Photosynthetic Responses of Wheat, *Triticum aestivum* L., Plants to Simulated Insect Defoliation During Vegetative Growth and at Grain Fill

TULIO B. MACEDO, ROBERT K. D. PETERSON,[1] AND DAVID K. WEAVER

Department of Land Resources and Environmental Sciences, 334 Leon Johnson Hall, Montana State University, Bozeman, MT 59717–3120

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ABSTRACT The impact of different levels of whole plant partial defoliation (WPPD) on the photosynthesis and primary metabolism of wheat, *Triticum aestivum* L., was evaluated at the vegetative and reproductive (grain-filling) developmental stages. Photosynthetic parameters such as photosynthesis, stomatal conductance, and transpiration, chlorophyll *a* fluorescence, and plant morphological parameters, such as main stem height, flag-leaf and undefoliated leaf areas, and number of tillers, were recorded 1 h and 1, 9, and 12 d after defoliation in 2004 and 1 h, 3 d, and 6 d after defoliation in 2005. Plants with high defoliation levels (i.e., defoliation $> 75\%$) had $\approx$21 and 20% greater photosynthesis rates compared with control and low defoliation level treatments, respectively. Our data show that stomatal conductance for flag leaves was not significantly affected by WPPD. In addition, we did not observe a significant effect of defoliation on intercellular CO_2 concentrations or on transpiration rates remaining flag leaf tissue. Similar responses were observed for the overall photosynthesis of defoliated plants during vegetative stages. Whole plant source-sink manipulation of wheat by WPPD during the major plant developmental stages (i.e., vegetative and reproductive) did not elicit any significant long-term modifications to growth, morphological, or primary physiological characteristics of wheat plants.

KEY WORDS whole plant partial defoliation, photosynthesis, herbivory, plant–insect ecophysiology

Source-sink manipulation of whole plants has been used to identify the potential mechanisms involved in plant photosynthetic responses to leaf-area reductions, such as insect defoliation (Peet and Kramer 1980, Dyer et al. 1991, Layne and Flore 1995, Wang et al. 1996, Paul and Foyer 2001). Whole plant partial defoliation (WPPD) is a technique that decreases the source while keeping actual sink demand unchanged. After defoliation, there are proportionally fewer source leaves available to supply the demanded photoassimilate to the sinks, and therefore, there are increases on the relative demand per unit of leaf area (Wareing et al. 1968, Gifford and Marshall 1973, McNaughton 1979). End-product inhibition (photo-assimilate accumulation in the source leaves) would not occur in partially defoliated plants, because this sink-limited condition is unlikely to occur (Wareing et al. 1968, Gifford and Marshall 1973, McNaughton 1979).

Unfortunately, the mechanisms involved in source-leaf responses to changes in demand for photo-assimilates are still uncertain. Changes in photosynthesis because of source-sink manipulation have been attributed to alterations in both mesophyll and stomatal conductance (Thorne and Koller 1974, Koller and Thorne 1978, Layne and Flore 1995). Increases in ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) activity and lower photorespiration have been suggested as possible contributors to higher mesophyll conductance in soybean, *Glycine max* L. Merr., pepper, *Capsicum annuum* L., and citrus, *Citrus madurensis* Lour. (Tung et al. 1973, Thorne and Koller 1974, Hall and Brady 1977).

Numerous studies have been conducted to characterize the effects of insect defoliators (leaf-mass consumers) on plant gas exchange (Poston et al. 1976, Hammond and Pedigo 1981, Ingram et al. 1981, Ostlie and Pedigo 1984, Welter 1991, Higley 1992, Peterson et al. 1992, 2004, 2005, Peterson and Higley 1996). Studies have shown that, as a result of defoliation, photosynthetic rates on the remaining leaves can either be increased (Wareing et al. 1968, Satoh et al. 1977, Aoki 1981, Von Caemmerer and Farquhar 1984, Baysdorfer and Bassham 1985, Williams and Farrar 1988, Tschaplinski and Blake 1989, Welter 1989, Layne and Flore 1992, 1993) or temporarily decreased (Alderfelder and Eagles 1976, Hall and Ferree 1976, Li and Proctor 1984). However, perhaps the most common response observed has been that defoliation does not elicit any photosynthetic changes on remaining tissue of injured leaves (Davidson and Milthorpe 1966,

[1] Corresponding author, e-mail: bpeterson@montana.edu.

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Poston et al. 1976, Syvertsen and McCoy 1985, Welter 1989, 1991, Higley 1992, Peterson et al. 1992, 1996, 2005, Peterson and Higley 1996, Burkness et al. 1999). It is important to point out that this type of response cannot be generalized for the entire plant. Different photosynthetic responses have been observed for uninjured leaves and new-leaf tissue. Increased photosynthetic rates in newly formed foliage (McNaughton 1979, 1983a, b, Belsky 1986, Paige and Whitham 1987, Crawley 1989, Ovaska et al. 1992) and delayed photosynthetic senescence of older, remaining leaves (Higley 1992, Peterson et al. 1992) have been observed as contributing mechanisms to the compensatory response after partial defoliation by herbivores.

Despite the increasing number of studies conducted to develop generalized models of plant physiological response to defoliation, most of the research to date has been on legumes such as soybean and alfalfa, *Medicago sativa* L. (Poston et al. 1976, Hammond and Pedigo 1981, Ingram et al. 1981, Ostlie and Pedigo 1984, Higley 1992, Peterson et al. 1992, 2004, Peterson and Higley 1993, 1996, Peterson 2001). A limited number of studies, using molecular approaches, have generated a better understanding of how tissue-consuming insects affect plant photosynthesis (Grant-Petersson and Renwick 1996, Stotz et al. 2000, Kliebenstein et al. 2002, Weinig et al. 2003, Bidart-Bouzat et al. 2004). Peterson et al. (2004) argued that characterizing physiological responses to defoliation injury to numerous plant species is crucial to better understand the strengths and limitations of generalized models of response that have been developed to date.

Removal of leaf tissue potentially has serious effects on plant development and yield of grasses. Detrimental effects of defoliation on plant fitness and yield might be related directly to reductions on the photosynthetic capacity of remaining tissue (Culy 2001). Wang et al. (1996) showed that defoliation of corn, *Zea mays* L., during reproductive stages caused a significant reduction of photosynthetic rates of remaining leaf tissue and a decline in grain yield. They suggested that, with the decrease of source leaves, the demand of photosynthates by sink tissues (e.g., ears) greatly exceeded the supply, forcing a remobilization of photosynthates from other parts of the plant. Conversely, Dyer et al. (1991) observed an increase in carbon fixation of a C4 African grass, *Panicum coloratum* L., after defoliation during the vegetative stage by grasshoppers. They suggested that storage of carbon reserves in sinks or pool tissues that are readily available to the plant may allow rapid mobilization of these plant resources after defoliation. Once a response has been induced, the effects may be evident over time (Satoh et al. 1977). Such diverse responses might be directly related to the level of biological organization, whether it is individual leaves, individual plants, or the plant canopy (Peterson and Higley 1993). In addition, plant developmental stage might be a physiological causal factor on photosynthetic response to defoliation (Welter 1989).

Simulated defoliation has been used to simulate the effects of insect herbivory on plant primary physiology, growth, and yield. Despite limitations associated with the use of artificial defoliation (Baldwin 1990), studies have shown that artificial defoliation can appropriately elicit many plant responses (including photosynthesis) in comparison with actual insect defoliation (Detling et al. 1979, Boote et al. 1980, Buntin and Pedigo 1985, Welter 1991, Peterson et al. 1992, Burkness et al. 1999).

Macedo et al. (unpublished data) found that defoliation of individual wheat leaves by fall armyworm, *Spodoptera frugiperda*, larvae and simulated defoliation resulted in no changes in photosynthesis of remaining tissue of individual injured leaves. However, as discussed above, responses at the individual leaf level can be different than at the whole plant level. Therefore, the objective of this study was to characterize the photosynthetic gas exchange responses of wheat to WPPD during the vegetative and reproductive developmental stages.

A continuous defoliation process was designed to simulate insect defoliation, similar to that caused by armyworms (Lepidoptera: Noctuidae) and grasshoppers (Orthoptera: Acrididae). Artificial defoliation imposed in an equal portion of the total defoliation over periods of time results in plant responses similar to actual insect defoliation (Ostlie 1984, Stewart and Sears 1988, Shelton et al. 1990, Stewart et al. 1990, Burkness et al. 1999, Ramachandran et al. 2000). To date, no related study to assess the short- and long-term effects of defoliation of whole plant defoliation in wheat plants has been conducted. This research represents an effort to characterize the impact of herbivory on primary physiology of wheat plants.

Materials and Methods

Plant Material and Experimental Conditions. Experiments were conducted during 2004 and 2005 in the Montana State University Plant Growth Center greenhouses, Bozeman, MT. Spring wheat, variety McNeal, was grown in 13.3 by 13.3 by 14.6-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). Plants were maintained in the greenhouse bay at 21 ± 1°C, photoperiod of 14:10 (L:D) h and 40–50% RH for the duration of the study. To increase light quality/intensity inside the greenhouse, supplemental lighting, consisting of GE Multi-Vapor lamps (MVR1000/C/U; GE Lighting; General Electric, Cleveland, OH) was provided. The light intensity in the greenhouse at the canopy level, under a clear sky at midday, was 970 μmol photons/m^2/s, recorded during photosynthetic measurements using a quantum sensor (model LI-190; Li-Cor, Lincoln, NE).

Defoliation Impact on Wheat Photosynthesis at Reproductive Stage. The experimental design consisted of a completely randomized design with five replications per treatment. Two experimental replications were conducted for a total of 10 (5 by 2) replications

per treatment. To impose WPPD treatments (control = 0%, low = 25–45%, medium = 50–75%, and high = ≥75%), plants at grain-filling developmental stage (i.e., Zadoks 58–59; Zadoks et al. 1974) were artificially defoliated using a pair of scissors. WPPD treatments were imposed on the entire plant, including tillers, during an interval of 3 d (one third total defoliation per day). The fourth completely expanded leaf from the top of the plant was left intact (undefoliated leaf).

Measurements of plant growth and development, such as main stem height (from the base of the head to the soil level), flag-leaf and undefoliated-leaf areas (calculated based on the measurements of the leaf length [from the ligule to the apices] and width [at 1 cm from the ligule]), and number of tillers were recorded at 1 h, 24 h, 9 d, and 12 d after defoliation in 2004 and 1 h, 3 d, and 6 d after defoliation in 2005.

Measurements of wheat photosynthesis (Ps) and closely related processes, such as transpiration (E), stomatal conductance (g_s), and intercellular CO_2 (C_i) rates were recorded from the flag leaf and the undefoliated leaf on the primary stem on each plant using a portable photosynthesis system (model LI-6400; Li-Cor) at 1200 μmol photons/m^2/s light intensity, 400 μmol/mol CO_2 reference concentration at a constant flow of 500 μmol/s. Data were recorded when the system was considered stable (i.e., photosynthesis changes were <0.1 μmol/m^2/s, and conductance changes were <0.05 μmol/m^2/s).

Additionally, in 2005, chlorophyll *a* fluorescence measurements were recorded from a subset of plants within each treatment ($n = 3$) on the flag leaf using a leaf chamber fluorometer (model LI-6400–40; Li-Cor). We performed a kinetic test to determine the photochemical efficiency of photosystem II. The parameters measured were nonvariable fluorescence (F_o), overall photochemical quantum yield (Y), apparent photosynthetic electron transfer rate (ETR), and the quenching coefficients, nonphotochemical quenching (qN), and photochemical quenching (qP). Chlorophyll *a* kinetics were measured at 400 μmol/mol CO_2 concentration, 1200 μmol photons/m^2/s light intensity, measuring intensity 1 Int, measuring modulation 0.25 kHz, measuring filter 1 Hz, measuring gain 10 Gn, flash duration 0.8 s, flash intensity 7, flash modulation 20 kHz, and flash filter 50 Hz.

All photosynthetic measurements were taken from flag leaves and from undefoliated leaves on the main stem (two measurements per plant), and all chlorophyll *a* fluorescence measurements were taken only from flag leaves at the same time interval described for plant parameter measurements.

Defoliation Impact on Wheat Photosynthesis at Vegetative Stage. WPPD was also imposed in early developmental stages and to determine short- and long-term effects of defoliation on wheat primary metabolism. We imposed three defoliation treatments (control = 0%, low = 25–50%, and high = 75–85%) on plants at the tillering developmental stage (i.e., Zadoks 22–23). Plants were artificially defoliated using the same procedures as described above. Photosynthetic parameters were measured 1 and 24 h and 1, 2, and 4 wk after WPPD was imposed. The time intervals corresponded to tillering (Zadoks 22–23), stem elongation (Zadoks 31–32 and 32–33), and flowering (Zadoks 64–65) developmental stages. Chlorophyll *a* fluorescence parameters were measured from the main stem flag-leaf 1, 2, and 4 wk after WPPD. Two experimental replications were conducted for a total of 10 (5 by 2) replications per treatment.

Statistical Analysis. Analysis of variance (ANOVA) procedures were performed to determine whether the variances were different between the experimental replications for each developmental stage by including experimental replication in the ANOVA model using PROC MIXED procedure (SAS Institute 2001). Data were pooled when interactions between experiment replication and treatments were not significant. Because of limitations on precise determination of leaf area with a nondestructive method, we treated defoliation levels as a categorical factor, such as control, low, medium, and high for WPPD at reproductive stage and control, low, and high for WPPD at vegetative stage experiments. To determine the WPPD effects on the parameters of interest, data were analyzed using repeated measures (PROC MIXED; SAS Institute 2001) with two factors: injured leaf (flag leaf or undefoliated leaf) and defoliation level. Means were separated by *t*-test ($\alpha = 0.05$).

Results and Discussion

When WPPD was imposed during vegetative stages, none of the defoliation levels had a significant effect on the number of tillers produced by individual plants. There were also no significant interactions between defoliation and time (i.e., days after defoliation treatment). Conversely, we observed a significant increase in the number of tillers produced by the wheat plants over time ($F = 127.74$, df = 4,83, $P < 0.0001$). Similar responses were observed for other plant parameters, such as stem height and undefoliated leaf area. However, we did observe a significant effect of defoliation treatments on the defoliated flag-leaf morphology. A significant reduction in leaf area was observed ($F = 162.62$, df = 2,21, $P < 0.0001$). Reductions of >34 and 68% were observed for low and high defoliation levels, respectively (Table 1).

We observed a significant effect of WPPD on the overall morphological parameters of plants defoliated during the reproductive stages (58–59; Zadoks et al. 1974). Main-stem height was significantly taller for plants with high defoliation levels (i.e., >75%) affected by defoliation ($F = 4.5$, df = 3,59, $P = 0.0065$). Defoliation did not have any significant effect on the number of tillers of injured plants ($F = 0.30$, df = 3,59, $P = 0.9707$; Table 2). We did not observe any significant interaction between time and the defoliation treatments on any plant morphological parameter measured (Table 2).

These results indicate that despite the differentiated stem elongation on plants defoliated at reproductive stages, WPPD during both vegetative and re-

Table 1. Mean ± SEM values of plant morphological parameters at vegetative developmental stage responses to defoliation levels at 1 and 24 h and 1, 2, and 4 wk after defoliation

Morphological parameters	Defoliation levels				
	Control (0%)	Low (25–45%)	High (>75%)		
Stem length (cm)	29.89 ± 10.5a	31.25 ± 12.1a	30.19 ± 10.3a		
Remaining flag leaf area (mm^2)	65.24 ± 4.9a	42.66 ± 7.1b	20.84 ± 8.6c		
Undefoliated leaf area (mm^2)	27.79 ± 12.8a	27.83 ± 12.7a	26.81 ± 12.8a		
Number of tillers	4.97 ± 2.9a	5.1 ± 3.2a	4.68 ± 3.0a		
	Time (h/wk after defoliation)				
	1 h	24 h	1 wk	2 wk	4 wk
Stem length (cm)	21.65 ± 2.85a	21.65 ± 2.86a	26.30 ± 2.59b	35.26 ± 7.77c	47.37 ± 1.19d
Remaining flag leaf area (mm^2)	62.62 ± 4.75a	62.61 ± 4.72a	65.09 ± 4.08a	68.56 ± 5.1a	65.27 ± 1.75a
Undefoliated leaf area (mm^2)	32.85 ± 1.5a	32.85 ± 1.58a	33.24 ± 1.48a	33.45 ± 1.15a	5.0 ± 2.58b
Number of tillers	2.75 ± 0.5a	2.75 ± 0.5a	4.0 ± 0.75b	5.75 ± 1.65c	9.26 ± 0.31d

Means ± SEM followed by different letters are significantly different at the 0.05 probability level.

productive stages did not elicit growth of new photosynthetically active tissue. Compensatory responses, by production of new foliage (McNaughton 1979, 1983a, b, Belsky 1986, Paige and Whitham 1987, Crawley 1989, Ovaska et al. 1992), were not directly related to wheat responses when challenged by levels of WPPD. In other plant systems, however, an elevated tolerance to partial defoliation caused by the plant's ability to increase its source strength size through production of new leaves after defoliation has been observed. Potato, *Solanum tuberosum*, and the citrus *C. madurensis* use this mechanism to avoid the accumulation of assimilates in leaves, which could result in inhibition of photosynthesis (Paul and Foyer 2001). Conversely, the wheat plants in our studies did not respond in a similar manner. This difference in plant response might be dependent on the developmental background (McNaughton 1979) and/or on the degree of injury imposed (Peterson and Higley 1993). For example, in a wheat plant at reproductive versus vegetative stages, the metabolic allocation of assimilates is not directed toward the development of new photosynthetically active tissues. Instead, acceleration of grain filling by increased remobilization of carbon reserves was observed on wheat plants coping with water stress (Yang et al. 2004).

Plant defoliation elicited a significant alteration in the overall photosynthesis of defoliated plants during vegetative stages. We observed a significant enhancement of photosynthesis of flag leaves from plants with high defoliation levels. Increases >41% ($T = 2.92$, df = 14, $P = 0.0113$) in photosynthesis rates were observed in flag leaves (Table 3). Interactions between WPPD and time were not significant.

Similarly, WPPD significantly affected photosynthesis of the remaining defoliated flag leaf for wheat plants at reproductive stage in both experiments ($F = 3.44$, df = 3,20, $P = 0.0366$). Plants with high defoliation levels (i.e., defoliation >75%) had ≈21 and 20% greater photosynthesis compared with control and low defoliation level treatments, respectively. This plant physiological response might not be directly related to changes in stomatal conductance, as suggested for other plant systems. In fact, our data show that stomatal conductance for flag leaves was not significantly affected by WPPD ($F = 0.10$, df = 3,20, $P = 0.9578$). Interactions between WPPD and time were not significant ($F = 0.09$, df = 6,40, $P = 0.9967$). In addition, we did not observe a significant effect of defoliation on intercellular CO_2 concentrations or on transpiration rates of remaining flag leaf tissue. Photosynthetic rates of undefoliated leaves were not significantly affected by defoliation in either experiment (Table 3).

In addition, WPPD did not impair any of the chlorophyll *a* fluorescence variables, such as nonvari-

Table 2. Mean ± SEM values of plant morphological parameters at reproductive developmental stage (grain-filling) responses to defoliation levels at 1 h and 1, 9, and 12d after defoliation

Morphological parameters	Defoliation levels			
	Control (0%)	Low (25–45%)	Medium (50–75%)	High (>75%)
Stem length (cm)	55.88 ± 1.7a	60.42 ± 1.8b	56.36 ± 1.8a	60.89 ± 2.0b
Remaining flag leaf area (mm^2)	34.4 ± 1.0a	17.85 ± 3.18b	13.38 ± 2.04c	9.75 ± 2.8d
Undefoliated leaf area (mm^2)	32.07 ± 0.5a	26.2 ± 0.6a	30.9 ± 0.7a	29.7 ± 0.4a
Number of tillers	3.3 ± 0.50a	3.6 ± 0.89a	3.7 ± 0.55a	3.9 ± 0.82a
	Time (days after defoliation)			
	0	1	9	12
Stem length (cm)	55.8 ± 1.8a	57.2 ± 1.6a	59 ± 2.0ab	60.6 ± 1.8b
Remaining flag leaf area (mm^2)	17.1 ± 1.0a	19.3 ± 1.5a	19.6 ± 2.0a	19.4 ± 1.01a
Undefoliated leaf area (mm^2)	29.7 ± 0.40a	30.0 ± 0.50a	29.9 ± 0.30a	29.4 ± 0.10a
Number of tillers	4.0 ± 0.3a	3.9 ± 0.2a	3.7 ± 0.4a	3.8 ± 0.3a

Means ± SEM followed by different letters are significantly different at the 0.05 probability level.

Table 3. Mean ± SEM wheat gas exchange responses, including photosynthesis (Ps), stomatal conductance (g_s), *intercellular* CO_2 (C_i), *and transpiration* (E), to defoliation levels and days after defoliation was imposed at the vegetative and reproductive stages

Physiological parameters	Wheat plants at vegetative stage (defoliation levels)			
	Control (0%)	Low (25–45%)	Medium (50–75%)[a]	High (>75%)
Ps (μmol $CO_2/m^2/s$)	14.2 ± 5.7a	17.29 ± 3.8a	-	20.15 ± 2.9b
g_s (mol $H_2O/m^2/s$)	0.186 ± 0.02a	0.164 ± 0.04a	-	0.224 ± 0.03a
Ci (μmol CO_2 mol/air)	201.2 ± 23.0a	182.5 ± 24.0a	-	229.1 ± 23.2a
E (mol $H_2O/m^2/s$)	2.24 ± 0.23a	2.01 ± 0.30a	-	2.54 ± 0.10a
	Wheat plants at reproductive stage (defoliation levels)			
	Control (0%)	Low (25–45%)	Medium (50–75%)	High (>75%)
Ps (μmol $CO_2/m^2/s$)	15.97 ± 4.5a	16.33 ± 3.1a	17.66 ± 3.6a	19.69 ± 2.7b
g_s (mol $H_2O/m^2/s$)	1.45 ± 1.12a	1.91 ± 1.1a	2.28 ± 1.0a	2.09 ± 1.13a
Ci (μmol CO_2 mol/air)	166.7 ± 82.3a	146.8 ± 90.6a	299.5 ± 62.1a	265.3 ± 52.1a
E (mol $H_2O/m^2/s$)	2.73 ± 0.45a	2.88 ± 0.56a	3.11 ± 0.40a	3.57 ± 0.86a

Means ± SEM followed by different letters are significantly different at the 0.05 probability level.
[a] There was no medium defoliation level for the exp with plants at vegetative stage.

able fluorescence, overall photochemical quantum yield, apparent photosynthetic electron transfer rate, and the quenching coefficients, nonphotochemical quenching, and photochemical quenching of plants defoliated during reproductive stages (F_o: $F = 1.85$, df = 3,31, $P = 0.158$; Y: $F = 1.35$, df = 3,31, $P = 0.278$; ETR: $F = 0.23$, df = 3,31, $P = 0.872$; qN: $F = 2.62$, df = 3,31, $P = 0.068$; qP: $F = 1.52$, df = 3,31, $P = 0.229$). Plants defoliated during vegetative stages showed similar responses (F_o: $F = 0.39$, df = 3,31, $P = 0.6933$; Y: $F = 0.22$, df = 3,31, $P = 0.8102$; ETR: $F = 4.75$, df = 3,31, $P = 0.058$; qN: $F = 0.27$, df = 3,31, $P = 0.7711$; qP: $F = 3.44$, df = 3,31, $P = 0.1013$).

Time (i.e., days after defoliation treatment) elicited significant changes in photosynthesis in both the flag leaf ($F = 6.93$, df = 2,40, $P = 0.0026$) and the undefoliated leaf ($F = 4.51$, df = 2,40, $P = 0.0171$) from plants during reproductive stages. We also observed a significant effect of time on all closely related photosynthetic parameters, such as stomatal conductance, intercellular CO_2 concentrations, and transpiration rates (g_s—flag leaf: $F = 17.82$, df = 2,40, $P < 0.0001$; undefoliated leaf: $F = 15.30$, df = 2,40, $P < 0.0001$; Ci—flag leaf: $F = 35.76$, df = 2,40, $P < 0.0001$; undefoliated leaf: $F = 18.08$, df = 2,40, $P < 0.0001$; E—flag leaf: $F = 35.76$, df = 2,40, $P < 0.0001$; undefoliated leaf: $F = 41.55$, df = 2,40, $P < 0.0001$). These results indicate that the photosynthesis rates were significantly reduced as the plants senesced, which is commonly observed for most plant species. We did not observe any significant interaction between time and defoliation.

Time also had a significant effect on all chlorophyll *a* fluorescence parameters measured (F_o: $F = 8.59$, df = 3,31, $P = 0.0003$; Y: $F = 3.95$, df = 3,31, $P = 0.017$; ETR: $F = 6.89$, df = 3,31, $P = 0.001$; qN: $F = 4.38$, df = 3,31, $P = 0.011$; qP: $F = 5.11$, df = 3,31, $P = 0.005$).

Additionally, we observed a significant effect of time on chlorophyll *a* parameters from flag leaves of plants during vegetative stages (F_o: $F = 22.15$, df = 2,11, $P = 0.0001$; Y: $F = 8.89$, df = 2,11, $P = 0.005$; ETR: $F = 33.32$, df = 2,11, $P < 0.0001$; qN: $F = 13.56$, df = 2,11, $P = 0.0011$; qP: $F = 25.68$, df = 2,11, $P < 0.0001$). In general, we observed a significant increase in nonvariable fluorescence and nonphotochemical quenching as plants senesced. An opposite trend was observed for the remaining parameters, overall photochemical quantum yield, apparent photosynthetic electron transfer rate, and the photochemical quenching, which decreased as plants senesced. No significant interactions were observed between defoliation and time.

Our results indicate that primary physiology of wheat was not negatively affected by whole plant source-sink manipulation. Defoliation was responsible for appreciably altering the relative source activity for a short period of time, with a transient increase in photosynthetic capacity. Although wheat source leaves had photosynthesis enhancement after defoliation, we did not observe any significant alteration in photochemical activity. In addition, we did not observe a significant enhancement in source leaf stomatal conductance. The lack of alteration of stomatal conductance values indicates that carboxylation efficiency and ribulose 1,5-bisphosphate regeneration may have been enhanced shortly after WPPD. This hypothesis is supported by previous studies (Thorne and Koller 1974, Koller and Thorne 1978, DeJong 1986, Tschaplinski and Blake 1989, Layne and Flore 1992, Peterson et al. 2004). Tschaplinski and Blake (1989) suggested that when enhancement of photosynthesis occurs after defoliation, it indicated that source leaves were operating below their maximum photosynthetic potential before defoliation. Layne and Flore (1992) found that photosynthetic enhancement of individual leaves to leaf-area reduction was caused by increased photochemical and carboxylation efficiencies and ribulose 1,5-bisphosphate regeneration rate on defoliated sour cherry trees, *Prunus cerasus.* They also observed enhanced stomatal conductance, which contributed to the observed photosynthetic response. Similar results were reported by Tschaplinski and Blake (1989) on leaves after decapitation of coppice shoots and by DeJong (1986) on fruiting peach trees, *Prunus persica.* Alterations in both stomatal and mesophyll conductance of soybean leaves after source-sink manipulation also have been reported (Thorne and Koller 1974, Koller and Thorne 1978).

Hudson et al. (1992) suggested that stomatal function is independent of total Rubisco activity. It might be a result of alterations in carbon pools, in which carbohydrate storage in source leaves decreases while phloem activity increases to retain the carbon supply to sink tissue. This has also been suggested as an important plant adaptation to defoliation in C4 grass (Dyer et al. 1991). However, the intensities of defoliation in our study did not elicit similar responses, which indicate that short-lived enhanced photosynthetic capacity might not be related directly to stomatal dynamics.

In other insect–plant systems, delayed senescence has been observed on remaining tissue after defoliation, which most likely was a consequence of increases in resources available to the remaining tissue. Delayed senescence is characterized by the maintenance of high photosynthetic rates and a delay in the normal progressive senescence pattern (Nowak and Caldwell 1984, Wallace et al. 1984, Mariko and Hogetsu 1987, Higley 1992, Peterson et al. 1992, Higley et al. 1993, Peterson and Higley 1993, Haile et al. 1998, Meyer 1998). The occurrence of delayed leaf senescence may depend on a series of factors, such as level of injury, timing of injury, and environmental resources (Hammond and Pedigo 1981, Pedigo et al. 1986, Haile et al. 1998). In our study, WPPD did not seem to result in any physiological modification of wheat senescence. Our data suggest that defoliation levels as much as 75% were not sufficient to elicit similar results observed in previous studies (Nowak and Caldwell 1984, Wallace et al. 1984, Mariko and Hogetsu 1987, Senock et al. 1991, Higley 1992, Peterson et al. 1992, Peterson and Higley 1993, Haile et al. 1998, Meyer 1998).

Based on our findings in this study, it seems that whole plant source-sink manipulation of wheat by WPPD during either of the major plant developmental stages (i.e., vegetative and reproductive) did not elicit any significant long-term modifications to growth, morphological, or primary physiological characteristics. Conversely, short-lived photosynthetic enhancements of plants with high levels of defoliation were observed for both vegetative and reproductive stages. However, such enhancement could not be related directly to modifications of other photosynthetic parameters, such as changes in photochemical efficiency or CO_2 uptake as reported by previous studies.

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