RESPONSE OF BARLEY CULTIVARS TO INFESTATIONS OF THE TWO SOUTH AFRICAN BIOTYPES OF THE RUSSIAN WHEAT APHID

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ABSTRACT

A second biotype of the Russian wheat aphid, *Diuraphis noxia* Kurdjumov code-named RWASA-2, a more virulent and fast breeder than the earlier RWASA-1, was reported from wheat farms in South Africa in 2007. There is an urgent need to characterize the effects of this new biotype on infested plants in order to assist the breeding programme in developing effective resistant cultivars that curb this emerging biotype and its destructive effects on our cultivated cereals. This study investigates and compares the feeding related damages caused by RWASA-1 and RWASA-2 through resulting chlorosis, evidence of leaf rolling as well as changes in aphid population levels on both resistant and non-resistant barley (*Hordeum vulgare*) cultivars. The results from this experiments revealed that RWASA-2 feeding caused a higher chlorosis levels in the non-resistant PUMA than was the case when exposed to feeding by RWASA-1. Interestingly, chlorosis ratings were significantly higher during RWASA-1 feeding than RWASA-2 feeding only in resistant barley lines. Leaf rolling was more severe on PUMA but lower in resistant cultivars. Population growth analysis revealed that RWASA-2 reproduced faster than RWASA-1, a reduction in growth was observed in resistant lines in comparison to the non-resistant PUMA, with a greater reduction recorded on a resistant - STARS-9301B line. Therefore, we suggest that the US developed resistant barley lines should be explored further as they may represent as yet unidentified resistant germplasm, which could be introduced into locally developed barley lines in South Africa and other regions of the world where this RWA is a problem.

Keywords: Barley, Chlorosis, Leaf roll, Resistance, Russian Wheat Aphid (RWA), Aphid Biotypes, Tolerance

INTRODUCTION

In 2007, a new biotype of the Russian wheat aphid (RWA), *Diuraphis noxia* Kurdjumov (Homoptera: Aphididae) was reported from wheat farms in the Eastern Free State of South Africa (Tolmay *et al.*, 2007). The biotype was designated RWASA-2 as done for the first biotype, RWASA-1 and it showed evidence of being a resistant-breaking biotype. It is virulent on many resistant wheat lines developed against RWASA-1 (Tolmay *et al.*, 2007; Walton and Botha, 2008). The RWA is also a devastating pest of barley, *Hordeum vulgare* L (Mornhinweg *et al.*, 2002; Bregitzer *et al.* 2003; Puterka *et al.*, 2006; Saheed *et al.* 2007a), but presently, it does not constitute a serious threat to barley growers in South Africa (Tolmay pers. Comm.).

However, in the United States of America (US), RWA had been a serious pest of barley to such an extent that growers in some areas stopped cultivating the crop (Bregitzer *et al.*, 2003). This has resulted in the development of RWA-resistant barley germplasm lines such as STARS-0502B, STARS-9301B and STARS-9577B among others (Mornhinweg *et al.*, 1995; 1999) against the US's Biotype 1 of RWA (RWA-1). These lines performed excellently in field trials against RWA infestations (Bregitzer *et al.*, 2003) and a follow-up study on the reactions of these RWA1-resistant lines to four subsequently identified biotypes of RWA showed that they retained their resistance genome (Puterka *et al.*, 2006).

In South Africa, RWASA-1 resistant cultivars have only been developed for wheat (*Triticum aestivum* L.). By 2007, about 27 resistant cultivars had been released to wheat growers, which have been integrated into pest control schemes against RWASA-1 (Tolmay *et al.*, 2007). Feeding damage caused by RWASA-1 in susceptible wheat cultivars is limited in resistant cultivars carrying the resistance gene, *Dn-1*. The emergence of a more virulent biotype, RWASA-2 which is unaffected by the *Dn-1* resistance gene poses a serious threat to small grain production in South Africa. Up to date, there is no RWA-resistant barley cultivar for commercial cultivation in South Africa.

It is necessary therefore, to identify potential source(s) of resistance in barley germplasm against known RWA biotypes before newer ones emerge. This is of importance as there are limited information on responses of barley cultivars to RWA infestation (Burd and Elliot, 1996; Gutsche

et al., 2009). The search for such resistant lines usually commences with studies on responses of available resistance germplasm lines against identified biotypes. This goes a long way into identifying resistance genes that can be incorporated into established locally developed lines in the battle against RWA. The South African strains of RWA are different from those in the US (Prinsloo pers. comm.). Earlier studies have indicated that RWA biotypes are morphologically similar; they only differ in their feeding behaviour, reproductive capacity and virulence (Puterka *et al*., 2006; Walton and Botha, 2008). To date, there is no report on development of resistant barley germplasm against RWA in South Africa.

The objectives of this study were to explore the response of some available US developed resistant barley lines to infestation by the two South African RWA biotypes. The purpose was to identify and ascertain which of the US tested resistant lines may show resistance against the South African RWA strains. These efforts we hope will provide background information for crop breeders towards development of resistant lines against these potential pests in South Africa and other barley growing parts of the world.

MATERIALS AND METHODS

Aphid colonies

RWASA-1 and RWASA-2 cultures were obtained from the Agricultural Research Council (ARC), Small Grain Institute, Bethlehem, South Africa. Their colonies were maintained on young feeder barley cv Clipper reportedly susceptible to RWASA1 (Saheed *et al*., 2007a and b). They were kept in insect cages in separate controlled environment (Conviron S10H Controlled Environments Ltd., Winnipeg, Manitoba, Canada)) at a daytime maximum temperature of 24°C and 66% relative humidity (RH) and at 22°C, 60% RH (night), with a 14-h photoperiod. Light source was a combination of fluorescent tubes (F48T12.CW/VHO1500, Sylvania, Danvers, MA) and frosted incandescent 60-W bulbs (Philips, Eindhoven, The Netherlands), with a PAR level of 250μmol^{-2}s^{-1} 30 cm below the light source. Fresh pots of two-week old feeder plants were introduced into the cages of each biotype at intervals of approximately two weeks. Each pot was usually infested with 30 apterous RWAs on older leaf segments placed at the axils of the feeder plants. Old pots were removed, discarded in waste bins and sprayed with aerosol pyrethroid insecticide (SC Johnson and Sons (Pty) Ltd., South Africa) before the aphids could produce alate (winged) forms in order to prevent cross-contamination of the biotypes' colonies.

Barley lines

Four barley lines tested in the experiments were STARS-0502B (PI 47541), STARS-9301B (PI 573080) and STARS-9577B (PI 591617), all developed at USDA-ARS, Aberdeen/Stillwater Oklahoma and known to be resistant to some US RWA biotypes (Webster *et al*., 1993; Mornhinweg *et al*.,1995, 1999; Puterka *et al*., 2006). PUMA, one of the widely cultivated barley cultivars grown commercially in South Africa, was used as non-resistant control. Seeds of the four lines were obtained from the ARC, Bethlehem, South Africa. The seeds were pre-germinated in Petri dishes and sown one seedling per pot in potting soil (50:25:25, garden soil: compost: vermiculite mixture) in 17cm diameter plastic pots in a green house maintained between 20-30ºC for one week. The seedlings were sprayed with aerosol pyrethroid insecticide to kill any insects that may have colonized them while in the greenhouse and were aired for another 24h (Jyoti *et al*., 2006). They were then removed to the growth cabinets (Conviron) where they grew for another two weeks to reach 2-3 leaf stage before they were manually infested with the aphids. They were fed twice a week with 50% Long Ashton nutrient solution (Hewitt, 1966).

Experimental Design

Two separate experiments, one for each biotype, were set up. Each experiment consisted of a growing barley plant enclosed under a ventilated clear cylindrical isolation cage. The plant, at the 3-leaf stage, was infested with 10 apterous form of each RWA biotype. Ten replicates of each treatment were prepared. The experimental procedures were repeated twice. The aphids were allowed a 24h period to transfer and acclimatize to their respective host plants.

Data Collection and Analysis

The plants were assessed for plant damage and aphid population changes. Plant damage was assessed using chlorosis and leaf roll ratings. Chlorosis rating was based on a ten-point scale of 0 to 9 as adapted from Webster *et al*. (1987), where 0 represented apparently healthy plants and 9 denoted plants that were either dead or expressing symptoms of severe feeding damage from which recovery was not possible. Leaf rolling was rated on a scale of 1 to 3 in which 1 represented plant

with flat leaves and no apparent rolling, 2 indicated leaves which were either folded or loosely rolled at the margins and 3 for leaves which were tightly or completely rolled (Burd *et al*., 1993). Plants were assessed for these ratings at seven, 14, 21 and 28 days after infestation (DAI). The population of aphids on each plant was recorded at seven and 14 DAI. The abaxial and adaxial surfaces of each plant were carefully examined with the aid of a hand lens and the number of live aphids recorded.
Data were analysed using Statistica version 9 (StatSoft, 2007). Statistical significance was determined using Repeated Measures ANOVA procedures to test for the effects of the four barley lines on the two South African RWA biotypes at 5% level in relation to the non-resistant control.

RESULTS

Interaction of the four barley lines with the two RWA biotypes using repeated measures of ANOVA was significant for chlorosis rating, leaf roll rating and population growth of aphids ($p<0.001$). Means of these parameters were subsequently subjected to *posthoc* tests. Leaf chlorosis that resulted from feeding by RWASA-2 became noticeable as early as seven DAI among the four barley lines (Table 1).

At 14, 21 and 28 DAI, there were no significant differences in the chlorosis ratings of PUMA infested with RWASA-1 and RWASA-2. Levels of chlorosis caused by the two biotypes recorded on PUMA were significantly higher than on the three resistant lines. On all the resistant lines, RWASA-1 caused higher levels of chlorosis than RWASA-2 at 14, 21 and 28 DAI (Table 1). There were significant differences between the levels of leaf chlorosis on PUMA and on the resistant lines due to feeding by RWASA-1 at 7 and 14 DAI. However, there were no significant differences among the four lines at 21 and 28 DAI regarding chlorosis ratings. RWASA-2 induced greater chlorotic effect on PUMA than on the resistant lines (Table 1). Generally, there were no significant differences in levels of chlorosis caused by RWASA2 on the resistant lines at each of 14, 21 and 28 DAI. Leaf rolling started from seven DAI in PUMA and STARS-0502B infested with RWASA1 and in the four lines infested with RWASA-2 (Table 1.). It was more pronounced in the non-resistant PUMA in which complete leaf roll was recorded on RWASA-2-infested plants at 14 DAI. Under infestation with both aphid biotypes, leaf roll ratings were generally higher on PUMA than on the resistant lines. Leaf roll ratings of PUMA infested with RWASA-1 were significantly lower than those infested with RWASA-2 at 5% level of significance. Also, leaf roll ratings recorded on resistant lines infested with RWASA-1 were lower compared to those infested with RWASA-2.
Comparative growth rates of the aphids on the test plants at seven and 14 DAI are shown in Fig.1. The four barley lines significantly affected the population growth of the two RWA biotypes ($p< 0.001$). The non-resistant PUMA recorded the highest number of either aphid per plant compared to the three resistant lines. Population of RWASA-2 was higher on the four lines compared to RWASA-1. At 7 DAI, populations ranged from an average of 35 (RWASA-1on STARS-0502B and STARS-9577B) to about 82 (RWASA-2 on PUMA) aphids per plant (SE range 1.9-6.86).

At 14 DAI, aphid populations ranged from about 101 (RWASA-1 on STARS-9301B) to an average of 310 (RWASA-2 on PUMA) per plant (SE range 4.10-16.30). At 7 DAI, there was no significant difference in the mean number of RWASA-1 growing on the four lines. However at 14 DAI, mean number of the aphid recorded on PUMA was significantly higher compared to those on the resistant lines. Mean population of RWASA-2 differ significantly across the four lines at 7 and 14 DAI. Highest mean population of this aphid was recorded on each day on PUMA compared to those recorded on the resistant lines. Deteriorating plant damage conditions observed on infested PUMA did not permit further assessment of aphid population growth beyond 14 DAI.

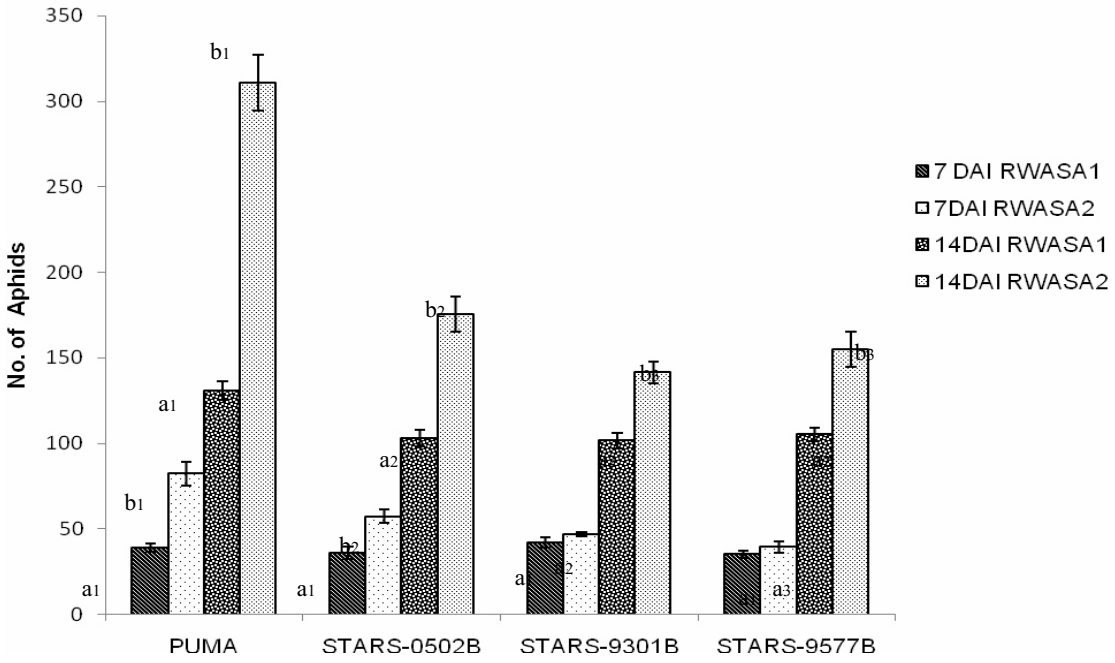

Fig. 1. Population Growth of RWASA-1 and RWASA-2 on the Four Barley Lines at 7 and 14 DAI.

Table 1: Mean† ± SE Barley Line Ratings‡ for Chlorosis and Leaf Rolling at 7, 14, 21 and 28 DAI with RWASA1 and RWASA2.

	Chlorosis Rating		Leaf Roll Rating	
	RWASA1	RWASA2	RWASA1	RWASA2
Cultivars		7 DAI		
PUMA	0.60±0.31 ^{a1}	1.80±0.20 ^{b1}	1.70±0.15 ^{a1}	2.30±0.15 ^{b1}
STARS-0502B	0.00±0.00 ^{a2}	1.00±0.00 ^{b2}	1.60±0.16 ^{a1}	1.70±0.15 ^{a2}
STARS-9301B	0.00±0.00 ^{a2}	1.00±0.00 ^{b2}	1.00±0.00 ^{a2}	1.70±0.15 ^{b2}
STARS-9577B	0.01±0.01 ^{a2}	1.00±0.00 ^{b2}	1.00±0.00 ^{a2}	1.70±0.00 ^{b2}
		14 DAI		
PUMA	6.70±0.15 ^{a1}	7.20±0.13 ^{a1}	2.30±0.15 ^{a1}	3.00±0.00 ^{b1}
STARS-0502B	4.20±0.32 ^{a2}	3.20±0.20 ^{b2}	2.00±0.21 ^{a2}	2.00±0.00 ^{a2}
STARS-9301B	3.90±0.50 ^{a2}	3.20±0.20 ^{b2}	1.20±0.13 ^{a3}	1.90±0.10 ^{b2}
STARS-9577B	3.10±0.28 ^{a3}	2.20±0.13 ^{a2}	1.30±0.15 ^{a3}	2.00±0.00 ^{b2}
		21 DAI		
PUMA	7.70±0.26^{a1}	8.70±0.15^{a1}	2.60±0.16^{a1}	3.00±0.00^{b1}
STARS-0502B	6.80±0.20^{a1}	4.70±0.26^{b2}	2.30±0.21^{a2}	2.40±0.16^{a2}
STARS-9301B	7.20±0.25^{a1}	3.00±0.14^{b3}	1.40±0.16^{a3}	2.00.00±^{b3}
STARS-9577B	6.90±0.18^{a1}	4.30±0.67^{b2}	1.50±0.17^{a3}	2.20±0.13^{b2,3}
		28 DAI		
PUMA	8.70±0.15^{a1}	9.00±0.00^{a1}	2.70±0.15^{a1}	3.00±0.00^{b1}
STARS-0502B	7.30±0.15^{a1}	5.40±0.26^{b2}	2.70±0.15^{a1}	2.50±0.17^{a2,3}
STARS-9301B	7.50±0.17^{a1}	4.70±0.21^{b2}	1.40±0.16^{a2}	2.30±0.15^{b3}
STARS-9577B	7.30±0.15^{a1}	5.40±0.52^{b2}	1.70±0.21^{a2}	2.60±0.16^{b2}

Note: Different letters and numbers indicate that means are significantly different between the two aphid biotypes across the four lines infested with a given biotype on each of 7 and 14 DAI at the 5% level of significance (n = 10) respectively.

DISCUSSION

Results from this study showed that PUMA is the most susceptible cultivar regarding infestation by RWASA-1 and RWASA-2 (Table 1). It was prone to the aphids' feeding damage as early as 14 DAI when chlorosis ratings were as high as 6.70 (RWASA-1) and 7.20 (RWASA-2) (see Table 1). By 28 DAI, PUMA plants rated 9.00 indicating plant deaths. These results are consistent with Puterka *et al.* (2006) where three susceptible barley entries recorded chlorosis ratings ranging from 7.00 to 8.40 after 14 days of feeding by five RWA biotypes. Mornhinweg *et al.* (1999) similarly reported a chlorosis rating of 9.00 on Morex, a susceptible barley cultivar in the US.

An interesting observation was that RWASA-1 which recorded a lower number of aphids compared to RWASA-2 on the resistant plants (Fig.1) caused higher levels of chlorosis in these lines. Our results are consistent with Puterka *et al.* (2006) who showed that the older biotype of the US strain of RWA caused higher levels of chlorosis than subsequently emerging biotypes on three resistant barley germplasm lines. We suspect that RWASA-1 may have ejected more wound callose initiating factor than does RWASA-2 when feeding on the resistant host plants. This may indicate that the stealthy RWASA-2 may contain a callose-degrading factor in its saliva that is capable of preventing host plants it fed on from responding to feeding injury, thereby sabotaging wound callose formation (Will *et al.*, 2007). Plants fed on by RWASA-1 responded rapidly to feeding injury through callose formation which may have caused complete physiological destruction of host plant tissues. Saheed *et al.* (2007a, 2007b) reported that RWASA-1 ejected massive saliva during feeding process which impairs the cells of the transport conduits of their host plants. This leads to chlorosis and streaking symptoms due to oxidative stress.

Mornhinweg *et al.* (see Puterka *et al.*, 2006) categorised chlorosis ratings of barley performance against RWA into four groups: resistant (1-3 rating), moderately resistant (4-5 rating), moderately susceptible (6 rating) and susceptible (7-9 rating). By applying this grouping in the present study, it may be speculated that at 28 DAI, while the resistant lines are susceptible to RWASA-1, they are only moderately susceptible to RWASA-2 (see Table 1). RWASA-2 caused higher leaf roll ratings than RWASA-1 among all plant entries (Table 1). It is higher in Puma than in the USDA germplasm lines. These results are consistent with Puterka *et al.* (2006) where susceptible barley plants recorded complete leaf roll (3.00 rating) while the resistant plants are generally not fully rolled at 14 DAI.

Leaf rolling is a form of gall which is critical to the biology of RWA feeding (Burd *et al.*, 1993). It is induced by apoplasmic and symplasmic isolation of xylem and phloem tissues during aphid feeding (Saheed *et al.*, 2007a, 2007b). Higher levels of leaf roll ratings obtained from RWASA2-infested plants could be due to lower water and nutrient transport capacity experienced by the translocatory conduits compared to RWASA-1 infestation. Transmission electron microscopy study by Saheed *et al.* (2007a, 2007b) showed that RWASA-1 ejected massive watery saliva which completely sealed xylem vessels responsible for conducting water and nutrients in host plants. Leaves that have been fed on by the more populous RWASA-2 may have been stuffed with more saliva and consequently rolled more rapidly than those fed on by RWASA-1.

Apparently, among the resistant lines, STARS-9301B germplasm grew least number of both aphids. It equally recorded least damage ratings. This germplasm line, developed against the first US biotype of RWA (Mornhinweg *et al.*, 1995) and STARS-9577B which was developed later (Mornhinweg *et al.*, 1999) represent key sources of resistance in barley against RWA. Reports by Puterka *et al.* (2006) further showed that emergence of new RWA biotypes in the US (eight as at 2008) virulent on wheat (Jyoti *et al.*, 2006) pose no threat to these resistance germplasm in barley. From the current study, the three USDA lines explored showed less damage, possibly as a result of reduced population growth rate when compared with the responses of South African PUMA cultivar. However, a comparison of data here with those of Puterka *et al.*, (2006) indicates that none of them is immune to the South African biotypes of RWA.

Colonies of RWASA-2 grew much faster than colonies of RWASA-1 on all cultivars. This finding is consistent with those of Walton and Botha (2008) and Jyoti *et al.* (2006) in wheat. The South African PUMA cultivar recorded the highest population of both RWASA1 and RWASA-2. This is contrary to the report of Puterka *et al.* (2006) in which susceptible barley lines recorded lower number of aphids than the resistant lines. They opined that the resistant lines tolerated aphids' breeding than the susceptible lines. In our study, the resistant lines may have shown antibiotic effects against the aphids,

thereby reducing the rates at which they breed on them. However, the fact that the two biotypes could reach the high population levels that we obtained on the resistant plants, leads us to believe that they only possessed mild antibiotic effects against the aphids. This view is consistent with the reports of Webster and Starks (1987) and Puterka *et al.* (2006) regarding STARS-9301B and STARS-9577B.

In summary, results from this study confirm report by Walton and Botha (2008) that RWASA-2 breeds faster than RWASA-1. We however find that in barley, as reported elsewhere (see Puterka *et al.*, 2006), RWASA-1 induced more leaf yellowing than RWASA-2 (only in resistant plants though). We foreclosed that RWASA-2 may contain a callose-degrading factor in its saliva with which it 'deceives' the plant in order to keep on feeding and breed faster. This is more evident in its (RWASA-2) causing higher levels of leaf rolling than RWASA-1 among the test plants. It is also shown that though all the barley lines recorded high number of aphids, the USDA resistant lines grew relatively lower number compared to the SA PUMA cultivar. Given the responses of the resistant lines to the two aphids, we speculate that these SA biotypes are different from the US strain of RWA. However, the USDA lines need to be explored further as they may potentially possess as yet unidentified resistant genes which could be introduced into locally developed barley lines in the on-going battle against RWA infestation in South Africa.

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