Characterization of the Impact of Wheat Stem Sawfly, *Cephus cinctus* Norton, on Pigment Composition and Photosystem II Photochemistry of Wheat Heads

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ABSTRACT Impact of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), feeding injury on chlorophyll content and photosystem II (PSII) photochemistry in heads of wheat, *Triticum aestivum* L., at the grain-filling developmental stage was evaluated by biochemically assessing the total chlorophyll, chlorophyll a (*Chla*), chlorophyll b (*Chlb*), chlorophyll a/b ratio (*Chla/b*), and carotenoid concentrations in the glumes in combination with a chlorophyll *a* fluorescence test. *C. cinctus*–infested stems had altered head glume pigment composition and photochemistry. Chlorophyll content, *Chl*a, *Chlb*, *Chla/b*, and total chlorophyll, and the photochemical efficiency of PSII were greater for glumes of heads developing on infested stems. Chlorophyll *a* fluorescence was also affected by *C. cinctus*. In this study, wheat plants in a controlled environment were able to compensate for injury imposed by *C. cinctus*. The mechanism underlying the compensatory processes seems to involve the alteration of wheat head physiology. Based on our results, either the photochemical efficiency of heads on infested stems was greatly improved or their senescence was delayed.

KEY WORDS *Triticum aestivum*, *Cephus cinctus*, herbivory, chlorophyll degradation, head physiology.

Wheat stem sawfly, *Cephus cinctus* Norton, is an important insect pest of wheat, *Triticum aestivum* L., in the continuous region including the northern Great Plains of the United States and the Canadian Prairies (Weiss and Morrill 1992, Morrill et al. 2001). This pest causes considerable economic losses, which might reach $25 million per year in Montana alone (Montana State University Extension Service 1997).

Emergence of *C. cinctus* adults begins in late May and may continue until late July (Criddle 1915, 1923, Wallace and McNeal 1966, Weiss et al. 1990, Weiss and Morrill 1992, Morrill and Kushnak 1996). The larvae develop inside wheat stems and require four or five instars (Ainslie 1920). At the onset of plant maturation, the large larvae chew a notch around the inside perimeter of the stem near ground level. As a result, infested stems usually lodge, which makes the collection of heads difficult at harvest (Ainslie 1920). Neonate larvae initially feed on parenchymous tissue near the oviposition site and disperse throughout the stem as they increase in size (Holmes 1954). Stem nodes are also injured by feeding, with possible disruption of vascular transport. This may result in the accumulation of material that appears as darkened regions below the nodes (Morrill et al. 1992a). Estimated losses for infested heads can reach 25% (Morrill et al. 1992b).

Photosynthetic processes such as photosynthesis, water–vapor transfer, and respiration are the primary processes determining plant growth, development, and, ultimately, yield (Peterson and Higley 1993). Therefore, it is important to understand how insect injury influences these parameters (Peterson and Higley 1993). In earlier studies, it has been suggested that the stem-boring injury, such as that imposed by *C. cinctus*, might impair photosynthetic capacity primarily because of damage to vascular tissue (Heichel and Turner 1973, Madden 1977). Reductions of ≈10–20% of photosynthetic rates have been observed in corn plants associated with larval stem boring by European corn borer, *Ostrinia nubilalis* (Hübner) (Godfrey et al. 1991), whereas Rubia et al. (1996) observed compensatory mechanisms leading to an increase in photosynthesis of borer-injured rice tillers. Furthermore, these processes (e.g., photosynthesis) respond very rapidly to external factors, so their measurement provides an immediate indication of plant stress (Peterson and Higley 1996, Peterson et al. 1998, 2005, Macedo et al. 2003, 2005, unpublished data, Li et al. 2005).

Photosynthesis can be limited by a multitude of factors, varying from intrinsic to extrinsic factors. According to Rosenthal and Kotanen (1994) "Intrinsic factors are those determined genetically or developmentally by the plant itself. Extrinsic factors include a

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broad range of variables such as the availability of resources in the environment to support regrowth, the type of herbivory experienced and its spatial distribution within a plant." Limitations in nutrient and/or water availability, elevated temperature, and herbicides are some examples of abiotic factors impacting photosynthesis.

In previous studies, we determined the impact of *C. cinctus* on photosynthetic capacity of flag leaves of wheat plants under a water deficit during the grain-filling stage (T.B.M., D.K.W., and R.K.D.P., unpublished data). Despite significant reductions in photosynthetic rates of flag leaves of *C. cinctus*–infested plants under water deficits, no negative impact was observed on yield parameters, such as head weight, number of seeds per head, and seed weight. These results led us to consider potential compensatory mechanisms involved in the interaction between *C. cinctus* injury and wheat grain filling.

Wheat grain filling is generally accepted as a process of starch biosynthesis and accumulation, once starch—the major form of carbon reserves—makes up to 65–75% of the final dry weight of the grain (Housley et al. 1981, Dale and Housley 1986, Hurkman et al. 2003). Four enzymes play key roles in starch biosynthesis, and their activities are considered to be regulated by a series of factors, such as temperature and water availability (Caley et al. 1990, Hawker and Jenner 1993, Keeling et al. 1993, Jenner 1994, Cheih and Jones 1995, Duke and Doehlert 1996, Wilhelm et al. 1999, Hurkman et al. 2003).

In addition to temperature and water availability, the grain-filling process also depends on carbon from assimilation and remobilization of reserves stored in the stem during pre- or postanthesis (Wardlaw 1990, Pheloung and Siddique 1991). Evans et al. (1975) showed that the main method of supplying assimilated carbon to grains in wheat is from photosynthesis in the flag leaf and the head. Estimates of the contribution of head photosynthesis to final grain weight, depending on the genotype and environment, ranges around 10–76% (Evans et al. 1975). Earlier studies showed that wheat varieties characterized by awned heads can make larger contributions to final grain yield than awnless varieties (Grundbacher 1957). It has been also suggested that, under drought conditions during grain filling, photosynthesis of wheat heads might contribute more than flag leaves to grain yield (Johnson and Moss 1976, Blum 1985). Araus et al. (1993) showed that, under certain environmental conditions, wheat heads are the main photosynthetic source of carbon to filling grains. Photosynthetic uptake by whole heads of wheat is significantly different from that for flag leaves (Knoppik et al. 1986). Higher maximal rates of photosynthesis at saturation CO_2, relative to the rates at normal atmospheric CO_2, is observed for wheat heads in comparison to flag leaves. In addition, the CO_2 uptake for the head is not saturated at intercellular CO_2 partial pressures below 180 Pa CO_2, whereas that of the flag leaf reaches saturation at a partial pressure of 80 Pa CO_2. Wheat heads also show greater amounts of CO_2 compensation than flag leaves (Knoppik et al. 1986).

The objective of this study was to characterize the impact of injury by *C. cinctus* on the photosynthetic pigment composition and photosystem II (PSII) photochemistry of wheat heads in a controlled environment.

Materials and Methods

In 2005, we conducted three experiments in greenhouses at the Montana State University Plant Growth Center, Bozeman, MT. Spring wheat, variety McNeal, 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 mix (Peters 20-20-20 General). Greenhouse conditions were maintained at 21 ± 1°C, photoperiod of 14:10 (L:D) h, and 40–50% RH for the duration of the study. Supplemental light was delivered by GE Multi-Vapor lamps (MVR1000/C/U; GE Lighting, General Electric Co., Cleveland, OH).

The experimental design consisted of a randomized complete block design, blocked by light source, with six replications per treatment. Treatments consisted of either uninfested (control) or *C. cinctus*–infested plants. Three experimental replications were conducted. To infest plants, small Plexiglas cages (4 by 60 cm), each containing the main stem of a wheat plant at developmental stage 32–33 (Zadoks et al. 1974), were infested with three male and six female *C. cinctus* adults. Insects were allowed to mate and oviposit freely for a period of 7 d, after which cages were removed.

PSII photochemistry was determined by chlorophyll *a* fluorescence measurements. Chlorophyll *a* fluorescence parameters were recorded from head glumes using a modulated chlorophyll fluorometer (model OS1-FL; Opti-Sciences, Tyngsboro, MA) at the grain-filling developmental stage (64–65 Zadoks scale), at 4 wk after treatment. One basic test was performed: 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 photosynthetic active radiance [PAR] value = 1,100 μmols electrons/m^2/s). The objective of this test was to determine the photochemical quantum yield (Y) of wheat leaves under experimental treatments. Parameters measured were steady-state fluorescence (Fs), steady-state maximal fluorescence (Fms), overall photochemical quantum (Y), incident PAR, and apparent photosynthetic electron transport rate (ETR). Measurements were taken from head glumes (i.e., the pair of bracts located at the base of a spikelet) of both *C. cinctus*–infested and noninfested stems. Three measurements were recorded for each head (i.e., 18 measurements/treatment).

Total chlorophyll, chlorophyll *a* (*Chla*), chlorophyll *b* (*Chlb*), chlorophyll *a*/*b* ratio (*Chla*/*b*), and carotenoid concentrations (mg/g glume) were quantified from a subset (n = 15) of head glumes of *C. cinctus*–

Table 1. Mean values for head glume pigment amounts measured by extraction (mg/g dry material)

Parameter	Treatments	
	C. cinctus–infested stem	Uninfested stem
Total chlorophyll	1.3635 ± 0.08a	0.8435 ± 0.09b
Chlorophyll *a*	0.885 ± 0.06a	0.579 ± 0.05b
Chlorophyll *b*	0.4785 ± 0.03a	0.2645 ± 0.03b
Chlorophyll *a*/*b*	1.8495 ± 0.01a	2.189 ± 0.02b
Carotenoids	0.3804 ± 0.019a	0.2445 ± 0.02b

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

Table 2. Mean values for chlorophyll *a* fluorescence parameters measured using an OS1-FL Modulated Chlorophyll Fluorometer

Parameters	Treatments	
	C. cinctus–infested stem	Uninfested stem
Fs	194.79 ± 8.27a	186.29 ± 8.3a
Fms	763.08 ± 30.16a	711.17 ± 30.2a
Fvs	534.96 ± 24.58a	499.88 ± 24.69b
Y	0.7021 ± 0.02a	0.6382 ± 0.02b
PAR	0.2667 ± 0.02a	0.2208 ± 0.019a
ETR	0.0804 ± 0.008a	0.06236 ± 0.01a

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

infested and uninfested stems by extraction using 80% aqueous acetone (vol:vol). Pigment extractions followed protocol described by Wang et al. (2004), and calculations of total chlorophyll, *Chla*, *Chlb*, and carotenoids concentration were based on the equation described by Bertrand and Schoefs (1997).

Measurements of plant yield parameters, such as head weight (HW), number of seeds per head (NS), and seeds weight (SW) were recorded from the remaining plants from each treatment ($n = 9$). Data were analyzed using an analysis of variance (ANOVA) in the PROC MIXED procedure of SAS (SAS Institute 2001). Means were compared using a Student's *t*-test ($\alpha = 0.05$).

Results

Our ANOVA test results indicated that there were no significant effects of experimental replicate and associated interactions with the imposed treatments for any of the chlorophyll parameters measured (Total *Chl:* $F = 0.87$, df = 2,24, $P = 0.4301$; *Chla:* $F = 0.73$, df = 2,24, $P = 0.4915$; *Chlb:* $F = 1.12$, df = 2,24, $P = 0.3428$; *Chla/b:* $F = 0.53$, df = 2,24, $P = 0.5953$; Carotenoids: $F = 0.99$, df = 2,24, $P = 0.3855$). Similarly, experimental replicate and associated interactions had no effect on Chlorophyll *a* fluorescence parameters (Fs: $F = 0.61$, df = 2,42, $P = 0.5459$; Fms: $F = 0.04$, df = 2,42, $P = 0.964$; Y: $F = 1.25$, df = 2,42, $P = 0.2972$; PAR: $F = 1$, df = 2,42, $P = 0.3748$; ETR: $F = 1.07$, df = 2,42, $P = 0.3513$). Therefore, each experimental replicate contributed 6 replications per treatment for a total of 15 replications per treatment (5 replications × 3 experiments) for pigment composition and 24 replications per treatment (8 replications × 3 experiments) for the chlorophyll *a* fluorescence statistical analysis.

Pigment quantities in the head glumes of *C. cinctus* injured stems were greater. We observed a significant increase of 62% in the total chlorophyll content in head glumes from *C. cinctus*–infested stems ($T = 4.20$, df = 14, $P = 0.0009$). This difference was concurrent with significant increases in both *Chla* and *Chlb* concentrations in head glumes from *C. cinctus*–infested stems ($T = 3.79$, df = 14, $P = 0.002$ and $T = 4.84$, df = 14, $P = 0.0003$, respectively). Similar results were observed for the *Chla/b* ratio (Table 1). We observed an increase of ≈24% in the *Chla/b* ratio on head glumes of the insect-injured stems. Carotenoid concentrations were also increased by *C. cinctus* injury ($F = 18.87$, df = 1,14, $P = 0.0007$; Table 1).

We observed a significant effect of *C. cinctus* feeding on the PSII photochemistry through increased chlorophyll *a* fluorescence parameters. Significant increases of 7 and 10% were observed on Fvs and Y parameters, respectively, for head glumes on infested stems (Fvs: $T = 2.45$, df = 23, $P = 0.0224$; Y: $T = 2.18$, df = 23, P 0.0397). No significant differences were observed for any other parameter measured (i.e., Fs, Fms, PAR, and ETR; Table 2).

We did not observe any significant effects of *C. cinctus* infestation on any of the yield parameters measured, such as HW, NS, and SW (HW: $F = 0.00$, df = 1,8, $P = 0.9764$; NS: $F = 1.52$, df = 1,8, $P = 0.2529$; SW: $F = 0.06$, df = 1,8, $P = 0.8165$; Table 3).

Discussion

Our data suggest that, under a controlled environment in a greenhouse, wheat stem sawfly feeding injury significantly increases pigment composition and alters the PSII photochemistry of wheat heads during the grain-filling period. In previous studies (T.R.M., D.K.W., and R.K.D.P., unpublished data), we determined that *C. cinctus* impaired the photosynthetic capacity of wheat flag leaves. However, we observed that the physiological alteration seems dependent on various factors, such as plant genetic background, nutritional status, and environmental variables. Although T.R.M., D.K.W., and R.K.D.P. (unpublished data) have observed significant photosynthetic reductions on flag leaves of infested plants under light and water deficits, yield parameters (such as HW, SW, and NS) were not significantly affected by *C. cinctus* feeding.

Table 3. Mean values for plant yield parameters: HW, NS, and SW

Parameters	Treatments	
	C. cinctus–infested stem	Uninfested stem
HW (g)	1.471 ± 0.14a	1.475 ± 0.2a
NS	44.89 ± 4.77a	51.89 ± 4.8a
SW (g)	0.032 ± 0.002a	0.028 ± 0.002a

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

These results led us to question whether other photosynthetically active organs, such as stems and heads, might compensate for injury caused by *C. cinctus* under optimal conditions. Based on *C. cinctus* feeding patterns and the resulting vascular disruption, sucrose generated in flag leaves would probably accumulate in the subnodal region, leading to an endproduct inhibition. In this phenomenon, phloem unloading attenuation can elicit elevated concentrations of soluble carbohydrates (Azcon-Bieto 1983, Plaut et al. 1987, Krapp et al. 1991, Murage et al. 1996), and certain enzymes involved in carbon fixation—most likely rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase—and regeneration are down-regulated. This process is driven by carbohydrates accumulated in the chloroplast (sucrose) and or cytosol (starch), through the impairment of the photosynthetic electron transport. The resulting accumulation of both ATP and reducing form NADPH (nicotinamide adenine dinucleotide) causes photo-oxidative stress in the photosynthetic light reactions (Külheim et al. 2002). Therefore, remobilization of carbon reserves stored in stems to grains seems to be greatly diminished or even disrupted.

Alternatively, head photosynthesis could generate an adequate quantity of carbon and mobilize it to grains. It has been shown that, along with flag leaves, heads are the main source of supplying assimilated carbon to grains during the grain-filling process in wheat plants (Evans et al. 1975). They estimated that photosynthesis in heads can contribute from 10 to 76% of the final grain weight, depending on the genotype and environment. It has also been suggested that, under drought conditions during grain filling, photosynthesis of wheat heads might contribute more than flag leaves to grain yield (Johnson and Moss 1976, Blum 1985).

In this study, our pigment and photochemical characterization of wheat heads leads us to suggest that, under certain conditions, *C. cinctus*–infested plants might use head photosynthesis as the major compensatory mechanism during grain filling. We have observed higher total chlorophyll content in head glumes on infested stems, possibly because of delayed chlorophyll degradation, increases in chlorophyll production, and/or resource reallocation of chlorophyll. Our data also show that both forms of chlorophylls (*Chla* and *Chlb*) were also more abundant in *C. cinctus*—infested stems, leading to a higher *Chla*/*b* ratio. *Chla* and *Chlb* are directly associated with photosynthetic light reactions. Both chlorophyll forms are present in the major light harvesting complex, and *Chla* is also associated with the photochemical reaction center, which generates the ATP and NADPH necessary to power carbon assimilation during the dark reactions of photosynthesis. This indicates that *C. cinctus* feeding might have an indirect impact on the photochemistry of wheat heads.

These findings also suggest that wheat heads of infested stems might have their senescence delayed. The most notable event in the senescence process is the disassembly of the photosynthetic apparatus. Conversely, our data show higher *Chla*/*b* ratios because of higher concentrations of both forms of chlorophyll. This indicates that senescence was not occurring. Our chlorophyll *a* fluorescence results support this hypothesis. We have observed that head glumes on infested stems have higher overall photochemical quantum yield of PSII (Y). Y is a good indicator of the efficiency in light use, i.e., how efficiently absorbed photon is converted into chemical products (Malkin and Niyogi 2000). Our results indicate that, in response to *C. cinctus* injury, plants might have a higher efficiency of light use. In addition, these results, combined with our pigment characterizations, suggest that these heads on *C. cinctus*–infested stems seem to have delayed senescence to improve CO_2 fixation, a phenomenon described in field measurements on moss and lichen (Green et al. 1998).

In this study, we were able to show that wheat plants, under a controlled environment, were able to tolerate and even compensate for injury imposed by *C. cinctus.* The mechanism underlying compensatory processes involved changes in head physiology. Based on our results, we can suggest that photochemical efficiency of heads on infested stems are either greatly improved or their senescence is delayed. We were also able to reveal broader considerations that are necessary when attempting to understand plant physiological responses based on local observations. In previous studies, T.B.M., D.K.W., and R.K.D.P. (unpublished data) suggested that one mechanism used by stressed plants is to shorten their growth cycle to decrease exposure to stress conditions. However, all observations were restricted to flag-leaf photosynthetic capacity. In this study, we were able to show that heads might remain green longer, allowing grain filling for an extended period of time. Studies have shown that some wheat varieties, such as 'Reeder', mature later, allowing longer grain-filling periods compared with 'McNeal', the variety used in this study (Talbert et al. 2001, Lanning et al. 2003). Our results, however, show that, under certain circumstances, such as *C. cinctus* herbivory, delayed senescence might be observed on 'McNeal' wheat plants.

Additional research is needed to better understand *C. cinctus*--wheat interactions. In particular, characterization of the physiology of wheat and its interaction with biotic (e.g., plant variety, plant developmental stage, and insect feeding behavior) and abiotic factors (e.g., water and nutrient availability) not only will improve models of insect–plant interactions, but also will provide a basis for improved integrated pest management programs for *C. cinctus.*

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