INFLUENCE OF POPULATION DENSITY AND PLANT
WATER POTENTIAL ON RUSSIAN WHEAT APHID
(HOMOPTERA: APHIDIDAE) ALATE PRODUCTION

by

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ABSTRACT

Little information is presently available on the environmental variables causing alate production in the Russian wheat aphid, Diuraphis noxia (Mordvilko). Our objectives were to determine if population density of aphids affects alate production and to determine the relationship between water potential of wheat and production of alates. Response to crowding was tested using a low density treatment of 10 - 20 aphids and a high density treatment of 150 - 200 aphids. No significant difference was found between the low and high density treatments. A pressure chamber was used to quantify the amount of water stress in wheat. Wing pad formation began within the range of -0.5 and -0.6 MPa and ended within the range of -1.21 and -1.31 MPa. From this range in water potential values, six water potential treatment ranges were established. Our results show a positive correlation between alate production and the leaf water potential of wheat, with maximum alate production occurring between -0.79 and -1.03 MPa. These data suggest that a response of the host plant which, in part, results from feeding damage is causing the production of alates.

Key Words: Russian wheat aphid, water potential, crowding, alate production

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CHAPTER I

INTRODUCTION

The Russian wheat aphid, Diuraphis noxia (Mordvilko), was recently discovered in the U.S.A. Indigenous to the Mediterranean area, this aphid is recorded in the Middle East, Central Asia, and North and South Africa (Blackman & Eastop 1984). In 1980, D. noxia was found in Central Mexico (Gilchrist & Rodriguez 1984) and was first identified in the U.S.A. in the Texas Panhandle in March of 1986 (Webster et al. 1987). Since its introduction, this aphid has spread throughout the small grain-growing regions of the Western United States and Canada.

The Russian wheat aphid can become a serious pest of small grain crops in the United States. These aphids can rapidly reproduce on their preferred hosts of wheat, barley, and triticale. The aphid usually feeds on the newest growth of the wheat plants, in the axils of the leaves, and within curled up leaves. In the latter growth stages of the plant, the aphid will infest the flag leaf. Infestations of wheat by this pest results in changes in the pigmentation of the leaves (Walters et al. 1980). Typical characteristics of D. noxia infestation are yellow and purple to reddish purple longitudinal streaks on the wheat leaves and an inward curling of the leaf edges. These symptoms are caused by a toxin in the saliva of the aphid (Kruger & Hewitt 1984).

The Russian wheat aphid is a relatively small green aphid, less than two millimeters in length with an elongate, spindle-shaped body. This aphid is easily distinguished from other aphids that infest wheat by its extremely short antennae and a characteristic projection above the cauda giving the aphid a double-tailed appearance (Walters et al. 1980).

In South Africa, the Russian wheat aphid reproduces parthenogenitically throughout the winter months (Kriel et al. 1984). The average lowest winter temperature in the Orange Free province, where the pest occurs, is milder than the winter temperatures found in the wheat growing regions of the U.S.A.. Harvey and Martin (1988) showed that Russian wheat aphids could survive temperatures as low as 20°C for 16 hours, which supports their field observations that this pest may survive winter conditions in Kansas. Webster and Starks (1987) tested the fecundity of D. noxia with 14:10 (L:D) and temperature regimes of 14-19, 19-21, and 26-28°C, and found that the reproductive period of D. noxia remained approximately the same over the wide range of temperatures. Michels and Behle (1988) discovered that natality patterns were not significantly different between 5 and 30°C. Therefore, spring and summer temperatures should not restrict the fecundity and, thus, dispersal into many of the small-grain growing regions on the United States.

Most adult D. noxia disperse before ripening makes the host plants unfavorable for aphid infestation (Hewitt et al. 1984);

therefore, alate formation becomes dominant in dense aphid populations in late stages of wheat growth (Kriel et al. 1984). Though normally weak flyers, alates can disperse great distances with the aid of the wind (Hughes 1988). Alate females will land on host plants, immediately begin to feed, and give birth to nymphs that develop into apterous females (Hewitt et al. 1984). Walters et al. (1980) and Hewitt et al. (1984) found in South Africa that alates began to appear in May, and that alate numbers increased in September through October as the wheat matured. Therefore, alatae appear to play an important role in the emigration from the ripening wheat crop.

Many factors can cause wing formation in aphids (Lees 1966) and some of these factors are environmental. In addition, appearance of alatae is closely related to the density of the aphid population on the host plant. Nutritional deficiency, temperature, and photoperiod have also been implicated. For example, Johnson (1966) showed that a higher percent of alate aphids are produced on mature, old and wilting plant tissues than on seedlings and growing shoots. A heavily infested host plant cannot supply enough of the needed nutrients, and therefore, dispersal from the plant is advantageous. Hardie (1987) found with the bean aphid, Aphis fabae Scopoli, that standard long days of 16:8 (L:D) resulted in 93% apterization, and that standard short days of 12:12 (L:D) resulted in 0.5% apterization. A regime of 16:12 (L:D) produced a short day response of 5% apterization. Kenton

(1955) found with the pea aphid, Acyrtosiphon pisum (Harris), that different regimes of photoperiod and temperature produced four main forms: apterous and alate virginoparae, males and oviparae. In investigations with green peach aphids, Myzus persicae (Sulzer) and the vetch aphid, Megoura vicia Buckton, Bonnemaison (1951), and Lees (1967) found that contact stimuli among aphids causes apterous adults to produce alate young, or apteriform larvae to develop into alatae. Lees (1966) suggested in his thorough review of polymorphism in aphids that the production of alate forms resulted from mechanical stimulation of one aphid by another. However, by isolating the aphids and removing the effect of the host plant different results were obtained. Mittler and Dadd (1966) showed that when various amino acids were omitted such as histidine and isoleucine, a higher percent of apterous morphs were produced. Sutherland and Mittler (1971) demonstrated that nutritional factors affect M. persicae wing dimorphism. In these studies, the greater number of alates were produced using 'balanced' artificial diets.

Upon examination of data involving water potential and its effects on aphids, a wide range of results are encountered. Michels and Undersander (1986) found that the greenbug, Schizaphis graminum (Rondani), responded differently to water-stressed and unstressed sorghum in both population numbers and distribution on the plant. Dorschner et al. (1986) showed that greenbug density increased on water-stressed wheat; whereas,

Sumner et al. (1983, 1986) found that the greenbug had a lower number of progeny per reproducing day and shorter longevity when fed on drought-stressed wheat. Fereres et al. (1988) found that the mean number of English grain aphid, Sitobion avenae (F.), nymphs per adult and the total progeny per adult exhibited a slight decline when plants were stressed. Wearing and van Emden (1967) observed that the bean aphid, Aphis fabae (Scopoli) reproduction was unaffected by water-stressed Vicia faba (L.), although reproductive rates of the cabbage aphid, Brevicoryne brassicae (L.), declined with increasing water stress in brussels sprouts, Brassica oleracea (L.), var. gemmifera DC. In this same study M. persicae was shown to have lower reproductive rates on brussels sprouts subjected to water stress; whereas, reproduction rates were highest at intermediate moisture levels. Barker and Tauber (1954) found that excess moisture and reduced light lowered the fecundity of the pea aphid, Acyrtosiphon pisum (Harris), on garden peas. Drought stress reduced reproduction in A. fabae on sugar beets (Kennedy & Booth 1959); whereas, fecundity increased on senescing sugar beet leaves rather than on middle-aged leaves that were not subjected to water stress (Kennedy et al. 1950).

We observed high numbers of Russian wheat aphid alates present in the field when population densities were high and when wheat began to desiccate and mature. Therefore, the objectives were to determine if population density of D. noxia affects alate

production and to determine the relationship between water potential of wheat and production of alates. A pressure chamber that measures leaf water potential was used to quantify the amount of water stress in wheat. Leaf water potential is composed of the osmotic and matric potential and the pressure potential arising from turgor, all of which affect the chemical potential of water in the leaf (Slatyer 1967).

CHAPTER II

MATERIALS AND METHODS

Effect of Crowding

The crowding test was attempted with two different studies and at two different times. The first test utilized 3 X 20 cm. glass tubes and 1 X 8 cm. micro vials, and the second crowding test utilized cylindrical plastic tubes (6.4 X 30.5 cm.).

Crowding test 1

To separate the effect of crowding from the effect of the host plant Lees' (1967) method of inducing the crowding response was used, but with some modification. Second, third, and fourth instar nymphs, and adults were crowded in 1 X 8 cm. vials at densities of 5, 10, 15, 20, 25, 30, 35, and 40 aphids for periods of 6, 12, and 24 hours. Cotton was placed in the bottom of the 1 X 8 cm. vials. Filter paper disks, cut to fit the diameter of the vials, were placed on top of the cotton. Once the aphids were placed in the vials, a cotton stopper was placed in the top of the vial to prevent escape. The vials were then placed in an environmental chamber for the desired time and at a temperature of 18° - 20°C. The control consisted of one aphid per crowding vial for the same time and temperature as the aphids being crowded.

To test the effect of crowding on the nymphs, individual apterous adult aphids were placed on wheat seedlings ('scout 66') grown in 6.5 X 9 cm. seed pots (4 plants/pot) and covered with a 3 X 20 cm. glass tube (1 plant/tube). Placing and removing aphids on or from the plants was accomplished using a suction hose fastened to the end of a micro pipette (5 μ l.). The adults were allowed to deposit two to three nymphs and then were removed from the plants. When the nymphs reached the instar to be tested, they were removed from the plant and placed in the crowding tubes. After the crowding stimulus, individual nymphs were placed on the wheat seedlings and the seedlings were covered with 3 X 20 cm. glass vials and were observed for the appearance of alates.

To test the effect of crowding on the adults, individual apterous female aphids were placed on the wheat plants and allowed to deposit one nymph. The plants were then covered with 3 X 20 cm. glass tubes. The adult was then removed from the plant, and the nymphs were left on the plant to mature to the adult stage. Second-generation adults were then removed and placed in the crowding tubes to receive the crowding stimulus. The second generation adults were used for the crowding test to insure that a crowding stimulus had not affected the aphids before the test began. After the crowding stimulus, the adults were again placed on the wheat plants and covered with the 3 X 20 cm. glass tubing. These adults deposited one nymph and were

removed from the plant, and the third-generation nymphs were monitored for the appearance of wing pads.

A complete randomized factorial design was used to determine the instars that received the stimulus and the interaction between numbers of aphids and the amount of time needed to provide the stimulus.

Crowding test 2

Wheat was grown in 6.5 X 9 cm. seed pots and placed in flats (30 pots per flat). A commercial potting medium was used, and the wheat plants were thinned to four plants per pot. The winter wheat cultivar used in all studies was 'scout 66'. When the third true leaf stage was reached, the wheat was inoculated by placing cut wheat leaves infested with aphids in each pot. Each pot was inoculated with ten to twenty fourth instar through adult D. noxia. Wheat plants were then removed from the greenhouse and placed in an environmental chamber at 12:12 (L:D) and at a temperature of 22°C. Cylindrical plastic cages (6.4 X 30.5 cm.) were placed over each pot to contain the aphids. Ventilation holes were cut in the top, and sides and were covered with chiffon cloth. A Bausch and Lomb® microscope light was used to locate the aphids on the plants. The light beam was projected through the leaf to illuminate the aphids on the plants and within curled up leaves. The wheat was watered once every

week or when wilting occurred. Nymphs of the second and succeeding generations were monitored for wing pads. Because we did not know which instar would respond to the stimulus and become alate, every instar was present in every pot and in each treatment.

The low density treatment contained 10 - 20 aphids per pot, and this population density was maintained by carefully stripping the excess aphids from the plants each day with soft forceps. A range was used because aphid removal did cause some disruption and mortality (though minimal), thereby making it difficult to maintain an exact number of aphids. The high density treatment was inoculated with 20 aphids per plant, and these aphid numbers were allowed to increase without inhibition. Each treatment was comprised of two flats, and the test was repeated twice resulting in a total of eight flats and 240 pots with 120 pots per treatment. Once wing pad formation began in the second and succeeding generation, the nymphs were observed for wing pads every other day until the test was terminated. Effects of crowding (number of pots containing alates) were analyzed using Student's t distribution ($P < 0.05$).

Effect of Water Potential

Wheat was grown in 6.5 X 9 cm. seed pots and placed in flats (30 pots per flat). A commercial potting medium was used, and the wheat plants were thinned to four plants per pot. The

winter wheat cultivar used was 'scout 66.' When the third true leaf stage was reached, the wheat was inoculated with ten to twenty Russian wheat aphids, and the plants were removed from the greenhouse and placed in an environmental chamber at 12:12 (L:D) and at a temperature of 22°C. Nymphs of the second and succeeding generations were monitored for wing pads. The wheat was watered once every week or when wilting occurred. First instar through adult aphids were present in every pot and in each treatment.

Cylindrical plastic cages (6.4 X 30.5 cm.) were placed over each pot to contain the aphids. Ventilation holes were cut in the top and sides and were covered with chiffon cloth. Approximately 50 to 100 aphids were present in each pot when sampling began, and the pots were sampled every other day until either the wheat plants or the aphids were dead. During each observation those nymphs with wing pads were removed, and the leaves upon which they were feeding were placed in the pressure chamber and the water potential obtained.

To measure water potential, the shoot or intact leaf was detached and quickly enclosed in a steel pressure chamber. The cut end of the stem or leaf protruded from the chamber, and the pressure inside was gradually increased by compressed oxygen or nitrogen until a small sap droplet appeared at the position of the xylem vessels on the cut surface. Droplets were detected with a 10x hand lens. Thus, pressure within the chamber increased the

water potential of leaf cells to a value equal to the osmotic potential of xylem sap at atmospheric pressure (Slavik, 1974). Readings of the pressure chamber were in pounds per square inch and were divided by 14.5 to provide pressure in bars (1 bar = 0.98 atmospheres). The negative of this value provides the water potential in bars (Klepper & Ceccato 1969), and one bar is equal to 10 megapascals (MPa).

Preliminary tests showed that alate production began within the range of -0.51 to -0.61 MPa of pressure and ended within the range of -1.2 to -1.3 MPa; therefore, six water potential treatment ranges were established. Treatments began with the range of -0.51 to -0.61 MPa of pressure and ended with -1.21 to -1.31 MPa of pressure with a 0.1 MPa increment between each range and a 0.04 MPa increment between each treatment. The test was repeated eight times with a total of 32 flats and 960 pots. Effect of water potential was analyzed using the χ^2 distribution ($df = 5$; $P < 0.05$). The hypothesis of no independence between water potential and the occurrence of alate nymphs was tested with a 6 X 2 contingency table. Simple linear regression ($df = 1, 371$; $P < 0.05$) was used to describe the relationship between alates (number per day and pots containing alates per day) and time, in which alates were the dependent variable and time in days was the independent variable (Cricket Software 1985). In addition, curvilinear regression ($df = 2, 22$; $P < 0.05$; second order polynomial) was also used to describe the

relationship between number of alates (dependent variable) and water potential (independent variable).

Effect of Water Stress and Population Density.

Wheat was grown in 6.5 X 9 cm. seed pots and placed in flats (30 pots per flat). A commercial potting medium was used, and the wheat plants were thinned to four plants per pot. The winter wheat cultivar used was 'scout 66.' When the third true leaf stage was reached, the wheat was inoculated with five to ten Russian wheat aphids. The pots were then removed from the greenhouse, covered with 6.4 X 30.5 cm. cylindrical plastic tubes, and placed in an environmental chamber at 12:12 (L:D) and at a temperature of 22° C. The treatments consisted of 10, 20, 30, 40, and 50 ml. of water applied to each pot once every week. The total number of nymphs and adults were counted every two days until the wheat plants had died. The statistical analysis was a complete randomized design with six replications for each treatment.

CHAPTER III

RESULTS

Response to Crowding

Response to crowding (test 1)

Two alate aphids were produced from the entire test. The immature aphids exhibited a high mortality rate due to either the physical action of removing the glass tubes from over the wheat plants or the relative humidity inside the glass tubes. Second, third, and fourth instar aphids are relatively small, less than 1.4 mm. Once these nymphs were physically knocked off the plants and had fallen into the potting medium, the chance of recovering and returning the nymphs to the plant was slight. Most of the mortality was due to the excess moisture inside the 2 X 20 cm. glass tubes. The moisture inside the tubes was due to evapotranspiration. Although cotton and later chiffon was used to cover the top of the tubes, these materials could not facilitate the escape of water vapor inside the tubes. The high relative humidity caused condensation to form on the inside of the glass tubes which caused the leaves to adhere to the side of the tube. The aphids would crawl from the plant to the wall of the tube and would become physically bound by the water and eventually died.

Along with the high humidity, fungal growth also appeared. Fungal growth started at the soil surface, and the hyphae extended to the tip of the leaves. Whether or not the fungus was

directly killing the aphids is not known, but the fungus may have stressed the plants resulting in decreased food quality. This change in food quality would cause the aphids to leave the plant in search of a richer food source, and thus eventually being bound by the free water on the inside the tube.

Response to crowding (test 2)

Mean number of pots containing alates in the low density treatment for the four tests were 30, 24, 27, and 27. Mean number of pots containing alates in the high density treatment were 30, 28, 25, and 28. No significant difference in the number of alates was detected between the low and high density treatments of 27.0 and 27.7 alates, respectively, ($t = 0.295$; $df = 238$; $P > 0.05$).

Response to Water Potential

Mean population density (Fig. 1) steadily increased from an average of 23 aphids on day one to 190 aphids on day 13. Number of pots containing alates (Fig. 2) and total number of alates (Fig. 3) decreased through time with coefficients of determination of 0.81 and 0.90, respectively ($df = 1, 5$; $P < 0.01$). Mean water potential decreased slightly from -0.8 MPa to -1.0 MPa (Fig. 4) with a low coefficient of determination of 0.19 ($df = 1, 371$; $P < 0.01$) through time. Number of pots with alates (Fig. 5) and total

numbers of alates (Fig. 6) exhibited curvilinear responses to decreasing water potential with relatively high coefficients of determination of 0.69 and 0.62, respectively ($df = 2, 22$; $P < 0.01$). Data in Table 1 show that the occurrence of alates is dependent on treatments. The range of -0.79 to -1.03 MPa was associated with higher number of pots containing alates ($\chi^2 = 73.5$; $df = 5$; $P < 0.01$).

Response of Density to Water Stress

The mean population density was not different ($P > 0.05$) when the individual populations (Table 2) were subjected to five different watering regimes ($F = 2.069$; $df = 4, 145$). The water potential in MPa (Table 3) was not different ($P < 0.05$) between the five different watering regimes ($F = 2.827$; $df = 4, 145$).

A difference was found in the mean population density when the aphids were exposed to the different water potential treatments (Table 4) with the treatment of -1.07 - 1.17 exhibiting the greater population density (Table 5).

Table 1. Effect of water potential of wheat on alate production of the Russian wheat aphid.

Water potential (-MPa)	Mean No. Alates	Pots with Alates ^a
.51 - .61	8.2	28
.65 - .75	10.4	60
.79 - .89	14.5	101
.93 - 1.03	16.5	90
1.07 - 1.17	11.3	64
1.21 - 1.31	4.8	33

Table 2. Analysis of variance for population density of Russian wheat aphid at each watering treatment.

SOV	df	SS	MS	F value
Treatment	4	1936.373	484.093	2.069
Error	145	33924.267	233.960	
Total	149	35860.640		

$F_{t 0.05 (4,145)} = 2.21$

Table 3. Analysis of variance for water potential (- MPa) at each watering treatment.

SOV	df	SS	MS	F-value
Treatment	4	86.007	46.502	2.827
Error	145	2385.520	16.452	
TOTAL	149	2571.527		

$F_t 0.05 (4,145) = 2.21$

Table 4. Analysis of variance for population density of Russian wheat aphid at each water potential treatment.

SOV	df	SS	MS	F value
Treatment	5	45981.330	9196.266	0.003
Error	420	1065817.534	2537.661	
Total	425	35860.640		

$F_t 0.05 (5, 420) = 2.37$

Table 5. Mean aphid densities at each water potential treatment.

Treatment (-MPa)	Mean
.51 - .61	57.4 a
.65 - .75	54.8 a
.79 - .89	55.2 a
.93 - 1.03	50.8 a
1.07 - 1.17	96.8 b
1.21 - 1.31	70.1 a

Means followed by the same letter are not significantly different ($P = 0.05$; least significant difference test).

Figure 1. Mean Russian wheat aphid densities through time

Figure 2. Total number of pots with Russian wheat aphid alates through time ($y = 77.64 - 3.36x$)

Figure 3. Total number of Russian wheat aphid alates through time ($y = 351.34 - 21.52x$)

Figure 4. Mean water potential of wheat through time ($y = 7.81 + 0.41x$)

Figure 5. Total number of pots with Russian wheat aphid alates regressed to decreasing water potential of wheat ($y = -88.81 + 24.59x - 1.34x^2$)

Figure 6. Total number of Russian wheat aphid alates regressed to decreasing water potential of wheat ($y = -378.22 + 103.152x - 5.66x^2$)

CHAPTER IV

DISCUSSION

Response to Crowding

The population density of Russian wheat aphids increased through time (Fig. 1); however, pots containing alates and total number of alates decreased through time (Figs. 2 & 3). If a response to crowding were inducing alate morphs, then the higher number of alates would occur when population densities reached their maximum (between days 10 and 15). However, maximum alate production occurred before the population density reached its maximum. These results confirm the results of the crowding test, suggesting that density does not appear to be a factor in alate production. Unlike Lees' results, (1967) with the vetch aphid, M. viciae, I found that the occurrence of alates was not affected by physical stimulation of one aphid by another as a result of crowding. Johnson (1965) cautions that any control, when studying alatae, must be exposed to conditions that promote apterous development. If this condition is not met, then the effect of crowding or tactile stimulation will not be detected. In this study, apterous females in both the low density and high density treatments were handled similarly, and both treatments were subjected to conditions that encouraged apterous forms. The fact that aphids were stripped from the low density treatments to maintain low numbers of aphids should not have

induced alatae because the aphids that remained were not affected by the removal procedure. In addition, aphids in the high density treatment were somewhat disturbed, but no more so than in the low density treatment. Therefore, the fact that no significant differences were detected between the two treatments indicate that tactile stimulation resulting from crowding is not a factor in alate production.

Crowding test number two yielded a higher number of alates for two reasons. The plastic cages allowed for more ventilation which eliminated the problems that are associated with condensation. The methodology in test one required extensive handling and moving of the aphids which could have led to the increase in mortality; whereas, the methodology in test two required little or no handling of the aphids, and thus resulting in less mortality.

One major difference exists when comparing the designs of the two crowding tests. Crowding test two combined the effects of the host plant and crowding; whereas, test one separated the effect of the host plant from the crowding stimulus. Therefore, crowding test one is not influenced by a plant interaction and would provide a more accurate conclusion as to the effect of crowding. But, because heavy populations of Russian wheat aphids affect the physiological condition of the host plant (Johnson 1966) and Russian wheat aphid saliva has been shown to adversely affects photosynthesis (Kruger & Hewitt 1984),

separating the effects of the host plant and crowding could possibly lead to false conclusions as to the true cause of alate production.

Response to Water Potential

As time increased, the water potential of wheat decreased slightly; however, the low coefficient of determination (Fig. 4) indicates that the decrease is not attributed to time, but to the effect of feeding damage by the aphids. Michels and Undersander (1986) observed the same trend with the greenbug, Schizaphis graminum (Rondani), in that the infested, stressed wheat plants also exhibited decreasing water potentials; whereas, infested non-stressed wheat plants did not. As time increased, the population density on each plant also increased, which resulted in increased feeding pressure. Feeding damage caused the plants to turn yellow and the leaves to curl inward. In addition, Kruger and Hewitt (1984) showed that D. noxia saliva adversely affects photosynthetic rates in vitro. Laboratory experiments by Fouche et al. (1984) showed that the arrangement of the chloroplasts in the cytoplasm became disrupted and eventually disintegrated when treated with D. noxia extract. This disruption of the chloroplasts and hence photosynthesis may have affected the health of the wheat plants, thus causing water potential readings in this study to decrease.

Numbers of pots containing alates and the total number of alates (Figs. 5 & 6) exhibited a curvilinear response when regressed to water potential with the greater number of alates occurring between -0.8 and -1.0 MPa. In addition, χ^2 analysis shows that the greater number of pots containing alates falls within the range of -0.79 to -1.03 MPa (Table 1). Mittler & Dadd (1966) and Johnson (1966) showed that diet or host quality is important in the production of alates. The increasing levels of water stress coupled with aphid feeding damage could have an effect on host quality, thus explaining the curvilinear regression of pots containing alates and total number of alates (Fig. 5 & 6). Between the range of -0.5 and -0.7 MPa, the wheat plants were starting to yellow thus affecting food quality, and this range may be the minimum threshold for initiation of wing development. The effect of water potential and feeding damage between the range of -0.8 and -1.0 MPa yielded plants that were yellowed and slightly bleached. The range of -0.8 and -1.0 MPa may be causing the maximum alate production we observed. Between the range of -1.1 and -1.3 MPa, the wheat plants were very chlorotic and bleached and therefore alate production declined.

Response of Density to Water Stress

The increase in population density through time (Fig. 1) causes an increase in feeding pressure on the wheat plants. This increased feeding pressure can be used to explain the effect of

water stress on the population densities of the aphids. No significant difference was detected in the mean water potential and the mean density of aphids when the plants were subjected to the five different watering regimes. The watering regimes were too even in magnitude, and feeding stress induced by the aphids negated the effect of the water stress. Preliminary data showed a decrease in water potential when the wheat plants were not subjected to aphid feeding. A significant difference was found in the mean aphid densities when the aphid populations were subjected to the different water potential ranges. The pressure ranges from -0.51 through -1.03 MPa occur more frequently early in time and, therefore, aphid density is relatively low and constant. The pressure ranges from -1.07 through -1.31 occur more frequently later in time when aphid density has increased. Due to the poor host quality of the wheat plants within the range of -1.21 through -1.31 MPa, the aphids exhibit a drop in density.

CHAPTER IV

CONCLUSIONS

This investigation showed that the occurrence of alates is not the direct result of increasing Russian wheat aphid densities. However, a positive correlation does exist between alate production and water potential of wheat, indicating that the host plant is involved in the production of alates. However, this study does not address the specific response that initiates alate production.

REFERENCES

- Barker, J. S., & O. E. Tauber. 1954. Fecundity of the pea aphid on garden pea under various combinations of light, moisture and nutrients. *J. Econ. Entomol.* 47: 113-116.
- Blackman, R.L. & V.F. Eastop. 1984. *Aphids on the World's Crops: an Identification Guide*. John Wiley, Chichester.
- Bonnemaison, L. 1951. Contribution a l'etude des facteurs provoquant l'apparition des formes ailees et sexuees chez les Aphidinae. *Ann. Epiphyt.* 2: 1-380.
- Cricket Software. 1985. Cricket graph, ver. 1.2 Philadelphia.
- Dorschner, K. W., R.C. Johnson, R.D. Eikenbary, & J.D. Ryan. 1986. Insect-plant interactions: greenbugs (Homoptera: Aphididae) disrupt acclimation of winter wheat to drought stress. *Environ. Entomol.* 15: 118-121
- Fereres, A., C. Gutierrez, P. Del Estal, & P. Castañera. 1988. Impact of the English grain aphid, Sitobion avenae (F.) (Homoptera: Aphididae), on the yield of wheat plants subjected to water deficits. *Environ. Entomol.* 17: 596-602.
- Fouche, A.M., R.L. Verhove, P.H. Hewitt, M. C. Walters, C. F. Kriel & J. de Jager. 1984. Russian aphid (Diuraphis noxia) feeding damage on wheat, related cereals and a Bromus grass species; In, Walters, M.C. (ed.), 'Progress in Russian wheat aphid (Diuraphis noxia Mordw.) Research in the Republic of South Africa'. Proceedings of a Meeting of the Russian Wheat Aphid Task Team held at the University of the Orange Free State, Bloemfontein, 5-6 May 1982. Republic of South Africa, Department of Agriculture Communication No. 191, 22-23.
- Gilchrist, L.I., & R. Rodriguez. 1984. The extent of freestate streak and Diuraphis noxia in Mexico, pp. 157-163 In 'Barley Yellow Dwarf', A proceedings of the workshop, CIMMYT.

- Hardie, J. 1987. The photoperiodic control of wing development in the black bean aphid, Aphis fabae. J. of Insect Physiol. 33: 543-549.
- Harvey, T. L., & T. J. Martin. 1988. Relative cold tolerance of Russian wheat aphid and Biotype-E Greenbug (Homoptera: Aphididae). J. Kansas Entomol. Soc. 61: 137-140.
- Hewitt, P.H., G.J.J. van Niekerk, M.C. Walters, C.F Kriel, & A. Fouche. 1984. Aspects of the ecology of the Russian wheat aphid, Diuraphis noxia, in the Bloemfontein district I. The colonization and infestation of sown wheat, identification of summer hosts and cause of infestation symptoms, pp. 3-13. In Tech. Commun. Dep. Agric. Repub. S. Afr. No. 191.
- Hughes, R.D. 1988. A synopsis of information on the Russian wheat aphid, Diuraphis noxia (Mordvilko). Division of entomology technical paper no. 28 CSIRO Australia. 39 pp.
- Johnson, B. 1965. Wing polymorphism in aphids-II. interaction between aphids. Entomologia Exp. Appl. 8: 49-64.
- Johnson, B. 1966. Wing polymorphism in aphids-III. The influence of the host plant. Entomologia Exp. Appl. 9: 213-222.
- Kennedy, J. S., & C. O. Booth. 1959. Responses of Aphis fabae Scop. to water shortage in host plants in the field. Entomol. Exp. Appl. 2: 1-11.
- Kennedy, J. S., A. Ibbotson, & C. O. Booth, 1950. The distribution of aphid infestation in relation to leaf age. I. Myzus persicae (Sulz.) and Aphis fabae Scop. on spindle trees and sugar beet plants. Ann. Appl. Biol. 37: 651-679.
- Kenton, J. 1955. The effect of photoperiod and temperature on reproduction in Acyrtosiphon pisum (Harris) and on the forms produced. Bull of Entomol. Res. 36: 599-624.

- Kriel, C.F., P.H. Hewitt, J. de Jager, M.C. Walters, A. Fouche & M.C. van der Westhuizen. 1984. Aspects of the ecology of the Russian wheat aphid, Diuraphis noxia in the Bloemfontein district. II. Population dynamics, 14-21. In, Walters, M.C. (ed.), 'Progress in Russian wheat aphid (Diuraphis noxia Mordw.) Research in the Republic of South Africa'. Proceedings of a Meeting of the Russian Wheat Aphid Task Team held at the University of the Orange Free State, Bloemfontein, 5-6 May 1982. Republic of South Africa, Department of Agriculture Technical Communication No. 191.
- Klepper, B., & R.D Ceccato. 1969. Determination of leaf and fruit water potential with a pressure chamber. Hort. Res. 9: 1-7.
- Kruger, G.H.J., & P.H. Hewitt. 1984. The effect of Russian wheat aphid Diuraphis noxia extract on photosynthesis of isolated chloroplasts: Preliminary studies, 34-37. In Tech. Commun. Dep. Agric. Repub. S. Afr. No. 191.
- Lees, A.D. 1966. The control of polymorphism in aphids. Adv. Insect Physiology 3: 207-277.
- Lees, A.D. 1967. The production of the apterous and alate forms in the aphid Megoura viciae Buckton, with special reference to the role of crowding. J. Insect Physiol. 13: 289-318.
- Michels, G. J. Jr., & R. W. Behle. 1988. Reproduction and development of Diuraphis noxia (Homoptera: Aphididae) at constant temperatures. J. Econ. Entomol. 79: 1097-1101.
- Michels, G.J. Jr., & D.J. Undersander. 1986. Temporal and spatial distribution of the greenbug (Homoptera: Aphididae) on sorghum in relation to water stress. J. Econ. Entomol. 79: 1221-1225.
- Mittler, T.E., & R.H. Dadd. 1966. Food and wing determination in Myzus persicae (Homoptera: Aphididae). Ann. Ent. Soc. Am. 59: 1162-1166.

- Slatyer, R.O. 1967. Plant water relations. New York: Academia Press.
- Slavik, B. 1974. Methods of studying plant water relationships. Academia; Publishing House of the Czechoslovak Academy of Sciences, Prague. Springer-Verlag, New York, Heidelberg, Berlin.
- Sumner, L. C., K. W. Dorschner, J. D. Ryan, R. D. Eikenbary, R. C. Johnson, & R. W. McNew. 1986. Reproduction of Schizaphis graminum (Homoptera: Aphididae) on resistant and susceptible wheat genotypes during simulated drought stress induced with polyethylene glycol. Environ. Entomol. 15: 756-762.
- Sumner, L. C., J. T. Need, R. W. McNew, K. W. Dorschner, R. D. Eikenbary, & R. C. Johnson. 1983. Response of Schizaphis graminum (Homoptera: Aphididae) to drought-stressed wheat, using polyethylene glycol as a matricum. Environ. Entomol. 12: 919-922
- Sutherland, O. R. W., & T.E. Mittler. 1971. Influence of diet composition and crowding on wing production by the aphid Myzus persicae. J. Insect Physiol. 17: 321-328.
- Walters, M. C. , F. Penn, F. du Toit, T. C. Botha, Y. K. Aalbersberg, P. H. Hewitt, & S. W. Broodryk. 1980. The Russian wheat aphid. Farming in South Africa, Leaflet Series, Wheat C3, 1-6. Also given as Appendix 1 In, Walters, M.C. (ed.), 'Progress in Russian wheat aphid (Diuraphis noxia Mordw.) Research in the Republic of South Africa'. Proceedings of a Meeting of the Russian Wheat Aphid Task Team held at the University of the Orange Free State, Bloemfontein, 5-6 May 1982. Republic of South Africa, Department of Agriculture Communication No. 191, 72-74.
- Wearing, C. H., & H .F. van Embden. 1967. Studies on the relations of insect and host plants on infestations by *Aphis fabae* (Scop.), *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.). Nature (London) 213: 1051-1052

- Webster, J. A., & K. J. Starks. 1987. Fecundity of *Schizaphis graminum* and *Diuraphis noxia* (Homoptera: Aphididae) at three temperature regimes. J. Kansas Entomol. Soc. 60: 580-582.
- Webster, J. A., A., K. J. Starks, & R. L. Burton. 1987. Plant resistance studies with *Diuraphis noxia* (Homoptera: Aphididae), a new United States wheat pest. J. Econ. Entomol. 80: 944-949.

Webster, J. A., & K. J. Starks. 1987. Fecundity of *Schizaphis graminum* and *Diuraphis noxia* (Homoptera: Aphididae) at three temperature regimes. J. Kansas Entomol. Soc. 60: 580-582.

Webster, J. A., A., K. J. Starks, & R. L. Burton. 1987. Plant resistance studies with *Diuraphis noxia* (Homoptera: Aphididae), a new United States wheat pest. J. Econ. Entomol. 80: 944-949.

APPENDIX

TABLE 6. 6 x 2 contingency table for pots containing alates and the six water potential treatments

Treatment	1	2	3	4	5	6	Total
Pots with alates	28	60	101	90	64	33	376
Pots without alates	932	900	859	870	896	927	5384
Total	960	960	960	960	960	960	960

TABLE 7. Russian wheat aphid density at each leaf water potential treatment

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
3	1	6	2	12	8
4	3	7	2	14	9
8	7	7	2	20	12
8	7	8	3	22	12
10	7	8	7	22	15
11	8	8	8	27	18
13	9	8	8	33	23
15	10	9	9	34	24
17	10	9	9	47	35
18	11	10	10	54	35
19	12	11	11	71	38
21	12	11	11	77	62
24	12	11	11	77	68
24	12	11	12	77	82
25	13	11	14	79	82
26	13	12	14	97	82
31	14	13	14	97	95
34	14	13	15	115	95
38	16	15	15	115	98

TABLE 7. (Cont.).

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
39	17	16	17	124	165
43	17	16	17	163	183
45	18	17	18	253	183
45	18	17	18	310	188
47	19	20	21	384	
49	20	20	23		
51	20	21	23		
52	21	21	24		
58	22	22	25		
61	24	22	25		
63	24	22	26		
65	24	23	27		
66	24	23	28		
70	25	24	28		
73	26	24	29		
96	27	27	29		
112	27	28	30		
142	27	29	31		
145	27	29	33		
161	28	30	33		

TABLE 7. (Cont.).

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
164	29	30	35		
203	29	31	36		
214	30	31	37		
	30	31	39		
	31	32	41		
	31	33	42		
	31	33	43		
	32	33	44		
	32	33	44		
	32	35	45		
	32	36	46		
	35	38	47		
	35	42	48		
	36	43	53		
	38	43	54		
	38	43	56		
	38	43	56		
	38	45	56		
	38	45	56		
	38	46	57		

TABLE 7. (Cont.).

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
	39	46	57		
	40	49	63		
	40	49	63		
	41	49	67		
	41	49	73		
	41	50	74		
	41	50	77		
	42	50	77		
	42	50	81		
	42	51	82		
	43	53	91		
	43	53	105		
	44	54	110		
	45	54	121		
	46	54	121		
	47	56	144		
	48	56	152		
	48	56	158		
	48	56	180		
	49	56	181		

TABLE 7. (Cont.).

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
	49	59	188		
	51	60	237		
	51	63			
	53	67			
	53	70			
	53	70			
	54	71			
	55	71			
	55	71			
	55	74			
	56	77			
	58	78			
	58	79			
	61	81			
	64	85			
	65	85			
	66	86			
	66	98			
	67	102			
	68	106			

TABLE 7. (Cont.).

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
	68	107			
	68	111			
	69	111			
	71	113			
	71	119			
	73	121			
	77	127			
	77	132			
	79	132			
	79	138			
	79	140			
	80	141			
	81	149			
	81	153			
	84	157			
	86	162			
	89	179			
	90	231			
	92				
	92				

TABLE 7. (Cont.).

Trt.1	Trt.2.	Trt. 3	Trt. 4	Trt. 5	Trt.6
	95				
	95				
	99				
	99				
	101				
	101				
	112				
	121				
	122				
	122				
	126				
	129				
	129				
	136				
	140				
	147				
	169				
	176				
	222				
	242				

TABLE 8. Total number of alates per leaf water potential treatment per day

Day	1	3	5	7	9	11	13
Trt.							
.51 - .61	39	35	14	6	7	0	0
.65 - .75	59	70	28	24	19	2	3
.79 - .89	85	64	73	70	24	18	23
.93 -1.03	69	114	76	80	43	14	12
1.07 -1.17	43	33	30	45	69	18	32
1.21 - 1.31	0	5	9	14	3	26	7
Total	295	321	230	239	165	78	77

TABLE 9. Water potential (-MPa) per day at each watering treatment

10ml.	20ml.	30ml.	40ml.	50ml.
<u>Day 1</u>				
448	.414	.414	.965	.586
1.034	.414	.448	.690	.414
.620	.483	.793	.621	1.034
.621	.828	.621	.483	1.138
.586	.414	.828	.655	.586
.690	.621	.690	.483	.621
<u>Day 3</u>				
.965	.965	.1.000	.655	.931
1.241	1.070	.655	1.138	1.172
1.241	.414	.862	.897	1.310
1.172	1.034	1.241	1.138	1.000
1.034	1.172	1.172	1.345	.862
1.069	1.310	1.034	1.379	1.034
<u>Day 5</u>				
.828	1.069	1.103	.897	1.138
1.345	1.310	1.345	1.586	1.517
1.207	1.345	1.310	.828	1.517
1.448	1.310	1.310	1.207	1.000

TABLE 9. (Cont.)

10ml.	20ml.	30ml.	40ml.	50ml.
1.172	1.345	1.034	1.000	.897
1.034	1.345	1.276	1.414	1.379
<u>Day 7</u>				
1.379	.965	1.276	1.103	.759
1.276	.828	1.310	1.103	.379
1.655	1.724	1.034	1.034	1.380
2.138	.724	1.724	.828	.965
1.724	1.517	1.207	.965	1.379
1.793	1.620	1.000	.897	.897
<u>Day 9</u>				
1.724	1.655	2.241	1.310	.828
2.207	1.103	1.310	1.793	1.448
1.931	1.379	1.241	1.379	1.379
2.345	2.414	1.241	.931	1.034
2.034	1.172	1.586	.965	1.448
1.931	1.413	1.552	1.172	1.069

TABLE 10. Population density counts (nymphs and adults) per day at each watering treatment

10ml.	20ml.	30ml.	40ml.	50ml.
<u>Day 1</u>				
6	5	14	0	9
4	4	3	3	15
1	2	2	2	10
1	9	3	2	1
2	7	1	8	2
2	3	15	11	2
<u>Day 3</u>				
13	14	25	0	16
12	1	1	1	26
1	2	0	2	13
6	13	4	20	1
1	1	20	9	12
13	2	9	1	1
<u>Day 5</u>				
48	26	28	0	24
24	0	0	31	40
18	0	7	0	2
0	29	0	22	39
13	0	26	16	2

TABLE 10. (Cont.)

10ml.	20ml.	30ml.	40ml.	50ml.
0	0	28	24	37
<u>Day 7</u>				
9	12	28	0	29
28	0	0	37	0
28	0	12	0	41
18	33	0	30	45
0	0	44	30	2
0	12	37	21	45
<u>Day 9</u>				
19	12	38	0	17
0	0	0	15	14
0	42	34	20	68
23	0	0	28	0
0	0	36	70	44
62	0	8	34	0