STUDIES ON SOME FACTORS THAT AFFECT CEREAL APHIDS (HOMOPTERA: APHIDIDAE) DISPERSAL AND COLONIZATION ON WHEAT (*Triticum aestivum* L.)

By

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DECLARATION

I declare that this thesis is my original work and it has not been previously presented in this or any other university for any degree

Signed ______________________ Date 14-9-02
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This Thesis has been submitted for examination with our approval as University Supervisors

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DEDICATION

To
my husband David, daughter Jacqueline, son Samuel and mum Esther
for their
prayers, encouragement and patience
during the research and thesis writing.

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ABSTRACT

Cereal aphids cause extensive direct and indirect damage on wheat. There is little information on their biology, ecology and host plant interaction. Experiments were conducted to observe the effect of environment, intrinsic and plant factors on dispersal and colonization of three aphid species namely: *Rhopalosiphum padi*, *Schizaphis graminum* and *Metopolophium dirhodum*. The intrinsic rate of increase (r_m) was done in a greenhouse using a CRD. The r_m for *R. padi* was higher than that of *S. graminum* and *M. dirhodum* which were both not significantly different ($P = 0.05$). The effect of temperature on r_m and alarysim was conducted in controlled environment chambers using RCBD in a split plot arrangement. The r_m for all species increased with temperature. *R. padi* had the highest response. Wing production increased with temperature in all the species. *M. dirhodum* had the highest percentage, followed by *R. padi* and then *S. graminum.* Dispersal capacity (wing production) was investigated by crowding fourth instar apterae and alate nymphs at different maternal ages. *M. dirhodum* had the highest response, followed by *R. padi* and then *S. graminum*. Maternal morph had an effect on subsequent wing formation. Only apterae mothers had a significant number of alate offsprings. The first born progeny offsprings of apterae had more alates. This declined gradually with age depending on species. Distribution patterns in time and space was observed in the field in factorial RCBD replicated four times using Fahari, Mbega and Duma wheat varieties sampled at six growth stages. Aphid populations differed among species, varieties and growth stages. *R. padi* had the highest aphid population followed by *M. dirhodum.* Duma variety recorded a higher population than the other two. *R. padi* colonised the stem, the lower and flag leaves and the ear. *S. graminum* colonised the lower leaves and *M. dirhodum* the underside of middle, upper and flag leaves.

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CHAPTER ONE

1. INTRODUCTION

1.1 Importance of wheat

Wheat (*Triticum aestvum*) is one of the most important cereals in the world. Irungu *et al.* (1997) reported that one third of the world's total cereal production was wheat. It is ranked second after rice in the world and second after maize in Kenya, among the most consumed cereal crops (GoK, 1997a; FAO, 1996). Wheat has continued to gain importance as food, especially for urban dwellers. In Kenya, the crop is grown on approximately 135,000 ha situated in high altitude areas lying between 1600m to 3000m above sea level (Cereal Growers Association 2001; Hassan *et al.,* 1993). Wheat is also an important cash earner for the farmers in these areas because traditional cash crops like coffee and tea are either scarce or absent.

Wheat production, which was traditionally grown on large scale operation, has now been adopted by small holders. In 1983 about 15% of the total wheat area was under small holder operation (Mulamula, 1983). This proportion has increased over the years, as a result of population pressure which has led to land subdivision and urbanisation (Kinyua, 1997).

Kenya has a potential to produce enough wheat for local consumption which is estimated at 600,000 MT annually (GoK 1997b). However, it was estimated by FAO (2000), KARI and MIAC (1993) that on average wheat yield in Kenya is about 2.0 MT/ha. The current annual national production of wheat is about 250,000 MT (Cereal Growers Association; 2001), which is far below the domestic demand. Therefore, the country continues to import over 50% of wheat annually to bridge the gap between production and national demand.

1.2 Production constraints

1.2.1 General constraints

Despite wide usage of high yielding quality seed, wheat yields in Kenya have remained low. The low yields especially in the high potential areas of Kenya can be partially attributed to poor land preparation and poor planting practices This is confounded by a decline in soil fertility as a result of continuous monoculture (Cheruiyot, 2000). Other constraints are poor technological packages, lack of credit facilities particularly for small scale farmers and high cost of inputs. The ever increasing human population and a fast decline in farm size has limited expansion of wheat production. There is also stiff competition for arable land in the high potential areas, from maize and higher value enterprises like dairy and horticulture.

Arama and Wanjama (1998), have stated that wheat production in the last few years has fallen below domestic demand due to low yields, citing pests and diseases as some of the major factors that cause yield reduction. Cereal aphids are among the most important pests of wheat in Kenya (Wangai *et al.*, 2000).

1.2.2 Cereal aphids (Homoptera: Aphididae) as constraints to wheat production

Aphids (plant lice) are soft bodied insects that suck sap from a wide variety of plants. They are the major pests of small grain cereals such as wheat, barley, oats and triticale in Kenya. Aphids affect plant growth directly through nutrient drain by sap sucking, especially when they are present in large numbers. Cabrera *et al.* (1995) observed that plants infested with aphids had lower water potential, carbon dioxide assimilation, soluble carbohydrates and proteins.

Some species of aphids cause extensive destruction of plant tissue through the injection of toxic saliva. Sugary excretions of aphids (honeydew) attract saprophytic fungi on leaf surfaces which cause accelerated aging and reduced photosynthetic area (Minks and Harrewjn, 1989; Dixon, 1997). All these, deprive the developing grain of nutrients thus causing low yields. It was estimated by Minks and Harrewjn (1989) that 23.3% of the 4.9% crop loss in North and Central America caused by insect pests through direct damage was attributed to the greenbug (*Schizaphis graminum*

(Rondani)). Kinyua *et al.* (2000) reported up to 40% yield losses in Kenya as being caused by the Russian wheat aphid (*Diuraphis noxia* (Kurdjumov). Elsewhere, a yield loss of as much as 60% has been reported in wheat and barley as being due to *Diuraphis noxia* (Archer and Bynum, 1992). *Metopolophium dirhodum* (Walker) causes direct yield losses of up to 10% (Empson, 1982), while yield losses due to *Rhopalosiphum padi* (Linnaeus) are comparable to those caused by *Schizaphis graminum* or *D. noxia* (Kieckhefer and Gellner, 1992).

Aphids are the most important insect vectors of plant viruses and transmit the majority of all viruses (Adane *et al.*, 1995). They are the only known vectors of Barley Yellow Dwarf Virus (BYDV) and in many cases, the vector-virus relationship is quite specific (Agrios, 1997). Even low numbers of aphids can cause significant crop losses if they transmit plant viral diseases. BYDV can cause yield losses of 8-54% under field conditions (Wangai and Torres, 1991). Eighteen species of aphids have been reported to transmit BYDV (Jeldsinki, 1981) but those considered to be the most important and commonly found on cereal crops are *Sitobion avenae* (Fabricious), *Metopolophium dirhodum*, *Rhopalosiphum padi* and *S. graminum* (Muthangya *et al.*, 1991; Wangai, 1994). The efficiency of virus transmission is influenced by the population of the vector and the virus source (McGrath and Bale, 1990). Disease spread is rapid and irreversible if initial inoculum is high and vector dispersal capacity is great.

In Kenya wheat is grown all the year round. It is planted in February-March in Lower Narok. In Nakuru and Uasin Gishu it is sown in April-June. Highlands, such as Mt. Kenya Region (Timau, Nyeri, Muiga) have two seasons. The first one starts in June and ends in early September. The second season starts in October and ends in January. This implies that aphids can be hosted throughout the year aided by their ability to migrate from one field to another or being airborne for many kilometres. Many perennial grasses also serve as alternate hosts of cereal aphids (Wangai, 1994; Donahue *et al.*, 2000).

One of the objectives of Kenya's National Development Plan (1997-2001) was to improve wheat production by exploring possibilities of utilizing marginal zones to increase wheat production (GoK, 1997a). The low altitude marginal areas of Kenya, have a potential of approximately 200,000 ha for wheat production (World Bank, 1989). KARI-Njoro and Kenya Seed Company, have bred varieties for such zones (Irungu *et al.*, 1997). Low elevation areas where wheat has already been introduced include Machakos, Naivasha, Koibatek and lower Narok among others (Kinyua, 1997). Aphid infestations in marginal zones have however been found to be higher (Hassan *et al.*, 1993) compared to high potential areas, indicating that environmental factors and especially high temperature and low moisture influence population increase and dispersal in cereal aphids.

1.3 Efforts made towards the management of aphids

Some of the collaborative work between Kenya Agricultural Research Institute (KARI)-Njoro and Kenya Breweries Limited, has been to monitor migration of cereal aphids through suction traps which catch aphids flying 12m above ground. Bulletins are prepared and sent to farmers to warn them of possible invasion. The exercise lacks precision because realistic values of population growth rates are needed in pest forecasting and Integrated Pest Management (IPM) programmes. Other than detection of infestation, pest surveillance should also include; estimates of pest population density and dispersal capacity and how all these factors change with time, an issue this study aimed to address. When the pattern of aphid infestation on crops is well documented, specific recommendations on dates of planting, choice of chemical and method of application and other management strategies on a local basis can be developed.

According to Macharia *et al* (1997), the spread of BYDV has been controlled by use of systemic insecticides both as a seed dress and foliar sprays on the vectors. Several applications may be required within a cropping cycle in some areas. This is heavy reliance on aphicides for the control of aphids, not only increasing wheat production costs, but also threatening the quality of environment. Aphicides only temporarily suppress these pests as there is always migration of aphids from other places. Biological pest control is an integral component of IPM and is based on a unique phenomena of population interaction in a complex environment (Hanning, 1987). Aspects of aphid biology like the intrinsic rate of natural increase, parthenogenesis, paedogenesis, polymorphism and how these are affected by the aphid ecology provide the most useful information in developing an IPM programme. The regulation of aphid dispersal by environmental factors are not well known but environmental conditions as well as genotypic traits have been found to influence the outcome. To develop, a sound IPM programme, a detailed knowledge of pest movement at several levels is required. A safe control strategy to check the spread of the aphids will also limit spread of the disease.

Available literature indicates that relatively few biological and ecological studies on cereal aphids indigenous to Africa, South America and India have been carried out. Information available is based on temperate regions. The results of this study which focussed on three cereal aphid species namely *Metopolophium dirhodum, Rhopalosiphum padi* and *Schizaphis graminum* are aimed at providing tools that will be useful in decision making for the management of most cereal aphids in a wheat crop in Kenya. It will also form a sound basis for development of pest management options.

1.4 Objectives and hypotheses

1.4.1 Objectives

The general objective of this research was to find out the contribution of environmental, plant and intrinsic factors to cereal aphid dispersal and colonization on wheat. The specific objectives were:

1. To compare the reproductive potential of three cereal aphid species: *M. dirhodum, R. padi* and *S. graminum* over time
2. To investigate and compare the effects crowding, aphid morph and maternal age in the stimulation of alate (winged forms) production in the three aphids.
3. To examine the pattern of distribution and colonization of the cereal aphid species in time and space on three wheat varieties (Duma, Fahari and Mbega) in a growing season.
4. To observe the effect of temperature (high, medium and low) on the reproductive rates and alarysim in the aphids.

1.4.2 Hypotheses

1 *M. dirhodum, R. padi* and *S. graminum* have different rates of population increase.

2. Alate production in aphid species have depend on crowding, aphid morph and maternal age.

3 The time of infestation and the distribution patterns within host plants differs among aphid species.

4. Temperature influences reproductive rate and alarysim in cereal aphids.

CHAPTER TWO

2. LITERATURE REVIEW

2.1 Importance and distribution of cereal aphids

The occurrence of several aphid species is common wherever cereal crops are grown. Their abundance and economic importance vary from one location to another. The major insect pests on field crops in Denmark and Northern Europe are the cereal aphids *Sitobion avenae* (Fabricous), *Rhopalosiphum padi* (Linnaeus), and to a lesser extent, *Metopolophium dirhodum* (Walker) (Sigsgaard, 2000). In Kenya, surveys conducted in Mau Escarpment, Kitale, Eldoret, Timau, and Nakuru by Muthangya *et al.* (1990) indicated that the distribution of various aphid species was widespread in these areas. *Metopolophium dirhodum* was the most common in all regions surveyed. Its population was highest in Timau and Njoro (Nakuru). *Schizaphis graminum* infestation was found to be very severe in Njoro while *Rhopalosiphum maidis* and *Rhopalosiphum padi* were also commonly found in all surveyed areas.

Diuraphis noxia infestation is also very severe and wide spread (Kinyua *et al.,* 2000). Beside their direct damage through feeding on plant sap, and extensive plant tissue destruction through the injection of salivary excretions by some species, aphids serve as vectors of serious viral diseases like Barley Yellow Dwarf Virus (BYDV) among others (Adane *et al.*, 1995). The major cereal aphid species have been reported to transmit BYDV (Gildow, 1984; Wanjama, 1990; Muthangya *et al.*, 1991) except *D. noxia* (Hein *et al.*, 1989).

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 because initial colonization of cereal fields is accomplished by flying aphids (Cannon, 1985).

2.2 Aphid dispersal

According to Scheider (1962) and Southwood (1962, 1981) dispersal refers to the scattering of a population, leading to an increase in the mean distance between individuals. The tendency to disperse is an evolved adaptation that has enabled aphids to spread the chance of survival in space, and to colonize quality plants (Johnson, 1969). Hein *et al.* (1996) reported that the ability of aphids to use flight for dispersal is an important factor that contributes to their status as pests. For example a major factor in the severity of the Russian Wheat Aphid (RWA), as a pest is its ability to disperse (Hein *et al.*, 1989).

By using suction traps, whose sampling efficiency is independent of wind speed and which segregate the aphids into hourly catches, Johnson *et al.* (1975) observed that the factors that determined *Aphis fabae* flying over a bean crop to be the rate of eclosion of the winged adults and the time it took them to complete their teneral development. Laboratory experiments to investigate movement of apterous *Sitobion avenae* using a 0.5 x 0.5 m grid of barley seedlings (plant spacing 6 cm) measured the proportion of aphids leaving the central plant and their subsequent movements. Results showed that aphid movements increased with aphid density, temperature, wind gusting and rain intensity (Mann and Harrington, 1995). Factors implicated in development of winged forms include: crowding, host plant quality, temperature, photoperiod and intrinsic factors (Kawada, 1987; Hein *et al.*, 1996; Dixon 1998). The production of alate morphs, in response to crowding, declining food quality or seasonal changes in day length and temperature, enables species to colonize more suitable seasonal host plants (Taylor and French, 1970).

2.2.1 Effect of crowding and polymorphism on aphid dispersal

Polymorphism (existing in many distinct forms or morphs) is characteristic of aphids (Dixon, 1985). Alary polymorphism in aphids allows for the expansion of the population (Blackman and Eastop, 1984). There is extensive literature concerning alary polymorphism in aphids and the phenomenon is complex (Wanjama, 1986) such that very few generalization can be applied in all aphid species.

The factors that induce the production of various morphs of cereal aphids have been investigated for some aphids only. Lees (1960) suggested that the production of emigrants in some holocyclic aphids was due to the action of an 'interval timer' within the aphid. For example, for a given aphid clone, emigrants were produced after a constant time interval and temperature. However, Dixon and Glen (1971) noted that no emigrants of *R. padi* developed when aphids were reared in isolation for six successive generations on actively growing plants of the primary host. Therefore, he suggested that the production of winged morphs was not due to interval timer but a combined action of poor nutrition and crowding which induced the production of emigrants in the second and third generations of *R. padi* on the primary host. Howard and Dixon (1992) found that very high levels of *M. dirhodum* alate occurred on wheat towards the end of the season, even when aphids were reared individually.

Crowding markedly influences the readiness with which aphids fly and thus disperse. Lees (1967) confirmed that tactile stimulation occurring among crowded aphids led to production of alatae. He found that the fourth larval instar and adult have the highest alatae production in response to crowding and that there is no response in the first instars in *M. viciae*. The more intense the crowding, the higher the proportion of alatae that develop, especially if both mothers and offspring experience crowding (Dixon, 1985). Reduced crowding of aphids, usually results in a lower fraction forming wings. On graminae, the highest proportion of alate developed when both females and their offsprings were crowded (Dixon and Glen, 1971). Dixon (1971) found out that production of winged emigrants is induced both by crowding and poor nutritional quality of the leaves.

Some species appear to "monitor" crowding continuously (Dixon, 1973). MacKay (1977) and MacKay and Wellington (1977) have shown that "maternal age effects" determine the production of alate producers in *Aphis pisum*. These authors found that firstborn progeny of apterae respond more strongly to a crowding stimulus than do later progeny. It may be assumed that maternal age effects operate also in cereal aphids in absence of similar data for these species.

In *S. avanae*, 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 and Dixon, 1981). However this cannot be generalised for all aphid species because in a study done by Migui (1996), nymphs from apterous mothers of *R. maidis, R. padi* and *S. graminum* developed into apterous adults but with *S. avenae*, the progeny of apterous mothers and alate mothers predominantly developed into winged and non-winged forms respectively.

2.2.2 Rate of increase in aphids and its influence on their dispersal

Aphid populations are favoured by extremely high reproductive capacities (upto ten offsprings per day) and short life cycles resulting in several generations (3-4 in one month) within a short time (Wanjama, 1986; Hein *et al.*, 1989). These factors enable a rapid population increase thus stimulating production of dispersers and progression of infestation and crop damage. Watt and Dixon (1981) and Cannon (1985) found that the proportion of alatiform larvae in the field was significantly correlated with aphid density.

Accelerated growth of populations in aphids is also due to their capacity of parthenogenesis (reproduction occurring through development of unfertilized eggs) (Hein *et al.*, 1996; Dixon 1997) which in turn is enhanced by neoteny or paedogenesis (reproduction in a juvenile stage) (Wanjama, 1986). This greatly reduces the generation time (Wyatt, 1961, 1963) because there is no time wasted in waiting or searching for a mate, which may never be found. Birch (1948) describes the intrinsic rate of increase as 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 as given by the following equations (1) and (2):-

$$\Sigma e^{-r_m x} l_x m_X = 1$$

$$T_c = \frac{Log_e \Sigma l_x m_X}{r_m}$$

Where r_m = intrinsic rate 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 (Migui, 1996).

The rate of increase of an aphid population depends on the speed of development, survival and fecundity. In many aphid species, reproduction rises rapidly in the early stages of adult life and the reproductive time required to contribute 95% to the natural intrinsic rate of increase (r_m) corresponds closely in value to the pre-reproductive period (Wyatt and White, 1977). 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, a simplified equation for the calculation of r_m and cohort generation time was formulated by Wyatt and White (1977) as follows:-

$$r_m = \frac{0.738(\log_e M_d)}{d}$$

$$T_c = 4d/3$$

where r_m = intrinsic rate of increase

d = pre-reproductive time i.e. the period (days) from birth to onset of reproduction

m_d = number of progeny(nymphs) produced within period equal to time d

T_c = cohort generation time

2.3 Aphid colonization

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 their survival.

Field studies on aphid populations on plants by Lowe (1984) and Kocourek *et al.* (1994) have confirmed that generally populations on plants are affected by the individual aphid (intrinsic), plant (host) and environmental factors. A colony is normally established by a closely aggregated group of up to about twenty progenies of immigrant alate adults. Multiplication rates dramatically decreases as the colony increases beyond relatively small optimum size. This was demonstrated in outdoor field-cage experiments in which multiplication rate of *Aphis fabae* was followed on whole plants (Way, 1968).

2.3.1 Effect of host plant on aphid colonization

Aphids like most phloem feeding insects commonly exhibit a high degree of host specificity. Plant specific chemical compounds are likely to serve as an important host selection cues for monophagous aphids and such substances could be present in aphid honey dew. In two specific experiments where apterous *Myzus persicae* and *Phorodon humuli* were reared on a buffered sucrose solution containing various aphid honey dew or a mixture of amino acid, the host-specific aphid *P. humuli* could grow and reproduce only on artificial diets containing honeydew collected from *P. humili* that had fed on hop (*Humulus lupulus*). *M. persicae* did not perform well on diets containing the same, perhaps because hop is a poor host (Dorscher, 1993). Aphid clones generally perform better on their original host than they do on the alternate host plants. Cereal aphids are also expected to have differential performance on different hosts even at varietal level. Hesler *et al*. (1999), found that MV4 wheat variety lowered the intrinsic rate of natural increase for *R. padi*. He also showed that the proportion of alate *R. padi* was greater on the same MV4 than most other accessions tested indicating that the former is not a suitable host for the pest

Glinwood and Pettersson (2000) suggested that a change in the intrinsic host preference in cereal aphids causes the switch between winter and summer hosts. Factors which influence host preference and winter host leaving by emigrants operate at the level of the individual aphid, as well as the aphid morph. The extreme hypersensitivity of alate colonists of some species to food plant quality may be taken as a mechanism of preventing colonization of some unsuitable plants (Kennedy and Stroyan, 1959). Host plant condition may indirectly intensify the crowding stimulus since aphids on a poor host will be more unsettled than those on one that is providing sufficient and satisfactory food (Lees, 1966).

2.3.2 Effect of niche and host growth stage on aphid colonization

Different species of aphids can occur on the same plant, but not compete for feeding sites. Aphid species on the same plant, have different feeding niches (Leather and Dixon, 1981; Migui, 1996). Adults of each species are more selective than juveniles in determining suitable locations for settlement, feeding and reproduction. Feeding site preferences are considered important, particularly in relation to the type and amount of damage caused by various aphid species (Vickerman, 1979).

The type of host plant and its growth stage markedly affect colonization and the subsequent rate of increase of aphid populations (Leather and Dixon, 1981; Guildemond *et al.*, 1998). Grima *et al.* (1990) reported that the highest intrinsic rate of increase (r_m) values for *Diuraphis noxia* was at the stem elongation stage of wheat except at high temperatures of 27-29 ^{0}C when the tillering stage was most suitable. Host quality has been found to vary with age. *S. avenae*'s reproductive rate is almost three times when it feeds on ears at the milk stage than when it feeds on the leaves (Watt, 1979). On the contrary, *M. dirhodum* reproduces poorly on the ears and best on leaves (Cannon, 1986).

The colonisation and subsequent population growth rate of *M. persicae* and *A. gossypii* is affected by the growth stage of the plant. Cultivar and aphid species interact with plant growth stage in influencing population growth rate (Guldemond *et al.*, 1998). Budding and flowering stages were found to be the most suitable in three out of four aphid x cultivar combinations. The relative growth rate of apterae *M. dirhodum* is mainly determined by temperature and the developmental stage of barley (Howard and Dixon, 1995). Flight activity is related to crop phenology (Kieckhefer and Lytle, 1976). This flight strategy enables *S. avenae* to colonise a sequence of ephemeral high quality habitats and to take advantage of any changes in host quality. Howard and Dixon (1992) proposed that the major induced plant factor contributing to the reduction in the growth of *M. dirhodum* populations on wheat in the fields is the production of alatae, which develop on mature plants even when the number of aphids on each plant is very low. Studies done by Kieckhefer *et al.* (1995) showed that accurate prediction of the yield loss caused by cereal aphids in wheat involves assessment of the aphid population density on plants, the duration of their feeding, and the growth stage of the crop at the time of feeding.

Research work by Leather and Dixon (1981), Wiktelius (1987) and Wiktelius *et al.* (1990) discussing patterns of within-plant distribution of *R. padi* have considered factors such as nutritional value of tissues and avoidance of extreme temperature in the field. Previous work by Jackson and Dixon (1996) on the same aphid, indicated that aphid distribution within the plant may be affected by plant quality, natural enemies or their interaction. These findings are supported by Hopkins and Dixon (1997) who observed that on non-flowering plants *R. padi* typically occurred on leaf sheaths or open blades where they were found to be easily captured by the lacewing predators compared to the *D. noxia* which fed within immature rolled leaves (Begerson and Messina, 1998).

Plant quality for herbivorous insects can decrease after feeding due to induced responses of the plant (Karban and Baldwin, 1997). Effects of induced responses on the within-plant distribution of the herbivore have also been reported by Edwards *et al.* (1991). They suggested that induced responses of wheat seedlings to aphid feeding play a role in shaping the within- plant distribution of *R. padi.* Gianoli (1999) found out that aphids feeding on the stem triggered an induced response that reduced aphid fecundity on the third leaf, whereas no effect on aphid fecundity on the stem was observed. In contrast, aphid feeding on the third leaf produced a local induced response that reduced aphid fecundity on this leaf, but did not affect aphid fecundity on the stem. *R. padi* selected the stem of cereal seedlings as its main feeding site. This may not be due to its nutritional value but rather to the avoidance of induced responses, which could occur if aphids fed on upper leaves.

2.4 Effect of environmental factors on the rate of increase, dispersal and colonisation of aphids

Bezermer *et al.* (1998) suggested that the abundance of *M. persicae* may increase under conditions of climatic changes. Aphid abundance which has a direct bearing on wing formation was found to be enhanced by both carbon dioxide and temperature treatment. Temperature affects the rate of development with each species having a different relationship with temperature (Dean, 1974; Cannon, 1984).

Pous and Tatchell (1995) found that drought stress had no effect on developmental time, nymphal mortality and the weight of teneral adults of *R. padi* and *S. avenae* clones up to the onset of reproduction in the first generation (F_1) . The subsequent reproductive capacity as measured by the effective and potential fecundity and reproductive rate were much reduced on drought stressed plants. There was however, only a small decrease in the intrinsic rate of increase. Population growth of chromosomal races of *Sitobion miscamthi* and a closely related species *S. near fragariae* was simulated from lab data for comparison with outdoor populations. Intrinsic rate of increase (r_m), mean relative growth rate (MRGR) and longevity at different temperatures in a controlled environment were compared to test whether the seasonal differences in abundance observed in Eastern Australia was related to temperature response. The study indicated significant differences in response to temperature regimes both in the laboratory and outdoor (Turak *et al.*, 1998).

The regulation of aphid dispersal by environmental factors is not well understood (Mann and Harrington, 1995). However, its known that environmental conditions as well as genotypic traits, influence the outcome. Studies on the effect of plant nutrient and four constant temperature of 10, 15, 20 and 25 ℃ on the biology of *Cinara cupressus* indicated that wing formation was not induced when apterae were reared for up to three generations. With continuous crowding in the supply cultures held at 21 ℃ wing formation increased with increase in temperature (Kairo and Murphy, 1999).

Dixon (1997) found out that aphids can produce different morphs (apterae and alatae) in response to environmental change and switch to sexual reproduction in the autumn. When wind and rain were compared, rain had the greatest effect on aphid dispersal. It was concluded that leaf disturbance caused by strong gusts of wind or large rain droplets are of considerable importance in the initiation of aphid dispersal but wetness alone was not (Mann *et al.*, 1995). The proportion of F_2 generations that was alate differed greatly between clones with *S. avenae* producing a significant number of alate on drought stressed wheat plants (Pous and Tatchell, 1995).

Previous research work by Howling *et al.*, (1993) has shown that, for *Myzus persicae*, there is a linear correlation between the date of first record in the trap each year and the mean temperature during the preceding winter. Data from 1966 to 1988 inclusive were used to generate models to predict the date of first record of this aphid species at Rothamsted, and the predictive values of the models using both simple and multiple regression were assessed using data from 1989 to 1992. Multiple regression however, identified relationship with other variables for time periods when the correlation with mean temperatures was weaker.

CHAPTER THREE

3. EFFECTS OF POPULATION INCREASE AND ALARYSIM ON APHID DISPERSAL

Abstract

A study on population increase in cereal aphids was done by comparing the intrinsic rate of natural increase (r_m) of three cereal aphid species in the green house. Single fourth instar nymphs from *Rhopalosiphum padi* (Linnaeus), *Metopolophium dirhodum* (Walker) and *Schizaphis graminum* (Rondani) were placed separately on potted and caged wheat plants. They were left to mature and start reproducing. Nymphs were counted and removed daily. The rate of increase for *R. padi* was higher ($P = 0.05$) than that of *S. graminum* and *M. dirhodum* which were not significantly different. The effect of temperature on the intrinsic rate of increase (r_m) and alarysim for the three species was conducted in controlled environment chambers set at three day/night temperature regimes of 4/ 11°C (low), 11/18° C (medium) and 18/25 C (high). Fourth instar aphids from each species were separately introduced onto potted plants, allowed to mature and reproduce. Nymphs produced were counted after every three days and transferred onto 6cm wheat leaf sections in petri-dishes and observed for percentage wing formation. The (r_m) increased with increase in temperature. *R. padi* had the highest response ($P = 0.05$). Low temperature reduced the rate of increase for all the aphids. Percentage alate also increased with temperature. *M.*

dirhodum had the highest proportion of its aphids forming wings followed by *R*. *padi* and *S. graminum.* A comparative study on dispersal capacity for the three aphid species was done by crowding 25 apterae and alate fourth instar nymphs separately in plastic vials. After 2h of crowding, the aphids were transferred onto 6 cm leaf sections of wheat. The aphids were reared to different ages so as to give progenies born within 24h, 48h and 72h. Observations were made on the proportion of these progenies that developed into alatae. Resultant alates were repeatedly allowed to reproduce and their offsprings monitored for wing formation, to determine whether the stimulus was passed from mother to offspring until no more alates were produced. *M. dirhodum* was observed to have the highest capacity to produce wings in both apterae and alate mothers. It was followed by *R. padi* and the least was *S. graminum.* Alate mothers from *S. graminum* and *R. padi* produced no alate offsprings but *M. dirhodum* produced a few alate only in their first generation. The first born progeny of apterae mothers had the highest proportion of alatiform. The number declined gradually with maternal age for all the three species. *M. dirhodum* apterae aphids passed the crowding stimuli by producing alatiforms up to the fourth generation but *R. padi* and *S. graminum* stopped after the first generation.

3.1 Introduction

Aphids can cause substantial losses by direct effects of their feeding or as vectors of several plant viruses (Kolbe and Linke, 1974; Haber, 1990). Some of the factors that enable an aphid to inflict economic damage in crops include high rate of population growth, high capacity for dispersal and ability to transmit plant diseases. The pest status of many aphid species is partly due to their remarkable rate of increase. Aphids reproduce parthenogenetically and their population can quickly reach damaging level when conditions are favourable in a given growing season. Development and reproduction are separate processes that together determine the size of aphid populations (Migui, 1996). Species that have a high rate of reproduction and development are likely to be important pests in regions where they occur. Detailed information on the biology and reproductive capacities of cereal aphids is essential in the determination of the relative effect of different aphid species on crops. To achieve this, reproductive capacities of *Rhopalosiphum padi* (Linnaeus), *Metopolophium dirhodum* (Walker) and *Schizaphis graminum* (Rondani) were compared under greenhouse conditions.

A survey conducted in Kenya by Hassan *et al.* (1993) revealed that aphid infestations are higher in marginal areas marked with high temperatures and low moisture. Temperatures are important in the ecology, evolution and pest status of aphids (Turak *et al.*, 1998). The production of alate morphs, in response to crowding, declining food quality or seasonal changes in day length and temperature, enables species to colonize more suitable seasonal host plants (Taylor and French, 1970). This study hypothesised that environmental factors and especially temperature, influence population increase and production of dispersers. Studies were initiated to confirm this hypothesis.

The factors that favour a rapid spread so that aphid infestation covers an entire field from initial colonization though not well understood can be greatly attributed to their dispersal capacity. Dispersal by aphids is an important factor that contributes to their pest status. A major factor in the severity of the Russian Wheat Aphid (RWA), as a pest is its ability to migrate (Hein *et al.*, 1989). In the field, aphids occur in both winged (alatae) and wingless (apterae). Only alate morphs are involved in long distance dispersal and initial colonization of new fields (Foster, 1978; Foster and Trehene, 1978). Crowding is the major stimulus for wing formation in aphids (Lees, 1967). Other factors implicated in the development of winged forms include: host plant quality, temperature, photoperiod and intrinsic factors (Kawada, 1987). A comparison of the third generation aphids with first generation showed that the experience of the mother in the second generation often influence the subsequent performance of its offspring (Borro *et al.,* 1995). The proportion of alatiform fourth instar larvae in the field has been used to estimate the production of alate emigrants or tendency to disperse (Lamb and MacKay, 1979; Watt and Dixon, 1981) as alate are likely to leave crop shortly after molting to the adult stage (Rabbinge *et al.*, 1979). Work was started to determine the effects of crowding on both apterae and alate morphs on the production of alate offsprings at different times of their adult life.

3.2 Materials and Methods

3.2.1 Production and maintenance of test plants

Throughout the study period a continuous supply of clean (aphid free) wheat seedlings required in the rearing of aphid cultures and the experimental work was maintained. A soil medium well mixed with diammonium phosphate fertilizer (18:46:0 NPK), at a rate of 100g per 1kg soil was used. Four seeds of wheat, variety Duma, were planted weekly in a number of pots (15 cm diameter and 25 cm deep) in the greenhouse. The plants were kept free from aphids by covering, the potted plants with a nylon net (0.3 mm mesh) supported on a wire frame (Plate 3.1). Approximately 10 days after planting, the first leaves were fully opened and seedlings were ready for use in the raising of aphid cultures. The plants used for experimental work were thinned to one per pot.

3.2.2 Rearing of aphid cultures

The three aphid species, *M. dirhodum, R. padi* and *S. graminum* were collected from fields within Njoro. They were identified according to the descriptions given by

Blackman and Eastop (1984) and Hein *et al.* (1996).

The rose grain aphid (*Metapolophium dirhordum*) wingless form is spindle shaped, yellowish-green with a distinct brighter green longitudinal mid-dorsal strip (Plate 3.2A). The antennae, legs and cauda are pale yellow. The winged form has a yellow abdomen without a dorsal abdominal marking.

The bird-cherry aphid (*Ropalosiphum padi*) wingless form is olive green with a reddish-orange (rusty) area at the base of the cornicles. The tips of its legs, cornicles and antennae are black (Plate 3.2B). The winged form of this aphid is darker than the wingless. The head, thorax and sphinculi are black making the aphid appear nearly black (Plate 3.3A).

The greenbug *(Schizaphis graminum)* is light green with a dark green colour stripe down the middle of the back. The tips of the legs and cornicles are black (Plate 3.2C). The winged form of the greenbug is darker (Plate 3.3B).

Adults of each aphid species from the three aphid cultures were separately settled on fresh leaf sections inserted in moist sand at the periphery of petri-dishes and allowed to larviposit. The nymphs were left to develop and one fourth instar nymph of each species was selected and transferred to separate potted plants in an aphid free well ventilated plexiglass cage (45 x 50 x 80 cm) (Plate 3.4). The cages were placed in the greenhouse to establish pure cultures of these aphid species. The greenhouse night temperatures ranged between 14-18°C and day temperature 20-28°C and natural light conditions of 12h daylength. Deteriorating plants were regularly replaced by fresh ones from the supply described under 3.2.1 above. From these cultures, a reliable supply of aphids of the three species was obtained for various experiments.

Plate 3.1. Potted plants covered with a 0.3 mm mesh nylon net

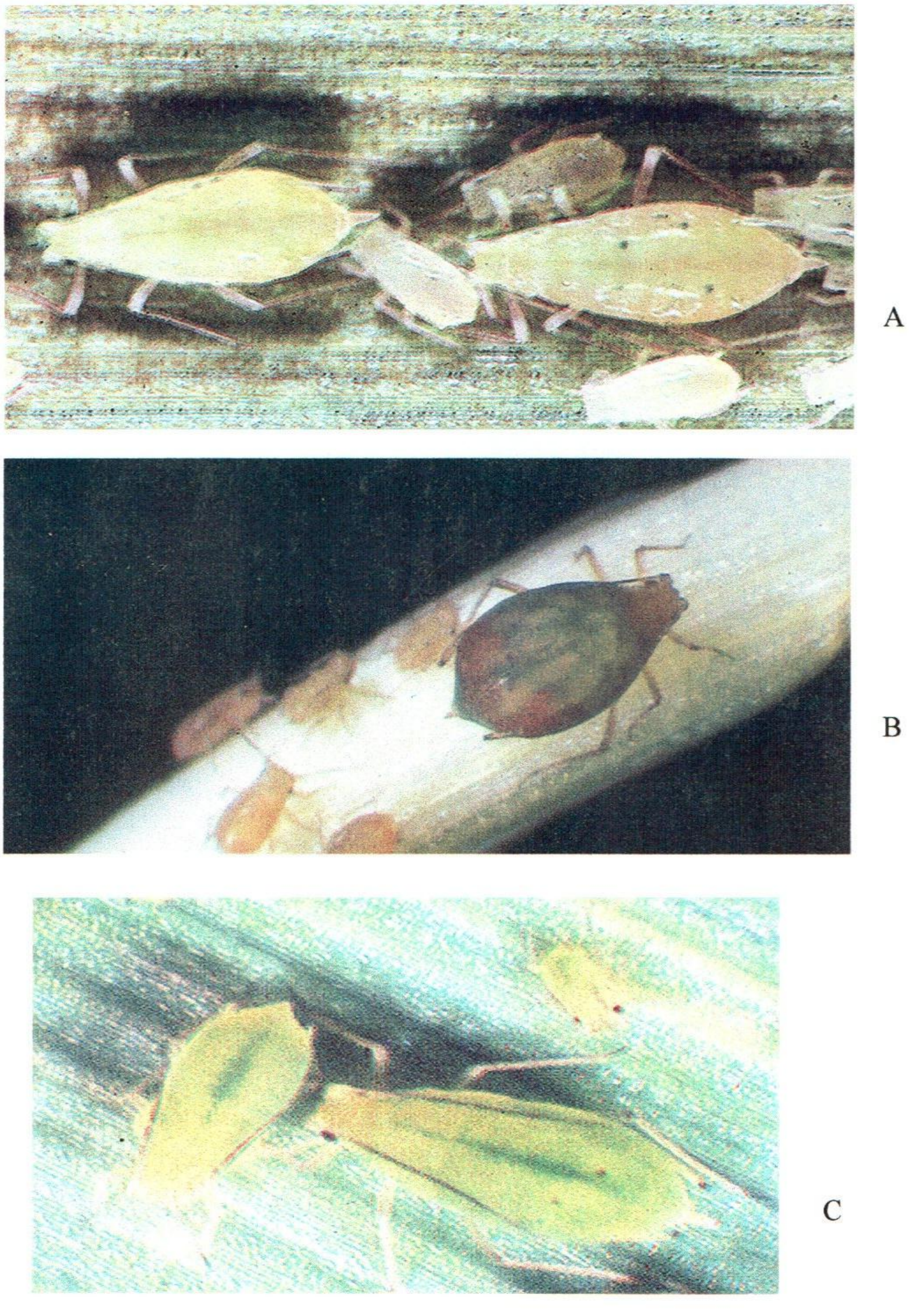

Plate 3.2. Three wingless aphid species, A: *M. dirhodum,* B: *R. padi* and C: *S. graminum* (Source: Ministry of Agriculture, Fisheries and Food, 1975)

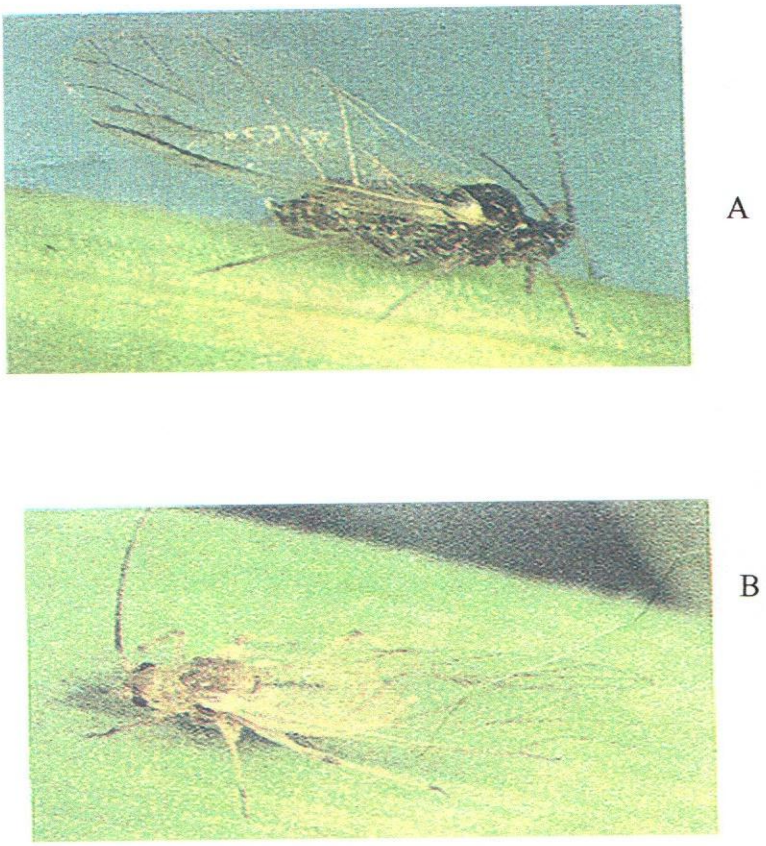

Plate 3.3. Winged aphids, A: *R. padi* and B: *S. graminum* (Source: Hein *et al.*, 1996)

Plate 3.4. A 45 x50 x 80 cm well ventilated plexiglass cage

3.2.3 Population increase of the three aphid species in the greenhouse

The experiment was conducted in a green house using a completely randomised design (CRD) replicated three times. The greenhouse temperature and relative humidity were recorded throughout the experimental period using a thermohygrograph. To obtain females of equal age for the experiment, three adult aphids from each species were selected from the reared cultures. These aphids were settled singly onto clean potted wheat plants (variety Duma) in separate plexiglass cage measuring 45 x 50 x 80 cm. They were left for 24h to larviposit. At this point, all the aphids including the larvipositing mother were removed to leave one nymph per plant. The remaining nymphs were of approximately the same age with 24h as maximum difference. Data was recorded on the developmental time 'd' (time from birth to production of first nymph), number of progeny (m_d) over a period equivalent to 'd' and population (intrinsic rate of increase, r_m) was calculated using Wyatt and White (1977) equation given as:

$$r_m = \frac{0.738(\log_e M_d)}{d}$$

where r_m = intrinsic rate of increase

d = pre-reproductive time i.e. the period (days) from birth to onset of reproduction

m_d = number of progeny (nymphs) produced within period equal to time d

The appearance of exuviae determined the end of instar periods. The start of the adult stage was therefore marked by the appearance of the exuviae at the end of the fourth instar. The number of offsprings for each female were recorded and removed daily using a fine paint brush (grade 00), for a period equivalent to the time ‘d’, from birth to production of first nymph. Care was taken to ensure that the mother did not fall off.

Data on the developmental time ‘d’ and the intrinsic rate of natural increase (r_m) was analysed using General Linear model of the Statistical Analysis Systems (SAS) package (SAS Institute 1996). Standard error (SE) was used to separate the treatment means.

3.2.4 Effect of temperature on population increase and alarysim

The experiment was conducted in controlled environment chambers (Plate 3.5) using split-plot design with three replications (Plate 3.6). The chambers were set at three day/night temperature regimes high (25/ 18°C) medium (18/11°C) and low (11/4°C) as main factors. Three aphid species namely; *M. dirhodum*, *R. padi* and *S. graminum* were observed as sub factors. Light was set at 12h of light and 12h of darkness (L12:D12) and the Relative humidity varied between 60-80%. Adult aphids from each species of the greenhouse cultures were placed singly using a fine paint brush onto potted wheat plants (variety Duma) at three tiller growth stage. The infested plants were then transferred into the controlled environment chambers. These adults were allowed to produce nymphs within a period of 24h. At this point, all the aphids including the larviposting mother were removed to leave one nymph per plant. The remaining nymphs were of approximately the same age with 24h as maximum difference. They were allowed to develop to maturity and start larviposting. All the nymphs produced by each female were counted, recorded and removed after every three days using a fine paint brush for a period equivalent to time from birth to first reproduction (d). The nymphs were then transferred onto leaf sections in petri dishes on laboratory benches. They were allowed to grow up to the fourth instar when they were observed for wing bud development. The effect of temperature on developmental time 'd' and number of progeny over a period equivalent to time 'd' were recorded. Population growth rate (r_m) using Wyatt and Whites' (1977) equation. The percentage alate (the proportion of progeny that developed wing buds at their fourth instar stage) were computed.

Data on the intrinsic rate of natural increase (r_m) and percent alate was analysed using general linear model of the statistical analysis systems (SAS) package (SAS Institute; 1996).

Plate 3.5. Controlled environment chambers

Plate 3.6. The experimental arrangement in the controlled environment chamber

3.2.5 Effect of Maternal age and aphid morph on percentage alate production

Six laboratory experiments were conducted to determine the effect of maternal morph (apterae and alatae) and maternal age (first, second and third larvipostion) on production of dispersers for the three aphid species as described in the following subheadings numbered (a) to (f).

(a) Percentage alatae in the progeny born within 24h from crowded apterae mothers

Twenty five (25) apterae (wingless) fourth instar nymphs from each of the three species were selected from the greenhouse cultures. The nymphs of each species were placed separately in a small plastic vial measuring 3mm diameter x 35mm depth, for 2h. This was to allow enough aphid to aphid contact and to give a strong crowding stimulus. The plastic vial was tapped lightly from time to time to increase aphid movement and hence more contact. Each aphid was then transferred and confined, on 6 cm long portion of wheat leaf in a petri-dish (Plate 3.7). The leaf was kept fresh by inserting its base into a heap of moist sand at the periphery of the dish, and replaced by a fresh one after every three days. The aphids were allowed to mature and start reproducing. The adults were removed to leave nymphs born within 24h of larviposition. These nymphs were raised to the fourth instar when observations were made and recorded on the proportion that developed into winged (alate) forms (as a percentage of total nymphs produced). Resultant alates were allowed to reproduce and their offsprings monitored for wing bud formation, to determine whether the stimulus was passed from mother to offspring. This was repeated until no more alate offsprings were produced.

(b) Percentage alatae in the progeny born between 24-48h from crowded apterae mothers

In the second experiment the procedure in 3.2.5(a) above was adopted but all nymphs were removed to select those produced between 24h-48h. These nymphs were raised to fourth instar and observed for wing development. Resultant alate nymphs were allowed to mature and reproduce and their offsprings monitored for wing formation, to determine wether the stimulus was passed from mother to offspring. This was repeated until no more alatae offsprings were produced.

c) Percentage alatae in the progeny of crowded apterae mothers born between 48-72h

The experimental procedures outlined in 3.2.5 (a) and (b) above were followed but the nymphs were constantly removed to select those produced between 48-72h. These nymphs were raised to fourth instar and observed for wing development. Resultant alate nymphs were allowed to mature and reproduce. Their offsprings were monitored for wing formation, to determine wether the stimulus was passed from mother to offspring. This was repeated until there was no more alatae offsprings.

(d) Percentage alatae in the progeny born within 24h from crowded alate mothers

Twenty five (25) alate (winged) fourth instar nymphs from each species were selected from the green house cultures. Each species was placed separately in small plastic vials measuring 3mm diameter x 35mm depth, for 2h. This was to allow enough aphid to aphid contact and to give a strong crowding stimulus. The plastic vial was tapped lightly from time to time to increase aphid movement and hence more contact. Each aphid was then transferred and confined, on 6 cm long portion of wheat leaf in a petri-dish. The leaf was kept fresh by inserting its base into a heap of moist sand at the periphery of the dish, and replaced by a fresh one after every three days. The aphids were allowed to mature and start reproducing. The adults were removed to leave nymphs born within 24h of larviposition. These nymphs were raised to the fourth instar when observations were made and recorded on the proportion that developed into winged (alate) forms (as a percentage of total nymphs produced). Resultant alates were allowed to reproduce and their offsprings monitored for wing formation, to determine wether the stimulus was passed from mother to offspring. This was repeated until no more alate offsprings were produced.

(e) Percentage alatae in the progeny born between 24-48h from crowded alate mothers

In the second experiment the procedure in 3.2.5(d) above was adopted but all nymphs were removed to select those produced between 24h-48h. These nymphs were raised to fourth instar and observed for wing development. Resultant alate nymphs were allowed to mature and reproduce and their offsprings monitored for wing formation, to determine wether the stimulus was passed from mother to offspring. This was repeated until no more alatae offsprings were produced.

(f) Percentage alatae in the progeny born within 48-72h from crowded alate mothers

The experimental procedures outlined in 3.2.5 (d) and (e) above were followed but the nymphs were constantly removed to select nymphs produced after 72h. The mothers were then removed and nymphs raised to fourth instar and observed for wing development. Resultant alate were allowed to mature and reproduce and their offsprings monitored for wing formation, to determine wether the stimulus was passed from mother to offspring. This was repeated until no more alate offsprings were produced.

The data was analysed using descriptive analysis.

Plate 3.7. Aphids confined to 6 cm wheat leaf sections in petri-dishes

3.3 Results

3.3.1 Population growth of the three aphid species in the greenhouse

The developmental days ‘d’ (time to first reproduction) for the three aphids was not significantly different under greenhouse conditions. *R. padi* had a bigger progeny size of 45.3 compared with 35.8 and 30.8 for *M. dirhodum* and *S. graminum* respectively within the same period of 8 days. The intrinsic rate of natural increase (r_m) for *R. padi* (0.373) was significantly higher than that of *S. graminum* and *M. dirhodum* (0.330 and 0.324) respectively, which were not significantly different ($P = 0.05$) (Table 3.1).

The thermohygrograph readings ranged between 12-28 °C for temperature and 65-90% for relative humidity during the experimental period.

Table 3.1 Developmental days (d), size of progeny (m_d) and intrinsic rate of increase (r_m) for *R. padi, M. dirhodum* and *S. graminum* reared under greenhouse conditions.

Aphid species	Developmental days (d)	Size of progeny (m_d)	Intrinsic rate (r_m)
R. padi	7.5a$^{\phi}$	45.3a	O.373a
M. dirhodum	8.0a	35.8b	0.330b
S. graminum	8.0a	30.8b	0.325b
SE	1.6	9.5	0.027
CV (%)	10.4	20.1	6.2

3.3.2 Effect of temperature on developmental time, size of progeny, intrinsic rate of population increase and alarysim in *R. padi*, *S. graminum* and *M. dirhodum*

Developmental time 'd'

Developmental time 'd' (the time the aphids took from birth to first reproduction) significantly depended upon aphid species and temperature regime (Table 3.2). There was a significant negative relationship between temperature and time 'd', but the magnitude differed among the three aphid species (Figure 3.1). Developmental time (d) from low to high temperatures regimes increased five times for *R. padi,* four times for *S. graminum* and twice for *M. dirhodum.*

Size of progeny

Table 3.3 indicates that at low temperatures *S . graminum* produced 70% of its progeny within 0.5'd' while *R. padi* and *M. dirhodum* had about 60%. Within the same temperature range, *R. padi* had close to hundred percent of its progeny at 0.75'd' while *M. dirhodum* and *S. graminum* had 90%. The scenario changed at medium temperature where except for *M. dirhodum* which had 54%, the other two aphids produced than 50% of their progeny within 0.5'd'. At 0.75'd', *R. padi* had only 65% of its progeny, *S. graminum* 71% and *M. dirhodum* 81%. At high temperatures *M. dirhodum* and *S. graminum* had about 60% of the progeny while *R.*

padi still had only 48% at 0.5'd'. All the aphids had produced 80-85% of their progeny by 0.75'd' at high temperature regime.

Intrinsic rate of increase (r_m)

Changes in time to first reproduction 'd' resulted in large changes in the intrinsic rate of increase (r_m) of aphid populations. At high temperature, *R. padi* took about 5 days from birth to first reproduction (Table 3.2) and produced a progeny size (m_d) of 37 nymphs (Table 3.4). At this temperature regime the intrinsic rate of increase (r_m) for this aphid species was 0.578 (Table 3.5). At low temperature, this aphid species took 24 days from birth to first reproduction and produced almost the same size of progeny but the r_m was only 0.111.

Intrinsic rate of natural increase (r_m) increased with temperature (Figure 3.2) for all the three species. The r_m for *R. padi* increased by more than 90% as temperatures rose from low to high, *S. graminum* by 80% and *M. dirhodum* by 70%. Low temperatures depressed the rate of increase in all the three species. While the intrinsic rate of natural increase (r_m) for *R. padi* was the same as *M. dirhodum* at low temperature, slightly different at medium, it was 37% more at high temperatures. The r_m was shown to be higher, early in the reproduction period and then declined at different rates depending on the temperature regimes and the aphid species (Figures 3.3-3.5).

Alarysim

There were significant differences in wing formation among the three temperature regimes (Table 3.6) for all the three aphid species (*P* = 0.05). The proportion of winged forms significantly increased with increase in temperature. Percentage wing production for the three aphid species increased from 10.1% at low temperature to 55.8% at high temperature. *M. dirhodum* had the highest average percentage wing production of 47% while *R. padi* and *S. graminum* had 27% and 12.3%, respectively. At low temperature *M. dirhodum* produced an insignificant number of alatae (29.5%) while *R. padi* and *S. graminum* produced 0.7% and 0%, respectively.

Table 3.2 Effect of temperature regimes on developmental days ‘d’ of *R. padi, M. dirhodum* and *S. graminum*

Aphid species	Developmental days with temperature		
	Low(11/4°C)	Medium(18/11°C)	High(18/25°C)
R. padi	24.3**b**	9.0**b**	4.7**b**
M. dirhodum	23.0**c**	12.3**a**	7.0**a**
S. graminum	29.3**a**	12.3**a**	7.3**a**
SE	0.8		
CV (%)	9.5		

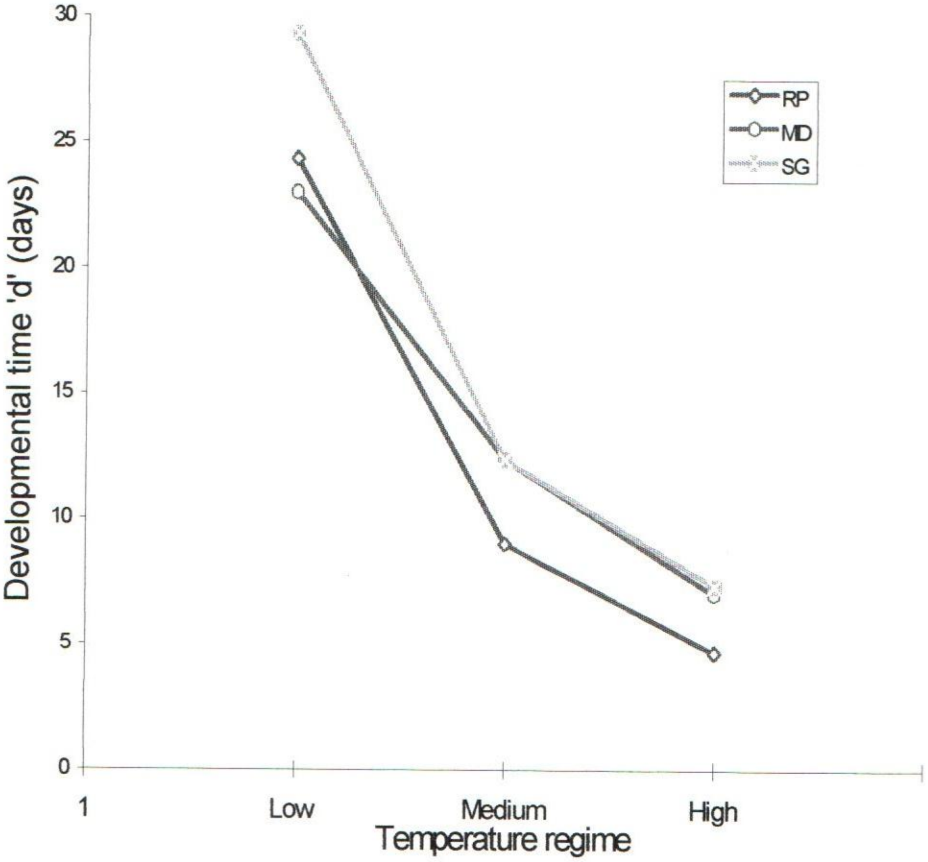

Figure 3.1 Effect of temperature regimes on developmental time of *R.padi, M. dirhodum* and *S. graminum*

Table 3.3 Effect of temperature regimes and species on cereal aphid cumulative percent progeny (m_d) at half, three quarter and full larviposition period equivalent to developmental days 'd'

Temperature regime	Fraction of d	Aphid species cumulative progeny (%)		
		R. padi	*M. dirhodum*	*S. graminum*
Low	Half 'd'	60.3	60.9	68.0
	Three quarter 'd'	97.8	89.4	88.9
	Full 'd'	100	100	100
Medium	Half 'd'	44.5	54.1	42.8
	Three quarter 'd'	65.1	81.3	70.7
	Full 'd'	100	100	100
High	Half 'd'	48.1	58.5	61.2
	Three quarter 'd'	79.2	86.5	85.4
	Full 'd'	100	100	100

Table 3.4. Effect of temperature regimes and species on cereal aphid size of progeny ($_{\text{Md.}}$)

Aphid species	Temperature regime			Temperature means
	Low	Medium	High	
R. padi	38	29	37	**34.7**
M. dirhodum	32	41	32	**35.0**
S. graminum	24	44	40	**36.0**
Species means	**31.3**	**38.0**	**36.3**	

Table 3.5. Effect of temperature regimes on the intrinsic rate of increase (r_m) of *R. padi, M. dirhodum* and *S. graminum*

Aphid species	Intrinsic rate of increase with temperature		
	Low	Medium	High
R. padi	0.111**a**	0.361**a**	0.578**a**
M. dirhodum	0.111**a**	0.223b	0.365**b**
S. graminum	0.081**a**	0.233**b**	0.373**b**
SE	0.316		
CV (%)	20.2		

Table 3.6. Effect of temperature regimes and species on percentage alate production in cereal aphids

Aphid species	Percentage alate with temperature			Species means
	Low	Medium	High	
R. padi	0.7	24.4	55.8	**27.0b**
M. dirhodum	29.5	35.6	76.0	**47.0a**
S. graminum	0.0	1.3	35.6	**12.3c**
Temp means	**10.1c**	**20.4b**	**55.8a**	
CV (%)	26.6			

SE = 3.0 and 2.6 for temperature and aphid species means respectively.

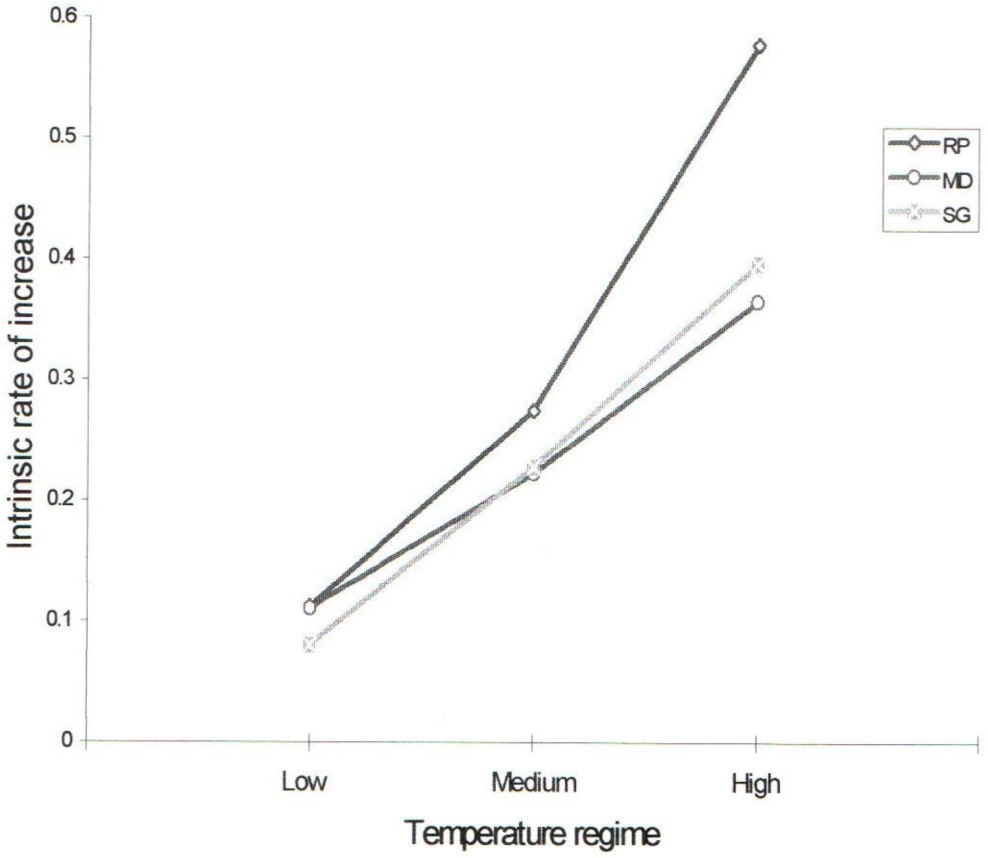

Figure 3.2 Effect of temperature regimes on intrinsic rate of increase 'r_m' of *R. padi, M. dirhodum* and *S. graminum*

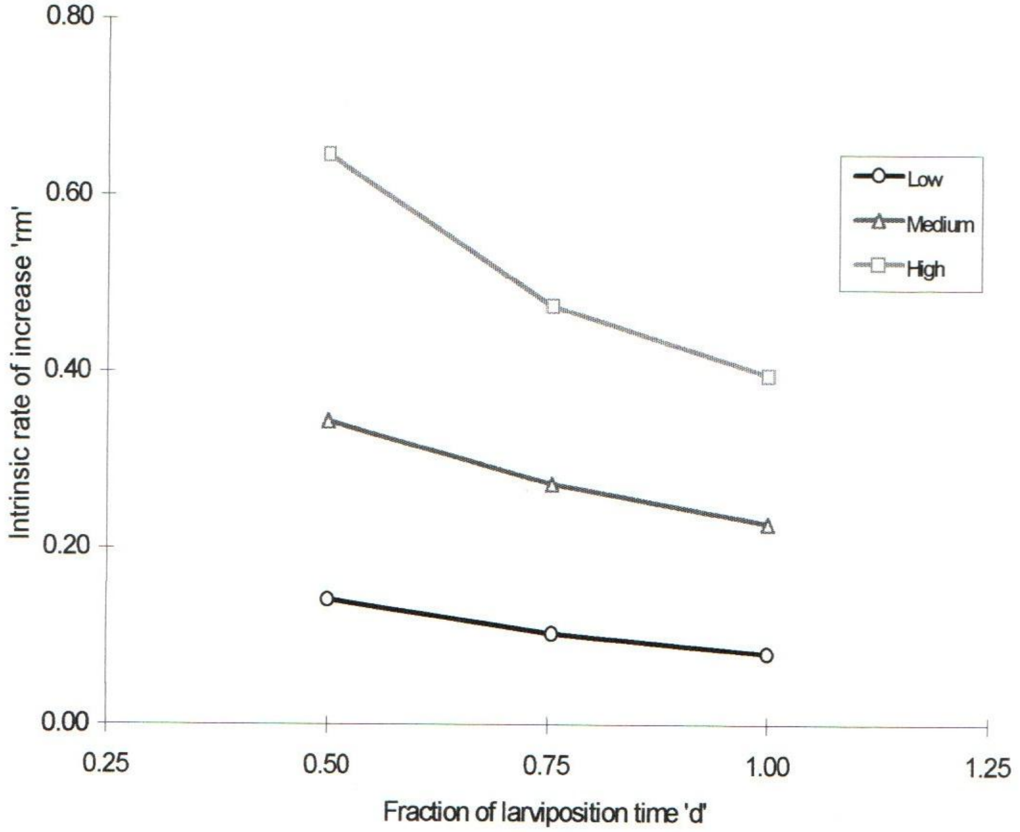

Figure 3.3 Effect of temperature regimes on intrinsic rate of increase ‘r_m’ of *R. padi*at 0.5, 0.75 and full larviposition period ‘d’

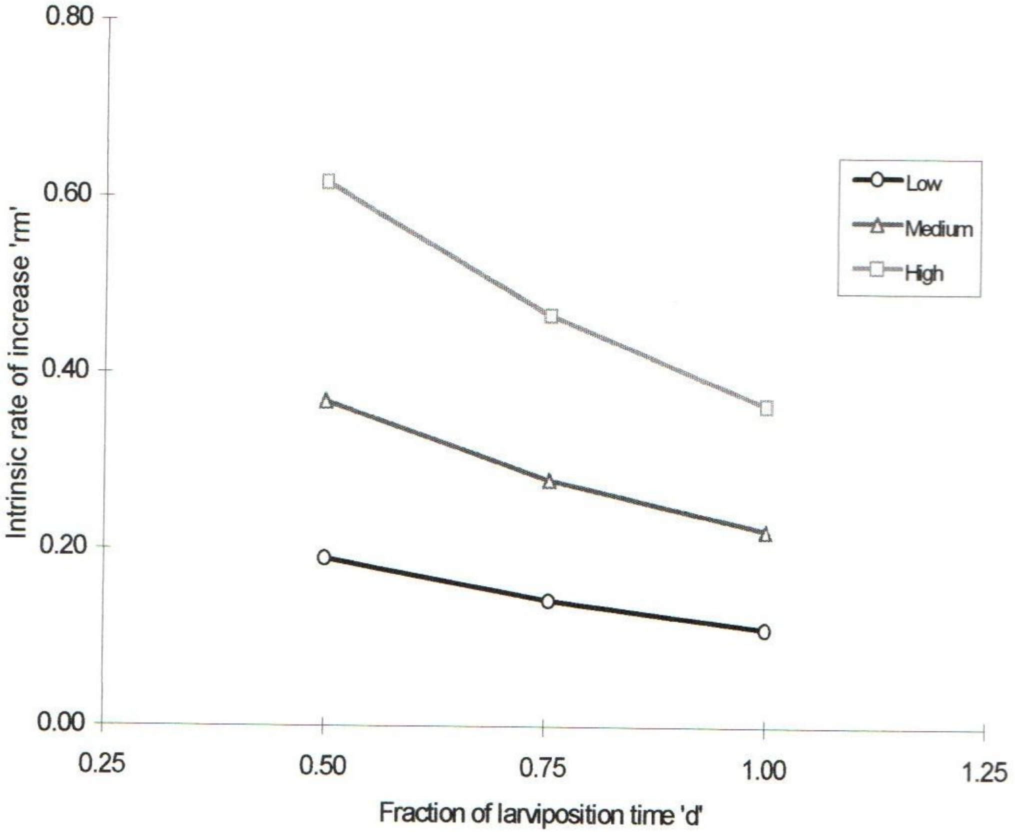

Figure 3.4 Effect of temperature regimes on intrinsic rate of increase 'r_m' of *M. dirhodum* at 0.5, 0.75 and full larviposition period 'd'

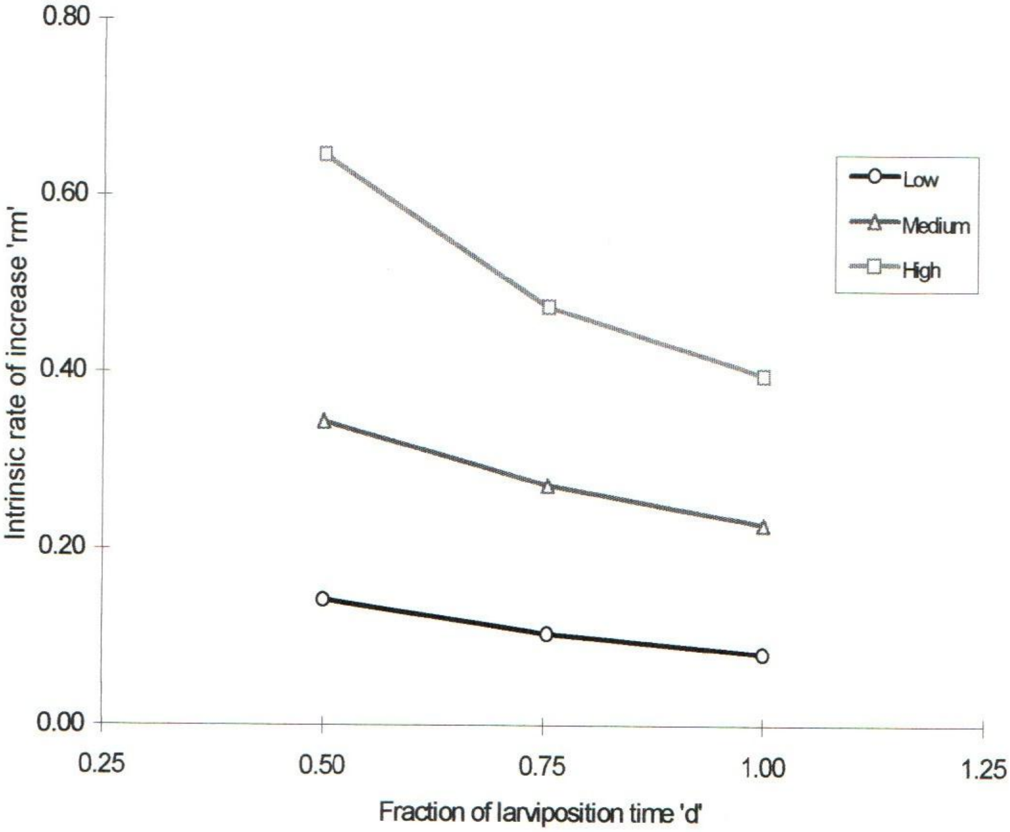

Figure 3.5 Effect of temperature regimes on intrinsic rate of increase 'r_m' of *S. graminum* at 0.5, 0.75 and full larviposition period 'd'

3.3.3 Effect of maternal age and aphid Morph on percentage alate production

There were marked differences among the species in their response to crowding, particularly for apterae aphids. The order of wing production in response to the two hours crowding at room temperature of 20-21°C in apterae aphids, from highest to the least was as follows: *M. dirhordum*, *R. padi* and *S. graminum* (Table 3.7a-c). Only the first born progeny of *R. padi* and *S. graminum* produced alatiforms at all maternal age levels. *M. dirhordum* produced alatiforms up to the fourth generation without further crowding.

There was a gradual decline in the production of winged forms with maternal age in all the species. *R. padi* had 48.6%, 42.2% and 23.3% in progenies born within 24h, 24-48h and 48-72h respectively. *M. dirhordum* had 78.5%, 61.4% and 46.3% in the first second and third maternal age level, while *S. graminum* had 30.1%, 23.8% and 14.9% respectively (Table 3.7a-c). In the progeny born within 24h, *R. padi* apterae mothers produced 2 nymphs that were intermediate morphs (adults with very short wings).

R. padi and *S. graminum* alates crowded at fourth instar for 2h produced only apterae aphids in their first progeny at all the three levels of maternal age tested. However, 10% of progeny from *M. dirhordum* developed winged forms in the progeny born within 24h and between 24-48h. No winged forms were produced in the progeny born between 48-72h (Table 3.8a-c).

Table 3.7. Percentage alate progeny from crowded apterae mothers of *R. padi, M. dirhodum* and *S. graminum*

a)Born within 24h

Aphid species	Factor	Progeny 1	Progeny 2	Progeny 3	Progeny 4	Progeny 5
R. padi	nymphs	144	154	-*	-	-
	alate	70(2)**	0	-	-	-
	% alate	**48.6**	**0**	-	-	-
M. dirhodum	nymphs	121	265	329	167	28
	alate	95	102	53	9	0
	% alate	**78.5**	**38.5**	**16.1**	**5.4**	**0**
S. graminum	nymphs	93	54	-	-	-
	alate	28	0	-	-	-
	% alate	**30.1**	**0**	-	-	-

b) Born between 24-48h

Aphid species	Factor	Progeny 1	Progeny 2	Progeny 3	Progeny 4	Progeny 5
R. padi	nymphs	154	243	-*	-	-
	alate	65	0	-	-	-
	% alate	**42.2**	**0**	-	-	-
M. dirhodum	nymphs	127	248	328	196	49
	alate	78	100	62	17	0
	% alate	**61.4**	**40.3**	**18.9**	**8.7**	**0**
S. graminum	nymphs	105	92	-	-	-
	alate	25	0	-	-	-
	% alate	**23.8**	**0**	-	-	-

* The dash (-) entry means no more alate were produced

** The number in parenthesis represents the intermediate morph (aphids with underdeveloped wings)

Table 3.7 continued

c) Born between 48-72h

Aphid species	Factor	Progeny 1	Progeny 2	Progeny 3	Progeny 4	Progeny 5
R. padi	nymphs	120	118	-*	-	-
	alate	28	0	-	-	-
	% alate	23.3	0	-	-	-
M. dirhodum	nymphs	121	190	213	103	12
	alate	56	65	31	4	0
	% alate	34.2	34.2	14.6	3.9	0
S. graminum	nymphs	87	33	-	-	-
	alate	13	0	-	-	-
	% alate	14.9	0	-	-	-

* The dash (-) entry means no more alate were produced

Table 3.8. Percentage alate in the progeny from crowded alatae mothers of *R. padi*, *M. dirhodum* and *S. graminum*

a) Born between 24h

Aphid species	Factor	Progeny 1	Progeny 2	Progeny 3	Progeny 4	Progeny 5
R. padi	nymphs	125	-*	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-
M. dirhodum	nymphs	101	110	-	-	-
	alate	10	0	-	-	-
	% alate	9.9	0	-	-	-
S. graminum	nymphs	86	-	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-

b) Born between 24-48h

R. padi	nymphs	120	-*	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-
M. dirhodum	nymphs	112	118	-	-	-
	alate	8	0	-	-	-
	% alate	7.1	0	-	-	-
S. graminum	nymphs	87	-	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-

* The dash (-) entry means no more alate were produced

Table 3.8. continued

c) Born between 48-72h

Aphid species	Factor	Progeny 1	Progeny 2	Progeny 3	Progeny 4	Progeny 5
R. padi	nymphs	116	-*	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-
M. dirhodum	nymphs	96	-	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-
S. graminum	nymphs	79	-	-	-	-
	alate	0	-	-	-	-
	% alate	0	-	-	-	-

* The dash (-) entry means no more alate were produced

3.4 Discussion

3.4.1 Population increase of the three aphid species in the greenhouse

The intrinsic rate of natural increase (r_m) for *R. padi* was found to be higher in this study compared to that of *S. graminum* and *M. dirhodum*. This aphid species appears to have many ovarioles (Walters and Dixon, 1983) since it produced a bigger progeny size of 45.3 against 35.8 and 30.8 (Table 3.4) for *M. dirhodum* and *S. graminum* respectively within the same period of 8 days. Species that have a high rate of development and reproduction are likely to be important pests in regions where they occur (Migui, 1996).

During a growing season, cereal aphids reproduce parthenogenetically and can quickly reach damaging population sizes when conditions are favourable. It can therefore be concluded that *R. padi* has a higher capacity to build up a population within a short time under optimal environmental conditions such as those provided in the greenhouse. High aphid populations cause significant losses in yields through sap removal and hence nutrient drain. Cabrera *et al.* (1995) observed that plants infested with high aphid densities have lower water potential, carbon dioxide assimilation, soluble carbohydrates and proteins. All these, deprive the developing grain of nutrients and cause low yields (Empson, 1982).

S. graminum and *M. dirhodum* did not show a very high r_m under the greenhouse conditions. It is however, known that *S. graminum* basically inflicts injury to crops through both direct feeding and injection of toxic saliva. The colonisation of *S. graminum* on wheat at seedling stage is the most probable cause of significant yield losses even at low aphid numbers. The chlorosis symptoms caused by this aphids species could also be a manifestation of changes in plant nitrogen availability (Dorscher, 1990). It was observed by Empson (1982*)* that *M. dirhodum* also causes yellowing and premature senescence of the leaves when present on leaves in large numbers. He noted that there is a negative correlation between the mean density of aphids per leaf and percent leaf nitrogen in the host plant (Mabry *et al.*, 1997).

A high rate of increase has a direct relationship with wing production. In a field situation, an increase in aphid density per host plant increases the frequency of aphid contacts and this brings about crowding. *R. padi* therefore, uses a fast population build up to increase its dispersal capacity. Lamb and Mackay (1987) observed a positive correlation between percentage of larvae with wing buds and total aphid density in the pea aphids (*Acrythosiphom pisum*).

3.4.2 Effect of temperature on population increase and alarysim in aphids

The period from birth to first reproduction 'd' for all the aphid species tested was greatly reduced as the temperature increased (Table 3.2). Small changes in time 'd' resulted into large changes in the intrinsic rate of natural increase of the aphid population which was consistent with the observations of Wyatt and White (1977). The capacity to reproduce early in an adult life and parthenogenesis accelerates the growth of populations in aphids (Hein, 1996; Dixon, 1997). Wyatt and White (1977) reported that the rate of increase of an aphid population depended on the speed of development, survival and fecundity. Therefore the intrinsic rate of increase r_m, increases with increasing temperature upto some optimal level. The magnitude of increase however varies with the aphid species. It can be concluded therefore that cereal aphids are serious pests in warm than in cool environments. *R. padi* is a very prolific insect in that its rate of increase is higher than that of *S. graminum* and *M. dirhodum* at all temperature regimes except low.

It was observed in this study that aphids tend to concentrate their reproduction within their first days of reproductive period when they experience temperature stress (Table 3.3). This is consistent with Wyatt and White (1977) who observed that in many aphid species, reproduction rises rapidly in the early stages of adult life. The reproduction pattern was however, observed to spread out peaking at 0.5'd' during favourable temperatures of 11/18°C. At the low temperature regime, *S. graminum* had about 70% of its progeny within 0.5'd' while *R. padi* and *M. dirhodum* had about 60% of their progeny (Table 3.3). *R. padi* and *M. dirhodum* can therefore be seen as being tolerant to low temperature regimes while *S. graminum* was sensitive.

Medium temperature regime appears to be optimum for the three aphid species because *M. dirhodum* had 54% while each of *R. padi* and *S. graminum* produced less than 50% of their progeny within 0.5‘d’. *M. dirhodum* and *S. graminum* which can be said to be sensitive to high temperature because they had about 60% of their progeny at 0.5‘d’ while *R. padi* still had only 48%. All the aphids had produced 80-85% of their progeny by 0.75‘d’ at high temperatures compared to the 90-100% produced at low temperatures. This has an impact on the trends of population growth in warm and cool areas. Aphid populations grow faster in warm areas (18-25°C) compared to cooler areas (4-11°C).

Temperature has a significant influence on the production of winged forms in all the aphid species tested (Table 3.6). The highest alate production was realised in high temperature regime of 18°C night and 25°C during the day. Unlike r_m there were insignificant differences in the effect of temperature on wing formation among the cereal aphids tested. *M. dirhodum* however, had the highest mean percentage wing formation. This indicates that intrinsic factors are playing a role in wing formation alongside temperature in this particular species. *R. padi* showed moderate response while *S. graminum* has the least. Generally, dispersal and spread of the three aphid species tested would be expected to be more efficient in warm areas. When this is combined with the high intrinsic rate of natural increase which has been observed to occur early in the aphid reproduction period in warm areas, the pest status of these insects is greatly increased. 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 (Wyatt and White, 1977).

3.4.3 Effect of crowding, maternal age and aphid morph on percentage alate production

The gradual decline in the production of winged forms with maternal age in all the crowded aphid species, is consistent with the results of MacKay and Wellington (1977) who found out that in *Aphis pisum,* the firstborn progeny of apterae respond more strongly to a crowding stimulus than do later progeny. This indicates that maternal age effects operate also in cereal aphids. The first born progeny of crowded colonies would therefore contribute to the dispersal of aphids to new habitats. The decline in alate offsprings in the later progenies can be seen as a strategy to guard against excessive dispersal (emigration) and maintenance of the colony as long as other factors such as the nutrition of the plant and other environmental factors are favourable.

The interval timer theory suggested by Migui (1996) for *S. avenae* whereby alatiforms were produced after a constant period of time was not evident in the test species and instead there was a constant decline in the production of alate offsprings with age. *R. padi* produced an intermediate morph (adults with very short wings) an observation similar to that of Wanjama (1986) for *S. graminum*. The occurrence of intermediates could therefore be common to other aphid species. Although the factors that contribute to the occurrence of this morph is not clearly understood it may be attributed to insufficient stimuli for complete wing production.

Maternal age effect on wing production in aphids differed with morph and aphid species Table 3.7-3.8). The first progeny of *R. padi* and *S. graminum* alate aphids crowded for 2h at fourth instar were all apterae; at least upto those born between 48-72h of the aphid reproductive period. The first progeny of *M. dirhordum* produced only 10% alate in its first generation progeny, indicating that intrinsic factors are playing a role in wing formation alongside crowding in this particular aphid species. In a similar study using *S. avanae*, the morph of the parent was found to be important in determining the proportion of alatae produced, with apterous parents producing more alate offspring than did alate parents (Watt and Dixon, 1981). The probable reason for alate mothers being poor in sensing the crowding stimuli is because initial colonization in the fields is accomplished by winged aphids (Cannon, 1985). Further dispersal should be delayed by producing non-winged forms that exploit the habitat. Emigration has a negative effect on the population growth rate in any given aphid colony (Walters and Dixon, 1982).

Migui (1996) reported that alate of *S. graminum* produced winged progeny only after a certain crowding threshold is reached. He observed non-responsiveness at a crowding period of 0, 4 and 8 hours and an abrupt change to responsiveness at 16 and 24 hours. Wanjama (1986) observed winged forms in the progeny of *S. graminum* alate when the aphids were crowded as fourth instar nymphs and soon after the final molt. This implies that for alate to produce winged forms in this species, the degree of crowding in the colonies must be so high and for a longer period. This is possible in years of high aphid infestations during warm and dry seasons as in the marginal areas. The crowding period of 2h in this study did not provide sufficient wing production stimuli to *S. graminum*. The conditions that determine the actual degree of wing production in the field however are not constant and involve a complex of variable factors that interact within a framework of species-specific behaviour. One of such factor is the condition of the host plant, which can trigger wing production by aphids even without crowding.

The fact that *M. dirhordum* produces alatiforms up to the fourth generation without further crowding (Table 3.6-3.7) and *R. padi* and *S. graminum* stopped at the first generation, indicate that *M. dirhordum* progenies are able to pick up the crowding stimuli from the mother while *R. padi* and *S. graminum* progenies are limited to the first generation only. This gives *M. dirhordum* an intrinsic capacity to produce winged forms compared to the other two aphid species. This condition may be viewed as an increase in migratory efficiency which enables this species to escape deteriorating plant conditions and maximise on favourable habitats within a short period. Increased production of alatae may lead to greater dispersal and potential to spread BYDV (Tremblay *et al.*, 1989).

CHAPTER FOUR

4. NICHE AND TEMPORAL DIFFERENCES IN APHID COLONIZATION ON WHEAT VARIETIES

Abstract

An experiment to determine the distribution patterns of *Rhopalosiphum padi* (Linnaeus), *Metopolophium dirhodum* (Walker) and *Schizaphis graminum* (Rondani) in time and space within host plants was conducted in Kenya Agricultural Research Institute, Njoro between May and August 2001 using a factorial RCBD replicated four times. Wheat varieties of Fahari, Mbega, and Duma were planted on field plots measuring 1.5m by 6m and sampled for aphid infestation at Zadok growth stages 12 (2-leaf), 22 (2-tiller), 32 (stem elongation), 45 (booting), 69 (flowering) and 91 (ripening). Aphid species differed in their time of colonisation. *R. padi* appeared on the wheat crop at GS 12 followed by *S. graminum* at GS 22 and *M. dirhodum* came later at GS 32. Aphid populations differed among the species, wheat varieties and crop growth stages. The species *R. padi*, wheat variety Duma and GS 69 had the highest aphid populations. The aphid species also differed in their points of colonisation. *R. padi* was most abundant on the wheat stems at seedling stage, the lower leaves, flag leaf and the ear as the crop aged. *S. graminum* mainly colonised the lower leaves and *M. dirhodum* was mainly on the underside of upper leaves including the flag leaf.

4.1 Introduction

Cereal aphids have distinct patterns of occupation on plants, both in spatial and temporal terms (Gianoli, 2000). Different aphids colonize a crop at different growth stages and in varying numbers. Virus infection on plants reduces yield directly, but the extent of this loss is influenced by the growth stage at which the plant is infested by the vectors. Greatest damage is caused when plants are infested at early growth stages (Watson, 1942; Doodson and Saunders, 1970). Feeding site preferences are considered important, particularly in relation to the type and amount of damage caused by various aphid species (Vickerman, 1979). Information on population fluctuations of cereal aphids is essential in determining the control strategies. The patterns of population buildup for the different cereal aphids on a wheat crop in Kenya have not been documented but can be better understood by studying the movement of individuals or colonies on the plants.

Much research has focused on various control measures against the various aphid species including manipulation of planting time and host plant resistance (Adugna, 1985). This study sought to understand varietal differences in the pattern of infestations and population buildup of three cereal aphids namely; *R. padi*, *S. graminum* and *M. dirhodum.*

4.2 Materials and Methods

Three wheat varieties (Duma, Mbega and Fahari) were planted at KARI-Njoro on 8 May 2001 using a factorial Randomised Complete Block Design (RCBD) replicated four times. The experimental plots measured 1.5m x 6 m with an inter-row spacing of 20cm. The plots and replications were separated by a 0.5m and 1m gap respectively. Di-ammonium phosphate (DAP) 18:46:0 (NPK) fertilizer at a rate of 90 kg/ha was drilled into the soil and well mixed before hand planting the wheat at a seedrate of 90 kg/ha. Hand weeding was done at growth stage 16 (Zadok *et al.*, 1974).

Observations were made and recorded on the time and location of colonisation on the three wheat varieties by the three cereal aphid species (*R. padi*, *S. graminum* and *M. dirhodum*), at six growth stages of the wheat varieties based on Zadok *et al.*, (1974) as follows: GS 12 (2-leaf stage) done at 21 days after planting, GS 22 (2-tiller stage) done at 34 days, GS 32 (stem elongation stage) done at 48 days, GS 45 (booting stage) at 62 days, GS at 69 (flowering stage) done at 72 days, and GS 91 (ripening stage) done at 86 days after planting (Appendix 2*)*. Data was taken from ten plants and their tillers, randomly selected in each plot.

The experimental field was located 50m away from the Rothamsted suction trap at KARI-Njoro. Migration of cereal aphids flying 12m above the ground were monitored through the suction trap catches throughout the experimental period. Suction trap records (Appendix 1) for the three aphid species were compared with those of time of colonisation in the field experiment. The temperature and rainfall records during the same period were also noted (Appendix 3).

Data on the mean number of aphids for each of the aphid species, wheat variety and growth stage were transformed using square root (1+x) to homogenise and stabilise the variance. General linear models (GLM) were done using Statistical Analysis Systems (SAS) package (SAS Institute; 1996). Data analysis for point of colonisation was done using descriptive analysis

4.3 Results

The aphid population of *R. padi* on the three wheat varieties was significantly higher (62.2), followed by *M. dirhodum* and *S. graminum* with means of, 21.3 and 14.3 aphids per plant respectively (Table 4.1). Duma had a higher aphid load (48.7) than Fahari and Mbega which had 32.8 and 27.8 respectively. There were distinct differences in the time of colonisation among the three aphid species (Figures 4.1-4.3). *R. padi* was observed on the wheat plants as early as growth stage 12 (2-leaf), *S. graminum* came at growth stage 22 (2-tiller) and *M. dirhodum* appeared later at stem growth stage 32 (stem elongation). There were no significant differences in the order and time of colonisation of the three cereal aphid among the three wheat varieties. Growth stage 69 (flowering), had the highest aphid population in all the three wheat varieties tested (Tables 4.2). The population of all the three cereal aphid species tested ($P = 0.05$), also was highest at growth stage 69 (flowering) (Table 4.3). Aphid populations dropped sharply at growth stage 91(ripening) for all the wheat varieties (Table 4.2), and all aphid species (Table 4.3). *S graminum* was almost absent at this stage.

Data from the suction trap catches (Appendix 2) indicated that *R. padi* was flying over the fields early as February. The population of *R. padi* caught, increased to an average of 2 aphids per catch by May when the experimental crop was planted and continued to increase throughout the experimental period. The highest populations of *R. padi* were caught in June and July. *S. graminum* populations were negligible between February and the beginning of the experiment in May. The numbers of *S. graminum* caught remained low, (less than one aphid per catch) in June and July, and almost absent in August. The populations of *M. dirhodum* was also negligible between February and the beginning of the experiment. There was a gradual increase for *M. dirhodum* in June, peaked in July and declined in August.

R. padi changed its sites of greatest colonization with the age of the plant. At seedling stage it was mainly on the stems. Majority of this aphid moved to the leaves and particularly close to the leave sheaths, during the stem elongation stage. At the latter stages *R. padi* was mainly observed on the flag leaves and the ears (Plate 4.1).

M. dirhodum was found on the underside of the middle and flag leaves (Plate 4.2). Unlike *R. padi* and *S. graminum, M. dirhodum* had a unique pattern of colonisation. Different growth stages of this aphid species were not found at the same point of the leaf particularly during its initial period of colonisation on the plant. The colonising adults of *M. dirhodum* moved away from the point of larviposition to other points of the same leaf or even further to other leaves after one or two days. The nymphs left behind which are of the same age and size were observed to be neatly arranged in a single file along the midrib. *M. dirhodum* shared a niche with *R. padi* at the few top green leaves including the flag leaf at ripening stage (Plate 4.3). Rarely did *M. dirhodum* move to the ears.

S. graminum colonies were found on the upper side of the lower leaves which turned necrotic within a few days of colonisation (Plate 4.4). The aphids completely destroyed the lower leaves and infestations progressed upwards to the middle leaves where they settled mainly at the angled points of these leaves. Rarely were the aphids found on the upper and flag leaves. They were completely absent on the ears.

Other aphids observed on all the wheat varieties with significant populations included *Diuraphis noxia*, *Sitobion avenae* and *R. maidis* in the order of colonisation. *D. noxia* was found in the rolled leaves and funnels. *S. avenae* was abundant on the middle leaves at earlier stages and on the ears even beyond ripening stage. *R. maidis* was in the leaf sheaths and funnels of particularly the flag leaf.

Plate 4.1. *R. padi* on the flag leaves and the ears of wheat

Plate 4.2. *M. dirhodum* on the flag leaves of wheat

Plate 4.3. *M. dirhodum* sharing a niche with *R. padi* at the few top green leaves including the flag leaf at ripening

Plate 4.4. *S. graminum* colonies on the upper sides of the lower leaves turning chlorotic

Table 4.1 Means of three cereal aphid species population per plant on three wheat varieties

Wheat Variety	Aphid species			Variety means
	R. padi	*S. graminum*	*M. dirhodum*	
Duma	74.7	19.4	43.2	**48.7a**$^{\phi}$
Fahari	50.8	14.7	33.0	**32.8b**
Mbega	53.0	9.5	20.9	**27.8b**
Species means	**62.1a**	**14.5c**	**21.3b**	

SE = 10.4 and 7.5 for variety and aphid species means respectively.

Table 4.2. Mean cereal aphid population per plant on three wheat varieties at six growth stages

Growth stage	Aphid population with variety			Growth stage means
	Duma	Fahari	Mbega	
2-leaf (GS 12)	0.8	0.2	1.3	**0.8d**
2-tiller (GS 22)	2.6	1.6	0.7	**1.6d**
Elongation (GS 32)	6.3	4.4	4.0	**4.9c**
Booting (GS 45)	25.6	11.3	6.6	**14.5b**
Flowering (GS 69)	94.0	72.9	65.9	**77.6a**
Ripening (GS 91)	16.8	8.1	5.0	**9.9b**
Variety GS means	**24.4a**	**16.4b**	**13.9b**	

SE = 14.1 and 3.5 for growth stages and variety population means respectively.

Table 4.3. Aphid population per plant at six growth stages

Growth stage	Aphid population with species		
	R. padi	*S. graminum*	*M. dirhodum*
2-leaf (GS12)	0.7**b**	0.0**b**	0.0**b**
2-tiller (GS22)	1.7**b**	0.3**b**	0.0**b**
Elongation (GS32)	3.1**b**	1.2**b**	0.5**b**
Booting (GS45)	5.6**b**	2.8**b**	3.0**b**
Flowering (GS69)	40.7**a**	11.9**a**	26.1**a**
Ripening (GS91)	9.3**b**	0.8**c**	2.9**b**
SE	5.5		

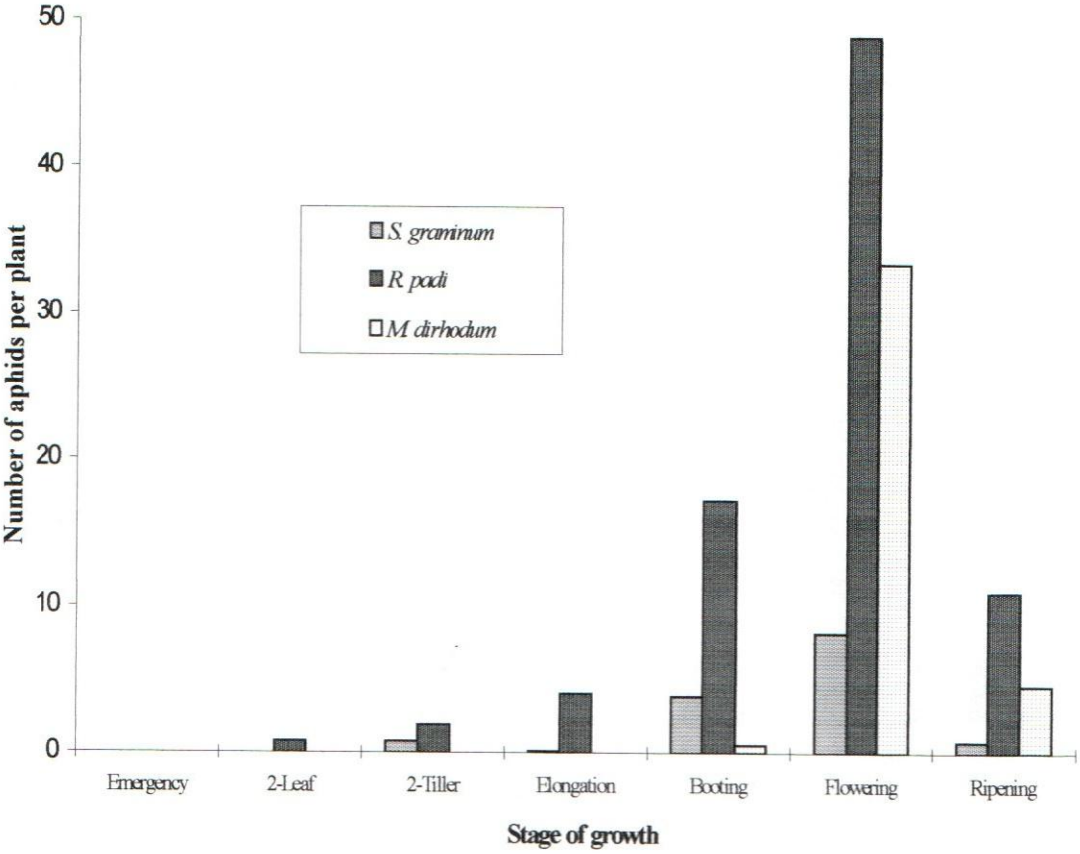

Figure 4.1. Mean numbers of *R. padi, M. dirhodum* and *S. graminum* aphids per plant at six growth stages on wheat cv. Duma

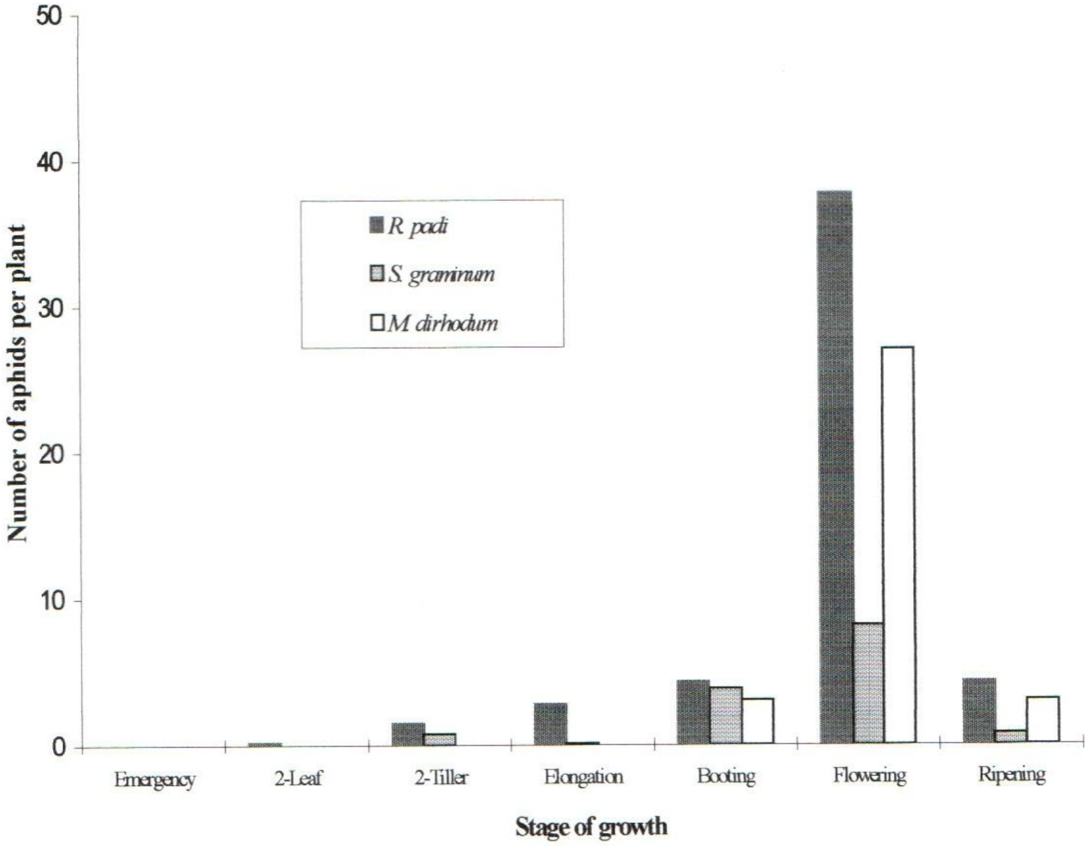

Figure 4.2. Mean numbers of *R. padi, M. dirhodum* and *S. graminum* aphids per plant at six growth stages on wheat cv. Fahari

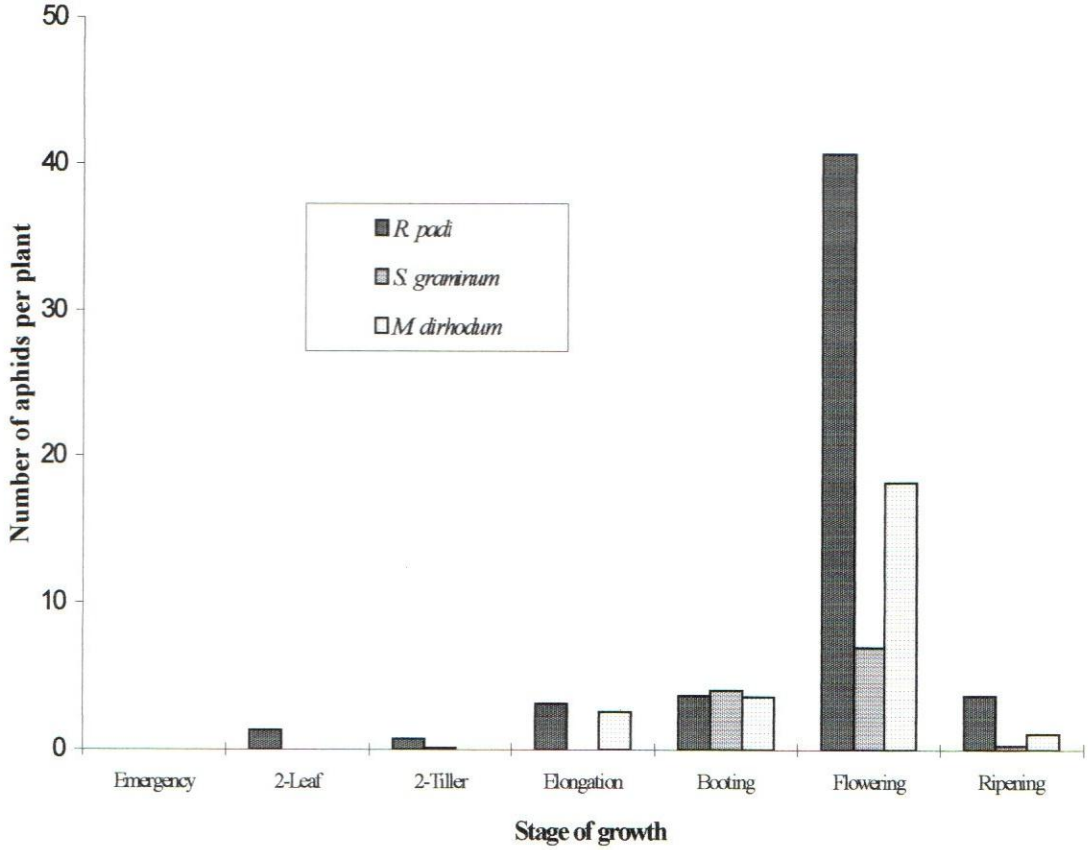

Figure 4.3. Mean numbers of *R. padi, M. dirhodum* and *S. graminum* aphids per plant at six growth stages on wheat cv. Mbega

4.4 Discussion

The three cereal aphids species studied were found to occupy different feeding sites on the wheat plants. The occurrence of different species of cereal aphids at different growth stages of the crop and at different feeding sites appears to reduce interspecific competition as a well as achieve full exploitation of the host plant. In this study, the results for *R. padi* are consistent with those obtained elsewhere. Holland and Thomas (1997) first found this aphid on crops four weeks after planting. Witkellius *et al.* (1990) observed that *R. padi* arrives first in the season (late spring-early summer) when cereals are in the seedling or early tillering stage. He further noted that the population peak is reached when plants attain the stem elongation stage, and then a decline during ear emergence. In this study however the population peaked at early flowering and drastically declined at early ripening stage (Figures 4.1-3).

The strategy of early colonisation (seedling) stage, gives *R. padi* a high pest status among cereal aphids. This is confounded by the ability of *R. padi* to exploit a wide range of host conditions i.e. from the tender and nutritious seedling stage to the deteriorating ripening stage, irrespective of variety as observed in this study. This aphid was found to aggregate its colonies at the tender stems during the seedling stage, the middle leaves during the elongation stage, the flag leaf and the ear in the latter stages. It is therefore a serious pest since it occurs in large numbers and inflicts serious direct damage through sap removal. Infestations by *R. padi* were found to reduce plant biomass dramatically, regardless of the growth stage (Gianolli, 2000). Populations as low as 25-30 aphids/stem at seedling stage significantly reduce yields (Kieckhfer and Kantack, 1980) with some components reduced by as much as 50% (Kieckhfer and Gellner, 1992). Densities of 30-40 aphids per stem at booting stage also caused reductions in most components of yield but no significant reductions in yield were recorded from mature plants even at high aphid densities.

S. graminum mostly exploits crops at seedling stage (Wanjama, 1986). It mainly feeds on leaves of the lower half of the plant (plate 4.4). Its preferred niche was on the angled points of the leaves probably to avoid extreme hot and dry field conditions or direct impact of rain splash. Given the direct and side effects of feeding by *S. graminum* whereby it causes injury to crops through sap removal and injection of toxic saliva, low pest populations are likely to cause severe crop damage particularly at early growth stages. Riedell and Blackman (1999) found out that the infestations of *S. graminum* also reduce dry weight, leaf area and chlorophyll concentration of upper and younger leaves. Offspring of *S. graminum* had almost killed the plant by the time records were taken about six days after infestation; plants were drooping and wilting. However, plants infested by the other cereal aphids species were still green and upright and did not show any symptoms of impending death. Pest outbreaks of *S. graminum* are likely to cause devastating crop losses.

M. dirhodum arrives later during stem (elongation). From the results on the effect of temperature on aphid performance and development in this study, it is evident that the percent progeny of *M. dirhodum* tends to decrease sharply at higher temperatures. This partly explains its time of colonisation. It comes in at the elongation stage when there is enough foliage cover and it mainly settles at the cooler underside. Its preference of the cool undersides of the dense canopy created by the middle leaves is avoidance of the extreme temperature in the field (Wiktelius, 1987). The populations of *M. dirhodum* drastically reduced as the foliage thinned out due to crop senescence. They shared a niche with *R. padi* at the few top green leaves including the flag leaf at ripening stage (plate 4.3) but none settled on the ear. However, in the greenhouse caged plants, *M. dirhodum* was observed to be colonizing the ears. This can be attributed to the extremely large colonies in the cages as a result of restricted migration justifying that experiments on the patterns of aphid colonisation give the best results when conducted in the fields. *M. dirhodum* has a unique pattern of colonisation as observed in this study. The adults move and larviposit on different parts of the plant thus allowing *M. dirhodum* to spread quickly within and between plants within a short time. It enables this aphid species to utilize favourable points of the crop plants and the field as a whole. This characteristic also makes this aphid an important and efficient vector of BYDV (Wangai, 1994).

Survival of most aphids on wheat that has reached ripening stage appeared to be poor, possibly because of reduced number of green leaves due to aging and hardening of the awns and grain kernels. A similar pattern particularly for *M. dirhodum* was observed by Watt (1979). Howard and Dixon (1992) proposed that the major induced plant factor contributing to the reduction in the growth of *M. dirhodum* populations on wheat in the fields is the production of alatae, which develop on mature plants even when the number of aphids on each plant is very low. This suggests that most of the aphid population become winged and leave the crop at this stage.

The temporal pattern of aphid colonisation in the field was closely related to the suction trap catches (Appendix 1). Results showed *R. padi* was flying over the fields long before the crop was planted. There is a possibility of this aphid landing on the volunteer crop and other grass species present in the unprepared fields (Donahue *et al.*, 2000), as early as February and migrating to the crop soon after emergency. The high populations of *R. padi* in the experimental field could have been as a result of dispersal from the nearby cereal fields and grasses or fresh landing from long distance flying aphids as it appeared in the suction trap catches throughout the experimental period. *S. graminum* populations were negligible between February and the beginning of the experiment in May. These results were consistent with those of Wanjama (1986) who observed no *S. graminum* flying between March and May. The numbers of *S. graminum* caught in this study remained low (less than one aphid per catch) in June and July, and almost absent in August. Population of this species were observed to increased from July 12-28 and then declined to zero by August. The population of *M. dirhodum* in the experimental field was also closely related to the suction trap results (Appendix 1). The period of maximum infestation in the field is correlated with the peak catches of this species.

Kenya Fahari and Mbega showed lower mean aphid loads compared to Duma (Table 4.1). This suggested some degree of resistance for these varieties though this experiment did not establish the mechanism of resistance. Wanjama (1986) also reported some resistance in Kenya Fahari to the greenbug (*S. graminum*) as it showed good performance for all mechanisms of resistance tested. Further work is required to establish whether this holds true for other aphid species.

CHAPTER FIVE

5. CONCLUSIONS AND RECOMMENDATIONS

From the greenhouse experiment it is evident that *R. padi* has an inherent capacity to build up a population faster than *S. graminum* and *M. dirhodum.* The controlled environment chamber observations indicate that warm conditions increased the population of all cereal aphids. Cool conditions greatly reduced cereal aphid populations.

All aphid species responded to crowding by producing winged forms. *M. dirhodum* had the highest capacity to produce winged forms compared to *S. graminum* and *R. padi.* Controlled chamber experiments revealed that high temperatures increased percentage wing production in aphids. Cool conditions greatly reduced percentage wing production in the cereal aphids. *M. dirhodum* showed rapid response in percentage wing production at high temperature and only a slight reduction under low temperatures. This implied that apart from temperature, in this aphid species, both crowding and intrinsic factors influenced wing development. Since *R. padi* produced a negligible percentage alate in low temperatures compared to medium and high, it can be concluded that in this aphid species dispersal is influenced by the effect of temperature, and its inherent ability to build up a high population fast. A large population brings about crowding which stimulates wing production. *S. graminum* had no winged forms under low temperatures and only a few in medium temperature conditions. Dispersal in this aphid species was therefore attributed to high temperatures and crowding brought about by high aphid population at this temperature conditions.

The low intrinsic rate of natural increase and percentage wing production observed at low temperatures implied that in cool areas aphid populations are low and dispersal is limited. Minimum chemical control measures are required to keep cereal aphid population below economic injury levels. On the other hand, the high intrinsic rate of natural increase and percentage wing production observed at high temperatures for all the aphid species indicate that cereal aphids can be serious pests in warm areas experiencing 18 to 25^{0}C. In these areas the cereal aphids have fast population build up, high dispersal capacity and hence fast spread within and between fields. The aphid populations quickly reach damaging levels, and this is particularly serious during prolonged dry weather. In addition to early planting in these areas, early maturing and drought resistant varieties should be planted. A seed dress followed by a foliar spray of a systemic aphicide before flowering stage is advisable because survival of most aphids on wheat after ripening stage was observed to be poor. Chemical control at this time is not likely be economical.

The field studies showed that there was a crop growth stage and feeding site preferences among cereal aphids. This is considered important, particularly in relation to the type and amount of direct damage caused by various aphid species. *S. graminum* and *R. padi* were found to infest the crop as early as seedling stage and inflict serious injuries in the cereal crops. From the Njoro suction trap records, *S. graminum* populations were negligible between February and the beginning of the experiment in May. This species population was observed to increase from mid July and then declined to zero by August. It can be recommended that for damages from this aphid specie to be minimised, late planting of wheat (end of May early June) be avoided so that the vulnerable seedling stage is passed before the insects appear in June or July. This should be combined with early maturing varieties and a seed dress before planting in medium temperature areas experiencing temperatures of 11-18^{0}C and sufficient moisture.

The suction trap records indicated that *R. padi* was flying over the fields long before the crop was planted. There is a possibility of this aphid landing on the volunteer crop and other grass species present in the unprepared fields. Avoidance of sites with alternative host plants can be recommended where land is not limiting but changing planting time is the most appropriate in small scale wheat production systems. In spite of the late arrival by *M. dirhodum*, its high dispersal capacity enables it to cover the entire field within a short time inflicting both direct damage and spreading BYDV. Studies done elsewhere have indicated that *M . dirhodum* produces alatiforms on mature plants even without crowding. Early maturing varieties will induce emigration and therefore provide some escape to this aphid species. The current study however did not focus on the effect of growth stage on the reproductive performance of various cereal aphid species which is measured as the intrinsic rate of natural increase (r_m). This will provide a better estimate of aphid population growth in relation to crop growth stage. It can also be very useful in forecasting aphid population growth.

The amount of direct and indirect damage caused by cereal aphids is proportional to their population. Any reduction in numbers as might be brought about by a natural enemy would be potentially beneficial. Reduction in aphid numbers would also reduce the probability of flying aphids on a host plant more than proportionally, because from this study it is clear that reduced crowding of aphids usually results in a lower fraction forming wings. Farmers should be advised to choose specific aphicides rather than broad-spectrum insecticides for use against cereal aphids. This is to encourage the build up of natural enemies like the ladybird beetles and hover fly and lacewing larvae, ground beetles etc to build up a sufficient population that can keep the aphid populations below Economic Injury levels (EIL). Cereal aphids as candidates for biological control require that approaches to be developed in future studies, should be appropriate to aphid features which include parthenogenesis, paedogenesis and polymorphism.

Kenya Fahari and Mbega showed a trend in aphid populations that suggested some degree of resistance in these varieties. Although Duma which is a drought resistant variety had the highest aphid infestation, its level of aphid tolerance was not established since the mechanism of resistance was not within the scope of this study. Further work on this, that will include crop loss assessment is required.

The use of resistant wheat varieties may reduce crop loss from cereal aphids and the economic and environmental costs associated with the use of aphicides. Early plant maturation can provide some degree of resistance to all cereal aphid species, since there was a sharp decline in aphid populations for all species tested at ripening stage in this study. On an aging plant, aphids become more restless, and are more likely to touch one another and hence emigration which has a negative effect on their population growth rate (Walters and Dixon 1982). Late maturing varieties support aphids for a longer period. Horward and Dixon (1995) observed that the survival of nymphs never fell below 95% in the field on barley or on wheat as long as the aphids fell on green leaves. Fikru *et al.* (1999) hypothesised that plant physiological responses, specifically photosynthesis, substantially contribute to plant tolerance to arthropod injury. Low levels of antibiosis can be important in limiting infestation levels of *R. Padi* on wheat and the subsequent spread of BYDV. There is therefore, need for further work as this can reduce the current frequency of aphicide application in wheat fields.

In conclusion, temperature, plant and intrinsic factors singly or collectively contribute to cereal aphid dispersal and colonization. All these factors should form basis for the development of sound cereal aphid management options.

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APPENDICES

Appendix 1. Suction Trap Catches at Njoro Feb-Aug 2001

	Feb			**March**			**April**			**May**			**June**			**July**			**Aug**		
Date	*Md*	*Sg*	*Rp*	*Md*	*Sg*	*Rp*	*Md*	*Sg*	*Rp*	*Mp*	*Sg*	*Rp*	*Md*	*Sg*	*Rp*	*Md*	*Sg*	*Rp*	*Md*	*Sg*	*Rp*
1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	3	0	1	3	1	0	0
2	0	0	0	0	0	1	0	0	1	0	0	2	0	1	6	0	0	5	0	0	0
3	0	0	0	0	0	1	0	0	0	0	0	4	1	0	8	0	1	4	0	0	3
4	0	0	0	0	0	2	0	0	1	0	0	0	0	2	3	1	0	3	1	0	4
5	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	3	2	2	0	0	0
6	0	0	1	0	0	0	0	0	0	0	0	0	1	0	4	3	0	6	1	0	3
7	0	0	1	0	0	1	0	0	0	0	1	2	1	0	2	1	0	2	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	4	0	4	0	0	5
9	0	0	2	0	0	1	0	0	0	0	0	2	0	0	0	6	1	7	2	0	3
10	0	0	3	0	0	1	0	0	1	0	0	2	1	0	2	0	2	5	0	0	4
11	0	0	0	0	0	1	0	0	0	0	0	3	0	1	4	5	0	4	2	0	3
12	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	3	0	4	1	1	4
13	0	0	1	0	0	2	0	0	0	1	0	0	1	0	2	6	0	7	0	0	2
14	0	0	1	0	0	1	0	0	1	0	0	0	0	0	3	4	0	0	1	0	4
15	0	0	2	0	0	0	0	0	0	0	0	1	1	0	5	8	1	0	1	0	3
16	0	0	1	0	0	1	0	0	0	0	0	2	0	0	6	2	0	0	1	0	5
17	0	0	2	0	0	1	0	0	0	0	0	0	0	2	2	3	0	5	2	0	1
18	0	0	1	0	0	0	0	0	0	0	0	3	2	1	3	4	2	8	0	0	0
19	0	0	2	0	0	0	0	0	0	0	0	5	0	2	2	2	0	4	0	0	4
20	0	0	0	0	0	0	0	0	0	0	0	2	0	3	0	1	0	3	1	1	2
21	0	0	1	0	0	1	0	0	1	1	0	0	1	1	3	0	1	4	2	0	3
22	0	0	2	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	1	0	4
23	0	0	1	0	0	2	0	0	0	0	1	2	3	2	4	0	0	7	3	0	2
24	0	0	1	1	0	0	0	0	0	0	1	4	1	0	7	1	0	5	1	0	4
25	0	0	0	0	0	1	0	0	2	1	0	2	2	0	6	0	0	3	3	0	2
26	0	0	1	0	0	1	0	0	0	0	0	2	0	0	4	0	0	2	2	0	3
27	0	0	1	0	0	0	0	0	0	1	0	3	1	0	3	3	0	6			
28	0	0	0	0	0	0	0	0	0	0	1	2	0	0	3	2	0	3			
29				0	0	0	0	0	0	0	0	4	0	1	4	3	0	2			
30				0	0	0	0	0	0	0	0	3	0	2	2	0	0	4			
31				0	0	1				0	0	3									
Total	**0**	**0**	**24**	**1**	**0**	**20**	**0**	**0**	**9**	**3**	**5**	**55**	**16**	**18**	**101**	**65**	**11**	**112**	**26**	**2**	**68**
Avg	**0**	**0**	**0.8**	**0**	**0**	**0.6**	**0**	**0**	**0.3**	**0.1**	**0.2**	**1.8**	**0.5**	**0.6**	**3.4**	**2.2**	**0.4**	**3.7**	**0.9**	**0.1**	**2.3**

Appendix 2. Growth stages of small grains

CODE	Description
0	**GERMINATION**
00	Dry seed
01	Start of imbibition
03	Imbibition complete
05	Radicle emerged from seed
07	Coleoptile emerged from seed
09	Leaf just at coleoptile tip
1	**SEEDLING GROWTH**
10	First leaf through coleoptile
11	First leaf unfolded
12	2 leaves unfolded
13	3 leaves unfolded
14	4 leaves unfolded
15	5 leaves unfolded
16	6 leaves unfolded
17	7 leaves unfolded
18	8 leaves unfolded
19	9 leaves unfolded
2	**TILLERING**
20	Main shoot only
21	Main shoot and 1 tiller
22	Main shoot and 2 tillers
23	Main shoot and 3 tillers
24	Main shoot and 4 tillers
25	Main shoot and 5 tillers
26	Main shoot and 6 tillers
27	Main shoot and 7 tillers
28	Main shoot and 8 tillers
29	Main shoot and 9 tillers
3	**STEM ELONGATION**
30	Pseudostem erection (winter cereals only)
31	1st node detectable
32	2nd node detectable
33	3rd node detectable
34	4th node detectable
35	5th node detectable
36	6th node detectable
37	Flag leaf just visible
38	Flag leaf ligule just visible
4	**BOOTING**
41	Flag leaf sheath extending
43	Boots just visibly swollen
45	Boots swollen
47	Flag leaf sheath opening
49	First awns visible
5	**EAR EMERGENCE**
51	First spikelet of ear emerged
53	One-fourth of ear emerged
55	One-half of ear emerged
57	Three-fourths of ear emerged
59	Emergence of ear completed
6	**FLOWERING**
61	Beginning of flowering
65	Flowering half-way complete
69	Flowering complete

Appendix 2 continued

CODE	Description	
7	**MILK DEVELOPMENT**	
71	Seed water ripe	
73	Early milk	
75	Medium milk	(An increase in the solids of the liquid of the endosperm
77	Late milk	is notable when crushing the seed between fingers)
8	**DOUGH DEVELOPMENT**	
83	Early dough	
85	Soft dough	(Fingernail impression not held)
87	Hard dough	(Fingernail impression not held; head losing chlorophyll)
9	**RIPENING**	
91	Seed hard (difficult to divide by thumbnail)	
92	Seed hard (can no longer be dented by thumbnail)	
93	Seed loosening in daytime	
94	Over-ripe; straw dead and collapsing	
95	Seed dormant	
96	Visible seed giving 50 percent germination	
97	Seed not dormant	
98	Secondary dormancy induced	
99	Secondary dormancy lost	

(Adopted from Zadok *et al.*, 1974)

Appendix 3. KARI-Njoro Rainfall and Temperature (February-August 2001)

Item	Months							Total	Mean
	Feb	March	April	May	June	July	Aug		
Rainfall (mm)	44.7	99.2	127.2	35.0	97.9	84.7	97.5	586.2	**83.7**
Temperature (°C)	26.0	25.1	22.0	23.3	22.5	21.5	22.3	162.7	**23.2**