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Physiological responses of resistant and susceptible barley, *Hordeum vulgare* to the Russian wheat aphid, *Diurpahis noxia* (Mordvilko)

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ORIGINAL PAPER

Physiological responses of resistant and susceptible barley, *Hordeum vulgare* to the Russian wheat aphid, *Diurpahis noxia* (Mordvilko)

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Abstract Knowledge of the physiological responses of barley, *Hordeum vulgare* L., to the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae) is critical to understanding the defense response of barley to aphid injury and identifying resistance mechanisms. This study documented the impact of *D. noxia* feeding on resistant ('Sidney') and susceptible ('Otis') barley through chlorophyll fluorescence measurements, chlorophyll content, and carbon assimilation ($A–C_i$) curves recorded at 1, 3, 6, 10, and 13 days after aphid introduction. All chlorophyll fluorescence parameters evaluated were similar between aphid-infested and control plants for both cultivars. $A–C_i$ curves showed that *D. noxia* feeding negatively impacts the photosynthetic capacity in both cultivars, but this effect was greater in the susceptible plants. From the $A–C_i$ curves, it is apparent that compensation occurs in resistant barley by day 10, but by the conclusion of the experiment, aphid populations reached levels that overwhelmed the resistant barley seedlings. Differences observed in carbon assimilation curves between control and infested plants show that *D. noxia* feeding impacts the dark reaction, specifically rubisco activity and RuBP regeneration. It is likely that declines in the photochemical efficiency and chlorophyll content of the plants may be a secondary effect and not the primary trigger of declines in host plant function.

Keywords Plant physiology · Plant resistance · Plant–insect interactions · Gas exchange · Chlorophyll content · Chlorophyll fluorescence

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Introduction

Diuraphis noxia (Mordvilko) (Hemiptera: Aphididae) is a serious pest of wheat, *Triticum aestivum* L., and barley, *Hordeum vulgare* L. The original *D. noxia* biotype has cost American wheat and barley producers billions of dollars in losses since it first appeared in the United States in 1986 (Pons 2004). These aphids prefer to feed within the leaf whorl and on new leaves (Macedo et al. 2003), which are strong sinks for phloem-mobile mineral nutrients, amino compounds, and carbohydrates. Damage symptoms include chlorotic leaf streaking and leaf rolling (Burd and Burton 1992). Leaf rolling is doubly damaging to host plants as it reduces photosynthetic area and provides an optimum environment for aphid reproduction. Leaf rolling also plays an important role in the effectiveness of certain management strategies, as it prevents the contact of insecticides and biological control agents with the aphids.

Because of the limited effectiveness of chemical and biological control methods, plant resistance is viewed as a viable approach (Webster and Kenkel 1999). *Diuraphis noxia*-resistant sources of barley have been identified (Mornhinweg et al. 1995, 1999, 2006, 2007a, b, 2008), although little is known about the physiological mechanisms that confer resistance.

Understanding how aphid feeding affects plant physiology (e.g. photosynthetic rates and fluorescence parameters)

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may help to explain the physiological mechanisms underlying plant resistance. Considerable progress has been made toward identifying the physiological responses of resistant and susceptible wheat to *D. noxia* (Burd and Elliott 1996; Franzen et al. 2007; Haile et al. 1999; Heng-Moss et al. 2003; Macedo et al. 2009), however; only limited information is available on the responses of resistant and susceptible barley to aphid feeding (Burd and Elliott 1996; Miller et al. 1994). Research on the physiological responses of resistant and susceptible cereals has focused on several different areas including; chlorophyll and protein content, chlorophyll fluorescence, gas exchange, and molecular pathways.

Several studies have reported that resistant and susceptible plants exhibit differences in chlorophyll maintenance in response to *D. noxia* feeding. Susceptible plants experience alterations in chlorophyll content (Ni et al. 2002) such as chlorosis development, reductions in chlorophyll (*a* and *b*) and carotenoids, and changes in chlorophyll fluorescence (Burd and Elliott 1996; Franzen et al. 2007; Heng-Moss et al. 2003; Miller et al. 1994; Rafi et al. 1997). In contrast, resistant plants have been shown to exhibit minimal differences in chlorophyll maintenance in response to *D. noxia* feeding (Burd and Elliott 1996; Franzen et al. 2007; Miller et al. 1994).

Differences in chlorophyll fluorescence and photosynthesis also exist between resistant and susceptible cereals. Haile et al. (1999) found that *D. noxia*-infested resistant and susceptible wheat plants had reduced chlorophyll fluorescence and photosynthetic rates when compared to control plants. After the aphids were removed (7 days after aphid introduction), the tolerant cultivar showed a complete recovery of photosynthetic capacity by 7 days after aphid removal, while photosynthetic recovery was not observed in the susceptible or antibiotic cultivars. Macedo et al. (2003) also found that *D. noxia* feeding caused reductions in photosynthesis and chlorophyll fluorescence for susceptible wheat, but only under continuous light. Under 72 h of continuous dark, aphid feeding did not cause damage symptom formation or reductions in gas exchange. This work demonstrates that the development of *D. noxia* damage symptoms on susceptible wheat seedlings may be a light-activated process even though the origin of the damage symptoms is aphid feeding.

Miller et al. (1994) used barley to examine chlorophyll fluorescence and stomatal resistance in response to *D. noxia* feeding. No significant differences were observed in the effectiveness of photosystem II between infested-resistant and -susceptible barley genotypes. *Diuraphis noxia* feeding did lead to closure of the stomates, but no differences were detected in stomatal closure between resistant and susceptible plants. Burd and Elliott (1996) examined chlorophyll fluorescence changes in resistant and susceptible wheat and barley in response to *D. noxia* infestation. In contrast, Miller et al. (1994) and Burd and Elliott (1996) found that photochemical efficiency was significantly decreased in the infested susceptible wheat and barley plants. However, declines were not observed in the resistant infested plants. Burd and Elliott (1996) concluded that wheat and barley exhibit similar responses to *D. noxia* feeding.

The most recent studies on the physiological responses of resistant and susceptible cereal to *D. noxia* were conducted by Franzen et al. (2007) and Macedo et al. (2009). Franzen et al. (2007) found that resistant wheat plants infested with *D. noxia* had photosynthetic rates similar to or greater than those of control plants, while susceptible-infested plants showed accelerated declines in photosynthesis. Measurements over time showed that infested-resistant plants had delays in photosynthetic senescence. Results from this study suggest that resistant plants subjected to *D. noxia* feeding compensated for aphid injury by altering their senescence pathways, while susceptible plants appeared to have accelerated senescence. Macedo et al. (2009) examined the impact of feeding injury by *D. noxia* and the non-symptomatic aphid, *Rhopalosiphum padi* on susceptible and resistant wheat. Photosynthetic measurements indicated that feeding by both *D. noxia* and *R. padi* caused reductions in photosynthetic activity and that these initial reductions are likely related to stomatal limitation or CO_2 uptake (Rafi et al. 1996 and Franzen et al. 2007).

The studies outlined have provided insights into differential responses between resistant and susceptible plants; however, relatively few studies have focused on how *D. noxia* feeding impacts the physiological responses of resistant and susceptible barley and the possible role of changes in photosynthesis and fluorescence as a mechanism for plant resistance. The objectives of this research were to document the physiological responses of resistant and susceptible barley to *D. noxia* over time and investigate photosynthetic processes as a mechanism for plant resistance to insect injury. The impact *D. noxia* had on resistant and susceptible plants was measured by examining number of aphids, chlorophyll content, photosynthetic responses, and chlorophyll fluorescence kinetics.

Materials and methods

Plant material and insects

Seeds of the susceptible barley cultivar 'Otis' and resistant cultivar 'Sidney' were planted in 'SC-10 Super Cell' Conetainers® (3.8 cm × 21 cm) (Stuewe & Sons, Inc. Corvallis, OR) containing a mixture of sand-soil-peat-perlite

(0.66:0.33:1:1). 'Sidney' (previously known as experimental line 98BX 28-58B) was developed through modified backcross breeding of Russian wheat aphid-resistant STARS 9301B into Otis. Three seeds of each cultivar were planted in a Cone-tainer® to a depth of approximately 2 cm and placed in Cone-tainer® racks. The Cone-tainer® racks were placed over a plastic tray (54 cm × 28 cm × 6 cm) filled with water to ensure that plants were watered uniformly from the bottom. Plants were grown to the four leaf stage (14 days) in a 36-m^2 greenhouse bay under 400-watt high intensity lamps with a 16:8 (L:D) h photoperiod, a temperature of 27 ± 3°C, and 40–50% relative humidity. Plants were thinned to one plant per Cone-tainer® once seedlings emerged from the soil.

Biotype 1 *D. noxia* were obtained from the United States Department of Agriculture-Agricultural Research Service research facility in Stillwater, OK. Aphids were maintained on susceptible 'Morex' barley and were kept in growth chambers (Percival Scientific, Perry, IA) at 21 ± 1°C, 40–50% RH, and a photoperiod of 16:8 (L:D) h.

The experiment utilized a completely randomized design with seven replications. The treatment design was a 2 × 2 × 5 factorial treatment design that included 2 barley cultivars, 2 aphid infestation levels (0 and 20 *D. noxia*), and 5 evaluation dates (1, 3, 6, 10, and 13 days after aphid introduction—rain delayed evaluation from 9 to 10 days). Barley plants were randomly designated to be a control plant or an infested plant. At the start of the experiment, ten aphids were introduced onto the first and second leaf blade (total of 20 aphids) of each designated infested plant. Aphids were confined to individual plants using tubular plexiglass cages (4 cm diameter × 30 cm height) with organdy fabric fastened by rubber bands to the top. Control plants were also caged. After aphid introduction, plants were kept in the greenhouse until each respective evaluation date.

Plants were evaluated for leaf chlorosis on each evaluation date using a 1–9 scale, where 1 = plants appear healthy and 9 = plant death or no recovery possible (Webster et al. 1991). The total number of *D. noxia* on infested plants was assessed through direct counting before aphid removal at each evaluation date.

Physiological responses of barley to *D. noxia*

Chlorophyll concentration

Chlorophyll levels were measured for each treatment from leaves of seven different plants (replicates) at 3 locations (near the base, the middle, and the tip of the leaf) on the first and second leaf blades at each evaluation interval using a chlorophyll meter (Model Spad-502, Minolta Camera Co., Osaka, Japan). The arithmetic mean of these measurements was used for all subsequent analyses.

Gas exchange responses

Photosynthetic responses were recorded at 3, 6, 10, and 13 days after aphid introduction (rain delayed evaluation from 9 to 10 days) using a portable photosynthesis system (model LI-6400, LI-COR, Lincoln, NE). Although plants were maintained in a greenhouse, measurements were performed o utdoors after plants had acclimatized for >1 h. Photosynthetic measurements included: assimilation rate (A) versus intercellular CO_2 concentration measurements ($A–C_i$ curves), where rates were measured at 1,400 µmol photons m^{-2} s^{-1} light intensity and CO_2 concentrations ranging from 50 to 1000 ppm. $A–C_i$ response curves were determined by the automated programs of the LI-6400.

Calculations of the stomatal and non-stomatal components of photosynthesis were made using the methods described by Farquhar and Sharkey (1982). By comparing A at a C_i of 400 µl l^{-1} CO_2 to A at the C_i corresponding to an intracellular CO_2 (C_a) of 400 µl l^{-1} CO_2, the stomatal limitation (SL) to photosynthesis can be calculated (Ryan et al. 1987).

The A versus C_i response curve can also be used to determine the CO_2 compensation point (the C_i value where A = 0, given in Pa), carboxylation efficiency (CE, the slope of the linear portion of the A versus C_i response curve), and changes in net CO_2 assimilation at saturating C_i (A_{max}). Analyses of the $A–C_i$ curves also allow for determination of maximum carboxylation velocity of rubisco (V_{cmax}—determined from the linear portion of the curve, µmol CO_2 m^{-2} s^{-1}) and maximum potential rate of electron transport contributing to ribulose-1,5-bisphosphate (RuBP) regeneration (J_{max}—µmol electrons m^{-2} s^{-1}). These values were calculated using the Photosyn Assistant Software (Dundee Scientific, Scotland, UK). For each treatment, response curves from leaves of three different plants (replications) were measured and estimated for SL, CE, CO_2 compensation point, A_{max}, V_{cmax}, and J_{max}.

Chlorophyll fluorescence

Chlorophyll fluorescence was measured at 1, 3, 6, and 10 days after aphid introduction (rain delayed evaluation from 9 to 10 days) using an OS5-FL modulated chlorophyll fluorometer (Opti-Sciences, Tyngsboro, MA). Leaves were dark adapted with clips for at least 30 min before measurements. Determinations were made of minimum fluorescence for dark-adapted leaves (F_o), maximum fluorescence for dark-adapted leaves (F_m), fluorescence under steady state conditions (F_s), maximal fluorescence under steady state conditions (F_{ms}), quantum yield ($Y = (F_{ms} - F_s)/F_{ms}$), photochemical quenching ($qP = (F_{ms} - F_s)/(F_{ms} - F_o)$), and non-photochemical quenching ($qN = (F_m - F_{ms})/(F_m - F_o)$) (see OS5-FL Manual for

additional details). For each treatment, fluorescence parameters from leaves of six different plants (replicates) were measured.

Data analysis

Mixed model analysis (PROC MIXED, SAS Institute 2002) was conducted for each measurement to detect differences in aphid number, chlorophyll levels, gas-exchange responses, and chlorophyll fluorescence measurements. When appropriate, the means were separated according to Fisher least significant difference (LSD) procedure. Statistical significance was assumed when $P \leq 0.05$.

Results and discussion

Leaf chlorosis

Aphid-infested susceptible and resistant plants showed limited visual damage at 1, 3, and 6 days after aphid introduction (data not shown). On days 10 and 13, infested plants of both cultivars (day 10: Susceptible = 2.1 ± 0.22, Resistant = 2.1 ± 0.36; day 13: Susceptible = 5.7 ± 0.32, Resistant = 4.6 ± 0.27) had significantly higher damage ratings than their respective control plants (day 10: Susceptible = 1.0 ± 0, Resistant = 1.0 ± 0; day 13: Susceptible = 1.0 ± 0, Resistant = 1.0 ± 0) ($F = 28.9$, df = 4, 120; $P = 0.0001$). There were no significant differences in visual damage between infested-resistant and -susceptible plants at 1, 3, 6, and 10 days (data not shown).

Aphid number

No significant differences were detected in numbers of aphids between the two barley cultivars at 1, 3, 6, 10, and 13 days after aphid introduction ($F = 0.4$; df = 2, 60; $P = 0.81$) (data not shown). The greatest number of aphids was recorded on the susceptible barley, Otis. The resistant cultivar, Sidney, supported numbers of aphids similar to the susceptible barley throughout the experiment, demonstrating that the resistant genotype was not adversely affecting the biology of the aphids.

Chlorophyll concentration

Aphid-infested resistant and susceptible plants (first leaf blade) had similar chlorophyll concentrations to control plants on all evaluation dates (data not shown). At days 1, 6, and 10, aphid infested-resistant and -susceptible plants (second leaf blade) had chlorophyll levels similar to those of their respective control plants (data not shown). However, on day 13 aphid infested-resistant (165.5 ± 14.6) and -susceptible plants (136.0 ± 21.5) had significantly lower chlorophyll levels when compared to their respective control plants (Resistant: 249.9 ± 31.9; Susceptible: 260.7 ± 13.8) (Resistant: $t = 2.3$; df = 120; $P = 0.02$; Susceptible: $t = 3.5$; df = 120; $P = 0.0008$). Interestingly, on day 3 the infested-resistant plants (171.0 ± 32.1) had a significantly lower chlorophyll concentration than resistant-control plants (318.4 ± 17.6) ($t = 4.1$; df = 120; $P = 0.0001$). For all evaluation dates evaluated, there were no significant differences between resistant- and susceptible-infested plants in the chlorophyll concentrations of the second leaf blade.

Photosynthetic responses

A_{max}

Susceptible plants infested with *D. noxia* exhibited declining A_{max} values over the course of the experiment with infested plants having lower values when compared to control plants (Figs. 1, 2, 3, and 4). Aphid-infested resistant plants had similar A_{max} values when compared to control plants at days 3, 6, and 10 (Figs 1, 2, and 3), but by day 13 resistant-infested plants had A_{max} values lower than those of control plants (Fig. 4). This research indicates that *D. noxia* feeding in the susceptible barley is associated with inhibiting the plants' ability to reach its maximum photosynthetic capacity.

Stomatal limitation

There was a significant aphid effect ($F = 4.5$; df = 1, 30; $P = 0.04$), however, stomatal limitation values between aphid treatments of interest were either not significantly different or did not follow an apparent trend (data not shown).

Carboxylation efficiency

At 3 days after aphid introduction similar declines in CE were documented in the aphid-infested plants of both barley genotypes (Table 1). For the susceptible barley on day 6, CE values of infested plants were similar to control plants (Fig. 2), but by day 10 CE values for the aphid-infested treatment experienced an almost 2 fold decline when compared to control plants (Fig. 3). Conversely, in the resistant barley, CE values of infested plants were slightly lower compared to those of control plants on day 6 (Fig. 2), but by day 10 CE values were similar (Fig. 3). Aphid infestation resulted in lower CE values for resistant

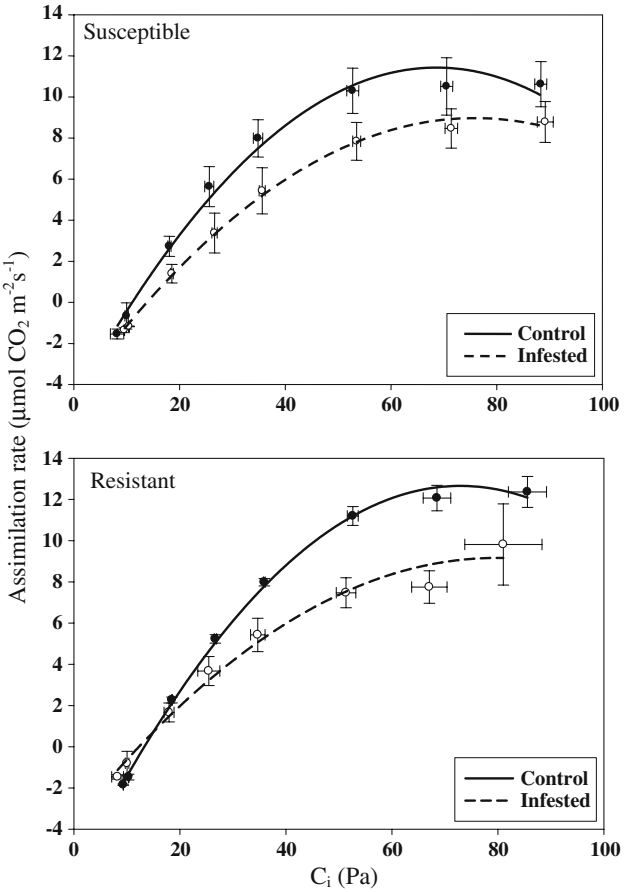

Fig. 1 Assimilation (µmol CO_2 m^{-2} s^{-1}) versus intercellular CO_2 concentration (Ci) in pascals (Pa) for susceptible and resistant barley at 3 days after aphid introduction

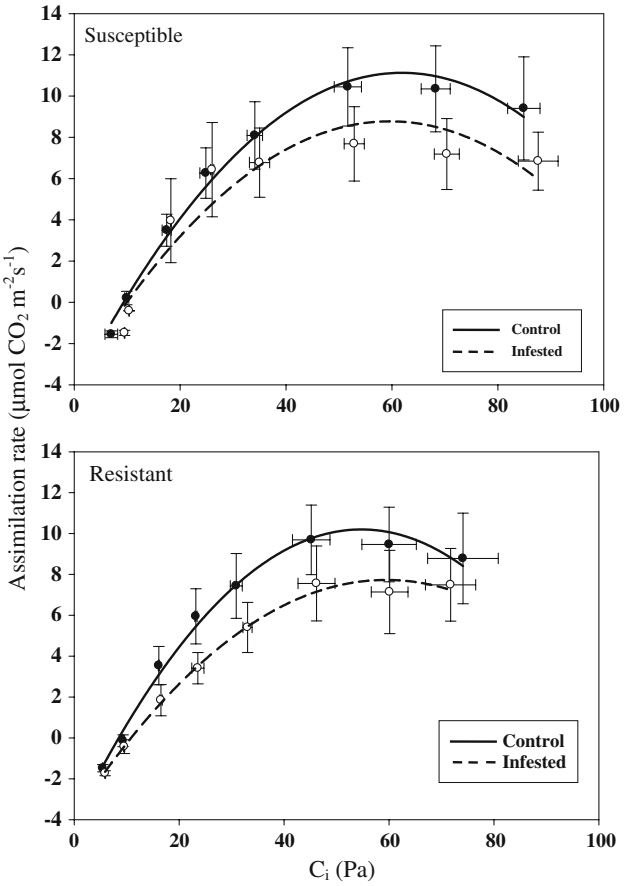

Fig. 2 Assimilation (µmol CO_2 m^{-2} s^{-1}) versus intercellular CO_2 concentration (Ci) in pascals (Pa) for susceptible and resistant barley at 6 days after aphid introduction

and susceptible plants on day 13, although susceptible plants experienced a more dramatic decline (Fig. 4).

CO_2 compensation point

There was a significant aphid effect ($F = 12.98$; df = 1, 30; $P < 0.001$) which showed that, across days, control plants had lower compensation points than *D. noxia*-infested plants. Infested plants of both cultivars showed CO_2 compensation points similar to those of their respective controls at 3, 6, and 10 days after aphid introduction (Figs. 1, 2, and 3). On day 13, aphid infested-resistant and -susceptible plants had significantly higher CO_2 compensation points when compared to their respective control plants (Resistant: t = −5.0; df = 32; $P = 0.001$, Susceptible: t = −2.0; df = 32; $P = 0.05$) (Fig. 4). Because the CO_2 compensation point represents the level at which oxygen production is zero, plants with lower CO_2 compensation points are able to produce oxygen at lower levels of carbon dioxide and, therefore, lower values are expected for the control plants.

V_{cmax}

Infested plants of both cultivars showed declines in V_{cmax} on days 3 and 6 when compared to their respective control plants (Table 1). At day 10 susceptible infested plants showed an almost 2 fold decline in V_{cmax} values when compared to control plants. Conversely, resistant infested plants had V_{cmax} values similar to those of their control plants on day 10. By 13 days after aphid introduction V_{cmax} values for infested plants were significantly lower than the control plants for both cultivars ($F = 31.9$; df = 1, 30; $P = 0.0001$) (Table 1). The difference in the responses of the two barley genotypes on day 10 indicates that the plant's ability to reach its maximum rate of rubisco-mediated carboxylation may be a key part of the resistance response.

J_{max}

Susceptible plants infested with *D. noxia* had declining J_{max} values over the course of the experiment, with infested plants having lower values when compared to control

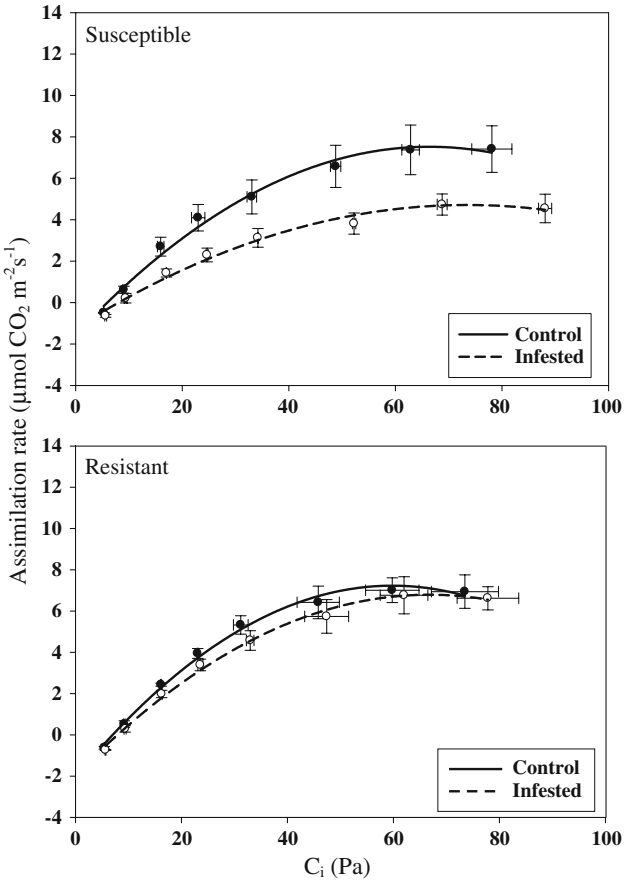

Fig. 3 Assimilation (μmol CO_2 m^{-2} s^{-1}) versus intercellular CO_2 concentration (Ci) in pascals (Pa) for susceptible and resistant barley at 10 days after aphid introduction

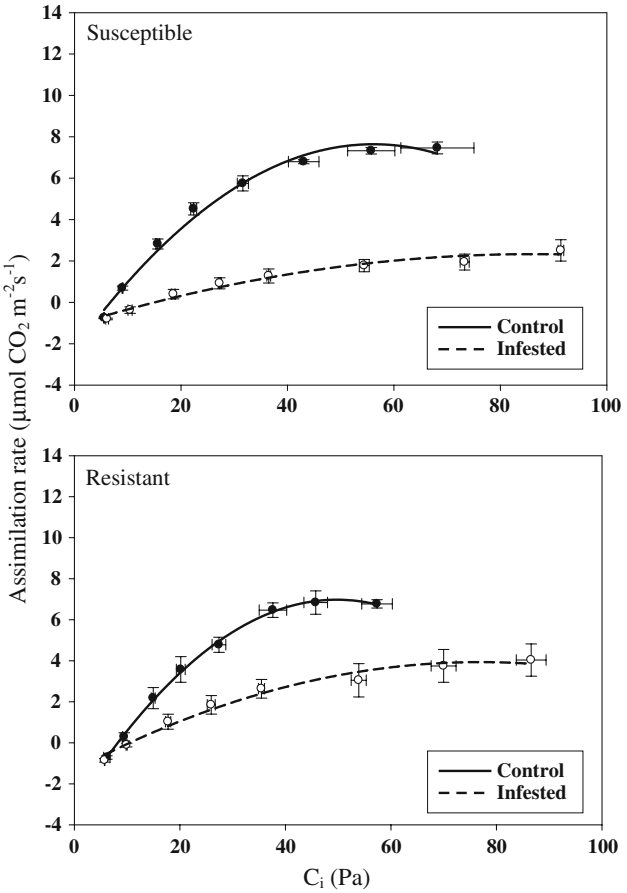

Fig. 4 Assimilation (μmol CO_2 m^{-2} s^{-1}) versus intercellular CO_2 concentration (Ci) in pascals (Pa) for susceptible and resistant barley at 13 days after aphid introduction

Table 1 Effect of *D. noxia* on gas-exchange responses of resistant and susceptible barley at 3, 6, 10, and 13 days

Mean ± SE

	CE[a]			V_{cmax}[b]			J_{max}[c]		
	Control	RWA	*P* value	Control	RWA	*P* value	Control	RWA	*P* value
Day 3									
Susceptible	0.41 ± 0.06	0.28 ± 0.08	0.11	30.7 ± 3.47	24.1 ± 3.66	0.25	71.9 ± 9.58	60.3 ± 6.76	0.16
Resistant	0.41 ± 0.08	0.30 ± 0.04	0.16	33.4 ± 0.71	22.2 ± 2.09	0.06	85.1 ± 3.70	58.2 ± 4.84	0.002
Day 6									
Susceptible	0.43 ± 0.08	0.47 ± 0.13	0.67	49.4 ± 6.76	42.9 ± 19.2	0.31	67.6 ± 8.18	50.4 ± 0.50	0.06
Resistant	0.41 ± 0.07	0.30 ± 0.06	0.17	39.1 ± 2.24	33.4 ± 3.97	0.33	58.1 ± 5.23	47.9 ± 7.92	0.21
Day 10									
Susceptible	0.27 ± 0.05	0.15 ± 0.09	0.14	21.3 ± 5.13	12.2 ± 3.86	0.12	39.3 ± 7.88	25.0 ± 6.95	0.09
Resistant	0.25 ± 0.02	0.23 ± 0.02	0.80	20.4 ± 3.70	17.0 ± 1.71	0.56	39.2 ± 2.64	37.1 ± 3.11	0.80
Day 13									
Susceptible	0.29 ± 0.03	0.08 ± 0.01	0.01	22.6 ± 1.64	6.1 ± 0.89	0.007	42.8 ± 0.32	17.1 ± 2.70	0.003
Resistant	0.27 ± 0.01	0.13 ± 0.03	0.09	22.7 ± 1.44	9.8 ± 1.83	0.03	42.9 ± 2.89	22.7 ± 4.16	0.02

[a] *CE* Carboxylation efficiency

[b] V_{cmax} Maximum Rubisco-mediated carboxylation (μmol CO_2 m^{-2} s^{-1})

[c] J_{max} Maximum potential rate of electron transport contributing to RuBP regeneration (μmol electron m^{-2} s^{-1})

plants (Table 1). Aphid-infested resistant plants had significantly lower J_{max} values when compared to control plants at days 3 and 6 (Figs. 1 and 2), but by day 10 resistant infested plants had J_{max} values similar to those of control plants ($F = 30.4$; df $= 1, 30$; $P < 0.0001$) (Table 1 and Fig. 3). By day 13 both cultivars showed declines J_{max} in response to intense aphid pressure (Fig. 4). These results suggest that the tolerance response of the resistant barley may be dependent on alteration of the rate at which RuBP becomes available.

Chlorophyll fluorescence response

In general, the non-variable minimal fluorescence (F_o), the maximal fluorescence (F_m), the total amount of variable fluorescence (F_v), and the photochemical efficiency of PSII (F_v/F_m) ratios of both cultivars were not significantly impacted by aphids (data not shown). Similarities in the chlorophyll fluorescence response values among aphid treatments strongly suggests that aphid feeding was not associated with photoinhibitory damage in the PSII reaction centers.

Infested-susceptible plants had Y values similar to those of control plants on days 1, 3, and 6, but by day 10, Y values were lower than control plants (Infested: 0.08 ± 0.03; Control: 0.21 ± 0.02). Over the course of the experiment, infested-resistant plants had Y values similar to control plants. Y is a good indication of how efficiently absorbed photons are converted into chemical products (Malkin and Niyogi 2000). Our results show that aphid feeding may play a role in the efficiency of converting photons to chemical products in the susceptible barley.

There was a significant aphid by day interaction for the photochemical fluorescence quenching (qP) ($F = 4.2$; df $= 3, 48$; $P = 0.001$) and non-photochemcial fluorescence quenching (qN) ($F = 2.7$; df $= 3, 48$; $P = 0.05$) (Table 2). However, quenching coefficient values between aphid treatments of interest were either not significantly different or did not follow an apparent trend.

Similar to those of Macedo et al. (2009), Franzen et al. (2007), and Macedo et al. (2003), our findings provide further evidence that chlorophyll may not be directly impacted by aphid injury, but rather that the carbon fixation reactions of photosynthesis may be more immediately impacted.

Integrated responses

Over the course of the experiment there was a decline in photosynthetic capacity for both barley genotypes. On days 3 and 6, resistant and susceptible plants experienced similar declines in photosynthesis in response to *D. noxia* feeding (Figs. 1 and 2). However on day 10, resistant and susceptible plants appeared to respond differently to *D. noxia* feeding (Fig. 3). At 10 days after aphid introduction resistant plants exhibited photosynthetic rates similar to those of control plants. In contrast, susceptible-infested plants had photosynthetic rates significantly lower than those of control plants. Differences observed in carbon assimilation curves and gas-exchange parameters,

Table 2 Mean ± SE of chlorophyll fluorescence responses of resistant and susceptible barley at 1, 3, 6, and 10 days after exposure to *D. noxia*

Mean ± SE						
	qP[a]			qN[b]		
	Control	RWA	*P* value	Control	RWA	*P* value
Day 1						
Susceptible	0.78 ± 0.05	1.22 ± 0.10	0.006	0.30 ± 0.08	0.41 ± 0.05	0.09
Resistant	0.76 ± 0.03	0.58 ± 0.26	0.25	0.82 ± 0.05	0.31 ± 0.07	0.0003
Day 3						
Susceptible	1.21 ± 0.04	0.91 ± 0.06	0.03	0.36 ± 0.04	0.30 ± 0.07	0.41
Resistant	1.05 ± 0.06	1.45 ± 0.04	0.004	0.40 ± 0.03	0.36 ± 0.06	0.50
Day 6						
Susceptible	0.98 ± 0.06	0.97 ± 0.04	0.93	0.45 ± 0.04	0.47 ± 0.08	0.74
Resistant	0.88 ± 0.07	1.40 ± 0.07	0.001	0.49 ± 0.03	0.45 ± 0.09	0.53
Day 10						
Susceptible	0.93 ± 0.09	0.72 ± 0.17	0.13	0.33 ± 0.02	0.27 ± 0.07	0.45
Resistant	0.54 ± 0.03	0.92 ± 0.16	0.01	0.07 ± 0.06	0.27 ± 0.08	0.001

[a] *qP* Photochemical quenching $(F_m - F_s)/(F_{ms} - F_o)$

[b] *qN* Non-photochemical quenching $(F_m - F_{ms})/(F_m - F_o)$

specifically, J_{max}, A_{max}, V_{cmax}, and CE, between control and infested plants show that *D. noxia* feeding negatively impacts the carbon-linked/dark reactions, specifically rubisco activity and RuBP regeneration, in susceptible barley. These reductions are consistent with photosynthetic reductions resulting from limitation in fixation.

The ability of the resistant-infested plants to compensate for aphid pressure and maintain levels of photosynthesis similar to control plants may be attributed to the resistant plant's ability to maintain normal levels of RuBP regeneration and rubisco carboxylation. However, by 13 days after aphid introduction, infested plants of both barley cultivars had photosynthetic rates significantly lower than those of controls (Fig. 4). By this point in the experiment aphid populations reached levels that overwhelmed the barley seedlings. Photosynthetic rates also declined for control plants by 13 days after aphid introduction (Fig. 4). This decline is likely due to senescence of the measured leaf blade over time.

Results documented in this study compare favorably with those of Franzen et al. (2007). Analysis of the A–C_i curves from Franzen et al. (2007) and this study suggests that an increase in rubisco carboxylation and RuBP regeneration in the resistant plants is the source of photosynthetic compensation. This study also demonstrates that short-term changes in photosynthetic compensation can be used to differentiate between resistant and susceptible genotypes. Additional studies are needed to determine the degree to which photosystems I and II are affected by aphid injury and the role of photosynthetic compensation in the tolerant barley.

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