J. Crop Prot. 2013, 2 (1): 81-92

Does leaf pubescence of wheat affect host selection and life table parameters of *Sipha maydis* (Hemiptera: Aphididae)?

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Abstract: The influence of leaf pubescence of three wheat cultivars (Pishtaz, Ghuds and Falat) on preference and biological parameters of *Sipha maydis* (Passerini) was investigated under greenhouse conditions (25 ± 2 °C, 70 ± 10% RH and 14: 10 h (L: D) photoperiod). The results showed that Pishtaz had a greater density of trichomes compared to the other cultivars. In the preference test with whole plant, the number of aphids on Pishtaz was significantly greater than that on other cultivars at 48 hrs after infestation. Similarly, in the preference test on leaves, the numbers of attracted aphids per leaf was highest on Pishtaz. In the life table study, there was no significant difference of intrinsic rate of natural increase (r_m) among the three studied cultivars but it was highest on Pishtaz (0.187 /day). Aphids' net reproductive rate, doubling time, mean generation time and finite rate of increases did not show significant differences between the tested cultivars. According to our results, leaf surface pubescence of wheat is not an effective resistance mechanism against *S. maydis*.

Keywords: trichomes, *Sipha maydis*, plant resistance, wheat cultivars

Introduction

Many plant species have different defense mechanisms used for their protection against herbivores attack. These defenses consist of chemical (e.g. toxic compounds, digestibility-reduceres and other secondary metabolites) and physical defense such as tissue toughness, surface waxes and trichomes (Schoonhoven *et al.,* 2005). Trichomes are the first plant structures contacted by insects during the preliminary stages of host acceptance (Shufran *et al.,* 1997; Khan *et al.,* 2000), consequently and are important physical barriers to oviposition of herbivore insects (Baur *et al.,* 1991; Handley *et al.,* 2005), their movement (Ramalho *et al.,* 1984; Eisner *et al.,* 1998) and/or feeding (Eisner *et al.,* 1998; Lam and Pedigo, 2001). However, the effect of pubescence on herbivores may be positive or neutral. For instance, some herbivores are protected by trichomes from natural enemies and/or moisture loss (Woodman and Fernandes, 1991; Lovinger *et al.,* 2000). Several studies also have shown that dense pubescence is correlated with higher rates of herbivore oviposition and feeding (McAuslane, 1996; Srinivasana and Uthamasa, 2005; Oriani and Vendramim, 2010).

Wheat, *Triticum aestivum* (L.) is the most produced cereal crop in Iran and worldwide (FAO, 2008). Production of wheat is limited by various pests, e.g. aphids, such as *Diuraphis noxia* (Mordvilko), *Rhopalosiphum padi* (L.), *Schizaphis graminum* (Rondani), *Sitobion avenae* (F.) and *Sipha maydis* (Passerini) are some of the most important ones (Blackman and Eastop, 2006). Pesticides are generally used in the management of the wheat aphids, however, development of population resistance to chemical pesticides as well as their potential adverse impacts on the

Handling Editor: Dr. Ali Asghar Talebi

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Received: 13 November 2012; Accepted: 12 February 2013

[DOR: 20.1001.1.22519041.2013.2.1.6.4]

environment and human health have led to alternative control methods, such as the use of resistant wheat cultivars (Wilde *et al.,* 2001; Edwards *et al.,* 2008). In several cases, varying degrees of antibiosis and/or antixenosis in resistant wheat cultivars have been found to wheat aphids (Schotzko and Bosque-Perez, 2000; Lage *et al.,* 2003; Jyoti and Michaud, 2005). Although the presence of chemical compounds (i.e. phenolics (Eleftherianos *et al.,* 2006) and hydroxamic acids (Givovich and Niemeyer, 1995) are involved in wheat resistance to aphids such as *R. padi* and *S. avenae*, leaf pubescence also could be one of the resistance factors against various wheat aphid species (Roberts and Foster, 1983; Webster *et al.,* 1994). For example, resistant wheat cultivars against *D. noxia* had a significantly greater trichome density compared with the susceptible wheat cultivars (Bahlmann *et al.,* 2003).

Sipha maydis feeds broadly on numerous species over 30 genera of Gramineae (Blackman and Eastop, 2006) in which wheat and barley are the most preferred hosts (Corrales *et al.,* 2007). The aphid is widespread in Eastern Europe, the Middle East and central Asia, North and South Africa, and South America (El-Yamani and Hill, 1991; Blackman and Eastop, 2006; Corrales *et al.,* 2007). In Iran, *S. maydis* is present in wheat fields at the seedling and maturing stages of host plant that could severely damages wheat (Rassipour *et al.,* 1996; Sabzalian *et al.,* 2004). In addition, management of *S. maydis* through biological control is difficult because the common aphid parasitoids attacking the other wheat aphids do not prefer this aphid as a host (Rakhshani *et al.,* 2008). Thus, the use of resistant wheat cultivars can be an ideal management tactic to reduce the spread and incidence of the pest. To our knowledge, there is no published information on the resistance potential of wheat cultivars to *S. maydis*, particularly from the perspective of physical defense. The specific aims of the present study were: (1) to examine the variation of leaf pubescence in selected commercial Iranian wheat cultivars and (2) to assess the relationship of leaf pubescence of the wheat cultivars and biological traits of the barely aphid, *S. maydis*.

Material and Methods

Plant rearing

Three extensively cultivated local cultivars of wheat, *Triticum aestivum* L., namely Pishtaz, Ghuds and Falat were selected for further investigation under controlled conditions. Seeds of these cultivars were prepared from Agricultural Research Center of Mashhad, Iran and were sown in pots (17 cm diameter, and 15 cm depth) consisting of 2.5 Kg sand and clay (Kumari coir, Singapore) at the ratio 2: 1 as a growing medium. Plants were irrigated routinely and kept at 26 °C day/ 23°C night, 70 ± 10% RH and a photoperiod of 14L: 10D.

Insect rearing

A clone of the *S. maydis* was started from a single individual from a culture maintained at the College of Agriculture, Ferdowsi University of Mashhad, reared on *Hordeum vulgare* cv. Kavir, at 25 ± 1 °C, 70 ± 10% RH and a photoperiod of 14L: 10D.

Assessment of trichomes density

1- *Scanning electron microscopy (SEM).* Leaf upper surfaces (1 mm × 1 mm) of the second fully expanded leaf from each wheat cultivar, at the five expanded-leaf stage, were fixed in glutaraldehyde (4% v/v, in phosphate buffer 0.2 M, pH 7) at 4°C for 24 hrs, then thoroughly rinsed in fresh phosphate buffer and dehydrated through an acetone series (25%, 50%, 75%, and 100% v/v) for 15 minutes at each concentration. Samples were mounted on SEM tubes and coated with a thin layer of gold. A LEO 1450VP SEM operating at 30 KV was used.

2- *Light microscopy*. Five leaf sections (1 mm × 1 mm) of the second fully expanded leaf from each cultivar (totally 15 samples) were cleared of chlorophyll by placing them in a 1:1 (v/v) chloral hydrate-phenol solution for 6 hrs. at 45°C, samples were then washed four times in distilled water for three min each time. Samples from each cultivar were mounted adaxial side up on microscopic slides. The numbers of trichomes were determined with light microscope using the 10 × objective and 10 × ocular lenses. The data

[DOR: 20.1001.1.22519041.2013.2.1.6.4]

were analyzed using one-way ANOVA in SAS v. 8.2 (SAS Institute 2000). If significant differences were detected ($P \leq 0.05$), Fisher's LSD test was used.

Preference tests

Choice preference test with whole plants

Seedlings of three wheat cultivars (one of each cultivar) were randomly planted in a circular pattern in 30-cm pot, 4 cm from the rim and 10 cm apart from each other in ten replications. When plants were at the five expanded leaf-stage, 30 apterous *S. maydis* adults were placed on the soil at the center of each pot. Adult aphids per plant were counted after 24 and 48 hr. and test plants were discarded. Aphid numbers were analyzed for effects of cultivars using one-way ANOVA. When significant effects were observed, means were separated using Fisher's LSD test ($P \leq 0.05$).

Choice preference test with leaves

The test was performed according to Martin and Fereres (2003). Briefly, the bottoms of Petri dishes (diameter 20 cm) were covered with agar (1%) (Krips *et al.,* 1999) and surface of agar lined with filter paper. At the edge of the paper, six pieces (8 × 40 mm) were cut out around the center of the dish and two leaf-disks from the second fully expanded leaf of each cultivar, at the five expanded-leaf stage, were placed alternately. Ten Petri dishes were prepared (i.e. 10 plants and 20 leaf disks for each wheat cultivar). Then, 20 apterous *S. maydis* adults, starved for three hours, were released at the center of each Petri dish. The dishes were then transferred to a growth chamber at 25 ± 1 °C, 70 ± 10% RH and 14: 10 h (L: D) photoperiod. The number of aphids located on each disk was counted at 1, 2, 3, 4, 6, 12, 24 and 48 hrs. after the aphids were released. The number of aphids per disk (n = 20 disks for each cultivar) was compared statistically with non-parametric Kruskal-Wallis test using Minitab v. 14.2 (Minitab Inc. State College PA USA).

Life table study

When the plants were at their five expanded leaf-stage, at least 35 female aphids were placed individually on the surface of the second fully expanded leaves in each cultivar (30 plants per cultivar). A ventilated clip cage (1.5 × 3 cm) encaged each individual aphid. Twenty-four hours later the initial adult aphids and produced nymphs except one were removed (n = 30). This single aphid was allowed to develop to adulthood. All aphids were examined daily for the onset of reproduction and every other day thereafter. The number of the young produced by each aphid (age-specific fecundity) was recorded for the remainder of its life. The plants and aphids were maintained in a climate chamber at 25 ± 1°C, 70 ± 10% RH and 14: 10 h (L: D) photoperiod.

To construct the age specific fertility life table, age specific survival rate (l_x) and average aphids progeny in x age class (m_x) were obtained. Based on these data, the intrinsic rate of natural increase (r_m, per day) was calculated by iteratively solving the equation (Birch, 1948): $\sum l_x m_x e^{-r_m x} = 1$

Where x is the age of the aphid in days, r_m is the intrinsic rate of natural increase, l_x is the age-specific survival, and m_x is the age-specific number of female offspring.

Other parameters of fertility life table including net reproduction rate ($R_0 = \Sigma l_x m_x$), generation time (T = (ln R_0) /r_m), population doubling time (DT = (ln 2) / r_m) as well as finite rate of increase ($\lambda = e^{r_m}$) were likewise computed (Carey, 1993).

To find differences in R_0, T, DT, λ and r_m values, jackknife method (Meyer *et al.,* 1986; Maia *et al.,* 2000) was used for producing pseudovalues. To assess the impact of varied trichome density, aphid performance parameters were subjected to One-way ANOVA.

Results

Assessment of trichome density

Scanning electron micrographs of the upper surface of second fully expanded leaves from each of cultivars are shown in Figure 1. The trichomes of three wheat cultivars were unicellular and nonglandular.

The number of trichomes per mm^2 was as Falat (14.4 ± 0.7) < Ghuds (23.6 ± 1.02) < Pishtaz (41.6 ± 1.43) which was significantly different between cultivars (One-way ANOVA, $F_{2, 42}$ = 156.04; $P < 0.01$).

[DOR: 20.1001.1.22519041.2013.2.1.6.4]

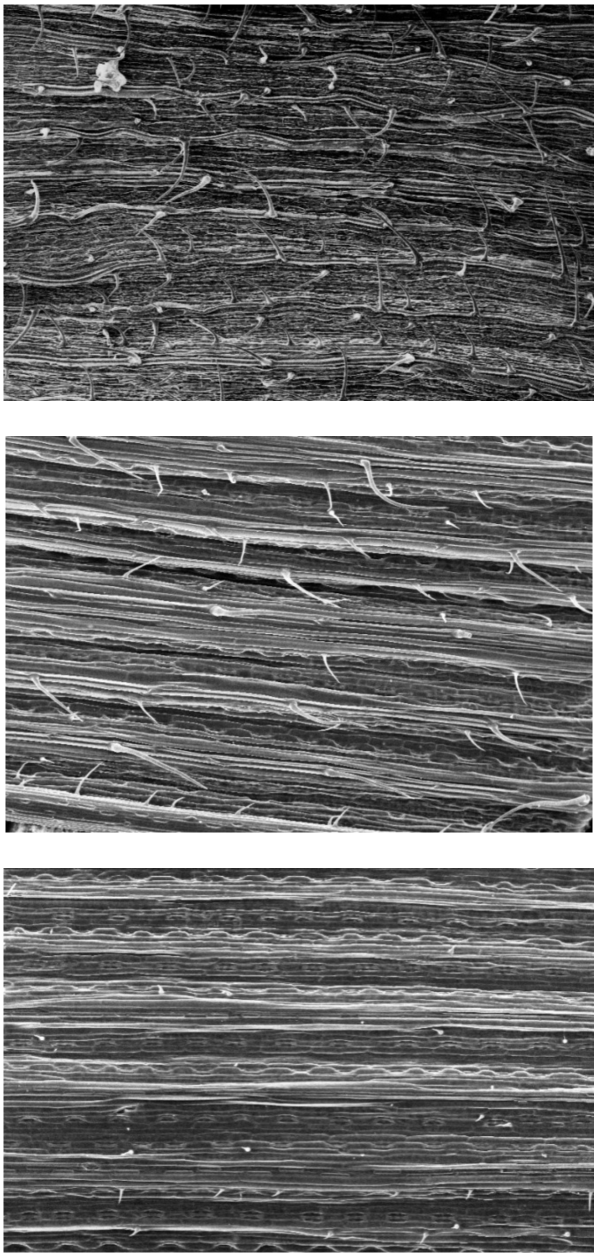

Figure 1 SEM micrographs showing the upper surface of second fully expanded leaves from three wheat cultivars a, Pishtaz; b, Ghuds; and c, Falat.

Preference tests

Choice preference test with whole plants

Up to 24 hrs. after release, the number of aphids per plant was not significantly different among cultivars (Figure 2a, One-way ANOVA, $F_{2,27} = 2.51$; $P = 0.1$). However, for longer assessment time, 48 hrs. after release, the number of aphids per plant varied significantly among cultivars (One-way ANOVA, $F_{2, 27} = 5.31$; $P = 0.01$). Significantly more number of aphids preferred Pishtaz cultivar than Falat and Ghuds (Figure 2a).

In addition, the linear regression analysis demonstrated a significant positive relationship between the number of aphids for various cultivars and trichome density 48 h after initiation of test (Figure 2b, $Y = 5.91 + 0.076 X$, $P < 0.05$, $R^2 = 0.35$).

Choice preference test with leaves

The results clearly indicate that, from the beginning of the experiment onwards, Pishtaz leaf disks were significantly more preferred than Ghuds or Falat ones (Table 1). However, in all assessment times, there was no significant difference between the numbers of aphids attracted to the leaf disks of Ghuds and those attracted to the leaf disks of Falat (Table 1).

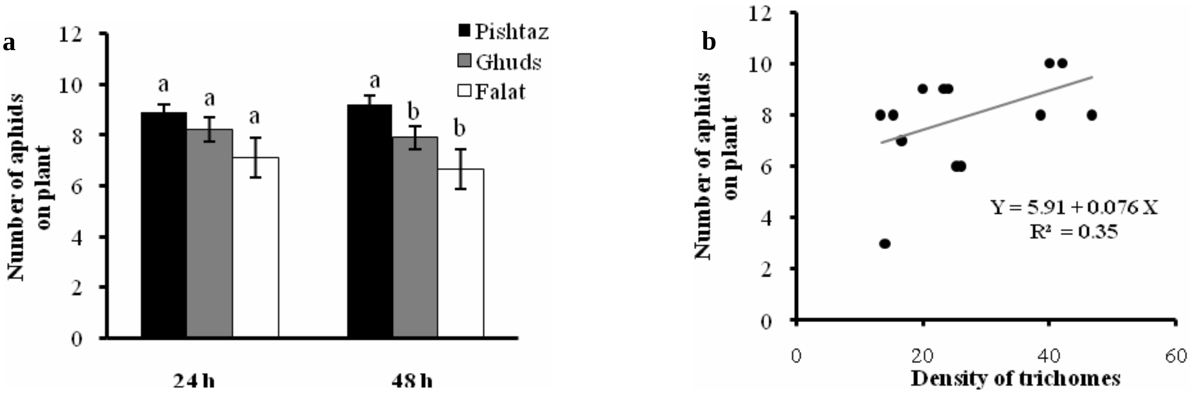

Figure 2 (a) Number of adult aphids (Mean ± SE) present on each wheat cultivar 24 and 48 h after release in preference test with whole plant; different letters indicate significant differences between cultivars (P < 0.01, LSD after one-way ANOVA), and (b) Relationship between the number of aphids present on plants and trichome density of wheat cultivars 48 h after initiation of test ($P < 0.05$, $R^2 = 0.35$), (n = 10).

Table 1 Number of adult aphids (Mean ± SE) located on leaf-disks of each wheat cultivar at different assessment times in preference test with leaves (n = 10).

Assessment Time	Wheat cultivars			H *
	Pishtaz	Ghuds	Falat	
1 h	6.2 ± 0.5 a**	3.9 ± 0.8 b	3.1 ± 0.8 b	7.94
2 h	6.4 ± 0.9 a	3.1 ± 0.6 b	2.1 ± 0.5 b	11.7
3 h	6.4 ± 0.9 a	3.3 ± 0.7 b	2.4 ± 0.6 b	10.1
4 h	7.5 ± 1 a	3.3 ± 0.7 b	2.5 ± 0.5 b	11.39
6 h	7.8 ± 1.1 a	3.4 ± 0.6 b	2.7 ± 0.5 b	12.1
12 h	7.6 ± 1.2 a	3.1 ± 0.6 b	2.8 ± 0.4 b	10.1
24 h	7.5 ± 0.1 a	3.4 ± 0.8 b	3 ± 0.4 b	12.5
48 h	7.6 ± 1.1 a	3 ± 0.9 b	2.9 ± 0.5 b	11.8

*Kruskal-Wallis H-test

**Means followed by different letter in a row are significantly different (P < 0.01, Bonferroni correction after Kruskal-Wallis)

[DOR: 20.1001.1.22519041.2013.2.1.6.4]

Life table study

Nymph developmental time and survivorship

Total pre-oviposition period (mean number of days from birth to first reproduction) of *S. maydis* was not significantly different among the tested cultivars (One-way ANOVA, $F_{2, 87} = 0.54$; $P = 0.57$). Although shortest developmental time was observed on Ghuds, it was not significantly shorter than that on other cultivars (Table 2). The lowest nymph survival rate (l_x) was obtained on Falat (96%) and the highest nymph survival rate was observed on Ghuds and Pishtaz (99% and 100%, respectively, Figure 3).

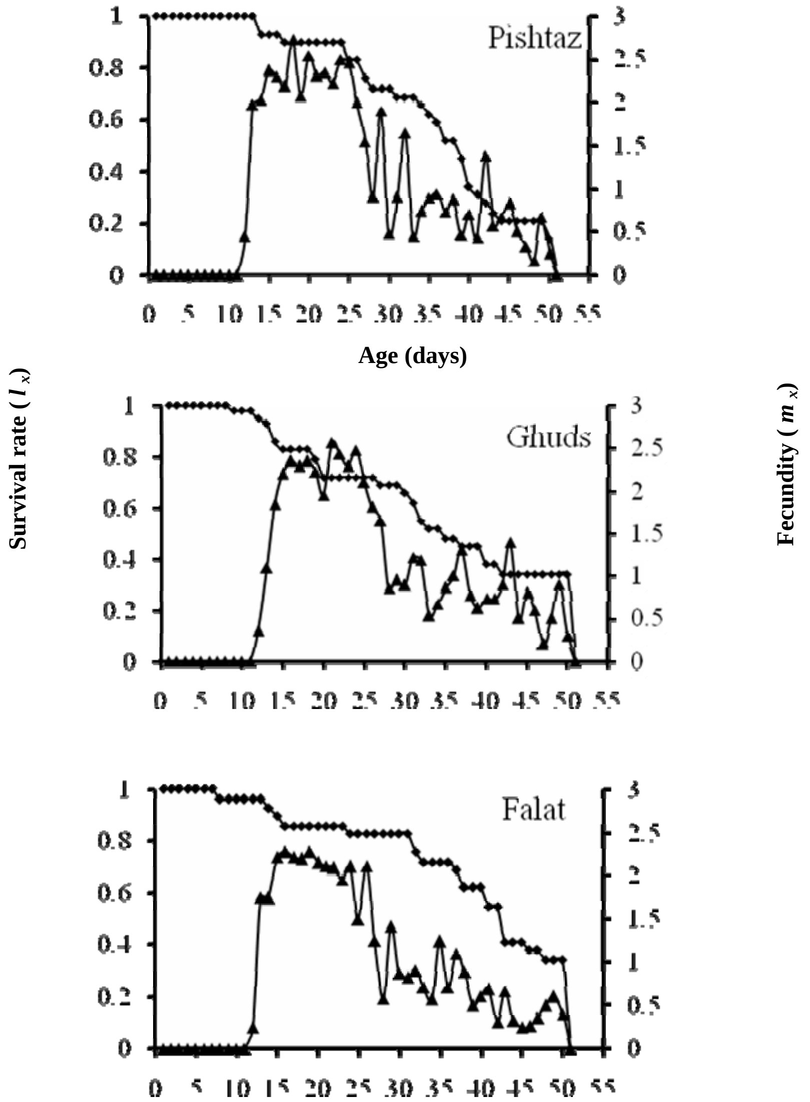

Figure 3 Survival rate (l_x) and fecundity (m_x) of *Sipha maydis* on three wheat cultivars under greenhouse conditions.

Table 2 Life-table parameters (Mean ± SE) of *Sipha maydis* on three cultivars of wheat in the life table test (n = 30).

Parameters	Wheat cultivars		
Adult longevity	**Pishtaz**	**Ghuds**	**Falat**
Total nymph produced per adult aphid	23.36 ± 2.11 **	25.83 ± 2.43 a	22.33 ± 2.75 a
Nymph development time	38.43 ± 3.51 a	36.83 ± 3.56 a	30.06 ± 2.13 a
r_m*	10.66 ± 0.09 a	10.13 ± 0.52 a	10.42 ± 0.38 a
R_0	0.187 ± 0.004 a	0.179 ± 0.005 a	0.170 ± 0.003 a
λ	38.04 ± 2.42 a	37.26 ± 3.68 a	30.85 ± 2.11 a
T	1.22 ± 0.09 a	1.19 ± 0.17 a	1.17 ± 0.12 a
DT	19.45 ± 0.45 a	20.18 ± 0.38 a	20.07 ± 0.33 a
Adult longevity	3.71 ± 0.11 a	3.91 ± 0.27 a	3.98 ± 0.14 a

*r_m, intrinsic rate of increase; R_0, net reproduction rate; λ, finite rate of increase; T, mean generation time (days); DT, doubling time (days)

**Means followed by the same letter in a row are not significantly different (P < 0.01, LSD)

Aphid adult longevity and reproductive ability

No significant difference was found in longevity of adult aphids among wheat cultivars (Table 2, One-way ANOVA, $F_{2,87}$ = 0.37; P = 0.66). Similar results were obtained for total number of offsprings per female aphid among the examined cultivars (One-way ANOVA, $F_{2,87}$ = 0.98; P = 0.39). The total number of offspring per female was the lowest on Falat but it was not significantly lower than that on the other cultivars (Table 2). The number of offsprings per female per day also showed no significant differences (One-way ANOVA, $F_{2, 87}$ = 0.18; P = 0.82, Figure 3).

Life table parameter

Age specific life table parameters of *S. maydis* on three wheat cultivars are presented in Table 2.

No significant differences were observed for net reproductive rate (R_0) (One-way ANOVA, $F_{2, 87}$ = 1.31; P = 0.27); mean generation times (T) (One-way ANOVA, $F_{2, 87}$ = 0.13; P = 0.88); doubling time (DT) (One-way ANOVA, $F_{2, 87}$ = 0.53; P = 0.58) and finite rate of increase (λ) (One-way ANOVA, $F_{2, 87}$ = 0.35; P = 0.71) of aphids among wheat cultivars. The intrinsic rate of natural increase (r_m) values of the aphids, in three studied cultivars (Pishtaz, Ghuds and Falat) were 0.187, 0.179 and 0.170/day, respectively. Statistical analysis showed that there was no significant difference in calculated r_m on wheat cultivars (One-way ANOVA, $F_{2, 87}$ = 0.45; P = 0.6).

Discussion

This study demonstrates considerable variability in the density of trichomes on the leaf surfaces of three wheat cultivars. The number of trichomes per mm^2 of leaf ranged from 14.4 ± 0.7 on Falat to 41.6 ± 1.43 on Pishtaz. This finding is in accordance with that of Webster *et al.* (1994) who reported 13.5 ± 3.8 to 53.3 ± 3.7 trichomes per mm^2 on the leaves of wheat lines and cultivars including PI 452264, PI 452262, CI9321, PI 452265, PI 452263, Downy, Abe and Fletcher. In addition, a range of trichome numbers per mm^2 on the leaves of wheat varieties reported by Hoxie *et al.* (1975) is compatible with our results.

Sipha maydis preference response to changing trichome density differed on the wheat cultivars. Contrary to expectation, aphid preference was positively correlated with trichome density, and hairy-leaf cultivar (Pishtaz) was significantly more preferred selected by aphids in the preference experiments. This is in agreement with the results reported by other authors for the preference of greenbug aphid, *S. graminum* on the pubescent wheat cultivars (Starks and Merkl, 1977). Similarly, Harvey *et al.* (1990)

[DOR: 20.1001.1.22519041.2013.2.1.6.4]

found that the landing efficiency of *Eriophyes tuliae* Keifer (Acari: Eriophyidae) positively increased on hairy-leaf cultivars of wheat. However, in contrast to our finding, there is considerable evidence to suggest that attraction and establishment of some wheat pests is negatively influenced by pubescent wheat cultivars (Roberts and Foster, 1983; Webster *et al.,* 1994). Therefore, probably less host acceptance of *S. maydis* on hairless-leaf wheat cultivar in the present study could be attributed to other morphological factors (e.g. quantity of epicuticular wax on leaf surface), (Weibel and Starks, 1986) and/or deterrent chemical profiles in tested cultivars (e.g. dihydroxyphenols) (Leszczynski *et al.,* 1995) which should be investigated further.

In the current study, the results of life table experiment revealed that the biological parameters of *S. maydis* were not significantly different among the wheat cultivars. The aphids reared on Pishtaz had longer duration of juvenile stage (10.7 days) than that on other cultivars. A range of data obtained here on the nymph developmental time of *S. maydis* on wheat cultivars (10.1-10.7 days) were slightly longer than that of previously reported on barely, *H. vulgare* cv. Pampa, (9.4) by Ricci and Kahan, (2005).

Total fecundity (number of offspring per female) of *S. maydis* was the lowest on Falat in the present study (30.1). The values of this parameter on Falat were lower than those for *S. maydis* reared on barely (37.1) (Ricci and Kahan, 2005) and wheat (cv. Pishtaz) (44.82) (Tazerouni and Talebi, 2012). However, total fecundity of *S. maydis* on Pishtaz and Ghuds (38.5 and 36.8, respectively) were very close to that estimated for this aphid on barely (Ricci and Kahan 2005).

The r_m value of *S. maydis* estimated in this study ranged from 0.170 on Falat to 0.187 on Pishtaz. These values were lower than that calculated for this aphid on barley (0.198) (Ricci and Kahan, 2005). The higher r_m of *S. maydis* found here on Pishtaz (hairy-leaf cultivar) is contrary to expectation that enhanced trichome density on the leaf surfaces of wheat should result in decreased aphid performance. Nevertheless, positive correlations between trichome densities and herbivore fitness have been demonstrated in other plant-herbivore systems (Flint and Parks, 1990, Srinivasana and Uthamasa, 2005; Horgan *et al.,* 2007). The reasons why hairy leaf cultivar caused the higher performance of aphids in our study remains unknown. However, when insect herbivore overcome trichome defenses of host plant, particularly relative to antixenosis resistance, the trichomes may increase herbivore fitness by protection against both UV radiation and water stress (Ehleringer, 1984; Butter and Vir, 1989).

Interestingly, the r_m value of *S. maydis* on Falat (the cultivar with the lowest trichome density) was relatively lower than that on the other tested cultivars. Although we did not investigate the reasons for this occurrence, some authors, e.g. Thackray *et al.,* (1990), found that some defensive metabolites, such as hydroxamic acids, caused low performance of aphids on wheat. It has also been revealed that either the level of amino acids or nitrogen in the phloem sap of wheat can affect the life table parameters of wheat aphids (Kazemi and Van Emden, 1992; Telang *et al.,* 1999).

In conclusion, based on the lack of significant differences among the life table parameters of *S. maydis* on tested cultivars, leaf pubescence density is probably not playing a role in plant defense against this aphid in these cultivars. However, it is important to consider that performance indices such as r_m are merely a comparative figure estimated under optimum condition which is likely different from field conditions. Thus, it is necessary to assess *S. maydis* population growth rate and associated yield losses on tested cultivars in the field where several biotic and abiotic components of environment interact simultaneously. Moreover, since plant morphological characteristics could influence the efficiency and behavior of natural enemies, further studies are planned to investigate the potential of using these cultivars integration with biocontrol agents, especially for the dominant native predatory bug, *Orius* *albidipennis* (Reuter) (Hemiptera: Anthocoridae), in IPM of *S. maydis*.

Acknowledgement

Ferdowsi University of Mashhad (Iran) and Iranian National Institute of Elites grant (No. 5/3521) to MH funded this research.

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آیا انبوهی تریکوم برگ گندم بر انتخاب میزبان و آماره های جدول زیستی شته‌ی *Sipha maydis* (Hemiptera: Aphididae) تأثیر دارد؟

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چکیده: تأثیر انبوهی تریکوم برگ بر مقاومت سه رقم گندم پیشتاز، قدس و فلات نسبت به شته‌ی Sipha maydis در مرحله‌ی پنج برگی گندم و تحت شرایط گلخانه‌ای (دمای ۲ ± ۲۵ درجه‌ی سلسیوس، رطوبت نسبی ۱۰ ± ۷۰ درصد و دوره‌ی روشنایی به تاریکی ۱۴:۱۰) مورد بررسی قرار گرفت. نتایج نشان داد که رقم پیشتاز نسبت به دیگر ارقام دارای انبوهی تریکوم بیش‌تر بود. در آزمون رجحان انتخابی با گیاه کامل، تعداد شته‌ها ۴۸ ساعت پس از شروع آزمون روی رقم پیشتاز به‌طور معنی‌دار بیش‌تر از دو رقم دیگر بود. به‌طور مشابه، در آزمون رجحان انتخابی دیسک برگی، تعداد شته-های جذب شده به برگ رقم پیشتاز بیش‌تر بود. مطالعه‌ی پارامترهای جدول زیست-باروری نشان داد که نرخ ذاتی افزایش جمعیت (r_m) شته جو بین ارقام مورد مطالعه تفاوت معنی‌دار نداشت. اما مقدار (r_m) شته جو روی رقم پیشتاز بیش ترین بود (۰/۱۸۷ / روز). نرخ خالص تولیدمثل، زمان دو برابر شدن جمعیت، متوسط طول یک نسل و نرخ متناهی افزایش جمعیت شته بین ارقام تفاوت معنی‌دار نشان نداد. بر اساس نتایج به‌دست آمده، انبوهی تریکوم برگ در ارقام گندم مورد مطالعه عامل مؤثری در مقاومت نسبت به شته‌ی S. maydis نبود.

واژگان کلیدی: تریکوم، Sipha maydi ، مقاومت گیاه، ارقام گندم