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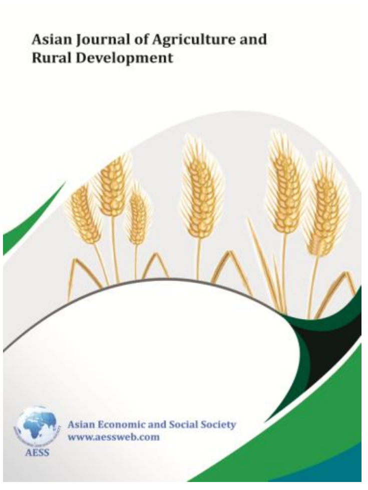

The Biology of the Red and Green Morphs of the Tobacco Aphid, *Myzus Persicae Nicotianae* (Blackman) on Flue-Cured Tobacco

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Abstract

The tobacco aphid, *Myzus persicae nicotianae* is an economically important pest of tobacco. Damage is through direct injury by sucking sap of infested plants as well as reduction of the quality of the leaf by leaving honey-dew which encourages the subsequent growth of sooty-mould. In addition to this, aphids also transmit economically important virus diseases such as the bushy-top virus, the alfalfa mosaic virus and the potato virus-Y. Before 2002, the main colour form of the tobacco aphid in Zimbabwe was green. However, during the 2003/2004 tobacco season, concerns were raised where red forms of the tobacco aphid were observed to be more prevalent than the green form. During the 2004/2005 tobacco season, green forms of the tobacco aphid could only be found with difficulty. In intensive research spanning three years, the days to adulthood, days to 1st nymph, nymphs/day, longevity, fecundity and survival of the red morph were compared to that of the green aphid. Across all years, days to adulthood were the same for the two forms. The red morph produced more nymphs/day than the green morph. Longevity was similar but fecundity was 1½ to 2 times higher for the red morph than the green aphid. The red morph survived longer than the green aphid. These parameters combined to give the red morph of the tobacco aphid a greater reproductive potential and rate of population increase over the green morph thereby partly explaining the sudden increase in this pest in the recent past.

Keywords: Aphid, Red morph, Green morph, Flue-cured tobacco

Introduction

The green peach aphid, *Myzus persicae persicae* (Sulzer) (Hemiptera: Aphididae) has a world-wide distribution and is an important vector of plant viruses, spreading diseases among many crops (Blackman & Eastop 2000). It is assumed to be of Asian origin because its primary host, peach (*Prunus persica* L.), on which sexual reproduction occurs, originated in Asia (Blackman & Eastop 2007). *Myzus persicae persicae* is known to develop populations specifically adapted to certain host plants (Margaritopoulos *et al*., 2000). The tobacco (*Nicotiana tabacum* L. (Solanaceae)) adapted form is considered to be a distinct subspecies and is known as the tobacco aphid, *M. persicae nicotianae* (Blackman) (Margaritopoulos *et al.,* 2000). This aphid exhibits morphometric (Blackman 1987; Blackman & Eastop 2007; Margaritopoulos *et al.* 2000) and genetic differences with respect to *M. p. persicae* (Blackman & Spence 1992; Margaritopoulos *et al*., 1998; Margaritopoulos *et al*., 2007). Relative preference for tobacco by *M. p. nicotianae* has been demonstrated experimentally (Margaritopoulos *et al*., 2005; Troncoso *et al*., 2005), suggesting that its capacity to detoxify and thus overcome allelochemicals from tobacco plants has been key during specialization (Cabrera-Brandt *et al*., 2010).

The tobacco aphid causes significant losses on tobacco directly by feeding and honeydew deposition and indirectly by contamination and as a vector of a wide range of viruses (Dixon, 1998). In Zimbabwe and other tropical regions, *M. p. nicotianae* has an anholocyclic lifecycle (not capable of producing sexual morphs or not producing viable eggs) and overwinters as active stages on crops and weeds such as *Nicandra* spp. Both winged and wingless forms can each produce about 80 offspring in a lifetime. Embryonic development begins before the mother's birth, in the body of the grandmother, whose food intake sustains three generations of about 6 000 individuals. This peculiar reproduction, together with a short life involves the telescoping of generations, providing high rates of population increase (Blair, 1990).

Colour variation among individuals of the green peach aphid is common and appears to be interclonal and sympatric in occurrence (Takada, 1981; Miyazaki, 1987). Two distinct colour forms are produced namely the green-yellow and red morphs. Although the benefit of colour dimorphism in *M. persicae nicotianae* is not clearly understood, the red morph is thought to able to absorb solar radiation and warm itself better than the green form (Markukula and Rautapaa, 1967). The colouration of aphids may reflect genetic differences (Muller, 1985, 1982) or be the result of environmental influences. Colour differences may be correlated with certain biological and ecological features, such as host specificity (Honek, 1982; Weber, 1985), insecticide resistance (Abdel-Aal, 1992), reproductive performance (Araya *et al*., 1996) and resistance to aphid parasitoids (Tomiuk and Wohrmann, 1980;). At times body colour serves as an indicator of a certain biotype or subspecies (Muller, 1985).

Before 2002, the main colour form of the tobacco aphid in Zimbabwe was green. However, during the 2003/04 tobacco season, red forms of the aphid were observed to be more prevalent than the green ones at Kutsaga Research Station, Zimbabwe. During the 2004/05 season, green forms could not be found and where they were found, constituted small numbers. Elsewhere in the world, the red form of the tobacco aphid had been observed as far back as 1985 in North Carolina, U.S.A. (Harlow & Lampert, 1990) and appeared to be a more serious pest than the green form.

The occurrence and subsequent dominance of the red form of *M. p. nicotianae* has brought about the need for a study of its biology as this is an important tool for the development of effective control strategies. The objective of this study therefore, was to compare the fecundity, longevity and survival of the red and green forms of the tobacco aphid *M. p. nicotianae* on flue-cured tobacco in Zimbabwe.

Materials and Methods

Aphid Culture

The aphid culture was collected from the most commonly grown variety of flue-cured tobacco, Kutsaga Rootknot 26 (K RK26), grown at Kutsaga Research Station. This culture was reared and maintained on K RK26 in the greenhouse until ready for use.

Determination of Aphid Fecundity, Longevity and Survival

From the greenhouse culture, 45 apterous adults of each morph were collected, marked with nail varnish and placed on 80 mm diameter flue-cured tobacco leaf discs. After reproducing for one day, 100 one-day-old nymphs from each morph were collected with a fine brush and placed in marked individual Petri-dishes (9.1 cm in diameter, 1.2 cm deep) containing moistened filter paper and one 30 mm leaf disc. Containers were kept in a constant temperature room at 24 °C with 16:8 (Day/Night) h photoperiod. Leaf discs were replaced three times a week (Lampert & Dennis 1987). Colonies were observed on alternate days until the first nymph was produced, then daily thereafter. On each observation, the instar of each aphid as evidenced by exuviae and their condition was recorded. Offspring present were counted and removed. From this data, days to adulthood, days to first nymph, longevity, mean nymphs per day and total nymphs per aphid and survival were calculated for both the red and green morph. The experiment was a factorial laid out in 4 randomised complete blocks with time (3 years) and aphid colour (Red and Green) as the main effects replicated 30 times. In addition a Life Table analysis was also performed. ANOVA was done on the data using Genstat Version 11.

Life Tables were used to describe the biology of the morphs according to Price, 1984 and Birch 1948 using the following parameters:

x = Age of the insect in days
l_x = Number of aphids alive at age x, out of 100
d_x = Number of deaths in the interval (x,x+1), out of 100, computed as $l_x - l_{x+1}$
q_x = probability of dying at age x. Also known as age specific risk of death, computed by d_x / l_x
$100q_x$ = Mortality rate at the age interval x and calculated using the formula

$$d_x / l_x \times 100$$

L_x = The number of aphids alive between age x and x+1, computed by:

$$(l_x + l_{x+1})/2, \text{ out of } 100$$

T_x = The total number of living aphids at age x and beyond computed as

$$T_x = L_x + L_{x+1} + L_{x+2} + \ldots + L_{x+n}$$

Finally, the average amount of time yet to be lived by members surviving to particular age/life expectancy:

$e_x = T_x / l_x$ Life expectancy, which is the mean number of age categories remaining until death for individuals surviving to the beginning of age category x.

M_x= The average number of offspring produced by an individual in age category *x while in that age category*..
Ro = $\sum l_x m_x$. Net Reproductive Rate represents the average lifetime number of offspring produced by an individual of maximum lifespan

Results

Days to adulthood

There was no interaction between year and colour, (Table 1) although the general trend was that the days to adulthood decreased from year 1 to year 3 (Table 1). No significant differences ($P > 0.05$) between the two forms were observed in the days taken to reach adulthood over the three year period (Table 1). However, significant differences were observed from the first to the third year where both forms took a significantly shorter time ($P < 0.001$) to reach adulthood (Table 1). Although the red morph tended to have a shorter time to adulthood, this was not significantly ($P > 0.05$) shorter than for the green morph (Table 1).

Days to 1st Nymph, Nymphs per Day and Total Number of Nymphs

There was no interaction between year and colour for days to 1st nymph, nymphs per day and total number of nymphs but consistently for 3 years the red morph, took a significantly shorter time ($P < 0.001$) to produce its first offspring, produced a significantly greater number ($P < 0.001$) of total nymphs (Table 1) and nymphs per day (Table 2) than the green morph.

Table 1: Days to Adulthood & to First Nymph, Fecundity, Nymphs per Morph, Longevity and Survival for the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae*

Year	Colour	Days to adulthood	Days to first nymph	Total nymphs/aphid (Fecundity)
1	Red	8.64	8.36	63.10
1	Green	9.39	10.22	40.10
2	Red	7.00	6.57	107.12
2	Green	7.18	8.17	63.40
3	Red	6.84	5.80	99.47
3	Green	7.23	7.92	50.90
Year * Colour: F-Probability		0.66	0.69	0.33
L.S.D		0.87	0.85	17.38

Colour	Red	7.46	6.89	90.97
	Green	7.89	8.73	52.21
	F-Probability	0.10	<0.001	<0.001
	L.S.D	0.51	0.50	14.35

Year	**Days to adulthood**		**Days to first nymph**		**Fecundity**	
	Red	Green	Red	Green	Red	Green
	8.64	9.39	8.36	10.22	63.10	40.10
	7.00	7.18	6.57	8.17	107.13	63.39
	6.84	7.23	5.80	7.92	99.47	50.90
F-Probability	<0.001	<0.001	<0.001	<0.001	0.002	0.18
L.S.D	0.85	0.90	0.88	0.84	24.54	24.95

Table 2: Nymphs / day, Longevity and Survival for the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae*

Year	**Colour**	**Nymphs/Day**	**Survival**	**Longevity**
1	Red	70.00	57.92	25.43
1	Green	46.70	50.57	22.13
2	Red	117.50	66.91	23.30
2	Green	79.20	56.58	22.50
3	Red	120.20	66.90	20.77
3	Green	87.50	56.38	18.67
Year * Colour: F-Probability		0.903	0.92	0.79
L.S.D		47.10	8.62	50.9
Colour	Red	100.20	63.60	23.17
	Green	69.30	54.30	21.10
	F-Probability	0.028	0.01	0.17
	L.S.D	27.54	7.11	2.94

Year	**Nymphs/Day**		**Survival**		**Longevity**	
	Red	Green	Red	Green	Red	Green
1	2.76	2.29	57.95	50.57	25.43	22.13
2	5.34	4.20	66.91	56.58	23.30	22.50
3	5.54	4.71	66.90	56.38	20.77	18.67
F-Probability	0.025	0.021	0.30	0.47	0.12	0.34
L.S.D	**2.26**	**1.81**	**13.36**	**10.14**	**4.46**	**5.71**

Longevity and Survival

There was no interaction between year and colour but the red morph survived for a significantly longer time ($P < 0.001$) than the green morph while longevity was the same for the morphs (Table 2). Over the three years no significant year differences ($P > 0.001$) were observed in survival or longevity for each morph (Table 2).

Life Tables

Figures 1to 3 show the age-specific fecundity of the red and the green morph of the tobacco aphid *Myzus nicotianae* from 2008 to 2010. The number of nymphs produced by the red morph reached two peaks on day 9 and 16 whilst that of that of the green morph reached peaks on day 12 and 20 for 2008 (Fig 1). The first peak for both morps was always smaller than that of the second. In 2009 the red morph peaked at age 17 while the green morph peaked 3 days later (Fig 2) while in 2010 thered morph peaked at 18 days and the green morph at 22 days (Fig 3). The general trend was that the red morph began to reproduce earlier than the green morph and reached peak reproduction earlier than the green morph (Fig 1, 2,3).

Figures 4-6 show the age-specific survival of the red and green morphs of the tobacco aphid *Myzus nicotianae*. From 2008 to 2010 the red morph consistently had higher survival than the green morph up to about day 25. Survival curves for both morphs fell similarly with time.

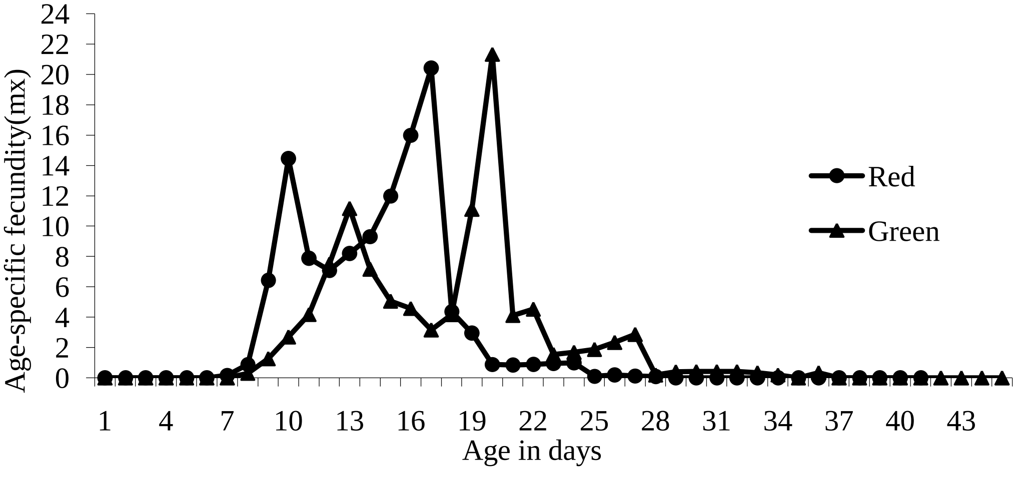

Fig 1: Age-specific Fecundity (m_x) of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae* in 2008

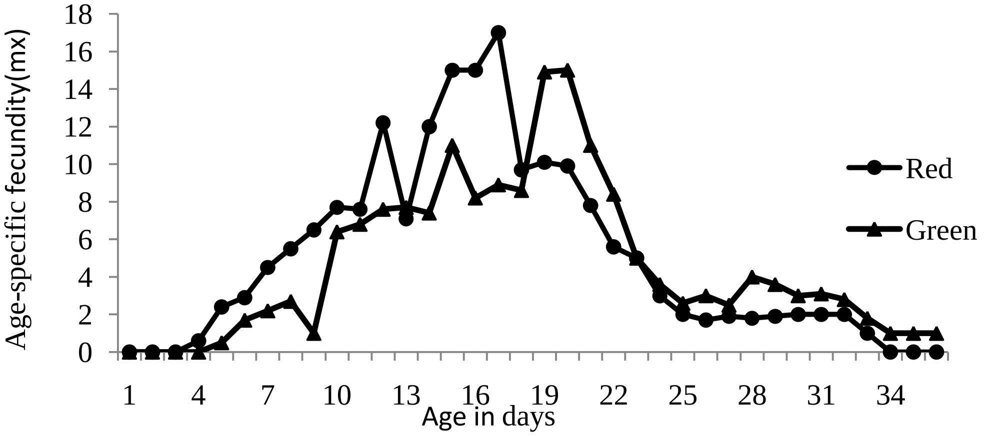

Fig 2: Age-specific Fecundity (m_x) of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae* in 2009

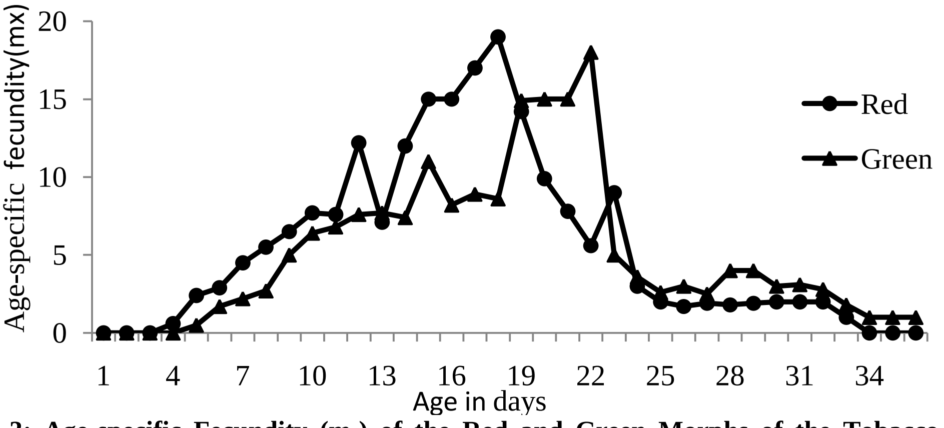

Fig 3: Age-specific Fecundity (m_x) of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae* in 2010

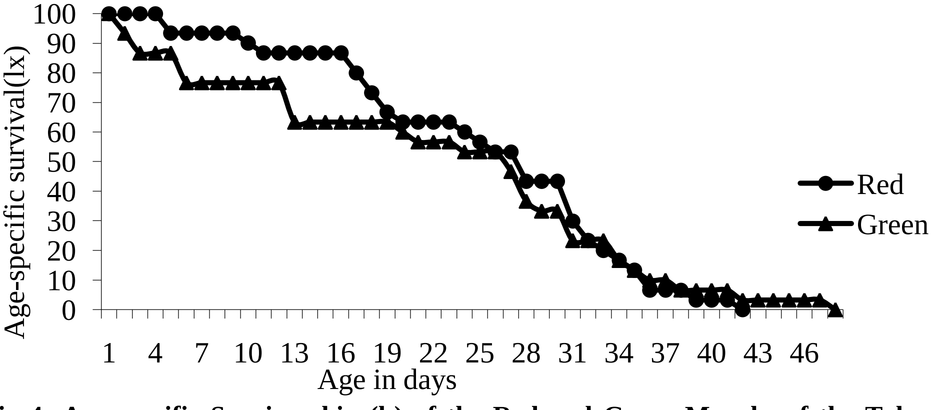

Fig 4: Age-specific Survivorship (l_x) of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae* in 2008

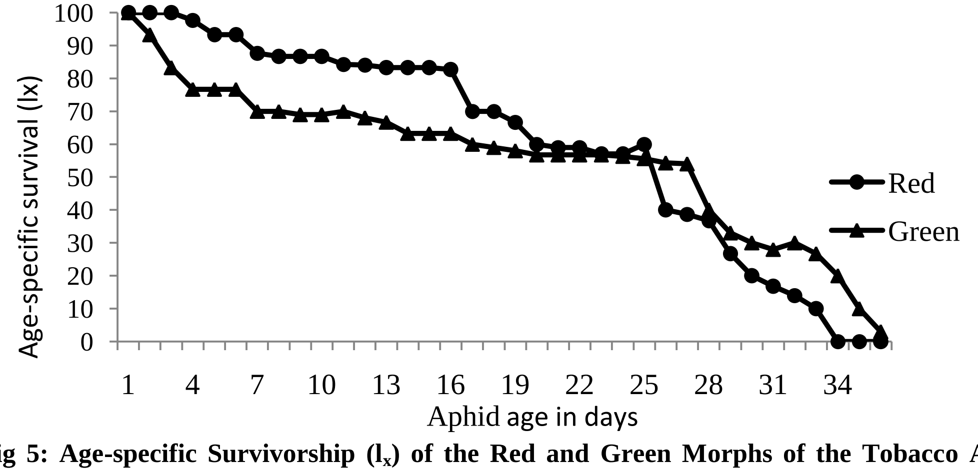

Fig 5: Age-specific Survivorship (l_x) of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae* in 2009

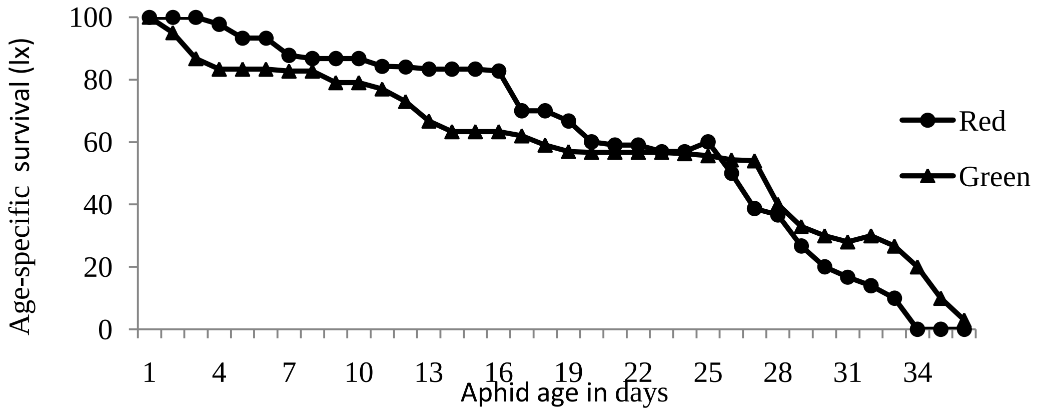

Fig 6: Age-specific Survivorship (l_x) of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae* in 2010

Analysis of the life table of green and red morphs of the tobacco aphid showed that the red morph consistently had a higher net reproductive rate (R_O) over the three year study than the green morph. However, for both morphs net reproductive rate increased between 2008 and 2010 (Table 3). The intrinsic rate (r_m) of increase was also higher for the red morph than the green and results of the mean generation time (T_c) showed that the red morph had a shorter mean generation time than the green morph (Table 3).

Table 3: Life-table Parameters of the Red and Green Morphs of the Tobacco Aphid, *Myzus nicotianae*

Year	Parameters	Red morph	Green morph
2008	R_o	**95.73**	**63.57**
	r_m	**0.349**	**0.256**
	T_c	**13.06**	**16.19**
2009	R_o	**129.3**	**87.40**
	r_m	**0.355**	**0.276**
	T_c	**13.71**	**16.21**
2010	R_o	**128.73**	**88.00**
	r_m	**0.353**	**0.262**
	T_c	**13.76**	**17.09**

R_0 = net reproductive rate, r_m = intrinsic rate of increase, T_c = mean generation time

Discussion

Understanding the biology of an insect is crucial in the development of an effective integrated pest management programme. A shorter period to adulthood would make an insect more competitive, since this could mean a shorter life cycle. However, in this respect the red morph only tended to develop in a shorter period than the green morph, suggesting that this did not give the red morph any related advantage over the green morph. However, the period to 1st nymph (to reproductive age) was shorter for the red morph than the green morph. This was also shown by the higher net reproductive rate and intrinsic rate of increase of the red morph. This would thus give the red morph a distinct advantage over the green morph in terms of capacity to quickly colonize a habitat. This could be one of the contributing factors to the success of the red morph as this may give the red aphids an advantage of early colony establishment. The present study agrees with findings by Goundoudaki *et al*. (2003) who indicated a shorter developmental time in the red morph of the tobacco aphid relative to the green morph. Araya *et al*. (1996) also showed that the pink English grain aphid, *Sitobion* *avenae* had a shorter reproductive period compared to the green form.

Not only did the red morph reach reproductive age earlier, but it also produced more nymphs per day giving it advantage over the green morph. However, longevity was comparable to that of the green morph, giving it no distinct advantage over the green morph. Higher longevity could mean an organism would produce more offspring in its lifetime and thus making it more competitive. Goundoudaki *et al.* (2003), however, showed a significantly higher longevity in the red morph relative to the green morph. Age-specific fecundity showed that the red morph reached its peak reproduction time earlier than the green morph and consistently had a higher survival than the green morph. In the present study, the red morph tended to have a greater longevity consistently but this was not significantly higher than for the green morph, perhaps showing that this "new" morph is still adapting to its new environment.

That the fecundity of the red morph was 1½ to 2 times higher than that of the green morph suggests that it would out-compete the green morph. This coupled with a greater survival implies greater competitive advantage and may explain the predominance of the red morph, particularly in warm temperatures. Reed & Semtner (1991) showed that the red morph could develop, reproduce and survive better than the green morph at 25 °C or higher, confirming earlier findings by Lampert & Dennis (1987).

Summary

Polyphenism, the production of two or more alternative phenotypes by a single genotype, is a characteristic feature of aphids (Dixon, 1998). Aphids exhibit a wide range of phenotypic plasticity characteristics, whereby the same genotype can respond to different environments by producing alternate phenotypes in a way that maximizes its fitness (Halkett *et al*. 2006). The predominance of the red morph in Zimbabwe is a new phenomenon in the country but the success of the red morph has been a worldwide experience (Blackman 1987; McPherson and Bass, 1990). This success could be linked to its ability to survive, reproduce and develop faster than the green morph (Reed & Semtner, 1991; Lampert & Dennis, 1987). Our work agrees with these findings and we postulate that the red morph will be a "new" menace in the region. This red morph has been conclusively associated with insecticide resistance (Blackman, 1987; Harlow & Lampert, 1990; McPherson & Bass, 1990).

Conclusions and Recommendations

The parameters studied in this study show that the red morph has competitive advantage in terms of days to 1st nymph, number of nymphs/day, fecundity and survival. These factors suggest that the increases in populations observed over the short period may be partly explained by these advantages. This study would therefore be useful in obtaining data for later use in the development of population models of tobacco aphids and development of integrated pest management strategies. In addition, we recommend more judicious use of insecticides and a need for a holistic approach to aphid control, utilizing perhaps natural enemies and insecticides not harmful to such enemies. More work is required to establish which of the pesticides available in the region the pest has already developed resistance to. Lastly, we recommend work in the area of biological control in order to augment insecticide usage.

References

Abdel-Aal, Y. A. I., Lampert, E. P., Roe, R. M. & Semtner P. J. (1992). Diagnostic esterases and insecticide resistance in the tobacco aphid, *Myzus nicotianae* Blackman. *Pesticide Biochemistry and Physiology*, 43, 123–133.

Araya, J. E., Cambron, S. E. & Ratcliffe, R. H. (1996). Development and reproduction of two colour forms of English grain aphid. *Environmental Entomology*, 25(2), 366–369.

Birch, L. C. (1948). The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology*, 17, 15-26.

Blackman, R. L. (1987). Morphological discrimination of a tobacco feeding form of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), and a key to New World *Myzus* (*Nectarosiphon*) species. *Bulletin of Entomological Research*, 77, 713–730.

Blackman, R. L. & Eastop, V. F. (2000). *Aphids on the world's crops: An identification and information guide*. Chichester, Wiley.

Blackman, R. L. & Eastop, V. F. (2007). Taxonomic issues. In: *Aphids as Crop Pests* (Eds, van Emden, H.F., Harrington, R.), pp. 1–29. CAB International, Wallingford, U.K.

Blackman, R. L. & Spence, J. M. (1992). Electrophoretic distinction between the peach–potato aphid, *Myzus persicae*, and the tobacco aphid, *M. nicotianae* (Homoptera: Aphididae). *Bulletin of Entomological Research,* 82, 161–165.

Blair, B. W. (1990). Insect and mite pests of tobacco in Zimbabwe. Technical Bulletin No. 1. Tobacco Research Board, Harare, Zimbabwe. P. 5.

Cabrera-Brandt, M. A., Fuentes-Contreras, E. & Figueroa, C. C. (2010). Detoxification metabolism in the aphid *Myzus persicae* (Hemiptera: Aphididae): effect of feeding on tobacco. *Chilean Journal of Agricultural Research,* 70, 567-575.

Goundoudaki, S., Tsitsipis, J. A., Margaritopoulos, J. T., Zarpas, K. D. & Divanidis, S. (2003). Performance of the tobacco aphid *Myzus persicae* (Hemiptera:Aphididae) on Oriental and Virginia tobacco varieties. *Agricultural and Forest Entomology,* 5, 285–291.

Halkett, F., Kindlmann, P., Plantegenest, M., Sunnucks, P. & Simon, J. C. (2006). Temporal differentiation and spatial coexistence of sexual and facultative asexual lineages of an aphid species at mating sites. *Journal of Evolutionary Biology,* 19, 809–815.

Harlow, C. D. & Lampert, E. P. (1990). Resistance mechanisms in two color forms of the tobacco aphid (Homoptera: Aphididae). *Journal of Economic Entomology,* 83, 2130–2135.

Honek, A. (1982). Colour polymorphism in *Acyrthosiphon pisum* in Bohemia (Homoptera, Aphididae). *Acta Entomologica bohemoslovaca,* 79, 406–411.

Lampert, E. P. & Dennis, C. A. (1987). Life history of the green peach aphid (Homoptera: Aphididae) on flue-cured tobacco. *Tobacco Science,* 31, 91–93.

Margaritopoulos, J. T., Mamuris, Z. & Tsitsipis, J. A. (1998). Attempted discrimination of *Myzus persicae* and *Myzus nicotianae* (Homoptera: Aphididae) by random amplified polymorphic DNA polymerase chain reaction technique. *Annals of the Entomological Society of America,* 91, 662–667.

Margaritopoulos, J. T., Tsitsipis, J. A, Zintzaras, E. & Blackman, R. L. (2000). Host-correlated morphological variation of *Myzus persicae* (Hemiptera: Aphididae) populations in Greece. *Bulletin of Entomological Research,* 90, 233–244.

Margaritopoulos, J. T., Tsitsipis, J. A., Goudoudaki, S. & Blackman, R. L. (2002). Life cycle variation of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) in Greece. *Bulletin of Entomological Research,* 92, 309–320.

Margaritopoulos, J. T., Tsourapas, C., Tzortzi M., Kanavaki, O. M. & Tsitsipis, J. A. (2005). Host selection by winged colonizers within the *Myzus persicae* group: a contribution towards understanding host specialization. *Ecological Entomology,* 30, 406–418.

Margaritopoulos, J. T., Malarky, G., Tsitsipis, J. A. & Blackman, R. L. (2007). Microsatellite DNA and behavioural studies provide evidence of host-mediated speciation *in Myzus persicae* (Hemiptera: Aphididae). *Biological Journal of the Linnean Society,* 91, 687–702.

Markkula M., & Rautapää, J. (1967). The effect of light and temperature on the colour of the English grain aphid, *Macrosiphum avenae* (F.) (Hom., Aphididae). *Annales Entomologici Fennici,* 33, 1–13.

Mcpherson, R. M., & Bass, M. H. (1990). Control of red and green forms of tobacco aphids (Homoptera: Aphididae) in flue-cured tobacco. *Journal of Entomological Science,* 25, 587–592.

Miyazaki, M. (1987). Forms and morphs of aphids, In: A. Minks and P. Harrewijn (Eds), *Aphids, Their Biology, Natural Enemies and Control*, Vol. 2A. Elsevier, Amsterdam. pp. 27–50.

Müller, F. P. (1982). The Problem Aphids. *Miscellanea Entomologica,* 94, 432–446.

Müller, F. P. (1985). Biotype formation and sympatric speciation in aphids. *Entomologica General,* 10(3/4), 161–181.

Price, P. W. (1984). Insect Ecology, 2nd Edition, John Wiley & Sons, New York.

Reed, D. T. & Semtner, P. J. (1991). Influence of temperature on population development of two color morphs of the tobacco aphid (Homoptera: Aphididae) on flue-cured tobacco. *Journal of Entomological Science,* 26, 33–38.

Takada, H. (1981). Inheritance of body colour in *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Applied Entomology and Zoology,* 16, 557–573

Tomiuk, J. & Wöhrmann, K. (1980). Population growth and population structure of natural populations of *Macrosiphum rosae* (L.). *Zeitschrift für Angewandte Entomologie,* 90, 464–473.

Troncoso, A. J., Vargas, R. R., Tapia, D. H., Olivares-Donoso, R. & Niemeyer, H. M. (2005). Host selection by the generalist aphid *Myzus persicae* (Hemiptera: Aphididae) and its subspecies specialized on tobacco, after being reared on the same host. *Bulletin of Entomological Research*, 95, 23–28.

Weber, G. (1985). On the ecological genetics of *Sitobion avenae* (F.). *Zeitschrift für Angewandte Entomologie,* 100, 100–110.