes (1988), observed that all non-winged aphids move from the natal ear before reproducing, and over 50% stay on one ear for less than 24 hours.

The present studies provide further evidence of the role of intra and interspecific population interactions in dispersal of aphids on barley. Larval dispersal was found to be an important component in the spread of infestations in some aphid species (Part III). Over 60% of *R. padi* larvae left their natal location soon after molting into the second instar and by the time aphid development reached adulthood, fewer than 10% of individuals were still in their natal location. For all species, increased larval movements

occurred soon after molting. Aphid feeding stops briefly during the molting process and prior to resumption of feeding aphids are likely to exhibit increased movements during the probing process as they search for phloem vessels. Hogson (1991) compared the dispersal of three aphid species *Megoura viciae* Buckton, *M. persicae* and *Brevicoryne brassicae* L., on their respective host plants, *Vicia faba*, *Brassica rapa* and *Brassica oleracea*, and reported that in each situation, the main emigrants are fourth instars and teneral adults. The studies of Johnson (1957) and MacKay & Downer (1979) emphasized the occurrence of a restless dispersive phase of teneral adults in several species of aphids. The findings of this study (Part III) show that among the four species studied, non-winged adults of *R. padi* had the highest frequency of movements (1.5 days) between natal locations, while *Sc. graminum* took the longest time (3 days). Dean (1974b) observed that winged *M. dirhodum* stays in one spot on a tiller for less time (1.8 days) than non-winged adults (2.3 days), while both morphs of *Si. avenae* are equally active (1.9 days). In this study it was apparent from experiments on seedlings in flats in the laboratory (Part III), that, adults of *R. padi* frequently moved between plants leaving a batch of first instar larvae on each stem visited. As the larvae developed to later instars, the groups fragmented as individuals

spread out to other locations and adjacent plants.

During the growing season, grain aphids have a remarkable rate of population growth due to the parthenogenetic mode of reproduction and can quickly reach damaging populations when conditions are favourable. In the field most aphid species continuously produce non-winged forms for several generations. The non-winged morphs have been observed often to be larger, reach maturity faster and be consistently more fecund than winged morphs in many species (Vickerman & Wratten, 1979; Dixon, 1987a). *R. padi*, *R. maidis* and *Sc. graminum* consistently produce higher proportions of non-winged aphids as long as host conditions are favourable.

The first 12 days of adult life appear to be the most important in determining individual contribution to population dynamics of each aphid species. Among the four species studied (Part I), *R. padi* ranked the highest in terms of developmental rate, fecundity and intrinsic rate of increase followed by *R. maidis*, *Sc. graminum* and *Si. avenae*. *R. padi* is reported to occur frequently in northern European countries and southern Australia and often achieves outbreak levels (Rautapaa, 1976; De Barro, 1992). Although serious outbreaks of this pest have not been reported in Manitoba, its occurrence every year poses a potential threat to grain production.

The occurrence of different species of cereal aphids at different growth stages of the crop and at different feeding sites (Parts II & V) appears to reduce interspecific competition as well as achieve full exploitation of the host plant. The four cereal aphid species in this study were all found to occupy different feeding sites on the barley plant. The feeding habits of each species affect the type and amount of damage done to the host plant. *R. maidis* prefers feeding within the youngest unfolding leaf near the growing point of immature plants, thereby depriving the growing region of essential nutrients required for growth. Inside the folded leaves, the pest is provided with a suitable environment with moderated fluctuations in temperature and humidity.

R. maidis has a tendency to aggregate, as large colonies were found in infested tillers (Part II). This behaviour, combined with favourable environmental conditions that promote a high rate of reproduction, such as warm dry weather would result in intense feeding and cause stunting of infested tillers. A heavy infestation by this species may also lead to a reduction in the number of tillers per plant, as some infested tillers die before maturity, or lead to a reduction in the number of grains per ear.

R. padi preferred to feed on the stems of young barley plants. Leather & Dixon (1981) found that *R. padi* is most

fecund while feeding on stems of earing barley and least fecund on oats, suggesting that barley is probably the most suitable cereal crop host for *R. padi*. Among the four aphid species studied, *R. padi* occupies the lowest strata of the habitat. The conditions at this level are probably most suitable for growth, development and survival of this species. The occurrence of this species under leaf sheaths near the ground level during mid-summer is probably a survival mechanism to protect it from from the hot and dry conditions.

Sc. graminum feeds on leaves of the lower half of the plant. The species occurs in tightly packed colonies on the underside of leaves. This species causes severe injury to crops by sap removal and injection of toxic saliva. Due to the compact pattern of distribution and the direct and side effects of feeding by *Sc. graminum*, low pest populations are likely to cause severe local damage, and pest outbreaks are likely to cause devastating losses. Damage is particularly serious during prolonged dry weather (Wanjama, 1979) and even light infestations may kill young plants (Muthangya *et al.*, 1990). For these reasons, assessment of aphid effects on field crops based on numbers per plant alone may not give a clear picture of their damage. Kieckhefer & Kantak (1986) reported that *Sc. graminum* and *R. padi* caused more yield losses than *Si. avenae* and *R. maidis* at similar population

densities. In the U.S.A., the occurrence of several biotypes of *Sc. graminum* with differential ability to attack various genotypes of grain cereals (Wood, 1961; Porter et al., 1982; Puterka et al., 1988) continues to cause a threat to grain production and insecticides are often used in an attempt to control the pest (Kring & Gilstrap, 1989). The occurrence of this species every year in Manitoba is suggestive of its potential impact on grain production.

The host plant and its stage of development are important in determining the feeding position of *Si. avenae* and in regulating its population dynamics. In immature plants, the species prefers to feed on the middle and upper leaves, but at flowering stage, *Si. avenae* rapidly colonizes the ears (Dean, 1973). Watt (1979), found the species to have its highest reproductive rate when feeding on ears of wheat and oats at milk stage and was almost three times as fecund as when feeding on leaves. The reproductive rate then rapidly declines as the grain ripens (Walters & Dixon, 1982). Judging by the aphid's developmental and reproductive rates, grasses in the early stages of earing provide *Si. avenae* with a high quality habitat.

In the field, *R. padi* and *Si. avenae* occurred in loose colonies and their widespread distribution was indicative of high dispersal capacity (Part III). The high abundance of *Si. avenae* throughout the season (Part V) indicated that

this pest was well adapted to the prevailing conditions in southern Manitoba in 1994 and was the most important cereal aphid in this region. On wheat, peak numbers of this species were recorded at milk stage, on 22 July (Part V), with most individuals feeding directly on the filling grain. This feeding behaviour combined with its high reproductive capacity (Watt, 1979) and rapid colonization of ears (Dean, 1973) largely accounts for its pest status.

R. maidis and *Sc. graminum* were present in very low numbers (Parts II & V) suggesting that either the conditions in southern Manitoba in 1994 were not suitable for growth and reproduction of these species or there may not have been sufficient or timely migrations from the south to enable development of noticeable infestations. As aphid infestations on cereal crops in Manitoba appear to depend on long range migration from the south, the timing of arrival of initial colonizers is possibly a major factor determining their effect on cereal crops.

Summary and conclusions

Populations of several species of aphids are usually present each year on fields of wheat and barley in Manitoba. Their establishment on field crops each spring is dependent upon migrants from the U.S.A., and subsequent dispersal within and between fields. The present studies focused on the potential for dispersal by each species in an attempt to

document their relative status as pests of cereal crops in Manitoba. All aphid species respond to crowding by producing winged dispersers (Part IV). *Si. avenae* has the highest capacity for production of winged forms. For this species, the morph of the parent is important in determining production of winged forms. Without crowding, *Si. avenae* produces winged and non-winged forms in alternate generations (Parts I & IV). *Sc. graminum* has the least capacity for production of winged forms when subjected to crowded situations. This species is unresponsive to short periods of crowding, but after a certain threshold crowding period is reached, there occurs a dramatic switch to production of winged forms.

Dispersal by non-winged adult and juvenile aphids between cereal plants in the field is a common phenomenon and plays an important role in spread of infestations. Non-winged adult aphids contribute to the spread of infestations by their movements between plants, leaving batches of offspring on the plants (Part III). The number of larvae deposited per natal location is related to the dispersiveness of the aphid species. Small larval group sizes are associated with species with a higher rate of dispersal, while large group sizes are associated with less dispersive species.

The four aphid species examined in these studies differ

in their developmental rates and reproductive strategies (Part I). *R. padi* has the greatest potential for population growth and development. The first 12 days of adult life appear to be the most important in determining individual contribution to population dynamics of cereal aphids.

Each aphid species appears to prefer a specific feeding location where reproduction also occurs. Regions of highest abundance for each species are, the central unopened leaf of immature plants for *R. maidis*, the lower leaf sheaths for *R. padi*, the underside of the proximal end of lower leaves for *Sc. graminum*, and the distal end of middle and upper leaves of immature plants and on the head of filling grain for *Si. avenae* (Part II).

Si. avenae appeared early in the cropping season in 1994, and its population remained higher than the other species throughout the season (Part V). Colony size was small and loosely aggregated for *R. padi* and *Si. avenae* and large and tightly aggregated for *R. maidis* and *Sc. graminum*. Because of their high dispersal capacity, *Si. avenae* and *R. padi* have widespread distribution within fields. On the basis of aphid abundance in 1994, and feeding behaviour, it is concluded that *Si. avenae* is the greatest threat to grain production in Manitoba. *R. padi* is second most important species in Manitoba. *R. maidis* and *Sc. graminum* did not occur in sufficient numbers to cause a threat to grain

production in 1994.

Future studies

Findings from this study indicate that among aphid species found on cereal crops in Manitoba, *Si. avenae* causes the greatest threat to grain production. Its high abundance throughout the season particularly during earing stage is suggestive of serious yield losses. Although effective insecticides are available, farmers rarely use them due to their high cost, fear of residue accumulation in grain and their unpleasant effect on the environment. There is need, therefore, to search for appropriate control strategies for control of aphid pests. Crop resistance against aphids is a useful alternative to insecticidal control.

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APPENDIX 1

COHORT LIFE TABLES OF CEREAL APHIDS

Calculation of intrinsic rate of increase using Birch (1948) method requires compilation of detailed life tables and fecundity schedules. This appendix contains the life tables of cereal aphids used in this study. The fecundity schedules of the aphids are contained in appendix 2.

Life table Analysis

x = age of aphids (days)

a_x = number of aphids alive

l_x = a_x /original number of aphids

d_x = $l_x - l_{x+1}$

q_x = (d_x/l_x) /interval

k_x = $\log_{10}(a_x/a_{x+1})$ /interval

Table 1. Cohort life table for *Rhopalosiphum padi* (Clone RP04) reared on barley in laboratory at constant conditions ($20 \pm 1^{\circ}$ C).

Age in days	Number surviving to day X	Proportion of original cohort surviving to the beginning of age class X	Proportion of original cohort dying during age class X	Daily mortality	Daily killing power
x	a _x	l _x	d _x	q _x	k _x
0	120	1.000	0.008	0.001	0
16	119	0.992	0.034	0.004	0.002
25	115	0.958	0.016	0.008	0.004
27	113	0.942	0.067	0.036	0.016
29	105	0.875	0.100	0.057	0.026
31	93	0.775	0.358	0.231	0.135
33	50	0.417	0.250	0.300	0.199
35	20	0.167	0.142	0.425	0.412
37	3	0.025	0.017	0.340	0.239
39	1	0.008	0.008	0.500	-
41	0	0	-	-	-

Table 2. Cohort life table for *Rhopalosiphum padi* (Clone RP06) reared on barley in laboratory at constant conditions ($20 \pm 1^{\circ} \text{C}$).

Age in days	Number surviving to day X	Proportion of original cohort surviving to the beginning of age class X	Proportion of original cohort dying during age class X	Daily mortality	Daily killing power
x	a_x	l_x	d_x	q_x	k_x
0	50	1.000	0.020	0.001	0.001
17	49	0.980	0.040	0.010	0.005
21	47	0.940	0.100	0.053	0.024
23	42	0.840	0.140	0.083	0.040
25	35	0.700	0.080	0.057	0.026
27	31	0.620	0.160	0.129	0.065
29	23	0.460	0.240	0.261	0.160
31	11	0.220	0.120	0.273	0.171
33	5	0.100	0.060	0.300	0.199
35	2	0.040	0.040	0.500	-
37	0	0	-	-	-

Table 3. Cohort life table for *Rhopalosiphum maidis* reared on barley in laboratory at constant conditions ($20 \pm 1^\circ \text{C}$).

Age in days	Number surviving to day X	Proportion of original cohort surviving to the beginning of age class X	Proportion of original cohort dying during age class X	Daily mortality	Daily killing power
x	a_x	l_x	d_x	q_x	k_x
0	38	1.000	0.026	0.001	0
33	37	0.974	0.027	0.014	0.006
35	36	0.947	0.052	0.027	0.012
37	34	0.895	0.158	0.088	0.042
39	28	0.737	0.263	0.178	0.096
41	18	0.474	0.211	0.223	0.128
43	10	0.263	0.210	0.399	0.349
45	2	0.053	0.053	0.500	-
47	0	0	-	-	-

Table 4. Cohort life table for *Schizaphis graminum* reared on barley in laboratory at constant conditions ($20 \pm 1^{\circ}$ C).

Age in days	Number surviving to day X	Proportion of original cohort surviving to the beginning of age class X	Proportion of original cohort dying during age class X	Daily mortality	Daily killing power
x	a_x	l_x	d_x	q_x	k_x
0	40	1.000	0.025	0.001	0
29	39	0.975	0.025	0.002	0.001
41	38	0.950	0.025	0.013	0.006
43	37	0.925	0.075	0.020	0.009
47	34	0.850	0.125	0.074	0.035
49	29	0.725	0.175	0.121	0.060
51	22	0.550	0.100	0.091	0.044
53	18	0.450	0.150	0.167	0.088
55	12	0.300	0.100	0.167	0.088
57	8	0.200	0.050	0.125	0.062
59	6	0.150	0.125	0.417	0.389
61	1	0.025	0.025	1.000	-
62	0	0	-	-	-

Table 5. Cohort life table for *Sitobion avenae* (Non winged)
 reared on barley in laboratory at constant conditions ($20 \pm 1^\circ \text{C}$).

Age in days	Number surviving to day X	Proportion of original cohort surviving to the beginning of age class X	Proportion of original cohort dying during age class X	Daily mortality	Daily killing power
x	a_x	l_x	d_x	q_x	k_x
0	65	1.000	0.046	0.005	0.002
10	62	0.954	0.016	0.002	0.001
18	61	0.938	0.015	0.001	0
41	60	0.923	0.031	0.017	0.007
43	58	0.892	0.046	0.026	0.012
45	55	0.846	0.123	0.073	0.034
47	47	0.723	0.092	0.064	0.030
49	41	0.631	0.093	0.074	0.034
51	35	0.538	0.061	0.057	0.026
53	31	0.477	0.154	0.161	0.085
55	21	0.323	0.200	0.310	0.210
57	8	0.123	0.046	0.187	0.102
59	5	0.077	0.062	0.403	0.349
61	1	0.015	0.015	0.500	-
63	0	0	-	-	-

Table 6. Cohort life table for *Sitobion avenae* (Winged) reared on barley in laboratory at constant conditions ($20 \pm 1^\circ \text{C}$).

Age in days	Number surviving to day X	Proportion of original cohort surviving to the beginning of age class X	Proportion of original cohort dying during age class X	Daily mortality	Daily killing power
x	a_x	l_x	d_x	q_x	k_x
0	54	1.000	0.019	0.001	0
35	53	0.981	0.018	0.002	0.001
43	52	0.963	0.037	0.019	0.009
45	50	0.926	0.111	0.060	0.028
47	44	0.815	0.167	0.102	0.050
49	35	0.648	0.074	0.057	0.026
51	31	0.574	0.148	0.129	0.065
53	23	0.426	0.185	0.217	0.124
55	13	0.241	0.093	0.193	0.105
57	8	0.148	0.092	0.311	0.213
59	3	0.056	0.037	0.330	0.239
61	1	0.019	0.019	1.000	-
62	0	0	-	-	-

APPENDIX 2

COHORT FECUNDITY SCHEDULES OF CEREAL APHIDS

This appendix contains a compilation of detailed cohort fecundity schedules of cereal used in this study. From these tables, and life tables (Appendix 1), the intrinsic rate of increase and cohort generation time can be calculated using Birch (1948) method.

Table 1. Cohort fecundity schedule for *Rhopalosiphum padi* (Clone RP04) reared on barley in laboratory at a constant temperature ($20 \pm 1^\circ \text{C}$).

Pivotal age in days	Proportion of original cohort surviving to age class x	Larvae produced per surviving individual in each stage	Larvae produced per original individual in each stage	
x	l_x	m_x	$l_x m_x$	$x l_x m_x$
6.5	1.000	1.275	1.275	8.288
7.5	1.000	7.075	7.075	53.063
8.5	1.000	7.958	7.958	67.646
9.5	1.000	10.433	10.433	99.117
10.5	1.000	9.633	9.633	101.150
11.5	1.000	10.075	10.075	115.863
12.5	1.000	9.933	9.933	124.167
13.5	1.000	8.883	8.883	119.925
14.5	1.000	6.542	6.542	94.854
15.5	0.992	3.739	3.709	57.491
16.5	0.992	1.571	1.558	25.714
17.5	0.992	0.874	0.867	15.173
18.5	0.992	0.479	0.475	8.791
19.5	0.992	0.261	0.259	5.049
20.5	0.992	0.193	0.191	3.925
21.5	0.992	0.067	0.066	1.422
22.5	0.992	0.042	0.041	0.930
23.5	0.967	0.009	0.009	0.211
24.5	0.958	0.017	0.016	0.391
			<u>79.001</u>	<u>903.167</u>
n = 120	$R_0 = 79.001$	$r_m = 0.431$		

Table 2. Cohort fecundity schedule for *Rhopalosiphum padi* (Clone RP06) reared on barley in laboratory at a constant temperature ($20 \pm 1^\circ \text{C}$).

Pivotal age in days	Proportion of original cohort surviving to age class x	Larvae produced per surviving individual in each stage	Larvae produced per original individual in each stage	
x	l_x	m_x	$l_x m_x$	$x l_x m_x$
6.5	1.000	2.960	2.960	19.240
7.5	1.000	7.940	7.940	59.550
8.5	1.000	8.220	8.220	69.870
9.5	1.000	10.040	10.040	95.380
10.5	1.000	11.140	11.140	116.970
11.5	1.000	10.240	10.240	117.760
12.5	1.000	9.680	9.680	121.000
13.5	1.000	9.820	9.820	132.570
14.5	1.000	5.460	5.460	79.170
15.5	1.000	3.440	3.440	53.320
16.5	0.980	2.082	2.040	33.660
17.5	0.980	0.837	0.820	14.350
18.5	0.980	0.286	0.280	5.180
19.5	0.980	0.102	0.100	1.950
20.5	0.940	0.149	0.140	2.870
21.5	0.880	0.023	0.020	0.430
			82.340	923.270
n = 50	$R_0 = 82.340$	$T_c = 9.868$	$r_m = 0.447$	

Table 3. Cohort fecundity schedule for *Rhopalosiphum maidis* reared on barley in laboratory at a constant temperature ($20 \pm 1^\circ \text{C}$).

Pivotal age in days	Proportion of original cohort surviving to age class x	Larvae produced per surviving individual in each stage	Larvae produced per original individual in each stage	
x	l_x	m_x	$l_x m_x$	$x l_x m_x$
6.5	1.000	0.263	0.263	1.711
7.5	1.000	7.211	7.211	54.079
8.5	1.000	7.658	7.658	65.092
9.5	1.000	6.079	6.079	57.750
10.5	1.000	7.211	7.211	75.711
11.5	1.000	8.816	8.816	101.382
12.5	1.000	7.684	7.684	96.053
13.5	1.000	7.921	7.921	106.934
14.5	1.000	7.474	7.474	108.368
15.5	1.000	6.474	6.474	100.342
16.5	1.000	4.816	4.816	79.461
17.5	1.000	4.316	4.316	75.526
18.5	1.000	1.263	1.263	23.368
19.5	1.000	1.158	1.158	22.579
20.5	1.000	0.684	0.684	14.026
21.5	1.000	0.395	0.395	8.487
22.5	1.000	0.105	0.105	2.368
23.5	1.000	0.105	0.105	2.474
24.5	1.000	0.026	0.026	0.645
25.5	1.000	0.026	0.026	0.671
			<u>79.684</u>	<u>997.026</u>

n = 38 $R_0 = 79.684$ $T_c = 10.678$ $r_m = 0.410$

Table 4. Cohort fecundity schedule for *Schizaphis graminum* reared on barley in laboratory at a constant temperature (20 ± 1° C).

Pivotal age in days	Proportion of original cohort surviving to age class x	Larvae produced per surviving individual in each stage	Larvae produced per original individual in each stage	
x	l_x	m_x	$l_x m_x$	$x l_x m_x$
7.5	1.000	0.100	0.100	0.750
8.5	1.000	3.925	3.925	33.363
9.5	1.000	5.650	5.650	53.675
10.5	1.000	5.425	5.425	56.963
11.5	1.000	6.300	6.300	72.450
12.5	1.000	7.075	7.075	88.438
13.5	1.000	6.750	6.750	91.125
14.5	1.000	6.225	6.225	90.263
15.5	1.000	6.125	6.125	94.938
16.5	1.000	6.400	6.400	105.600
17.5	1.000	4.525	4.525	79.188
18.5	1.000	4.300	4.300	79.550
19.5	1.000	4.100	4.100	79.950
20.5	1.000	2.675	2.675	54.838
21.5	1.000	1.425	1.425	30.638
22.5	1.000	1.225	1.225	27.563
23.5	1.000	0.500	0.500	11.750
24.5	1.000	0.375	0.375	9.188
25.5	1.000	0.175	0.175	4.463
26.5	1.000	0.300	0.300	7.950
27.5	1.000	0.025	0.025	0.688
			<u>73.600</u>	<u>1073.325</u>

n = 40

$R_0 = 73.600$

$T_c = 12.569$

$r_m = 0.342$

Table 5. Cohort fecundity schedule for *Sitobion avenae* (Non-winged) reared on barley in laboratory at a constant temperature ($20 \pm 1^{\circ}$ C).

Pivotal age in days	Proportion of original cohort surviving to age class x	Larvae produced per surviving individual in each stage	Larvae produced per original individual in each stage	
x	l_x	m_x	$l_x m_x$	$x l_x m_x$
7.5	1.000	0.400	0.400	3.000
8.5	1.000	4.662	4.662	39.623
9.5	0.954	4.919	4.692	44.577
10.5	0.954	5.661	5.400	56.700
11.5	0.954	5.500	5.246	60.331
12.5	0.954	4.323	4.123	51.538
13.5	0.954	3.887	3.708	50.054
14.5	0.954	4.145	3.954	57.331
15.5	0.954	4.613	4.400	68.200
16.5	0.954	3.371	3.215	53.054
17.5	0.938	4.133	3.877	67.846
18.5	0.938	3.608	3.385	62.615
19.5	0.938	3.592	3.369	65.700
20.5	0.938	3.559	3.338	68.438
21.5	0.938	3.379	3.169	68.138
22.5	0.938	3.494	3.277	73.731
23.5	0.938	2.772	2.600	61.100
24.5	0.938	2.280	2.138	52.392
25.5	0.938	2.526	2.369	60.415
26.5	0.938	1.624	1.523	40.362
27.5	0.938	1.476	1.385	38.077
28.5	0.938	1.115	1.046	29.815
29.5	0.938	1.017	0.954	28.138
30.5	0.938	0.738	0.692	21.115
31.5	0.938	0.558	0.523	16.477
32.5	0.938	0.623	0.585	19.000
33.5	0.938	0.262	0.246	8.246
34.5	0.938	0.164	0.154	5.308
35.5	0.938	0.164	0.154	5.462
36.5	0.938	0.066	0.062	2.246
37.5	0.938	0.049	0.046	1.731
38.5	0.938	0.016	0.015	0.592
39.5	0.923	0.017	0.015	0.608
40.5	0.923	0.050	0.046	1.869
41.5	0.908	0.017	0.015	0.638
			<u>74.785</u>	<u>1284.469</u>
$n = 65$	$R_0 = 74.785$	$T_c = 13.000$	$r_m = 0.332$	

Table 6. Cohort fecundity schedule for *Sitobion avenae* (Winged) reared on barley in laboratory at a constant temperature ($20 \pm 1^\circ \text{C}$).

Pivotal age in days	Proportion of original cohort surviving to age class x	Larvae produced per surviving individual in each stage	Larvae produced per original individual in each stage
x	l_x	m_x	$l_x m_x$
7.5	1.000	0.019	0.019
8.5	1.000	0.093	0.093
9.5	1.000	1.778	1.778
10.5	1.000	5.204	5.204
11.5	1.000	2.741	2.741
12.5	1.000	3.000	3.000
13.5	1.000	3.704	3.704
14.5	1.000	3.278	3.278
15.5	1.000	3.259	3.259
16.5	1.000	3.981	3.981
17.5	1.000	4.056	4.056
18.5	1.000	2.796	2.796
19.5	1.000	2.926	2.926
20.5	1.000	2.444	2.444
21.5	1.000	2.741	2.741
22.5	1.000	2.481	2.481
23.5	1.000	2.611	2.611
24.5	1.000	2.833	2.833
25.5	1.000	3.056	3.056
26.5	1.000	2.537	2.537
27.5	1.000	3.019	3.019
28.5	1.000	1.759	1.759
29.5	1.000	1.574	1.574
30.5	1.000	1.333	1.333
31.5	1.000	1.259	1.259
32.5	1.000	1.056	1.056
33.5	1.000	0.630	0.630
34.5	0.981	0.396	0.389
35.5	0.981	0.321	0.315
36.5	0.981	0.170	0.167
37.5	0.981	0.038	0.037
38.5	0.981	0.019	0.019
39.5	0.981	0.076	0.074
40.5	0.981	0	0
41.5	0.981	0.019	0.019
42.5	0.963	0.019	0.019
43.5	0.944	0	0
44.5	0.926	0	0
45.5	0.889	0.021	0.019
			<u>67.222</u>
			<u>1329.185</u>

$n = 54$ $R_0 = 67.222$ $T_c = 15.358$ $r_m = 0.274$

APPENDIX 3

EFFECT OF CROWDING ON WING PRODUCTION BY SEVEN CLONES OF *Rhopalosiphum padi*

The potential for production of winged dispersers by seven clones of *Rhopalosiphum padi*, RP02, RP04, RP06, RP07, RP08, RP09 and RP10, maintained in Dr. P.A. MacKay's laboratory, Department of Entomology, University of Manitoba, was evaluated by crowding a group of 10 adults in petri-dishes for 24 hours and later determining the proportion of their progeny that developed into winged forms. Twenty pre-reproductive adults of each clone were selected for use in the crowding experiment (see Chapter 3 and Chapter 4, Part IV for information on pre-crowding rearing conditions, crowding process and post-crowding rearing conditions). The crowding periods were 0, 4, 8, 16 and 24 hours for each clone. Experiments on each crowding period were replicated three times for each clone. The first clone initially tested (RP04) (for use in Part IV) showed a relatively low response compared to the response reported in literature (Noda, 1959; Dixon & Glen, 1971; MacKay & Lamb (in press)). Therefore, a number of *R. padi* clones were screened and a more sensitive clone (RP06) was selected.

Fig. 1 shows the results of the crowding experiment. Wing production by all clones increased as the crowding period was increased. However, for each crowding period,

the response among clones differed. RP06 had the highest response in wing production while RP02 had the lowest. Aphid response to crowding appeared to fall into two groups, those with a high response (RP06, RP08, RP09 and RP10) and those with a low response (RP02, RP04 and RP07). Four clones, RP02, RP04, RP06 and RP07 had a lightly coloured cuticle and the other three, RP08, RP09 and RP10 were dark coloured. These colour differences were very distinct and the two colour groups could be easily differentiated by the naked eye in both adults and larvae. All three of the dark coloured clones produced a higher proportion of winged forms. However, one of the light coloured clones (RP06) also produced high proportions of winged forms. This suggests that these two characteristics, wing production and colour may not be in any way linked, and makes it unlikely that these differences represent a strain or subspecies differences. It is not clear why there appears to be a large clonal variation in *R. padi* in wing production as a response to the crowding stimulus.

Fig. 1. Mean (\pm s.e.) proportion of winged progeny produced by *R. padi* clones after groups of 10 non-winged adults of each clone were separately crowded in petri-dishes for different time periods. Each test of 10 was replicated three times per crowding time.

