

Article

Effects of Leaf Cutting on *Fusarium* Head Blight Disease Development, Photosynthesis Parameters and Yield of Wheat under *F. graminearum* Inoculation Condition

Qianglan Huang^{1,2} and Peigao Luo^{1,3,*} 

¹ Provincial Key Laboratory of Plant Breeding and Genetics, Sichuan Agricultural University, Chengdu 611130, China; huangqianglan@swust.edu.cn

² Wheat Research Institute, School of Life Sciences and Engineering, Southwest University of Science and Technology, Mianyang 621010, China

³ State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences (CAAS), Beijing 100193, China

* Correspondence: lpglab@sicau.edu.cn

Abstract: *Fusarium* head blight (FHB), caused by *Fusarium graminearum*, occurs mainly on developing wheat seeds, which are important energy sinks. Leaf cutting (removing a portion of the energy sources) could have an effect on the damage caused by *F. graminearum*. To determine the effects of leaf cutting on disease development, photosynthesis parameters, and yield components between resistant and susceptible wheat genotypes, the wheat FHB-resistant line L693 and FHB-susceptible line L661, which have similar genetic backgrounds, were used in this study. Different numbers of leaves were removed before inoculation with *F. graminearum*, and photosynthesis parameters, including the net photosynthesis rate (P_n), stomatal conductance (G_s), and intercellular CO_2 concentration (C_i), were measured at various time points both before and after *F. graminearum* infection. The number of diseased spikelets (NDS) and yield components were also measured. The greenhouse and field experiments results showed that cutting leaves could decrease the NDS and alleviate the damage from FHB, which could partly compensate for the yield loss caused by *F. graminearum* under *F. graminearum* inoculation condition. Leaf cutting did not significantly change the total grain weight per spike (GWS) after *F. graminearum* inoculation in both L661 and L693. Further study found that the P_n obviously differed between L661 and L693 after infection with *F. graminearum* and cutting leaves could aggravate the P_n difference between L661 and L693, which revealed cutting leaves could change the balance between source and sink, with the change of P_n , which may refer to FHB resistance. This study provides new insights into both energy sources and sinks for future studies on the physiological mechanism underlying systematic resistance against FHB.

Keywords: *Fusarium graminearum*; spikelet; source-sink relationship; *Triticum aestivum* L.; yield component



Citation: Huang, Q.; Luo, P. Effects of Leaf Cutting on *Fusarium* Head Blight Disease Development, Photosynthesis Parameters and Yield of Wheat under *F. graminearum* Inoculation Condition. *Agriculture* **2021**, *11*, 1065. <https://doi.org/10.3390/agriculture11111065>

Academic Editor:
Ana Isabel López-Sesé

Received: 5 September 2021
Accepted: 25 October 2021
Published: 28 October 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Fusarium head blight (FHB), which is caused mainly by *Fusarium graminearum* Schwabe and *Fusarium culmorum* WG Smith, is a destructive disease of wheat (*Triticum aestivum* L.) worldwide [1,2]. FHB threatens food security and quality through contamination with mycotoxins such as deoxynivalenol (DON), which affects the health of both animals and humans [3,4]. FHB resistance is also a complex trait with multiple components. Five type resistances were included, such as resistance to initial penetration of the pathogen (type I), resistance to disease spread within a spike (type II), resistance to accumulation of DON in infected kernels (type III); resistance to *Fusarium*-damaged kernels (type IV) and tolerance to FHB (type V) [1]. In five type resistances, type II resistance is characterized extensively and used in cultivar improvement due to its stability and robustness, such as the number of diseased spikelets.

Photosynthesis is a key link between grain yield and carbon assimilation in natural ecosystems. The infection of plant tissue with fungal pathogens is definitively associated with variation in metabolic pathways, including pathways associated with photosynthesis [5]. At present, the effects of pathogen infection on photosynthesis parameters are highly contrasting. Some studies have shown that the net photosynthesis rate (P_n) decreased after pathogenic infection, as was the case for summer squash infected with *Bemisia argentifolii* [6], Douglas-fir (*Pseudotsuga menziesii*) infected with *Pheocryptopus gaeumannii* [7], grapevine (*Vitis vinifera* L.) infected with *Uncinula necator* or *Plasmopara viticola* [8] and rice infected with *Bipolaris oryzae* [9]. In contrast, other studies have shown that the P_n increased after pathogenic infection, as was the case for wheat inoculated with *Septoria nodorum* at the three-leaf stage [10].

In terms of energy, plant tissues attacked by pathogens can be divided into energy sources or energy sinks. Wheat leaves are major energy sources and synthesize energy-rich carbohydrates via photosynthesis, whereas developing seeds are a type of carbohydrate energy sink [11]. Therefore, various diseases that occur in different types of plant tissues could have different and even contrasting effects on photosynthesis. Powdery mildew caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*) [12] and stripe rust caused by *Puccinia striiformis* f. sp. *tritici* [13] are two important leaf diseases that occur mainly in source tissues, while the causal agents of *F. graminearum* infect mainly the energy sinks of developing wheat seeds [14]. Therefore, powdery mildew, stripe rust, and FHB compose a source and sink disease system that can be used to identify the effects of pathogen infection of energy-associated organs on photosynthesis in wheat. However, whether the effects of disease on the photosynthesis of hosts with different resistance abilities are similar and whether artificially induced changes to the balance between sources and sinks influence disease development are currently unknown.

Host resistance to disease can have different effects on photosynthesis. For example, 3–6 days after pathogen infection, the P_n of flag leaves significantly decreased in the stripe rust-susceptible line Mingxian 169, while the P_n of flag leaves significantly increased in the stripe rust-resistant wheat line 88357 [15]. A similar effect of stripe rust infection on photosynthesis was also shown by another independent study [16]. Similarly, a recent study showed that there were significantly different effects of *Bgt* infection between the photosynthesis parameters of the powdery mildew-susceptible genotype L1095 and the powdery mildew-resistant genotype L693 [17]. In a previous study, *F. graminearum* infection caused more significant reductions in the P_n and stomatal conductance (G_s) of flag leaves and a smaller reduction in 1000-grain weight (TGW) and total grain weight per spike (GWS) in the FHB-resistant genotype L699 than in the FHB-susceptible genotype L661 [18]. We further demonstrated that photosynthesis is involved in FHB resistance and suggested that *F. graminearum* infection could cause brief susceptibility in local spikes and that the brief susceptibility response further increased the expression of genes previously identified to be involved in systemic acquired resistance in the FHB-resistant genotype L693 [14].

To determine the different effects on disease development, photosynthesis parameters and yield components of wheat with different FHB resistance capabilities under various leaf-cutting treatments, a resistant line L693 and a susceptible line L661 [19,20], were used. Photosynthesis parameters such as the net photosynthesis rate, stomatal conductance, and intercellular CO_2 concentration (C_i) were measured via an LI-6400 photosynthesis measurement system. In addition, the yield index, including the number of kernels per spike (NKS), total grain weight per spike, and 1000-grain weight was also investigated. The number of diseased spikelets and the percent of *Fusarium*-damaged kernels (PFDK) were evaluated as the disease index (DI) of FHB in this study.

2. Materials and Methods

2.1. Plant Materials and Cultivation

Two sister wheat lines, the FHB-resistant genotype L693 (Reg. No. GP-974, PI 672538) and the FHB-susceptible genotype L661, derived from an MY11/YU25 cross [20] were selected and planted in a greenhouse in 2019 and 2020, and a field in Wenjiang (30.70° N; 103.83° E) at Sichuan Agricultural University in 2021.

In the greenhouse, more than 200 seeds of each genotype were planted in round plastic basins (top diameter = 20 cm, bottom diameter = 15 cm, height = 15 cm) filled with organic nutrient soil in 2019 and 2020 year. Many seeds are germinated by running water on the tray. Four germinated seeds of the same state were randomly selected and evenly distributed in each basin and just covered the seeds with a little nutrient soil in a day. The light intensity was $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ and persisted for 15 h per day. The air temperature was maintained at 17 °C before the seedlings elongated, after which point the air temperature was maintained at 19 to 20 °C. The relative humidity, an important factor influencing FHB development, was approximately 60%.

The field experiments were conducted in a field of Wenjiang (30.70° N; 103.83° E) at Sichuan Agricultural University, where the climate was warm and rainy and the soil type was loam. The soil with homogeneous fertility and moisture was selected in our study. Wheat seeds were sowed on 25 October 2020. The previous crop is rice. The soil was deep tilled twice using a cultivator on 22 October. Each genotype was sown in six rows with a blank row between two genotypes and six rows in each genotype were divided into two groups. Each group contains three rows in each genotype. Each row was 1.5 m long with 30 seeds and a row spacing of 30 cm. The field aisle is 50 cm. N-P-K compound fertilizer (1280 kg) was used per hectare during sowing time in winter. The field was managed using standardized management.

2.2. Leaf Cutting Treatment and Host FHB Resistance Screening

In the greenhouse, to test the effects of cutting different numbers of leaves on disease development and yield parameters, various leaves were respectively cut at the beginning of flowering stage one day before *F. graminearum* inoculation in 2019 and 2020 year; this time point was denoted as minus one (−1) day after inoculation (DAI). Three treatments, including no cutting, cutting all leaves except the flag leaf, and cutting all leaves, were applied. More than 20 randomly selected spikes of each treatment of each genotype were then inoculated with *F. graminearum* No F₁₅. The *F. graminearum* No F₁₅ was provided by Professor Gong Guoshu, Plant Pathology Laboratory, Sichuan Agricultural University. The *F. graminearum* No F₁₅ was used as inocula, and conidia were prepared as follows. The strain was rejuvenated for 4 days at 25 °C using Potato Dextrose Agar (PDA). PDA contains 200 g/L peeled potatoes, 20 g/L agar, and 15 g/L glucose. Then the conidia propagation was cultured for 3 days in the liquid CMS medium in a shaking table at about 28 °C. CMS medium contains 7.5 g/L sodium carboxymethyl cellulose, 0.5 g/L yeast paste, 0.5 g/L dipotassium hydrogen phosphate and 0.25 g/L magnesium sulfate. The concentration of conidia was calculated using a hemocytometer under a light microscope. The final concentration of inocula was adjusted to 100,000 conidia per ml. At early anthesis, 10 μL conidial suspension (~1000 conidia/spike) was respectively injected into two small flowers in a central spikelet of a spike using a syringe (Hamilton, Reno, NV, USA). The inoculated spikes were then covered with plastic bags to maintain a relatively high humidity, and the plastic bags were removed at 72 h after inoculation. The disease index NDS that was associated with the content of DON was used to evaluate the FHB spread resistance. The number of diseased spikelets (NDS) at 7 and 14 DAI were recorded as NDS1 and NDS2, respectively, and the average of all the inoculated spikes of the same treatment was used to represent the value of the treatment. The NDS1 in 2019, NDS1 in 2020, and NDS2 in 2020 year were investigated.

In the field, the experiment was divided into two groups. To test the effects of cutting different numbers of leaves on disease development and yield parameters, various leaves were respectively cut at the beginning of the flowering stage one day before *F. graminearum* inoculation in each group in 2021. Three treatments, including no cutting, cutting all leaves except the flag leaf, and cutting all leaves, were applied in each group. Each treatment of each genotype was respectively conducted in a row in each group. More than 14 randomly selected spikes of each treatment of each genotype in a group were then inoculated with *F. graminearum* No F₁₅ using the above method. The inoculated spikes were then covered with plastic bags to maintain a relatively high humidity, and the plastic bags were removed at 72 h after inoculation. The NDS at 14 and 21 DAI were recorded as NDS1 and NDS2, respectively, and the average of all the inoculated spikes of the same treatment was used to represent the value of the treatment.

2.3. Measurement of Photosynthesis Parameters

To estimate the different effects of leaf cutting and *F. graminearum* inoculation on the photosynthesis of wheat with different FHB resistance levels, photosynthesis parameters such as the photosynthesis rate, stomatal conductance, and intercellular CO₂ concentration (*C*_i) were measured in the middle of the flag leaves with an LI-6400 photosynthesis measurement device (LI-COR, Lincoln, NE, USA), with an air temperature from 19 to 20 °C, a vapor pressure deficit (VPD) from 0.55 to 0.65 kPa and an actinic light intensity of 1000 μmol m⁻² s⁻¹ in 2019. To compare the different effects of disease infection on photosynthesis parameters at various stages under different leaf cutting conditions, the day before inoculation (−1 DAI) was set as the first time point to compare the two genotypes under the no cutting control conditions. The second time point was set at 1 DAI, which is considered an important time point at which plants develop systemic resistance to *F. graminearum* infection [14]. The final time point was set at 7 DAI, at which point disease development visibly differs between resistant and susceptible genotypes [18]. More than four plants of each genotype (L661 and L693) were randomly selected from among the *F. graminearum* inoculation. The mean value of two measurements of one flag leaf per plant represented a replicate sample, and the mean from all four plants represented the value for a given genotype at a given time point. The measurements of photosynthetic parameters were made in the middle of the flag leaf, based on leaf width. Each measurement took approximately 30 s.

2.4. Measurement of Yield Components and the Percent of *Fusarium*-Damaged Kernels

In 2019, 2020, and 2021, the seeds of the inoculated spikes of each genotype were harvested by hand to avoid the loss of severely wrinkled grains and then dried in an oven. To estimate the different effects of leaf cutting and *F. graminearum* inoculation on yield parameters, the number of kernels per spike, total grain weight per spike, and 1000-grain weight were determined. In addition, to evaluate the effect of cutting leaves and *F. graminearum* inoculation on kernels, the percent of *Fusarium*-damaged kernels per spike (PFDK) was investigated by artificial recognition. The mean value of all the inoculated spikes under the same treatment represented the treatment value.

2.5. Statistical Analysis

Significant differences in disease index, photosynthesis parameters, and yield parameters between L693 and L661 were evaluated separately for each treatment using one-way ANOVA tests and multiple comparison tests (LSD test) with IBM SPSS Statistics 19 software (SPSS Inc., Chicago, IL, USA). In addition, the photosynthesis parameters of adjacent time points were performed using multiple comparison tests (LSD test) using the same software.

3. Results

3.1. FHB Resistance of Wheat under Various Leaf Cutting Treatments

In the greenhouse, all the plants displayed visible FHB symptoms at 7 DAI, with FHB fully developed at 14 DAI (Figure 1), while in the field all the plants also displayed visible FHB symptoms at 14 and 21 DAI (Figure 2). The NDS1 and NDS2 in the greenhouse in 2019 and 2020 were significantly ($p < 0.05$) bigger than in the field in 2021 under the same leaf-cutting treatments (Table 1). This illustrated that the FHB severity in the greenhouse in 2019 and 2020 was obviously heavier than in the field in 2021. Four experiments in the greenhouse and field showed that the NDS1 and NDS2 of L661 were obviously greater than those of L693 under leaf-cutting treatments, and most differences were significant at the $p = 0.05$ level at the same time points (Table 1). This illustrated that host resistance is an important factor that influences disease development.

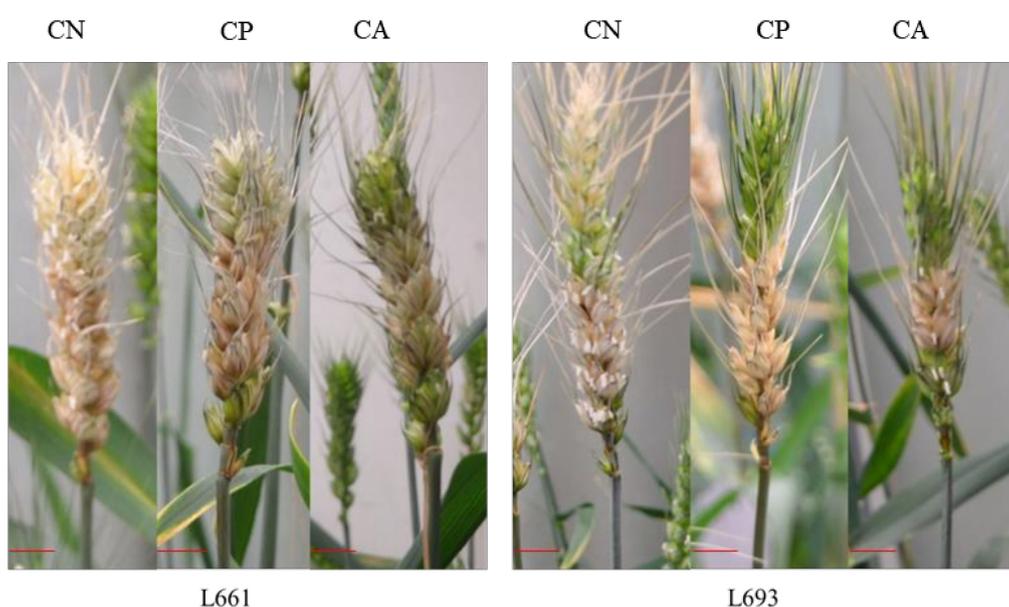


Figure 1. *Fusarium* head blight symptoms at 14 DAI in greenhouse for L661 and L693. CN, CP, and CA—cutting no leaf, cutting some leaves (flag leaf remains), and cutting all leaves, respectively. Scale bar, 1.0 cm.

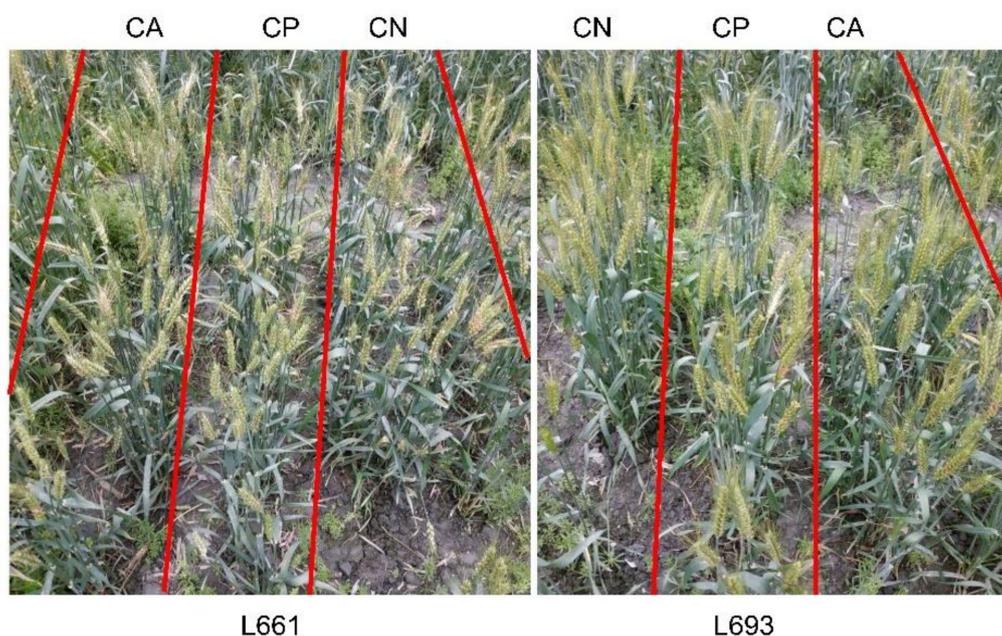


Figure 2. *Fusarium* head blight symptoms at 21 DAI in field group 1 for L661 and L693. CN, CP, CA—cutting no leaf, cutting some leaves (flag leaf remains), and cutting all leaves, respectively.

Table 1. Evaluation FHB resistance and yield indices in the greenhouse and field.

Year	Genotype	Treatments	N	NDS1	NDS2
2019 greenhouse	L661	No leaf cutting	29	6.34 ± 0.35 a A	-
		Flag leaf remains	27	6.07 ± 0.42 a A	-
		Cutting all leaves	27	4.92 ± 0.34 b A	-
	L693	No leaf cutting	22	4.00 ± 0.42 b A	-
		Flag leaf remains	24	3.42 ± 0.31 b A	-
		Cutting all leaves	26	3.50 ± 0.33 b A	-
2020 greenhouse	L661	No leaf cutting	29	6.24 ± 0.24 a A	7.93 ± 0.28 a A
		Flag leaf remains	28	5.61 ± 0.24 a b A	7.25 ± 0.26 a b A
		Cutting all leaves	31	5.55 ± 0.23 b A	7.03 ± 0.22 b A
	L693	No leaf cutting	27	3.56 ± 0.28 c A	5.96 ± 0.33 c A
		Flag leaf remains	29	3.66 ± 0.23 c A	5.48 ± 0.35 c d A
		Cutting all leaves	25	3.04 ± 0.20 c A	4.83 ± 0.41 d A
2021 field group 1	L661	No leaf cutting	24	3.70 ± 0.30 a B	5.15 ± 0.62 a B
		Flag leaf remains	19	2.56 ± 0.20 b c B	3.89 ± 0.42 b B
		Cutting all leaves	31	2.81 ± 0.18 b B	3.76 ± 0.31 b B
	L693	No leaf cutting	24	2.17 ± 0.10 c B	2.24 ± 0.12 c B
		Flag leaf remains	14	2.21 ± 0.11 bc B	2.50 ± 0.18 c B
		Cutting all leaves	23	2.00 ± 0.00 c B	2.18 ± 0.11 c B
2021 field group 2	L661	No leaf cutting	20	3.42 ± 0.27 a B	4.17 ± 0.38 a B
		Flag leaf remains	22	2.95 ± 0.23 a b B	3.87 ± 0.35 a B
		Cutting all leaves	23	2.80 ± 0.24 b B	3.17 ± 0.23 b B
	L693	No leaf cutting	26	2.19 ± 0.19 c B	2.16 ± 0.10 c B
		Flag leaf remains	26	2.09 ± 0.09 c B	2.12 ± 0.09 c B
		Cutting all leaves	16	2.03 ± 0.03 c B	2.06 ± 0.06 c B

All the indices are described as the means ± standard errors; N-the number of spikes inoculated with *F. graminearum*; NDS1-The number of diseased spikelets at 7 DAI in greenhouse in 2019 and 2020, and 14 DAI in field in 2021 year; NDS2-the number of diseased spikelets at 14 DAI in greenhouse in 2019 and 2020, and 21 DAI in Field in 2021; The means in a column followed by the same lowercase letter(s) are not significantly different at the 5% probability level in the same year. The means in a column followed by the same capital letter(s) are not significantly different at the 5% probability level in the same treatments and different year.

Moreover, four experiments in the field and greenhouse showed that cutting some or all leaves could decrease the NDS1 and NDS2 of FHB-susceptible L661 and alleviate the damage of L661 caused by *F. graminearum* inoculation (Table 1). However, in FHB-resistant L693, cutting some or all leaves could only decrease the NDS2 in the greenhouse, where the FHB is heavy, but could not significantly change the NDS1 and NDS2 in the field in 2021, and NDS1 in the greenhouse in 2019 and 2020 (Table 1).

3.2. Effects of FHB on Photosynthesis Parameters under Various Leaf Cutting Treatments

In 2019, no differences in the P_n , G_s , or C_i at day -1 were detected (Figure 3), which perhaps resulted from the similar genetic makeup between L661 and L693 [19]. The results showed that the P_n of the L693 plants rapidly increased from -1 DAI to 1 DAI, while the P_n of the L661 plants rapidly decreased during the same timeframe (Figure 3A). Further analysis revealed that the difference in the change in P_n between L693 and L661 increased when only some leaves were cut (only the flag leaf remained) (CP) compared with that when no leaves were cut (CN), so that the P_n of the L693 plants of CP was significantly ($p < 0.05$) greater than the P_n of the L661 plants of CP (Figure 3A). In addition, the P_n of the L693 plants of CP and the L693 plants of CN rapidly decreased, while the P_n of the L661 plants of CP rapidly increased. The change in the P_n of other plants of CN was minimal from 1 day to 7 days (Figure 3A). Last, the change in both G_s and C_i between L693 and L661 differed to some extent among the different treatments, although the patterns of change were similar (Figure 3B,C).

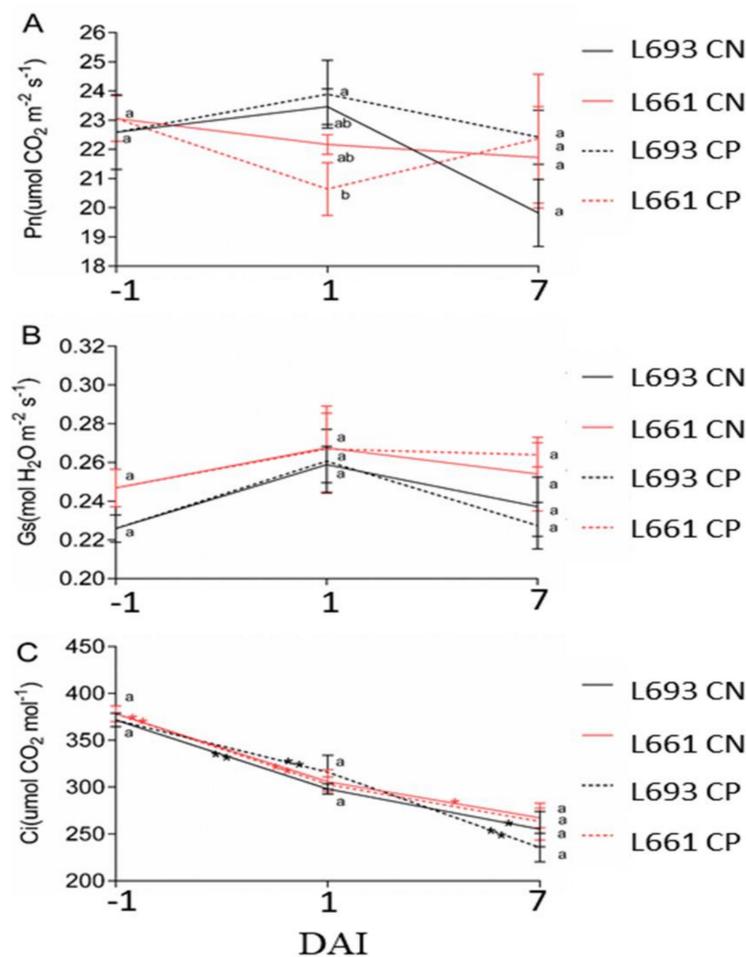


Figure 3. Changes in photosynthesis parameters of plants in the greenhouse. (A–C) represent changes in the P_n , G_s , and C_i in the greenhouse, respectively. P_n —the net photosynthesis rate, G_s —stomatal conductance, and C_i —the intercellular CO_2 concentration. CN—cutting no leaves; CP—cutting some leaves (flag leaf remains). The asterisks represent statistically significant differences, as follows: ** $p < 0.01$ and * $p < 0.05$. An asterisk on the trend line represents the difference between two adjacent time points for the same genotype and treatment. The same lowercase letter(s) at each time point are not significantly different at the 5% probability level in different genotypes and treatments.

3.3. Effects of FHB on Yield Components

Yield component analysis found that cutting some leaves (flag leaf remains) and all leaves resulted in an obvious decrease in NKS in FHB-resistant L693 in four experiments, and significantly ($p < 0.05$) in field group 1 in 2021 (Table 2). In FHB-susceptible L661, cutting some leaves and all leaves could also result in a decrease in NKS in the greenhouse, although it resulted in an increase in NKS in field group 1 and field group 2 (Table 2).

For GWS, In FHB-susceptible L661, cutting some leaves and all leaves resulted in no significant change of GWS in four experiments. In FHB-resistant L693, cutting some leaves and all leaves also resulted in no significant change of GWS in the greenhouse in 2019 and 2020, but a significant ($p < 0.05$) decrease in field group 1 and field group 2 in 2021 (Table 2), which might be associated with the FHB severity.

For PFDK, In FHB-susceptible L661, cutting some leaves and all leaves resulted in a little decrease of PFDK in four experiments in the greenhouse in 2019 and 2020 and in the field in 2021, and significantly ($p < 0.05$) in field group 1 in 2021. However, in FHB-resistant L693, cutting some leaves and all leaves resulted in no significant change of PFDK in four experiments (Table 2).

Table 2. Yield indices and PFDK in the greenhouse and field.

Year	Genotype	Treatments	N	NKS	TGW	GWS	PFDK
2019 greenhouse	L661	No leaf cutting	29	26.3 ± 1.3 a C	4.72 ± 0.43 b B	0.13 ± 0.02 c C	0.77 ± 0.05 a A
		Flag leaf remains	27	25.4 ± 1.2 a b B	5.06 ± 0.39 b B	0.13 ± 0.01 c B	0.75 ± 0.06 a A
		Cutting all leaves	27	25.5 ± 1.5 a b C	5.90 ± 0.67 b B	0.15 ± 0.02 b c C	0.67 ± 0.05 a A
	L693	No leaf cutting	22	21.8 ± 2.2 b c B	14.13 ± 3.17 a C	0.31 ± 0.06 a B	0.44 ± 0.30 b A
		Flag leaf remains	24	21.0 ± 1.3 c B	11.29 ± 1.64 a B	0.24 ± 0.04 a b B	0.46 ± 0.04 b A
		Cutting all leaves	26	20.0 ± 1.6 c B	11.67 ± 1.30 a B	0.25 ± 0.04 a B	0.32 ± 0.07 b A
2020 greenhouse	L661	No leaf cutting	29	16.0 ± 1.0 a D	5.06 ± 0.42 c B	0.08 ± 0.01 b C	0.68 ± 0.04 a A
		Flag leaf remains	28	15.6 ± 1.1 a C	4.98 ± 0.50 c B	0.08 ± 0.01 b B	0.66 ± 0.06 a A
		Cutting all leaves	31	10.8 ± 0.9 b D	7.56 ± 1.48 b B	0.06 ± 0.01 b C	0.64 ± 0.06 a A
	L693	No leaf cutting	27	16.9 ± 0.8 a B	9.26 ± 1.35 a b B	0.16 ± 0.03 a B	0.52 ± 0.04 b A
		Flag leaf remains	29	16.7 ± 1.0 a B	10.59 ± 1.21 a b B	0.19 ± 0.03 a B	0.45 ± 0.04 b A
		Cutting all leaves	25	15.9 ± 0.8 a B	11.99 ± 1.43 a B	0.18 ± 0.02 a B	0.40 ± 0.05 b A
2021 field group 1	L661	No leaf cutting	24	31.5 ± 2.7 c B	25.61 ± 2.76 b A	0.83 ± 0.13 c B	0.30 ± 0.04 a B
		Flag leaf remains	19	32.5 ± 2.8 c A	29.18 ± 2.80 b A	0.98 ± 0.14 c A	0.22 ± 0.04 b B
		Cutting all leaves	31	33.3 ± 2.0 c B	26.62 ± 1.19 b A	0.90 ± 0.07 c B	0.11 ± 0.01 c B
	L693	No leaf cutting	24	47.8 ± 2.2 a A	49.14 ± 1.60 a A	2.35 ± 0.14 a A	0.05 ± 0.01 c B
		Flag leaf remains	14	44.2 ± 3.4 a B A	43.75 ± 2.99 a A	1.94 ± 0.20 b A	0.08 ± 0.03 c B
		Cutting all leaves	23	40.8 ± 1.6 b A	44.53 ± 1.79 a A	1.83 ± 0.10 b A	0.05 ± 0.01 c B
2021 field group 2	L661	No leaf cutting	20	38.05 ± 3.02 c A	29.29 ± 2.25 b A	1.13 ± 0.13 c A	0.24 ± 0.02 a b B
		Flag leaf remains	22	35.41 ± 2.99 d A	31.21 ± 2.28 b A	1.14 ± 0.14 c A	0.26 ± 0.03 a B
		Cutting all leaves	23	39.96 ± 1.78 b c A	29.61 ± 1.69 b A	1.20 ± 0.10 c A	0.2 ± 0.03 b B
	L693	No leaf cutting	26	47.19 ± 1.72 a A	51.17 ± 1.43 a A	2.42 ± 0.11 a A	0.08 ± 0.01 c B
		Flag leaf remains	26	44.54 ± 2.24 a b A	48.66 ± 1.49 a A	2.16 ± 0.12 a b A	0.06 ± 0.01 c B
		Cutting all leaves	16	43.44 ± 1.87 a b c A	43.77 ± 2.05 a A	1.90 ± 0.12 b A	0.03 ± 0.00 c B

All the indices are described as the means ± standard errors; N—the number of spikes inoculated with *F. graminearum*; NKS—the number of kernels per spike; TGW—1000-grain weight; GWS—grain weight per spike; PFDK—the percent of *Fusarium*-damaged kernels; the means in a column followed by the same lowercase letter(s) are not significantly different at the 5% probability level in the same year. The means in a column followed by the same capital letter(s) are not significantly different at the 5% probability level in the same treatments and different years.

4. Discussion

F. graminearum primarily infects developing wheat seeds [1], making it a typical disease that attack photosynthesis energy sinks. There is usually a balance between energy sources and energy sinks, but the balance can change because of biological factors such as pathogen attack [21] and plant development [22,23] and because of abiotic factors such as light intensity [24,25] and temperature [26]. This suggests that an artificial change in the balance between sources and sinks could have an effect on disease development, physiological responses, and yield components. Therefore, in the present study, wheat plants were subjected to different leaf-cutting treatments, both the resistant and susceptible cultivars were inoculated with *F. graminearum*, after which photosynthesis parameters and the yield index were measured.

Various studies have demonstrated that natural genetic variation exists between both species and genotypes with respect to photosynthesis after wheat heading, especially during grain filling [12,27–29]. We found that the difference in photosynthesis parameters between L661 and L693 at -1 DAI was very low and that the difference was largest at 1 DAI (Figure 3). This result can be explained by the slight difference before inoculation resulting from the similar genetic makeup of the hosts [19], while the largest difference at 1 DAI could be due to *F. graminearum* inoculation. Our previous study suggested that photosynthesis is involved in FHB resistance [18] and that the change in photosynthesis during the early stage plays a crucial role in the development of systemic acquired resistance in response to FHB [14]. However, other studies have suggested that systemic acquired resistance conversely results in changes in photosynthesis during the later stage (usually 2 days or more), after *F. graminearum* inoculation [18,30,31]. In addition, some previous reports indicated that a broad range of defense responses in early incompatible interactions similarly occurred in late compatible interactions [32,33]. In the present study, within 1 day after *F. graminearum* inoculation, the *Pn* increased rapidly in the L693 plants but decreased rapidly in the L661 plants, and the tendency for the *Pn* to change after 1 day after *F. graminearum* inoculation in L661 was similar to that before 1 day

after *F. graminearum* inoculation in L693 (Figure 3). Furthermore, the rate of change in the P_n of both L661 and L693 after some leaves cut was faster than that when no leaves were cut (Figure 1), which suggested that cutting some leaves could increase the robustness of the physiological adaptations of both the FHB-susceptible and FHB-resistant wheat during the early stage after *F. graminearum* inoculation.

In our study, the NDS1 and NDS2 of L693 were significantly lower than L661 (Table 1), which illustrated that the FHB resistance of L693 is significantly stronger than L661. Further study found that leaf cutting could decrease the NDS1 and NDS2 in both FHB-resistant L693 and FHB-susceptible L661 in the greenhouse (Table 1), which demonstrated that the decrease in NDS after leaf cutting was a physiological response. Further results showed that leaf cutting could also decrease the NDS1 and NDS2 in FHB-susceptible L661 in the field (Table 1), which further supported that the decrease in NDS after leaf cutting was a physiological response. However, leaf cutting did not significantly change the NDS1 and NDS2 in FHB-susceptible L693 in the field in 2021 (Table 1), which may be explained by the field environmental condition not being conducive to FHB disease for FHB-resistant L693 and the decreased NDS content depended on host resistance to FHB.

Researchers were usually attracted by the accumulation of mycotoxins produced by *Fusarium*, which cause acute food poisoning in both humans and animals that consume infected grains [34]. In the present study, leaf cutting could decrease the PFDK of L693 and L661 shortly after *F. graminearum* infection in the greenhouse and field (Table 2). This indicated that leaf cutting could decrease the mycotoxins content produced by *Fusarium*.

In fact, FHB also severely reduces wheat yield [1,2] and leaf cutting also could reduce wheat yield [35]. In the present study, we observed that *F. graminearum* infection led to an abundance of shriveled seeds for both L661 and L693, with impacts being greater in L661 (Figure S1), which indicated that the shriveled or incompletely developed seeds caused by *F. graminearum* inoculation might be the important factor responsible for the reduced yields. Further study found that, under the condition of *F. graminearum* inoculation, leaf cutting did not significantly change the GWS of wheat in L661 and L693 and the GWS of L693 is higher than L661 in the greenhouse in 2019 and 2020 (Table 2). This could be explained by the fact that leaf cutting could decrease the NDS (Table 2), which could partially compensate for the yield loss caused by leaf cutting and *F. graminearum* infection, resulting in no significant change of GWS. Furthermore, FHB could severely reduce wheat yield [1,2] and the NDS of L693 is lower than L661 under different leaf-cut treatments. This indicated that the decrease in GWS after cutting leaves and *F. graminearum* inoculation major depended on host resistance to FHB, not cutting leaves.

5. Conclusions

Leaf cutting could alleviate FHB, which is a physiological response and the effect of leaf cutting and *F. graminearum* inoculation on yield depend on the FHB resistance of the host. This study provides new insights into the physiological mechanism of systematic resistance against FHB.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/agriculture11111065/s1>, Figure S1: Kernels affected by Fusarium head blight.

Author Contributions: Conceptualization, P.L. and Q.H.; methodology, Q.H.; software, Q.H.; validation, P.L.; formal analysis, Q.H.; investigation, Q.H.; resources, P.L.; data curation, Q.H.; writing—original draft preparation, Q.H.; writing—review and editing, P.L.; visualization, Q.H.; supervision, Q.H.; project administration, P.L. and Q.H.; funding acquisition, Q.H. and P.L. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Doctor Foundation of Southwest University of Science and Technology, grant number 21zx7118 and the Provincial Science and Technology Foundation of Sichuan, China, grant number 2017JY0012.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Bai, G.; Shaner, G. Management and resistance in wheat and barley to Fusarium head blight. *Annu. Rev. Phytopathol.* **2004**, *42*, 135–161. [[CrossRef](#)]
- Li, X.; Xiang, Z.; Chen, W.; Huang, Q.; Liu, T.; Li, Q.; Zhong, S.; Zhang, M.; Guo, J.; Lei, L. Reevaluation of Two Quantitative Trait Loci for Type II Resistance to Fusarium Head Blight in Wheat Germplasm PI 672538. *Phytopathology* **2017**, *107*, 92–99. [[CrossRef](#)]
- Sobrova, P.; Adam, V.; Vasatkova, A.; Beklova, M.; Zeman, L.; Kizek, R. Deoxynivalenol and its toxicity. *Interdiscip. Toxicol.* **2010**, *3*, 94–99. [[CrossRef](#)] [[PubMed](#)]
- Zwart, R.S.; Muylle, H.; Van Bockstaele, E.; Roldán-Ruiz, I. Evaluation of genetic diversity of Fusarium head blight resistance in European winter wheat. *Theor. Appl. Genet.* **2008**, *117*, 813–828. [[CrossRef](#)]
- Hill-Ambroz, K.; Webb, C.A.; Matthews, A.R.; Li, W.; Gill, B.S.; Fellers, J.P. Expression Analysis and Physical Mapping of a cDNA Library of Fusarium Head Blight Infected Wheat Spikes. *Crop Sci.* **2006**, *46*, S15. [[CrossRef](#)]
- Zhang, Z.B.; Zhang, H.J.; Duan, G.Q.; Jing, X.W.; Chen, Z. Comparison of photosynthetic physiological and anatomical features of gene and virus controlled silver leaf mottling of summer squash. *Chin. J. Eco-Agric.* **2007**, *15*, 123–125.
- Stone, J.K.; Hood, I.A.; Watt, M.S.; Kerrigan, J.L. Distribution of Swiss needle cast in New Zealand in relation to winter temperature. *Australas. Plant Pathol.* **2007**, *36*, 445–454. [[CrossRef](#)]
- Moriondo, M.; Orlandini, S.; Giuntoli, A.; Bindi, M. The Effect of Downy and Powdery Mildew on Grapevine (*Vitis vinifera* L.) Leaf Gas Exchange. *J. Phytopathol.* **2005**, *153*, 350–357. [[CrossRef](#)]
- Dallagnol, L.J.; Rodrigues, F.A.; Martins, S.C.V.; Cavatte, P.C.; DaMatta, F.M. Alterations on rice leaf physiology during infection by *Bipolaris oryzae*. *Australas. Plant Pathol.* **2011**, *40*, 360–365. [[CrossRef](#)]
- Rooney, J.M.; Hoard, G.V. Compensation in Growth and Photosynthesis of Wheat (*Triticum aestivum* L.) Following Early Inoculations with *Septoria nodorum* (Berk.) Berk. *New Phytol.* **1989**, *113*, 513–521. [[CrossRef](#)]
- Sturm, A.; Tang, G.-Q. The sucrose-cleaving enzymes of plants are crucial for development, growth and carbon partitioning. *Trends Plant Sci.* **1999**, *4*, 401–407. [[CrossRef](#)]
- Luo, P.G.; Luo, H.; Chang, Z.; Zhang, H.; Zhang, M.; Ren, Z. Characterization and chromosomal location of Pm40 in common wheat: A new gene for resistance to powdery mildew derived from *Elytrigia intermedium*. *Theor. Appl. Genet.* **2009**, *118*, 1059–1064. [[CrossRef](#)] [[PubMed](#)]
- Luo, P.G.; Ren, Z.L.; Zhang, H.Q.; Zhang, H.Y. Identification, Chromosome Location, and Diagnostic Markers for a New Gene (YrCN19) for Resistance to Wheat Stripe Rust. *Phytopathology* **2005**, *95*, 1266–1270. [[CrossRef](#)]
- Li, X.; Zhong, S.; Chen, W.; Fatima, S.A.; Huang, Q.; Li, Q.; Tan, F.; Luo, P. Transcriptome Analysis Identifies a 140 kb Region of Chromosome 3B Containing Genes Specific to Fusarium Head Blight Resistance in Wheat. *Int. J. Mol. Sci.* **2018**, *19*, 852. [[CrossRef](#)] [[PubMed](#)]
- Shen, X.; Li, H.; Jia, Q.; Feng, H.; Li, M.; Liang, H. Influence of wheat (*Triticum aestivum* L.) stripe rust infection on photosynthetic function and expression protein D1 of wheat leaves. *Acta Ecol. Sin.* **2008**, *28*, 669–676.
- Li, X.; Liu, T.; Chen, W.; Zhong, S.; Zhang, H.; Tang, Z.; Chang, Z.; Wang, L.; Zhang, M.; Li, L. Wheat WCBP1 encodes a putative copper-binding protein involved in stripe rust resistance and inhibition of leaf senescence. *BMC Plant Biol.* **2015**, *15*, 239. [[CrossRef](#)] [[PubMed](#)]
- Ma, L.; Zhong, S.; Liu, N.; Chen, W.; Liu, T.; Li, X.; Zhang, M.; Ren, Z.; Yang, J.; Luo, P. Gene expression profile and physiological and biochemical characterization of hexaploid wheat inoculated with *Blumeria graminis* f. sp. *tritici*. *Physiol. Mol. Plant Pathol.* **2015**, *90*, 39–48. [[CrossRef](#)]
- Yang, S.; Li, X.; Chen, W.; Liu, T.; Zhong, S.; Ma, L.; Zhang, M.; Zhang, H.; Yu, D.; Luo, P. Wheat resistance to fusarium head blight is associated with changes in photosynthetic parameters. *Plant Dis.* **2016**, *100*, 847–852. [[CrossRef](#)] [[PubMed](#)]
- Huang, Q.; Li, X.; Chen, W.; Xiang, Z.; Zhong, S.; Chang, Z.; Zhang, M.; Zhang, H.; Tan, F.; Ren, Z. Genetic mapping of a putative *Thinopyrum intermedium*-derived stripe rust resistance gene on wheat chromosome 1B. *Theor. Appl. Genet.* **2014**, *127*, 843–853. [[CrossRef](#)] [[PubMed](#)]
- Liu, Z.; Xu, M.; Xiang, Z.; Li, X.; Chen, W.; Luo, P. Registration of the Novel Wheat Lines L658, L693, L696, and L699, with Resistance to Fusarium Head Blight, Stripe Rust, and Powdery Mildew. *J. Plant Regist.* **2015**, *9*, 121–124. [[CrossRef](#)]
- Gamm, M.; Héloir, M.-C.; Bliigny, R.; Vaillant-Gaveau, N.; Trouvelot, S.; Alcaraz, G.; Frettinger, P.; Clément, C.; Pugin, A.; Wendehenne, D. Changes in carbohydrate metabolism in *Plasmopara viticola*-infected grapevine leaves. *Mol. Plant-Microbe Interact.* **2011**, *24*, 1061–1073. [[CrossRef](#)] [[PubMed](#)]
- Liang, C.; Wang, Y.; Zhu, Y.; Tang, J.; Hu, B.; Liu, L.; Ou, S.; Wu, H.; Sun, X.; Chu, J. OsNAP connects abscisic acid and leaf senescence by fine-tuning abscisic acid biosynthesis and directly targeting senescence-associated genes in rice. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 10013–10018. [[CrossRef](#)]
- Yu, S.-M.; Lo, S.-F.; Ho, T.-H.D. Source–sink communication: Regulated by hormone, nutrient, and stress cross-signaling. *Trends Plant Sci.* **2015**, *20*, 844–857. [[CrossRef](#)]

24. Chang, T.-G.; Zhu, X.-G. Source–sink interaction: A century old concept under the light of modern molecular systems biology. *J. Exp. Bot.* **2017**, *68*, 4417–4431. [[CrossRef](#)] [[PubMed](#)]
25. Liu, Q.-H.; Xiu, W.; Chen, B.-C.; Jie, G. Effects of low light on agronomic and physiological characteristics of rice including grain yield and quality. *Rice Sci.* **2014**, *21*, 243–251. [[CrossRef](#)]
26. Abdelrahman, M.; Burritt, D.J.; Gupta, A.; Tsujimoto, H.; Tran, L.-S.P. Heat stress effects on source–sink relationships and metabolome dynamics in wheat. *J. Exp. Bot.* **2019**, *71*, 543–554. [[CrossRef](#)]
27. Luo, P.; Ren, Z.; Wu, X.; Zhang, H.; Zhang, H.; Feng, J. Structural and biochemical mechanism responsible for the stay-green phenotype in common wheat. *Chin. Sci. Bull.* **2006**, *51*, 2595–2603. [[CrossRef](#)]
28. Luo, P.; Deng, K.; Hu, X.; Li, L.; Li, X.; Chen, J.; Zhang, H.; Tang, Z.; Zhang, Y.; Sun, Q. Chloroplast ultrastructure regeneration with protection of photosystem II is responsible for the functional ‘stay-green’ trait in wheat. *Plant Cell Environ.* **2013**, *36*, 683–696. [[CrossRef](#)]
29. Thomas, H.; Howarth, C.J. Five ways to stay green. *J. Exp. Bot.* **2000**, *51*, 329–337. [[CrossRef](#)] [[PubMed](#)]
30. Khan, W.; Prithiviraj, B.; Smith, D.L. Photosynthetic responses of corn and soybean to foliar application of salicylates. *J. Plant Physiol.* **2003**, *160*, 485–492. [[CrossRef](#)]
31. Lorenzini, G.; Guidi, L.; Nali, C.; Ciompi, S.; Soldatini, G.F. Photosynthetic response of tomato plants to vascular wilt diseases. *Plant Sci.* **1997**, *124*, 143–152. [[CrossRef](#)]
32. Lamb, C.J.; Ryals, J.A.; Ward, E.R.; Dixon, R.A. Emerging Strategies for Enhancing Crop Resistance to Microbial Pathogens. *Biotechnology* **1992**, *10*, 1436–1445. [[PubMed](#)]
33. Tao, Y.; Xie, Z.; Chen, W.; Glazebrook, J.; Katagiri, F. Quantitative Nature of Arabidopsis Responses during Compatible and Incompatible Interactions with the Bacterial Pathogen. *Plant Cell* **2003**, *15*, 317–330. [[CrossRef](#)] [[PubMed](#)]
34. Modrá, H.; Svobodová, Z. Incidence of animal poisoning cases in the Czech Republic: Current situation. *Interdiscip. Toxicol.* **2009**, *2*, 48–51. [[CrossRef](#)]
35. Liu, W.-D.; Yin, J.; Zhu, G.-J. Effects of Leaf Removal on Dry Matter Accumulation and Grain Yield in Different Spike-type Wheat Varieties. *Sci. Agric. Sin.* **2007**, *40*, 1353–1360.