

ISSN 1678-3921

Journal homepage: www.embrapa.br/pab

For manuscript submission and journal contents,
access: www.scielo.br/pab

Physiological and yield parameters of wheat as affected by tiller removal and defoliation




Abstract – The objective of this work was to evaluate the photosynthetic parameters, yield potential, and response to defoliation of wheat (*Triticum aestivum*) plants subjected to tiller removal. Two experiments were conducted under greenhouse conditions. In the first, the two following cultivars were evaluated for complete tiller removal: TBIO Audaz and BRS 394, with a high and low tillering capacity, respectively. In the second, only 'TBIO Audaz' was subjected to detillering and defoliation at post-anthesis. Tiller removal increased the yield potential of the main stem of both tested cultivars and the CO₂ assimilation potential of the flag leaf, which was possibly a strategy to meet the demands for an increased sink strength, as evidenced by the response curves to irradiance and leaf internal CO₂ concentration. The partial defoliation of 'TBIO Audaz' increased daily CO₂ assimilation, both in intact and detillered plants. Detillered plants show a higher photosynthetic and yield potential of the main stem, but also a greater sensitivity to defoliation in the post-anthesis period.

Index terms: *Triticum aestivum*, photosynthesis, source-sink relationship, tillering.

Parâmetros fisiológicos e produtivos de trigo afetados pela remoção de perfilhos e pela desfolha

Resumo – O objetivo deste trabalho foi avaliar os parâmetros fotossintéticos, o potencial produtivo e as respostas à desfolha de plantas de trigo (*Triticum aestivum*) submetidas à remoção de perfilhos. Dois experimentos foram conduzidos em cultivo protegido. No primeiro, as duas seguintes cultivares foram avaliadas quanto à remoção total de perfilhos: TBIO Audaz e BRS 394, com alto e baixo potencial de perfilhamento, respectivamente. No segundo, apenas 'TBIO Audaz' foi submetida à remoção de perfilhos e à desfolha no período de pós-antese. A remoção dos perfilhos aumentou o potencial produtivo do colmo principal das duas cultivares testadas e a assimilação de CO₂ da folha bandeira, que, possivelmente, foi uma estratégia para suprir a maior demanda de drenos, como evidenciado pelas curvas de resposta à irradiância e à concentração foliar interna de CO₂. A desfolha parcial de 'TBIO Audaz' aumentou a assimilação diária de CO₂, tanto em plantas intactas quanto nas com perfilhos removidos. As plantas submetidas à remoção de perfilhos apresentam maior potencial fotossintético e produtivo do colmo principal, mas, também, maior sensibilidade à desfolha no período de pós-antese.

Termos para indexação: *Triticum aestivum*, fotossíntese, relação fonte-dreno, perfilhamento.

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Received
October 14, 2022

Accepted
March 06, 2023

How to cite

FIGEZE, S.L.; BORGA, I.; RIBEIRO, E.C. Physiological and yield parameters of wheat as affected by tiller removal and defoliation. *Pesquisa Agropecuária Brasileira*, v.58, e03156, 2023. DOI: <https://doi.org/10.1590/S1678-3921.pab2023.v58.03156>.



Introduction

Wheat (*Triticum aestivum* L.) yield is limited by sink capacity (Lawlor & Paul, 2014; Borrill et al., 2015), being influenced by the ability of plants to allocate resources and by the size and number of sinks (Smith et al., 2018). Therefore, cereal yield can be increased by modifying sink capacity through genetic improvement or management practices (Furbank et al., 2019).

A promising approach to enhance sink strength in wheat plants is the use of signaling molecules, such as trehalose-6-phosphate, to increase sugar allocation in reserve tissues (Griffiths et al., 2016). Tiller inhibition (*tin*) mutants (Kebrom et al., 2012; Kebrom & Richards, 2013; Hendriks et al., 2016) and artificial tiller removal (Guo & Schnurbusch, 2015; Fioreze et al., 2020, 2021) can also be used to increase the yield potential of the ear and provide important information about the effect of inter-stem competition on source-sink relationships.

Researches on *tin* lines have shown that tiller suppression improves main stem development and yield (Mitchell et al., 2013; Hendriks et al., 2016), enhancing the strength of spike sinks. Dreccer et al. (2013) added that low-tillering wheat genotypes have high concentrations of water-soluble carbohydrates in the main stem, which may explain the higher yield potential of individual spikes in detilled plants (Guo & Schnurbusch, 2015; Fioreze et al., 2019). According to Furbank et al. (2019), this finding is related to the competition between sinks already in the early growth stages of wheat plants, when tillering represents an intense process of competition between the main stem and tillers for water, nutrients, and light, as well as for photoassimilates.

Despite these important results, there are no known studies on the photosynthetic behavior of detilled plants after anthesis and the impact of detillering on grain filling. Defoliation simulated after anthesis has shown that there may be a long period of limited assimilate availability for grain filling in plants, forcing those with normal tillering to remobilize carbon metabolites from stems or to improve ear photosynthetic activity (Zhang et al., 2020).

The objective of this work was to evaluate the photosynthetic parameters, yield potential, and response to defoliation of wheat plants subjected to tiller removal.

Materials and Methods

Two experiments were conducted under greenhouse conditions during the winter of the 2019 growing season in the municipality of Curitiba, in the state of Santa Catarina, Brazil (27°16'26.55"S, 50°30'14.41"W, at 988 m altitude). The experimental design was a randomized complete block with four replicates, in a 2x2 (experiment 1) and 2x3 (experiment 2) factorial arrangement.

In experiment 1, the following two wheat cultivars with contrasting tiller capacities were evaluated: TBIO Audaz and BRS 394, with a high and low capacity, respectively. Both cultivars were subjected to two treatments: free tillering (control, with no detillering) and complete detillering of the main stem. For detilled plants, all late-emerging tillers were manually removed. In experiment 2, only 'TBIO Audaz' was evaluated, being subjected to detillering (control and detillering) and defoliation at post-anthesis (control, partial defoliation, and total defoliation). Leaves were removed at the beginning of plant anthesis, and only the flag leaf was maintained for partial defoliation.

The plants used in the study were grown in 3.6 L plastic pots filled with a Cambissolo Háplico (Santos et al., 2018), i.e., a Haplic Inceptisol (Soil Survey Staff, 2014) of clayey texture (550 g kg⁻¹ clay), limed with 1.51 g dm⁻³ limestone at 40 days before sowing. A base fertilizer, consisting of 120 mg dm⁻³ potassium chloride (60% K₂O) and 2.16 g dm⁻³ triple superphosphate (42% P₂O₅), was mixed with the soil. In each pot, four seeds were sown at a 3.0 cm depth, and, after emergence, seedlings were thinned to two. Side dressing nitrogen fertilization was carried out every 15 days between emergence and anthesis, using urea (45% nitrogen) applied in solution (25 mg dm⁻³ N) to reach 150 mg dm⁻³ N. Soil moisture was maintained close to field capacity throughout the growing period by manual irrigation. The maximum temperature of the greenhouse was set to 30°C with natural irradiation. The propiconazole fungicide was applied between the jointing and flowering stages as a protective management of foliar diseases.

Gas exchange was measured at anthesis using the LI-6400XT portable photosynthesis meter (LICOR Biosciences Lincoln, NE, USA). The curves of the responses to photosynthetic light (A_n versus I) and CO₂ (A_n versus C_i) were plotted in experiment 1, where A_n is the net photosynthetic rate, I is irradiance, and

C_i is leaf internal CO_2 concentration. Light-response curves were obtained by varying I from 1,800 to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, at 25°C , in a fixed CO_2 concentration of 400 $\mu\text{mol mol}^{-1}$. The linear portion of the response curve was subjected to the linear regression analysis in order to determine apparent quantum yield and light compensation point according to Habermann et al. (2003).

The A_n versus C_i curve was determined at 1,600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 25°C , with measurements starting at 400 $\mu\text{mol mol}^{-1} \text{CO}_2$. Once the steady state was reached, the CO_2 concentration was gradually decreased to 50 $\mu\text{mol mol}^{-1}$ and, then, increased stepwise to 1,500 $\mu\text{mol mol}^{-1}$. CO_2 assimilation and the corresponding internal CO_2 values for the linear portion of the response curve were subjected to the linear regression analysis in order to determine carboxylation efficiency (Farquhar & Sharkey, 1982). In addition, CO_2 assimilation values at a leaf external (AC_e) and internal (AC_i) CO_2 concentration of 400 $\mu\text{mol mol}^{-1}$ were used to determine the relative effect of stomatal resistance on photosynthesis (S) as described in Farquhar & Sharkey (1982).

Since wheat is markedly known as a sink-limited plant (Lawlor & Paul, 2014; Borrill et al., 2015), in experiment 2, defoliation aimed to simulate a long period of limited assimilate availability for grain filling. A daily curve of net carbon assimilation was plotted in the anthesis stage (except for fully defoliated plants) at ten days after defoliation. During measurements, the CO_2 concentration was fixed at 400 $\mu\text{mol mol}^{-1}$. Photon influx to the chamber was adjusted according to external I values at 6:00 a.m., 9:00 a.m., noon, 3:00 p.m., and 6:00 p.m. The flag leaf of fully defoliated plants was collected and evaluated for length and width.

In the two experiments, plants were harvested at maturity and the main stems were individually evaluated for the following morphological and yield parameters: rachis length, number of spikelets, number of fertile spikelets, number of grains, grain weight, and thousand-grain weight. Basal stem diameter and peduncle diameter were determined only in experiment 2.

Data were subjected to the analysis of variance by the F-test at 5% probability, and means were compared by Tukey's test at 5% probability using the SISVAR software (Ferreira, 2011).

Results and Discussion

In experiment 1, tiller removal increased the photosynthetic response of the two wheat cultivars under high radiation (Figure 1). The absence of intraspecific competition due to detillering resulted in higher maximum A_n values for both cultivars. By contrast, apparent quantum yield was slightly lower in detillered plants, whereas the light compensation point was higher, particularly in 'BRS 394'. Moreover, tiller removal increased carbon assimilation potential under high radiation, and, given that apparent quantum yield was little affected, there also seemed to be an increase in metabolic carbon consumption via dark respiration. According to O'Leary et al. (2017), dark respiration is highly related to plant carbon and nitrogen status.

The increase in the radiation response of detillered plants can be explained by the increase in stomatal conductance (g_s), C_i , and transpiration rate (E) (Figure 2). For both cultivars, g_s , C_i , and E increased with detillering, particularly in BRS 394. Given that the differences between treatments were observed in the region of the curve that represents a limitation of photosynthesis by CO_2 diffusion, g_s acts there as a pathway for increasing C_i values and CO_2 assimilation in detillered plants (Zhao et al., 2020).

Detillering, therefore, caused changes in plant photosynthetic activity in response to the increase in internal CO_2 concentration (A_n versus C_i) (Figure 3). 'TBIO Audaz' showed better responses to tiller removal (Figure 3 A). In the plants of both cultivars, detillering caused a higher catalytic capacity of Rubisco (Figure 3 B and D), but did not affect the AC_e , AC_i , and S parameters (Table 1).

The enhanced photosynthetic potential of the plants might be associated with a high foliar nitrogen content, mainly through the increase in the maximum carboxylation velocity of Rubisco (Cabrera-Bosquet et al., 2009). This can be a key process to explain the highest values of leaf area and photosynthetic activity in detillered wheat plants as a consequence of reduced intraspecific competition. Hendriks et al. (2016) found that an increased root/shoot ratio and foliar nitrogen content in wheat lines expressing the *tin* gene improved water availability, which is another determining factor for maintaining stomatal opening throughout the day.

Considering morphological and yield parameters, tiller removal promoted an increase in the yield

potential of the main stem in both cultivars (Table 1). Detilled plants showed a higher rachis length, grain number per spike, and grain weight per spike, regardless of the cultivar. The interaction between wheat cultivar and tiller removal affected the number of fertile spikelets and thousand-grain weight. In this case, 'TBIO Audaz' plants subjected to tiller removal had a higher number of spikelets, as well as a greater thousand-grain weight (Table 2), although the latter parameter was increased in the two cultivars due to detilling. This finding can be attributed to the higher tillering potential of 'TBIO Audaz' (seven tillers per plant, $n = 4$) compared with 'BRS 394' (four tillers per plant, $n = 4$). Fioreze et al. (2020, 2021) highlighted

that, the greater the competition between main stem and tillers, the greater the effect of tiller removal.

In experiment 2, the flag leaf length of 'TBIO Audaz', determined in plants subjected to total defoliation, was significantly longer in detilled plants (Figure 4); however, leaf width was not affected. The differences between treatments were observed mainly under high irradiance, similar to the pattern found for the $A_n \times I$ curves (Figure 1). Detilled plants, whether partially defoliated or not, showed the highest daily carbon assimilation (Figure 5), whereas partially defoliated plants exhibited a higher assimilation than those of the control, regardless of the tillering treatment (without and with detilling). This finding is in alignment with that of Macedo et al. (2006), who concluded that the

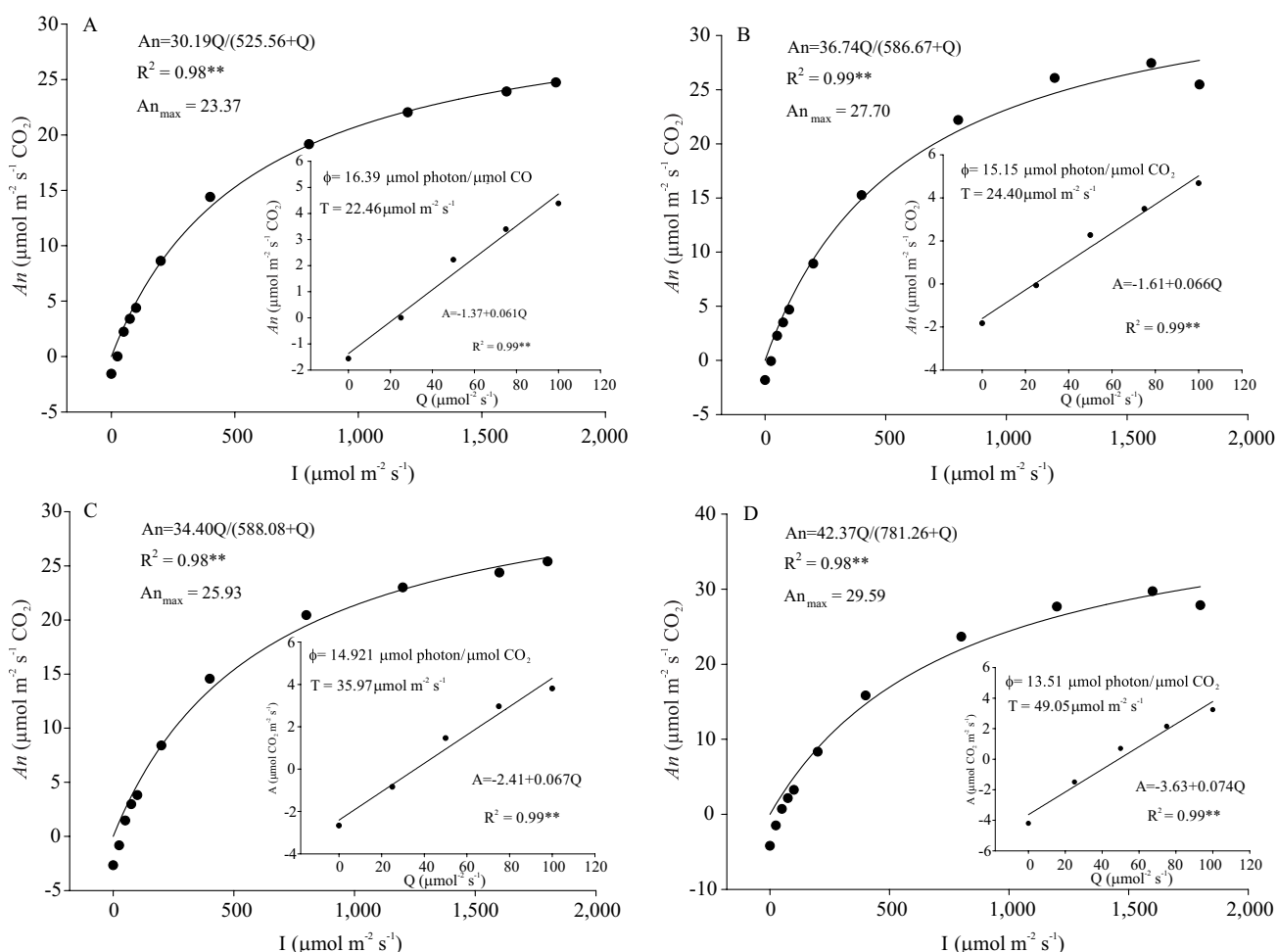


Figure 1. Irradiance (I) versus net photosynthetic rate (A_n) of the TBIO Audaz (A and B) and BRS 394 (C and D) wheat (*Triticum aestivum*) cultivars at anthesis as affected by tiller removal (B and D). Internal figures present the apparent quantum yield (Φ) and light compensation point (Γ). **Significant at 1% probability.

photosynthetic activity of the flag leaf was adjusted to mitigate the effects of defoliation; however, the

participation of the ear in CO₂ assimilation must also be considered (Zhang et al., 2020).

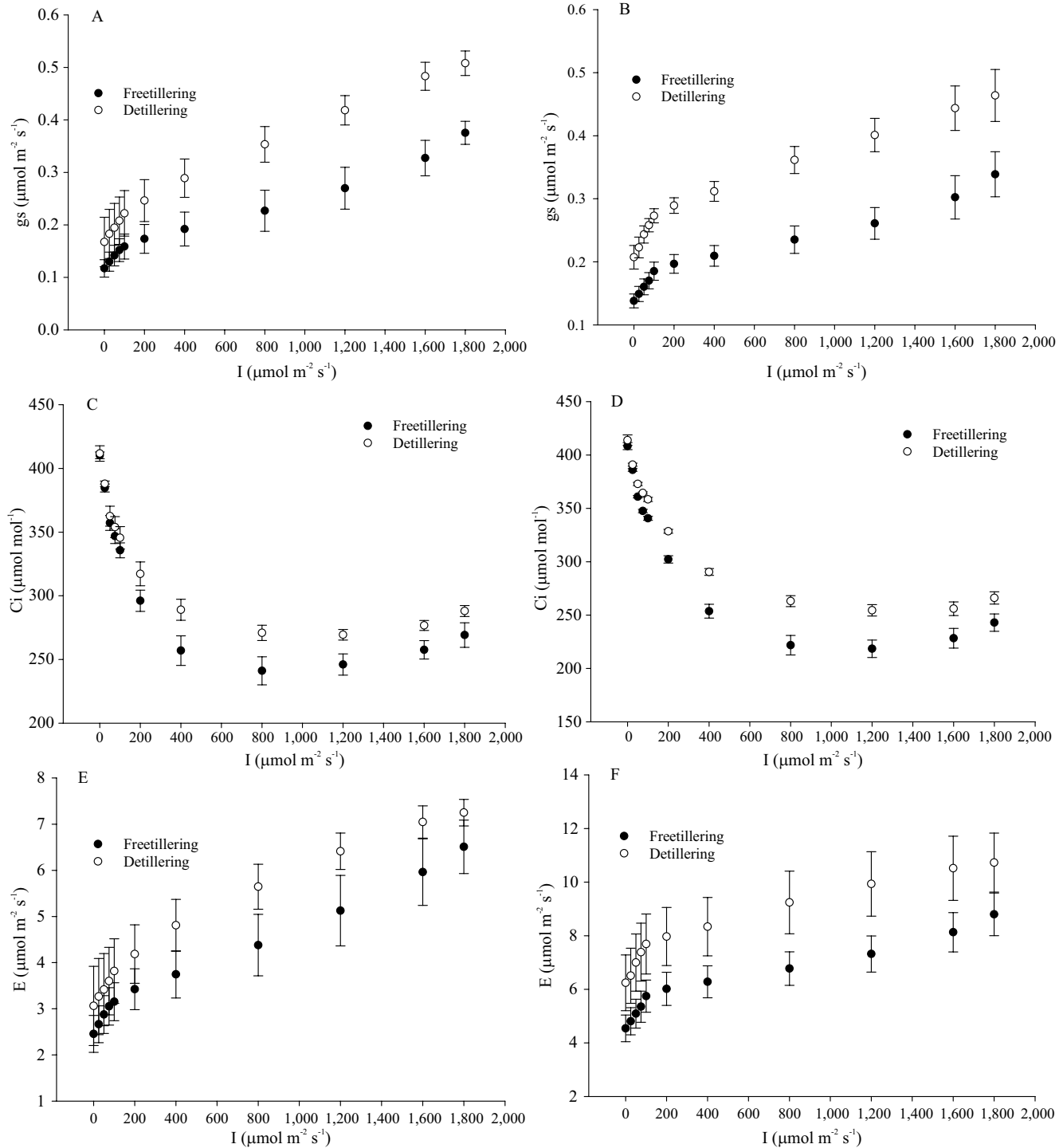


Figure 2. Response of stomatal conductance (g_s), leaf internal CO₂ concentration (C_i), and transpiration rate (E) to irradiance (I) of the TBIO Audaz (A, C, and E) and BRS 394 (B, D, and F) wheat (*Triticum aestivum*) cultivars at anthesis as affected by tiller removal.

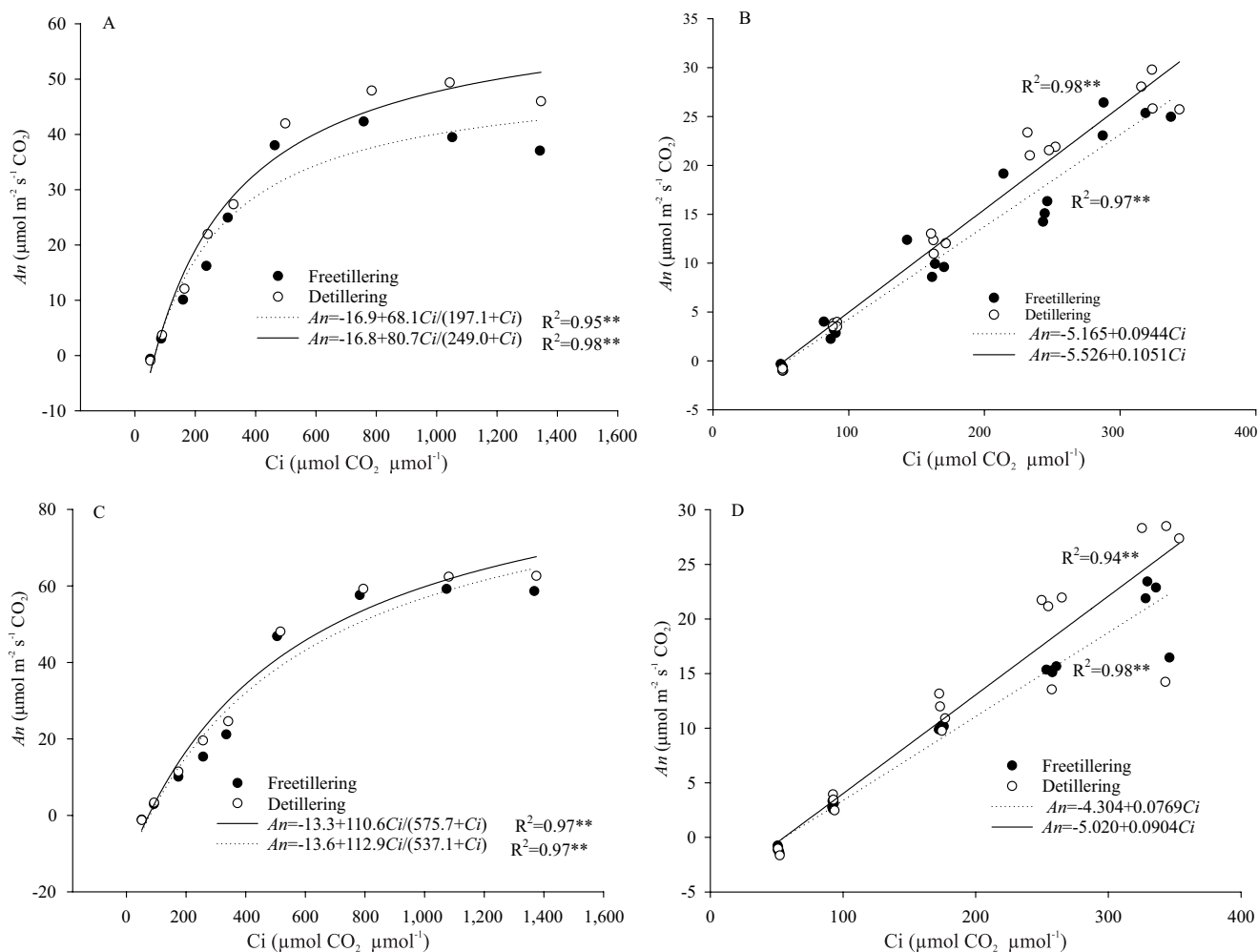


Figure 3. Net carbon assimilation (An) versus leaf internal CO_2 concentration (C_i) (A and C) and carboxylation efficiency (B and D) of the TBIO Audaz (A and B) and BRS 394 (C and D) wheat (*Triticum aestivum*) cultivars at anthesis as affected by tiller removal. ******Significant at 1% probability.

Table 1. Net carbon assimilation at different leaf internal (AC_i) and external (AC_e) CO_2 concentrations, relative effect of stomatal resistance on photosynthesis (S), and yield parameters for the main stem of wheat (*Triticum aestivum*) plant cultivars as affected by tiller removal⁽¹⁾.

Cultivar (C)	AC_i ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	AC_e ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	S (%)	RL (cm)	NS	NFS	NG	GW (g)	TGW (g)
TBIO Audaz	46.89	26.15	44.21	10.6	23.3a	22.1a	84.8	3.4	37.9b
BRS 394	45.61	22.88	50.29	11.0	20.5b	20.1b	81.1	3.6	44.1a
p	0.46	0.14	0.09	0.26	0.00	0.00	0.40	0.21	0.01
Tiller removal (T)									
No detillering	44.51	23.05	48.26	9.8b	21.9	20.6b	67.3b	2.3b	34.4b
Detillering	48.00	25.97	46.23	11.8a	21.9	21.6a	98.6a	4.7a	47.6a
p	0.07	0.18	0.54	0.00	1.00	0.00	0.00	0.00	0.00
C × T (p)	0.89	0.81	0.64	0.06	1.00	0.03	0.47	0.07	0.02
CV (%)	7.24	16.31	13.59	7.35	5.11	2.84	10.04	12.18	8.24

⁽¹⁾Means followed by equal letters do not differ by Tukey's test, at 5% probability. AC_i , net carbon assimilation when the leaf internal CO_2 concentration is $400 \mu\text{mol mol}^{-1}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$); AC_e , net carbon assimilation when the external CO_2 concentration is $400 \mu\text{mol mol}^{-1}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$); RL, rachis length; NS, number of spikelets; NFS, number of fertile spikelets; NG, number of grains; GW, grain weight; TGW, thousand-grain weight; p, probability by the F-test; and CV, coefficient of variation.

As in experiment 1, high carbon assimilation rates coincided with high g_s values, which resulted in higher E values (Figure 5 C). Considering that transpiration was markedly higher in plants with an increased photosynthetic activity, water use efficiency was slightly lower in detillered plants (Figure 5 D). In a previous work, Hendriks et al. (2016) found that *tin* lineages have a higher leaf photosynthetic potential

Table 2. Effects of the interaction tiller removal \times cultivar on number of fertile spikelets and thousand-grain weight on the main stem of wheat (*Triticum aestivum*) plants⁽¹⁾.

Cultivar	Number of fertile spikelets		Thousand-grain weight (g)	
	No detillering	Detillering	No detillering	Detillering
'TBIO Audaz'	21.3Ba	23.0Aa	29.0Bb	46.8Aa
'BRS 394'	20.0Ab	20.3Ab	39.8Ba	48.4Aa
LSD	0.96		5.40	

⁽¹⁾Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ by Tukey's test, at 5% probability. LSD, least significant difference.

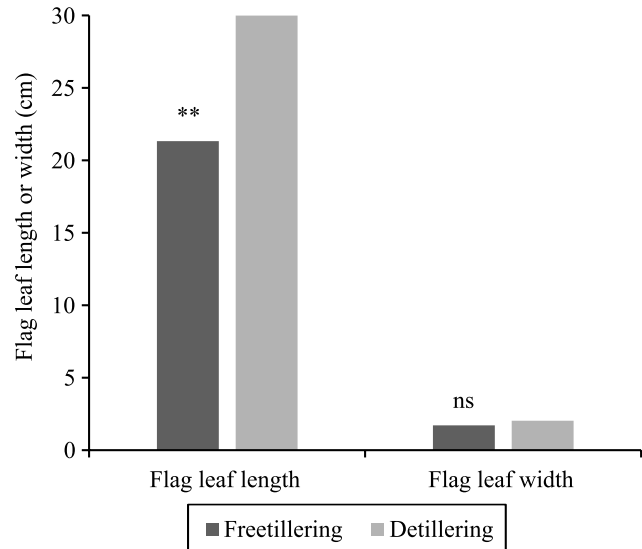


Figure 4. Flag leaf length and width of the TBIO Audaz wheat (*Triticum aestivum*) cultivar as affected by tiller removal. **Significant by Tukey's test at 1% probability. nsNonsignificant.

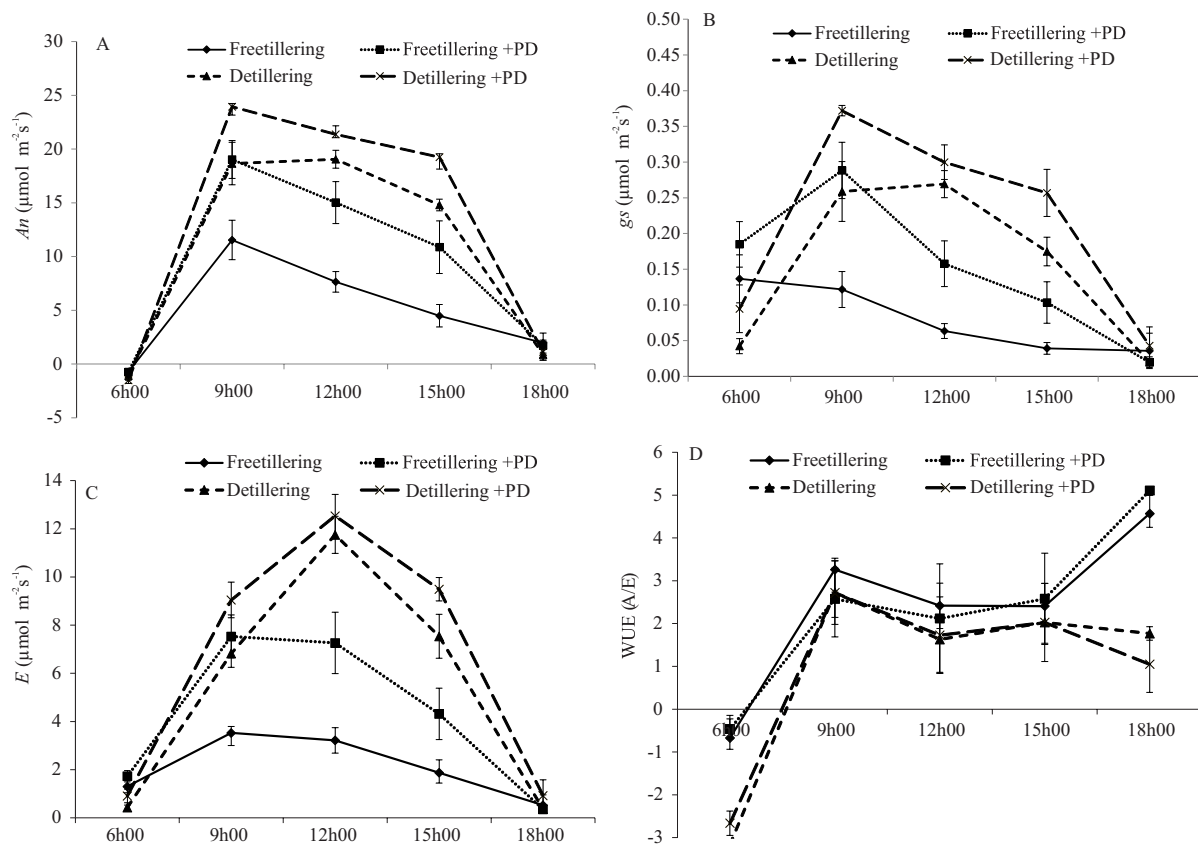


Figure 5. Graphs showing: A, daily net carbon assimilation (An); B, stomatal conductance (g_s); C, transpiration rate (E); and D, photosynthetic water use efficiency (WUE) of the TBIO Audaz wheat (*Triticum aestivum*) cultivar as affected by tiller removal and partial defoliation (PD).

even under field conditions. Considering that days with I values greater than $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ were frequent in the present study, this response is of great importance for carbon accumulation, indicating a lower need for the dissipation of excess-light energy. A similar pattern was observed for daily CO_2 assimilation since detillered plants exhibited a greater daily CO_2 accumulation (Figure 5).

Grain number and weight per spike, as well as thousand-grain weight, were significantly affected by the interaction between tiller removal and defoliation (Table 3). Grain number per spike increased significantly in detillered plants, regardless of defoliation, as observed in experiment 1. Furthermore, this parameter was not influenced by defoliation in plants that were not detillered, but showed the highest values in partially-defoliated detillered plants, which did not differ from those of the control. Similar results were found for grain weight per spike. In detillered

plants, thousand-grain weight, grain number per spike, and grain weight per spike reduced drastically as a result of total defoliation (Table 4). However, tiller removal and defoliation did not affect thousand-grain weight and plants that were not detillered, respectively (Table 3).

Yield components were not affected by partial or total defoliation in plants that were not subjected to detillering. Interestingly, in partially defoliated plants, yield potential was maintained due to the increase in the photosynthetic activity of the flag leaf. This increased activity is probably associated with the almost two-fold increase in the grain number of detillered plants, which enhanced sink strength.

An increase in yield potential was observed with the increase in the photosynthetic potential of the main stem, combined with the decreased competition for water and nutrients, as evidenced by the higher number of spikelets and initiated flowers. Similar effects were reported for wheat plants subjected to tiller removal, attributed to a greater availability of resources during flower initiation and differentiation (Guo & Schnurbusch, 2015). Furthermore, there was a significant increase in grain weight and thousand-grain weight caused by the increase in the photosynthetic activity of detillered plants at post-anthesis. In this case, the increase in thousand-grain weight can be explained by an increase in nitrogen contents, which is known to occur in the leaves and grains of *tin* lineages (Hendriks et al., 2016), whereas the increase in the photosynthetic activity of detillered plants can be explained by the increase in sink capacity (grain number and size). Such findings underscore the importance of increasing sink strength as a strategy to enhance source activity in wheat, as shown by Griffiths et al. (2016).

The increase in the daily CO_2 assimilation of partially defoliated plants added to the reduced grain

Table 3. Morphological and yield parameters of the main stem of 'TBIO Audaz' wheat (*Triticum aestivum*) plants as affected by tiller removal and defoliation⁽¹⁾.

Tiller removal (T)	RL (cm)	NG	GW (g)	TGW (g)
No detillering	12.0	78.2	3.02	38.8
Detillering	15.1	136.5	5.31	37.8
p	0.00	0.00	0.00	0.61
Defoliation (D)				
Control	13.1	112.4	4.63	40.9
Partial defoliation	14.3	119.1	5.14	42.3
Total defoliation	13.2	90.5	2.73	31.5
p	0.25	0.00	0.00	0.00
T × D (p)	0.11	0.04	0.00	0.02
CV (%)	10.66	12.98	21.01	12.42

⁽¹⁾RL, rachis length; NG, number of grains; GW, grain weight; TGW, thousand-grain weight; p, probability by the F-test; and CV, coefficient of variation.

Table 4. Effects of the interaction tiller removal × defoliation on number of grains, grain weight, and thousand-grain weight of the main stem of 'TBIO Audaz' wheat (*Triticum aestivum*) plants⁽¹⁾.

Treatments	Number of grains		Grain weight (g)		Thousand-grain weight (g)	
	No detillering	Detillering	No detillering	Detillering	No detillering	Detillering
Control	87.0Ba	137.8Aab	3.47Ba	5.80Aa	39.8Aa	42.0Aa
Partial defoliation	78.8Ba	159.5Aa	3.14Ba	7.13Aa	40.1Aa	44.6Aa
Total defoliation	68.8Ba	112.2Ab	2.46Aa	3.00Ab	36.3Aa	26.7Bb

⁽¹⁾Means followed by equal letters, uppercase in the lines and lowercase in the columns, do not differ by Tukey's test, at 5% probability. LSD, least significant difference.

yield in detilled plants subjected to total defoliation allow of inferring that spike yield potential is more dependent on source capacity in detilled plants. Although the present work was carried out under greenhouse conditions, this result can help to explain why wheat lines expressing the *tin* gene are more susceptible to severe water deficit at post anthesis (Moeller & Rebetzke, 2017; Houshmandfar et al., 2019), which causes a reduction in the photosynthetic metabolism of plants.

Conclusions

1. Tiller removal increases grain number and weight on the main stem of wheat (*Triticum aestivum*) plants.
2. Tiller removal enhances the photosynthetic capacity of the flag leaf.
3. Detilled wheat plants are more sensitive to total defoliation at post-anthesis.

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