Photosynthesis in Wheat at the Grain Filling Stage Is Altered by Larval Wheat Stem Sawfly (Hymenoptera: Cephidae) Injury and Reduced Water Availability[1]

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Abstract The impact of larval feeding by wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), and reduced water availability on the photosynthesis and primary metabolism of wheat, *Triticum aestivum* (L.), was evaluated at the grain-filling developmental stage. Photosynthetic parameters measured included photosynthesis (*Ps*), stomatal conductance (g_s), and transpiration (E) in the flag leaves. The parameters were measured at 4 wks after the treatments were imposed. Additional concomitant chlorophyll *a* fluorescence measurements were taken using both dark- and light-adapted tests. Photosynthesis was significantly affected by *C. cinctus* injury and suboptimal water availability. However, no significant interaction was observed between the two treatment factors. Plants under a reduced or suboptimal watering regime had *Ps* rates that were 43.7% lower than plants that were watered daily. We also observed a 12% higher *Ps* rate in uninfested plants compared to plants infested by *C. cinctus*. Several chlorophyll *a* fluorescence parameters also were affected by *C. cinctus*. Specifically, reductions in the photochemical efficiency of photosystem II (PSII) of *C. cinctus* infested plants were observed for plants under reduced water availability. This study demonstrates that wheat plants at the grain filling stage have reduced photosynthetic capacity when watered less frequently or when subjected to *C. cinctus* larval feeding injury. Less frequent watering and larval feeding injury did not have significant impacts on yield in this greenhouse study.

Key Words *Triticum aestivum, Cephus cinctus*, herbivory, photosynthesis, ecophysiology

The wheat stem sawfly, *Cephus cinctus* Norton, is one of the most important insect pests of dryland wheat, *Triticum aestivum* L., in the Prairie Provinces of Canada and in the northern Great Plains of the US (Weiss and Morrill 1992, Morrill et al. 2001). Injury by *C. cinctus* can cause considerable economic loss, with losses in Montana totaling $25 million per year (Montana State Univ. Ext. Serv. 1997).

Adults of *C. cinctus* emerge in late spring or early summer and oviposit in the stem lumen of developing wheat plants (Criddle 1915, 1923, Wallace and McNeal 1966, Weiss et al. 1990, Weiss and Morrill 1992, Morrill and Kushnak 1996). Oviposition by *C. cinctus* occurs at wheat stem elongation, between developmental stages 32 and 69 on the Zadoks decimal scale (Zadoks et al. 1974). Neonate larvae initially feed on parenchyma tissue surrounding the oviposition site (Holmes 1954). Developing larvae feed throughout the stem lumen, and the stem nodes are injured by feeding. The possible disruption of vascular tissues, which are constricted at the nodes, may cause

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an accumulation of material that appears as darkened areas below nodes (Morrill et al. 1992).

Despite the well-known biology and economic importance of this insect pest in wheat production, comparatively little is known about the effect of *C. cinctus* injury on physiological components underlying wheat yield (Macedo et al. 2005). Most studies have evaluated host quality, morphological, and yield components of wheat, but photosynthetic responses have not been extensively studied (Seamans et al. 1938, Platt 1941, Munro 1945, Farstad and Platt 1946, Platt and Farstad 1946, Munro et al. 1947, Platt et al. 1948, McNeal et al. 1955, Macedo et al. 2005). Photosynthesis and the closely-associated processes of water-vapor transfer and respiration are the primary processes determining plant growth, development, and, ultimately, yield. Therefore, it is important to understand how insect injury influences these parameters (Peterson and Higley 1993). Heichel and Turner (1973) and Madden (1977) suggested that the type of injury imposed by insects like *C. cinctus* (i.e., stem boring) might impair photosynthetic capacity mainly because of injury to vascular tissue. Godfrey et al. (1991) observed photosynthetic reductions of about 10-20% associated with larval stem boring by European corn borer, *Ostrinia nubilalis* (Hübner), in corn, *Zea mays* (L.). They concluded that alterations of source-sink relationships may be related to these reductions.

Reduced or suboptimal water availability might affect plant response to injury by herbivorous insects by altering the compensatory ability of plants during and after injury. Dunn and Frommelt (1998) suggested that water limitation plays an important role in carbon allocation patterns of plants coping with herbivory. Haile et al. (1998a, b) demonstrated that in nonwater stressed soybean, herbivory had no negative impact on yield. However, significant reductions in yield were observed when water availability was suboptimal. A combination of factors such as the reallocation of resources to new leaves during regrowth and delayed maturity of defoliated plants contributed to offset the impact of defoliation.

Macedo et al. (2005) found that *C. cinctus* injury did not impair photosynthesis of wheat in two greenhouse experiments and one field study. However, photosynthesis was impaired in an environmental chamber experiment. Consequently, Macedo et al. (2005) hypothesized that environmental interactions, such as light quality and/or plant-water availability, may be responsible for impairment of photosynthesis. Therefore, the objective of this study was to characterize the impact of injury by wheat stem sawfly, *C. cinctus,* and its interactions with suboptimal water availability on wheat leaf gas exchange under controlled conditions.

Materials and Methods

Experiments were conducted during 2005 in greenhouses at the Montana State University Plant Growth Center, Bozeman, MT. The spring wheat variety, 'Reeder', was grown in 10.15-cm pots in a mixture of 'Sunshine' soil mix and sand mix (1:1 ratio) in a greenhouse bay (32 m^2). Plants were watered regularly and fertilized twice per week with a 100 ppm N-P-K mix (Peters 20-20-20 General, Scotts-Sierra Hort. Prod. Company, Marysville, OH). Plants were maintained in the greenhouse bay at 21 ± 1°C, on a photoperiod of 14:10 (L:D) h, and at 40-50% RH for the duration of the study. The light intensity in the greenhouse was supplemented with GE MultiVapor Lamps (MVR1000/C/U, GE Lighting, General Electric Co., Cleveland, OH).

The experimental design consisted of a 2 × 2 factorial (2 infestation levels × 2 watering regimes) in a randomized complete block design (RCBD) with 6 replications per treatment. Treatments were: 2 infestation levels, infested and uninfested (control); and, suboptimal water availability regimen (i.e., irrigation 2× per week) and optimal water availability (i.e., irrigation every day). To infest plants, 3 male and 6 female *C. cinctus* adults were placed in small Plexiglas (United States Plastic Corp., Lima, OH) cages (4 × 60 cm), each containing the main stem of a wheat plant at developmental stage 32-33 (Zadoks et al. 1974). Insects were allowed to mate and oviposit freely for a period of 7 d, after which cages were removed. Water treatments were imposed after the termination of the infestation period. The experimental procedure was repeated three times.

Measurements of wheat photosynthetic parameters, such as photosynthesis (*Ps*), transpiration (*E*), stomatal conductance (g_s), and intercellular CO_2 (C_i) rates, were recorded from the flag leaf of the primary stem on each plant using a portable photosynthesis system (Model LI-6400, Li-Cor Inc., Lincoln, NE). Measurements were taken from wheat flag leaves at the grain filling developmental stage (64-65 on the Zadoks scale), which occurred about 4 wks after the initiation of the treatments. Photosynthetic measurements were taken under 1200 µmol photons/m^2/sec light intensity, with 400 µmol/mol CO_2 reference concentrations at a constant flow of 500 µmol/sec. Data were recorded when system was considered stable (i.e., photosynthesis changes were less than 0.1 µmol/m^2/sec, and conductance changes were less than 0.05 µmol/m^2/s).

In addition, chlorophyll *a* fluorescence measurements were recorded from a subset of plants within each treatment ($n = 5$). These were taken on the flag leaf using a modulated chlorophyll fluorometer (Model OS1-FL, Opti-Sciences, Tyngsboro, MA). Two basic tests were performed: a dark-adapted test (modulation intensity = 40 µmol electrons/m^2/s; saturation intensity = 190 µmol electrons/m^2/s; duration = 8 s; and detector gain = 80), and a light-adapted test (modulation intensity = 200 µmol electrons/m^2/s; saturation intensity = 230 µmol electrons/m^2/s; duration = 8 s; and detector gain = 80; default PAR (Photochemically Active Radiance) value = 1100 µmol electrons/m^2/s). The ultimate objectives of these tests were to determine the photochemical efficiency of photosystem II (*Fv/Fm*) and the photochemical quantum yield (*Y*) of wheat leaves under experimental treatments.

After plant maturation, measurements of plant yield parameters, such as head weight, number of seeds per head, and seed weight were undertaken. Data were analyzed as a 2 × 2 factorial by analysis of variance using PROC MIXED procedure (SAS Institute 2001). When appropriate, treatment means were separated using Fisher's least significant difference (LSD) procedure ($\alpha = 0.05$).

Results and Discussion

The ANOVA test results indicated that (1) there were no significant effects of trial, and (2) trial did not significantly interact with the treatments imposed for any of the photosynthetic parameters measured (*Ps*: $F = 0.94$; df = 2, 56; $P = 0.3948$; g_s: $F = 0.87$; df = 2, 56; $P = 0.4247$; C_i: $F = 0.47$; df = 2, 56; $P = 0.628$; and *E*: $F = 0.97$; df = 2, 56; $P = 0.3858$). Therefore, there were a total of 18 replications per treatment (6 replications × 3 trials) in a combined statistical analysis.

No significant interactions were observed between the treatment factors ($F = 0.44$; df = 1, 47; $P = 0.51$). However, each factor had a significant effect on the flag-leaf

photosynthetic capacity (Table 1). Photosynthesis was significantly affected by *C. cinctus* injury and suboptimal water condition ($F = 5.28$; df = 1, 47; $P < 0.0261$ and $F = 106.58$; df = 1, 47; $P < 0.0001$, respectively). Plants under water limited conditions had *Ps* rates that were 43.7% lower than plants under well watered conditions ($t = 10.32$; df = 47; $P < 0.0001$). We also observed a 12% higher *Ps* rate for uninfested plants compared with *C. cinctus* infested plants ($t = 2.30$; df = 47; $P < 0.0261$) (Table 1).

Unlike *Ps*, other closely associated processes, such as g_s, C_i, and E, were not significantly affected by *C. cinctus* injury (g_s: $F = 1.46$; df = 1, 47; $P = 0.2333$; C_i: $F = 0.39$; df = 1, 47; $P = 0.5357$, and E: $F = 0.40$; df = 1, 47; $P = 0.5308$). Conversely, the water treatments had a significant effect on both g_s and E rates (g_s: $F = 42.76$; df = 1, 47; $P < 0.0001$; and E: $F = 17.89$; df = 1, 47; $P < 0.0001$). Plants under suboptimal water treatments had 66.5% lower g_s values when compared with adequately-watered plants ($t = 6.54$; df = 47; $P < 0.0001$). Similarly, we observed 54.8% lower E rates on water-limited plants ($t = 4.23$; df = 47; $P < 0.0001$) when compared with their adequately watered counterparts (Table 1). No significant differences were elicited by any of the factors (i.e., *C. cinctus* injury and water limitation) for C_i for any imposed treatments (Table 1).

Chlorophyll *a* fluorescence parameters measured in both dark- and light-adapted tests were significantly affected by the treatment factors imposed in this study (Table 2). A significant interaction between treatment factors was observed for the photochemical efficiency of photosystem II (PSII) ($F = 9.56$; df = 1, 39; $P = 0.0037$), with

Table 1. Mean ± SEM values for photosynthetic capacity parameters: photosynthesis (*Ps*), stomatal conductance (g_s), intercellular CO_2 (C_i), and transpiration (*E*) measured 4 wk after *C. cinctus* infestation

	Treatments	
	C. cinctus	
Photosynthetic parameters	Uninfested	Infested
Ps (μmol $CO_2/m^2/s$)	15.53 ± 1.03a	13.71 ± 1.04b
g_s (mol $H_2O/m^2/s$)	0.18 ± 0.02a	0.15 ± 0.02a
C_i (μmol CO_2 mol/air)	225.0 ± 74.9a	292.0 ± 77.1a
E (mol $H_2O/m^2/s$)	3.39 ± 0.4a	2.97 ± 0.5a
	Watering regime	
Photosynthetic parameters	Regular (7d/wk)	Reduced (2d/wk)
Ps (μmol $CO_2/m^2/s$)	18.7 ± 1.03a	10.53 ± 1.0b
g_s (mol $H_2O/m^2/s$)	0.26 ± 0.02a	0.06 ± 0.03b
C_i (μmol CO_2 mol/air)	213.4 ± 76.05a	303.58 ± 75.92a
E (mol $H_2O/m^2/s$)	4.66 ± 0.47a	1.71 ± 0.5b

Means ± SEM followed by same letters within rows are not significantly different at $\alpha = 0.05$.

Table 2. Mean ± SEM values for chlorophyll *a* fluorescence parameters: minimal fluorescence yield (Fo), variable fluorescence (Fv), maximal fluorescence yield (Fm), photochemical efficiency of PSII (Fv/Fm), and photochemical quantum yield (Y)

	Treatments			
	Regular water availability (7d/wk)		Reduced water availability (2d/wk)	
Parameters	Uninfested	*C. cinctus*-infested	Uninfested	*C. cinctus*-infested
Fo	333.4 ± 21.9a	316.9 ± 21.8a	356.7 ± 22.0a	344.4 ± 21.8a
Fv	1233.2 ± 109.5a	1254.4 ± 108.9a	1305.6 ± 110a	1100.4 ± 109.1b
Fm	1566.28 ± 130.3a	1564.4 ± 129.8a	1657.24 ± 130.9a	1441.0 ± 129.9b
Fv/Fm	0.78 ± 0.01a	0.79 ± 0.01a	0.78 ± 0.02a	0.73 ± 0.01b
Y	0.73 ± 0.01a	0.73 ± 0.01a	0.71 ± 0.01a	0.69 ± 0.01a

Means ± SEM followed by same letters within rows are not significantly different at $\alpha = 0.05$.

significantly lower Fv/Fm values for *C. cinctus* infested plants under suboptimal water conditions when compared with uninfested plants under the same watering condition ($t = 3.77$; df = 39; $P = 0.0005$) or to *C. cinctus* infested plants under regular water regimen ($t = 5.14$; df = 39; $P < 0.0001$). We did not observe any significant difference for Fv/Fm values for either of the regularly watered treatments. Lower Fv/Fm values for plants under suboptimal water availability treatments were accompanied by higher Fv and Fm values and lower Fo values. Photochemical quantum yield (Y), on the other hand, was not significantly affected by either *C. cinctus* injury or by the interactions between the two treatment factors. However, lower Y values were observed for plants under suboptimal water availability in comparison with the regular watering regimen ($t = 3.07$; df = 41; $P = 0.0037$) (Table 2).

We did not observe any significant yield effects of the treatments in this study. We also did not observe significant interactions between the treatment factors on any of the yield parameters measured, such as head weight ($F = 1.09$; df = 1, 24; $P = 0.3073$), number of seeds/head ($F = 0.44$; df = 1, 24; $P = 0.5130$), and seed weight ($F = 1.97$; df = 1, 24; $P = 0.1739$) (Table 3).

Our results indicate that the photosynthetic capacity of wheat was sensitive to *C. cinctus* injury under greenhouse conditions at specific developmental stages. Plants were photosynthetically impaired by both *C. cinctus* injury and the suboptimal water availability imposed in this study. Conversely, Macedo et al. (2005) observed that *C. cinctus* did not affect photosynthesis of wheat plants under greenhouse conditions, although photosynthesis was affected in injured plants in an environmental chamber experiment.

The discrepancies between our results and those of Macedo et al. (2005) could be attributed to several factors. First, Macedo et al. (2005) measured photosynthetic parameters more than once, during both the vegetative and reproductive stages, which included grain filling. However, in the present study, photosynthetic parameters were measured only at grain fill. There is evidence that the photosynthetic capacity during plant development is variable, which is driven by the source-sink relationship (Pheloung and Siddique 1991, Wardlaw and Willenbrink 1994, Yang et al. 2000, 2001, 2004). It also has been demonstrated that the grain filling of wheat depends on carbon from the current assimilation and from the remobilization of reserves stored in the stem either pre or postanthesis (Pheloung and Siddique 1991, Wardlaw and Willenbrink 1994, Yang et al. 2000, 2001, 2004).

Second, the wheat variety used in this study was different from that used in Macedo et al. (2005). Differences in plant material may result in different plant response to stressors. For example, Yang et al. (2004) indicated that conflicting responses from wheat plants at the grain-filling stage as a result of water deficit might be dependent on plant variety. The variety used in the present study, 'Reeder,' is characterized by a slightly later maturation compared with 'McNeal' (Talbert et al. 2001, Lanning et al. 2003). Consequently, 'Reeder' plants stay green longer and the grain filling period is extended, as long as moisture is available. Plant varieties that have longer grain filling and a low harvest index because they remain green for a long period, can remobilize prestored assimilate comparatively poorly to the grains (Yang et al. 2000).

Our results show that wheat photosynthetic capacity was significantly impaired by suboptimal water availability. We cannot characterize the mechanism(s) directly involved in the plant response. Based on this, one can only explore or speculate about possible scenarios that have been reported in the literature.

Table 3. Mean ± SEM values for plant yield parameters: head weight (HW), number of seeds per head (NS), and seeds weight (SW)

	Treatments			
	Regular water availability (7d/wk)		Reduced water availability (2d/wk)	
Parameters	Uninfested	*C. cinctus*-infested	Uninfested	*C. cinctus*-infested
HW (g)	0.865 ± 0.10a	0.955 ± 0.09a	0.812 ± 0.07a	0.715 ± 0.08a
NS	28.0 ± 2.7a	30.99 ± 2.3a	24.73 ± 2.12a	24.64 ± 2.12a
SW (g)	0.63 ± 0.08a	0.69 ± 0.07a	0.61 ± 0.07a	0.48 ± 0.06a

Means ± SEM followed by same letters within rows are not significantly different at $\alpha = 0.05$.

First, plant photosynthetic responses observed under suboptimal water availability might be related to stomatal closure. Cornic (2000) demonstrated that stomatal closure is a highly efficient way to prevent leaves from losing water. We have observed significantly lower g_s and E values in plants under water limitations, independent of *C. cinctus* infestation. This might be a consequence of stomatal closure. However, g_s and E values were not significantly depressed for *C. cinctus* infested plants, which may indicate that there may be a different mechanism from the one elicited by suboptimal water conditions.

Second, based on *C. cinctus* feeding behavior and the possibility of vascular disruption because of injury, sucrose unloading would be inhibited, thereby causing increases in sucrose accumulation in the nodes (Morrill et al. 1992). This could ultimately lead to end-product inhibition. Decreases in phloem unloading can elicit elevated concentrations of soluble carbohydrates (Azcon-Bieto 1983, Plaut et al. 1987, Krapp et al. 1991, Murage et al. 1996). Enzymes involved in carbon fixation, most likely rubisco, ribulose-1,5-bisphosphate (RuBP), are then down-regulated by carbohydrates accumulated in the chloroplast (sucrose) and/or cytosol (starch), through the impairment of photosynthetic electron transport. This causes an accumulation of ATP and reducing form NADPH resulting in photo-oxidative stress in the photosynthetic light reactions (Külheim et al. 2002). Our results show that photochemical efficiency of PSII was impaired. In addition, we observed higher F_o values on plants under water stress regimes, which suggests oxidative inhibition of the photosynthetic light reactions due to accumulation of reactive oxygen species.

Finally, one could argue that the observed plant response might be directly associated with the suboptimal greenhouse light intensity/quality for wheat to perform photosynthesis. When exposed to the higher light intensity (i.e., 1200 µmol photons/m^2/sec light intensity) during photosynthetic measurements, photochemical energy is not converted into chemical energy, generating long-lived, excited states of chlorophyll which can modify the photosystem II reaction center in the presence of oxygen (Barber 1994, Oxborough et al. 1996, Hong and Xu 1999, Barth et al. 2001). Electrons and reducing forms can accumulate in the thylakoid membrane when the photodamage is elevated and as a consequence, the overall photosynthetic quantum yield of photosynthesis is diminished, resulting in photoinhibition (Powles 1984, Asada 1994, Ke 2001). Increases in light intensity also can be responsible for accumulation of ATP and reducing form NADPH causing photo-oxidative stress in the photosynthetic light reactions (Külheim et al. 2002).

Although the importance of light has been demonstrated in other studies, it might have only a minor impact on the results reported herein, as we observed significant differences in the photosynthetic responses of treated and untreated plants, which were maintained in the same greenhouse conditions. However, more detailed studies are being undertaken to fully evaluate this possibility.

Our data indicate that neither treatment factor had a significant effect on the yield parameters measured. In part, this may be complicated by innate discrimination of plants with higher yield potential by ovipositing *C. cinctus* (Morrill et al. 1992). However, this also raises questions pertaining to the contribution of the severity of moisture deficit and the degree of injury imposed by *C. cinctus* on the vascular tissue. It is possible that either the severity of water limitation imposed in our study was mild and/or the degree of vascular tissue damage was not sufficiently severe to affect grain yield. It has been demonstrated that under controlled water limitation plants which are allowed to rehydrate benefit from this water-limited condition, and can enhance the

remobilization of carbon reserves from vegetative tissues to the grain. This accelerates starch accumulation and the rate of grain filling. Under these conditions, the grain weight and grain yield would not necessarily be reduced (Yang et al. 2004).

In addition to physiological modification, plants are able to cope with water stress by shortening their growth cycle. In fact, our chlorophyll *a* results indicate that plants under stressful conditions started to senesce earlier than nonchallenged plants. The leaf senescence event is marked by the disassembly of the photosynthetic apparatus within chloroplasts, which causes a concomitant decrease in the photosynthetic activity (Woolhouse 1984, Grover and Mohanty 1992). Therefore, decreases in photosynthetic activity during leaf senescence generally occur earlier than for photosystem II photochemistry (Humbeck et al. 1996). Lu and Zhang (1998) observed that PSII activity seemed to be affected only slightly; whereas a substantial decrease in photosynthesis occurred during leaf senescence. The combination of our photosynthetic and fluorescence data suggests that plants under water-limited conditions showed an accelerated senescence process compared with well-watered plants. The data also suggest that *C. cinctus* plants senesced earlier than noninfested plants under water-stress conditions.

Based on the results from this study, suboptimal water availability and *C. cinctus* feeding injury impair photosynthesis in wheat. However, yield was not significantly reduced under these greenhouse conditions. Future research should be directed toward examining the role of other environmental factors, such as light conditions and potential interactions with water and nutrient availability for infested plants. Variability in varietal response to *C. cinctus* larval feeding injury also should be measured under the same conditions.

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