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Effects of Defoliation at Different Fertility Stages on Material Accumulation, Physiological Indices and Yield of Cotton

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Abstract: In recent years, severe hailstorms have caused damage to cotton leaves and stalks. In order to identify the effects of cotton leaf damage on its dry matter accumulation, protective enzyme activity and yield in different periods, in this experiment, different intensities of hail were simulated by manual leaf cutting. In this study, the effects of leaf damage on dry matter accumulation, chlorophyll fluorescence, POD (peroxidase), SOD (superoxide dismutase) and MDA levels (malondialdehyde), and yield of cotton were studied in field experiments at three stages (bud, full bud and flower boll stages) and in sub-plots with different artificial defoliation intensities (0%, 25%, 50%, 75% and 100%). Removing the leaf sources had differently sized effects on the "sink" at each stage, and these are ordered as follows: flowering and boll stage > full bud stage > pregnancy stage. The greater the intensity of leaf removal, the greater the impact on the "sink". Among them, after removing 50% of the leaves at the full bud stage, the total dry matter of the cotton plant increased by 12.46% compared to that of the control, and the boll formation rate per plant increased by 14.99%, resulting in overcompensation. Mo, Vj and φDo all showed a tendency to decrease and then increase with the increase in defoliation intensity at different periods of the treatment, and the lowest values of Mo, Vj and φDo, and the largest values of φpo, ψo and φEo were found in the 50% defoliation treatment at the gestational bud stage. The values of ψo and φEo were at the maximum in the 25% defoliation treatment at the full bud stage. The values of Mo and Vj in the different defoliation treatments at the bolling stage showed a tendency to increase and then decrease with the increase in defoliation intensity, with the highest values in the 25% treatment and the smallest values of φpo, ψo and φEo in the 25% defoliation treatment. The POD enzyme activity level was elevated in the defoliation treatments at the three different periods, and the highest value was observed in the 50% defoliation group at the full bud and boll stages, which is a reflection of supercompensation. The SOD enzyme activity level tended to increase with the intensity of defoliation, and defoliation at the gestational and full bud stages first enhanced and then weakened the stress on the cotton plants. The differences between treatments decreased after 12 weeks. The stress of defoliation on cotton plants was weakened at the boll stage. With the increase in defoliation intensity, the content of MDA showed a gradual increasing trend. The cotton MDA content was higher than that of the other treatments at 75% defoliation at both the post-fertilized bud and full bud stage.

Keywords: cotton; defoliation; dry matter accumulation; protective enzymes; yield

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1. Introduction

Cotton, an important cash crop in southern Xinjiang, had a planting area of 1.567 million hectares in 2022 (accounting for 63.7% of Xinjiang) and suffered from hailstorms over 19,100 hectares, with a loss of CNY 630 million. In south Xinjiang, strong hail generally occurs from April to August, with the least occurring in April and August and the most

occurring in June to July [1]; these latter months are critical for cotton growth [2]. Through rapid, intensive ice ball strikes, the crop canopy parts are smashed, and the leaves, stem and branch phloems, growth points, stalks, flowers and fruits are damaged and shed, seriously affecting the growth of the crop. At the same time, a short-term deterioration of the micro-environment of the farmland occurs, resulting in a drop in temperature, humidity increases, etc., which promote diseases and insect pests, so that the crop has significantly reduced yields and lower quality. However, cotton, as an infinite-growth annual plant, has a strong secondary function in June to July (full bud ~ boll stage); after the disaster, it can achieve better recovery growth, reasonable regulation, and form a certain yield [3].

Chlorophyll fluorescence is a novel technology developed on the basis of photosynthesis, and its role in plant stress tolerance experiments has been increasingly emphasised [4]. Chlorophyll fluorescence and photosynthesis are closely related, and the effect of any adversity on photosynthesis can be reflected by changes in the kinetic parameters of chlorophyll fluorescence [5]. Currently, the studies on the effects of defoliation stress on plant photosynthetic physiology are mainly focused on economic crops or exotic invasive plants [6,7], and there are fewer studies on defoliation on cotton photosynthesis and chlorophyll fluorescence. In this paper, by studying different defoliation periods and defoliation intensities, we explored the photosynthetic physiological response mechanism of cotton to defoliation stress by analysing the changes in the kinetic parameters of cotton chlorophyll fluorescence, with a view to providing a scientific theoretical basis for the late field management of damaged cotton.

The content of reactive oxygen species (ROS) in normal plants is in dynamic equilibrium, whereas under adverse conditions, the gradual accumulation of ROS causes lipid membrane peroxidation, which ultimately leads to cell death [8]. In order to adapt to various adversities, plants have produced antioxidant enzyme systems during long-term evolution, in which superoxide dismutase (SOD) and peroxidase (POD) can effectively remove the ROS accumulated in the cells, reduce the damage caused to the plant cell membranes, and provide stable internal environments for the plant's growth and development, as well as protect the cell membrane system to a certain extent [9]. Malondialdehyde (MDA) is the end product of lipid peroxidation in the cell membranes, and its content has been used by many researchers as a relevant indicator of the degree of plant stress caused by adversity [10]. Many experts have found that the activities of antioxidant enzymes and the malondialdehyde content are closely related to plant stress tolerance in the studies of wheat [11], maize [12], rice [13] and other crops. This paper simulates the defoliation stress caused by leaf damage when cotton suffers from hailstorms through defoliation experiments and explores the changes in the activities and contents of three enzymes, SOD, POD and MDA, under different defoliation periods and intensities, with the aim of revealing the roles of these enzymes in coping with cotton leaf damage in different fertility periods. By studying the effects of cotton leaf damage on the protective enzymes at different times, the physiological mechanism of stress growth in hail-damaged cotton was revealed, providing a theoretical basis for future research on the efficient production of hail-damaged cotton.

2. Materials and Methods

2.1. Overview of the Test Site

This experiment was conducted in 2022 and 2023 in the net room of the experimental station of Tarim University. The site is located on the northwestern edge of the Tarim Basin (40°33′ N, 81°16′ E), which is a typical extremely arid desert area, with an average annual temperature of 11.2 °C, an average annual precipitation of 45.70 mm, an average annual evapotranspiration of 1988.40 mm and an average annual relative humidity below 55%. The test site contained sandy loam soil with a dry soil mass of 1.22 g/cm^3, a field water holding capacity of 23.80% and a medium-to-high soil fertility level.

2.2. Design of the Experiment

A two-factor split-zone design was used, with the main zone containing cotton in three different fertility periods: post-fertilized bud bud stage—cotton plants were defoliated when they had four fruiting branches (20 May); full bud stage—cotton plants were defoliated when they had eight fruiting branches (18 June); and boll stage—defoliation of cotton plants after topping (15 July). There were four defoliation treatments: (1) 25% defoliation (each unfolded leaf was cut from the tip to half of the midrib, and then cut perpendicular to the midrib, without injuring the midrib); (2) 50% defoliation (half of each unfolded leaf was cut from the tip along the midrib, without injuring the midrib); (3) 75% defoliation (half of each unfolded leaf was cut from the tip along the midrib, and then half of the unfolded leaf was cut from the top along half of the midrib, and then cut perpendicular to the midrib to the midrib); and (4) 100% defoliation (each unfolded leaf was cut, and the petiole was retained). No defoliation (0%) was used as a control (CK). Each treatment represents a different intensity of hail damage. Each treatment was repeated three times, with a total of 45 plots. Adopting a (66 + 10) cm × 11 cm machine-picked cotton strip seeding pattern, the theoretical density was 15,950 holes/mu, the area of each plot was 10.5 m × 2.3 m = 24.15 m^2, and a drip irrigation belt was placed in the middle of the narrow rows under the film. The other patterns are consistent with field management.

Leaf treatment is as follows: use scissors to fully expand the leaves to cut the leaves one by one, the order of leaf cutting on the whole plant from the first and then down, first cut the upper part of the cotton plant leaves, and then cut the basal leaves. Specific operations are as follows: 25% defoliation, first from the top of the cotton leaf blade along the mid-vein to cut off one-quarter of the leaf surface of each leaf, without injuring the mid-vein. Then the remaining half of the leaf will be cut with scissors along the middle of the leaf vein perpendicular to the leaf vein and then cut off half, and the remaining leaf surface is near the axis part of three-quarters of the leaf surface. For 50% defoliation, cut half of the foliage of each leaf from the top of the cotton leaf blade along the midrib without injuring the midrib. The remaining leaf surface is the half-leaf surface with the main stem. Seventy-five percent of the leaves, first from the top of the cotton leaf blade along the midvein to cut off half of the leaf surface of each leaf, without injuring the midvein. Then the remaining half of the leaf is cut with scissors along the middle of the leaf vein perpendicular to the leaf vein and then cut half, the remaining leaf surface is near the axis part of one-quarter of the leaf surface. For 100% defoliation, cut the leaf surface with scissors along the point where the leaf surface meets the petiole, leaving the petiole on the cotton plant.

2.3. Observation Indicators and Measurement Methods

2.3.1. Determination of Dry Matter

During each period, 2 rows of cotton plants were cut side by side, with 3 consecutive plants in each row (6 plants in total), At the cotton fluffing stage and the different organ (stem, leaf, bud + flower + boll) samples were put into an oven at 105 °C for 30 min to kill the green parts. Then, they were dried at 80 °C to a constant weight, taken out, and weighed after cooling.

2.3.2. Determination of Chlorophyll Fluorescence Kinetic Parameters

The fluorescence parameters of the second or third fully expanded leaf from the top of the cotton plant were measured three times for each treatment on sunny and cloudless days during the main reproductive period. The leaves were treated in the dark for 30 min, and then the fast chlorophyll fluorescence induction kinetic curves and related parameters were determined at the blooming bud period and cotton bolling stage using a Yaxin-1105 portable photosynthesiser (Beijing Ya Xin Li Yi Technology Co., Ltd., Beijing, China) in saturated pulsed light (3000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) after exposure to ls [14], as shown in Table 1.

Table 1. Formulas and terminology used in OJIP assay analyses.

Terms and Equations	Definitions
Fo	Minimum fluorescence intensity after dark adaptation
Fj	Fluorescence intensity at point J (2 ms)
Fi	Fluorescence intensity at point I (30 ms)
Fp	Fluorescence intensity at the point of maximum fluorescence (point P)
Fm = Fp	Maximum fluorescence intensity after dark adaptation
Fv = Ft − Fo	Variable fluorescence intensity at t
Vt = (Ft − Fo)/(Fm − Fo)	Relative variable fluorescence intensity at time t
Vi = (Fi − Fo)/(Fm − Fo)	Relative variable fluorescence intensity at time I
Vj = (Fj − Fo)/(Fm − Fo)	Relative variable fluorescence intensity at point J
Mo = 4 (F300μs − Fo)/(Fm − Fo)	Initial slope of the OJIP fluorescence induction curve
φPo ≡ TRo/ABS = 1 − (Fo/Fm)	Maximum photochemical efficiency of PSII
φEo ≡ ETo/ABS = [1 − (Fo/Fm)]ψo	Quantum yield for electron transfer
ψo ≡ ETo/TRo = (1 − Vj)	Probability that an exciton captured in the reaction centre will transfer an electron to other electron acceptors after the primary quinone acceptor (QA)

2.3.3. Determination of Enzyme Activity and Content

During each reproductive period after treatment, leaves of the main stem were selected, and the POD and SOD enzyme activities and MDA content were determined using the kits provided by Beijing Haobo Biotechnology Co. (Beijing, China). The POD activity was measured by the addition of the substrate to the extracted enzymes, and the enzyme activity was expressed in a unit activity. The SOD activity was measured by the addition of the substrate to the extracted enzymes, and the enzyme activity was expressed in a unit activity. The MDA content was measured by adding substrate to the extracted enzyme and the enzyme content was expressed as unit weight.

2.3.4. Production and Production Structure

During the first frost episode (25 October), the number of cotton plants in each plot was counted, all the seed cotton spitting fluffy bells were picked, the number of effective bolls per plant and the actual seed cotton yield in each plot were calculated, and the quality of a single boll was determined.

2.4. Analysis of Data

The experimental data were statistically analysed using Excel 2021, and the data were subjected to analysis of variance (ANOVA) using SPSS26.0 (SPSS Inc., Chicago, IL, USA) statistical analysis software, and the significance of difference was tested by the least significant difference (LSD) method. The graphs were prepared by using origin2021 (Origin Lab Corporation, Northampton, MA, USA) software.

3. Results

3.1. Effect of Defoliation at Different Periods on Dry Matter Changes in Cotton

As can be seen in Figure 1, the defoliation treatments at different periods significantly reduced the biomass of dry matter of the bud and flower bells. As the intensity increased, the biomass of the leaves showed a tendency to decrease and then increase under the treatments at the post-fertilized bud bud and full bud stages, but there was no significant difference between them, and the respective biomasses of the leaves were 1.44 g and 1.27 g higher than that of the control at 100 percent defoliation. The treatments at the boll stage caused a gradual decrease, and at 100% defoliation, the biomass of the leaves was 9.67 g less than that of the control. The biomasses of the stalks did not differ much among the treatments during the three different treatment periods and showed a decreasing and then increasing trend at both the full bud and boll stages. The biomass of the reproductive organs behaved differently during the different treatment periods. The biomass of the reproductive organs decreased with the increase in treatment intensity at the gestational bud and boll

stages, decreasing by 6.27, 17.31, 38.86 and 49.35 percent, respectively, compared with that of the control at the gestational bud stage. These values were 9.52%, 24.28%, 38.34% and 53.85% less than that of the control at the boll stage, respectively. When defoliation was carried out at the full bud stage, the biomass of the nutrient organs showed a tendency to decrease and then increase with the increase in defoliation intensity. The maximum biomass of the nutrient organs was recorded for the 50% defoliation treatment, with a 12.46% increase over that of the control, and the minimum biomass was recorded for the 100% defoliation treatment, with a 51.66% decrease over that of the control.

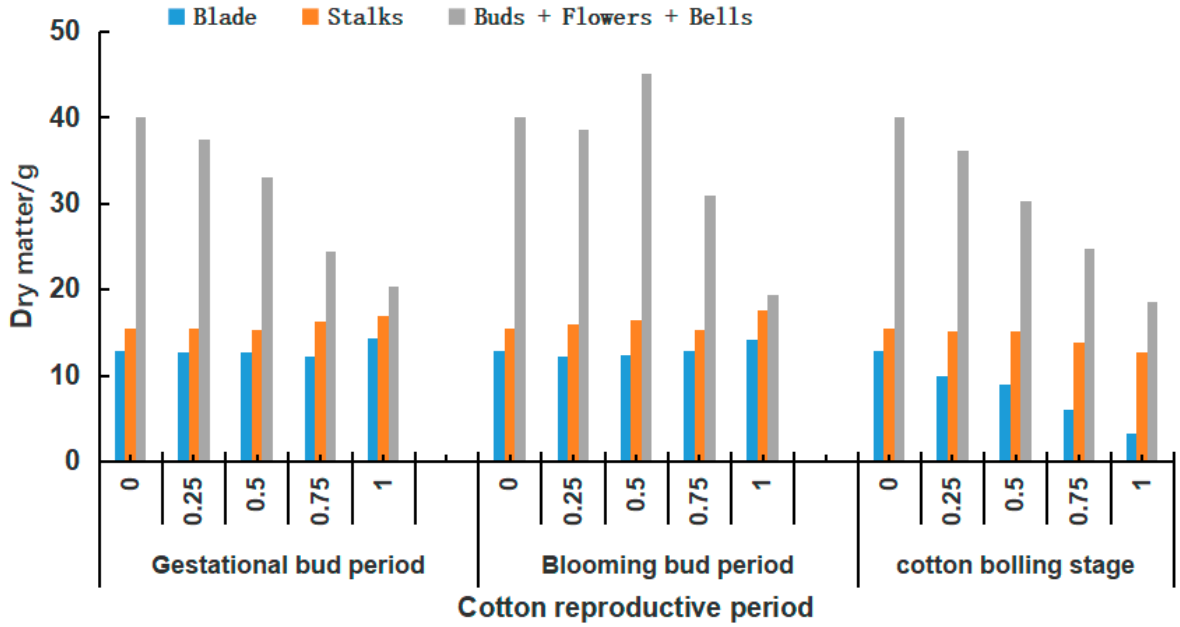

Figure 1. Effect of defoliation at different periods on dry matter changes in cotton.

3.2. Effect of Defoliation at Different Periods on Chlorophyll Fluorescence Parameters

3.2.1. Effect of Different Treatments on Kinetic Parameters of Chlorophyll Fluorescence Induction in Cotton at Full Bud Stage

Chlorophyll fluorescence is a rapid and noninvasive method of determining the photosynthetic performance of leaves, and it systematically reflects the indicators of absorption, transmission, dissipation and distribution of light energy in the plant leaves. The parameters, such as Mo, Vj, φpo, ψo, φEo and φDo, mainly reflect the changes in the PSII receptor side [15]. Mo reflects the initial slope of the OJIP fluorescence induction curve and the maximum rate at which the primary quinone receptor (QA) content is reduced. When the activity of the reflecting centre decreases, the rate at which the QA content is reduced increases, i.e., Mo will increase [14]. The results of different intensities of damage to the leaves at the different reproductive periods of cotton are shown in Table 2, with significant differences in the kinetic parameters of chlorophyll fluorescence at the full bloom stage. Mo, Vj and φDo showed a decreasing and then increasing trend with the increase in defoliation intensity at both the gestational and full bud stages, and the lowest values of Mo, Vj and φDo were found for the 50% defoliation treatment at the gestational bud stage, which decreased by 54.24%, 48.94% and 48.65%, respectively, compared with that of the control. φpo, ψo and φEo showed the largest values for the 50% defoliation treatment at the gestational bud stage, and the smallest values were found in the control. The 50% defoliation treatment caused increases of 28.57%, 43.40% and 79.41%, respectively, over that of the control. The values of Mo and Vj in the different defoliation treatments at the full bud stage showed a tendency to decrease and then increase with the increase in defoliation intensity, and the values were the lowest in 25% treatment, which were 76.74% and 64.86% lower than that of the control, respectively. The φpo, ψo and φEo of the different defoliation

intensities increased compared with that of the control, and the values of ψo and φEo were the largest for the 25% defoliation treatment, which increased by 38.10% and 36.9%, respectively, compared with that of the control.

Table 2. Effects of different treatments at full bud stage on chlorophyll fluorescence-induced kinetic parameters in cotton (values are means ± standard errors).

Period	Treatment	M_o	V_j	φ_{po}	ψ_o	φ_{Eo}	φ_{Do}
Gestational bud period	0%	0.59 ± 0.02 a	0.47 ± 0.01 a	0.63 ± 0.01 b	0.53 ± 0.03 c	0.34 ± 0.04 e	0.37 ± 0.02 a
	25%	0.29 ± 0.01 d	0.28 ± 0.02 e	0.79 ± 0.02 a	0.72 ± 0.01 a	0.57 ± 0.02 b	0.21 ± 0.04 d
	50%	0.27 ± 0.02 d	0.24 ± 0.03 d	0.81 ± 0.02 a	0.76 ± 0.02 a	0.61 ± 0.01 a	0.19 ± 0.05 e
	75%	0.34 ± 0.01 c	0.33 ± 0.02 c	0.75 ± 0.02 a	0.67 ± 0.02 b	0.5 ± 0.03 c	0.25 ± 0.02 c
	100%	0.51 ± 0.02 b	0.44 ± 0.01 b	0.66 ± 0.03 c	0.56 ± 0.04 c	0.37 ± 0.02 d	0.34 ± 0.02 b
Blooming bud period	0%	0.43 ± 0.02 a	0.37 ± 0.02 a	0.73 ± 0.02 b	0.63 ± 0.05 b	0.46 ± 0.05 b	0.27 ± 0.02 b
	25%	0.1 ± 0.05 c	0.13 ± 0.05 b	0.73 ± 0.02 b	0.87 ± 0.01 a	0.63 ± 0.02 a	0.28 ± 0.02 a
	50%	0.12 ± 0.02 c	0.14 ± 0.04 b	0.75 ± 0.01 a	0.86 ± 0.02 a	0.65 ± 0.02 a	0.25 ± 0.02 d
	75%	0.13 ± 0.02 b	0.14 ± 0.03 b	0.75 ± 0.02 a	0.86 ± 0.02 a	0.64 ± 0.01 a	0.25 ± 0.01 cd
	100%	0.14 ± 0.01 b	0.16 ± 0.02 b	0.76 ± 0.02 a	0.85 ± 0.01 a	0.64 ± 0.02 a	0.25 ± 0.03 bc

Note: Different lowercase letters indicate that the difference between different treatments of the same index is significant ($p < 0.05$).

3.2.2. Effect of Different Treatments on Kinetic Parameters of Chlorophyll Fluorescence Induction in Cotton at Boll Stage

The chlorophyll fluorescence parameters of each treatment were measured at the flowering stage, and the results are shown in Table 3. The values of Mo, Vj and φDo first decreased and then increased with the increase in defoliation intensity at the bud stage, and the values were the lowest for the 50% treatment, which decreased by 24.32%, 23.08% and 6.25%, respectively, compared with that of the control. The values of φpo, ψo and φEo were the highest for the 50% defoliation treatment at the bud stage, and the values of the control were the smallest, which increased by 2.94%, 14.75% and 19.51%, respectively, compared with that of the control. The values of Mo, Vj and φDo for the different defoliation treatments at the peak bud stage first increased and then decreased with the increase in defoliation intensity, and the values were the highest for the 25% treatment, which increased by 23.08%, 6.45% and 7.69%, respectively, compared with that of the control. The values for the 100% treatment were the lowest, which were 23.08%, 32.26% and 23.08% lower than that of the control, respectively. The values of φpo, ψo and φEo first decreased and then increased with the increase in defoliation intensity of the different treatments, and the values of φpo, ψo and φEo were the lowest for the 25% defoliation treatment, which were 2.70%, 2.90% and 5.88% lower than that of the control, respectively. The values for the 100% treatment were the highest, which increased by 8.11%, 14.49% and 23.53%, respectively, compared with that of the control. The Mo and Vj values of the different defoliation treatments at the lowering boll stage first increased and then decreased with the increase in defoliation intensity, and the values were the highest for the 25% treatment, which increased by 66.67% and 56.52%, respectively, compared with that of the control. The values of φpo, ψo and φEo first decreased and then increased with the increase in defoliation intensity, and the values were the lowest for the 25% defoliation treatment, which decreased by 11.11%, 20% and 28.13%, respectively, compared with that of the control.

Table 3. Effects of different treatments at flowering stage on chlorophyll fluorescence-induced kinetic parameters in cotton (values are means ± standard errors).

Period	Treatment	M_o	V_j	φ_{po}	ψ_o	φ_{Eo}	φ_{Do}
Gestational bud period	0%	0.37 ± 0.01 b	0.39 ± 0.03 a	0.68 ± 0.02 c	0.61 ± 0.04 a	0.41 ± 0.04 e	0.32 ± 0.02 a
	25%	0.27 ± 0.03 d	0.3 ± 0.05 c	0.68 ± 0.03 c	0.7 ± 0.03 a	0.48 ± 0.03 b	0.32 ± 0.01 ab
	50%	0.28 ± 0.04 c	0.3 ± 0.03 c	0.7 ± 0.01 a	0.7 ± 0.01 a	0.49 ± 0.01 a	0.30 ± 0.03 ab
	75%	0.37 ± 0.03 b	0.38 ± 0.01 a	0.69 ± 0.03 b	0.62 ± 0.03 a	0.43 ± 0.03 d	0.31 ± 0.03 ab
	100%	0.39 ± 0.03 a	0.35 ± 0.03 b	0.71 ± 0.01 ab	0.65 ± 0.05 a	0.46 ± 0.03 c	0.29 ± 0.03 b
Blooming bud period	0%	0.26 ± 0.04 b	0.31 ± 0.03 ab	0.74 ± 0.03 b	0.69 ± 0.02 d	0.51 ± 0.05 d	0.26 ± 0.04 ab
	25%	0.32 ± 0.03 a	0.33 ± 0.01 a	0.72 ± 0.02 c	0.67 ± 0.03 e	0.48 ± 0.03 e	0.28 ± 0.03 a
	50%	0.22 ± 0.02 c	0.24 ± 0.03 c	0.74 ± 0.03 b	0.76 ± 0.01 b	0.56 ± 0.01 b	0.26 ± 0.02 ab
	75%	0.21 ± 0.03 cd	0.28 ± 0.04 b	0.75 ± 0.03 b	0.72 ± 0.03 a	0.54 ± 0.03 c	0.25 ± 0.03 b
	100%	0.20 ± 0.03 d	0.21 ± 0.05 d	0.8 ± 0.01 a	0.79 ± 0.01 c	0.63 ± 0.02 a	0.2 ± 0.03 c
cotton bolling stage	0%	0.18 ± 0.05 d	0.23 ± 0.05 d	0.81 ± 0.01 a	0.8 ± 0.01 a	0.64 ± 0.01 a	0.19 ± 0.05 d
	25%	0.30 ± 0.03 b	0.36 ± 0.01 a	0.72 ± 0.03 d	0.64 ± 0.05 e	0.46 ± 0.04 d	0.28 ± 0.03 b
	50%	0.24 ± 0.02 c	0.27 ± 0.03 c	0.77 ± 0.01 bc	0.73 ± 0.03 c	0.57 ± 0.02 b	0.23 ± 0.02 c
	75%	0.31 ± 0.03 a	0.33 ± 0.03 b	0.74 ± 0.02 c	0.67 ± 0.01 b	0.5 ± 0.03 c	0.26 ± 0.03 b
	100%	0.29 ± 0.03 ab	0.24 ± 0.02 d	0.79 ± 0.03 b	0.77 ± 0.03 d	0.54 ± 0.03 c	0.33 ± 0.01 a

Note: Different lowercase letters indicate that the difference between different treatments of the same index is significant ($p < 0.05$).

3.3. Effect of Defoliation on POD Enzyme Activity in Cotton at Different Stages

3.3.1. Effect of Defoliation at the Gestation Bud Stage on POD Enzyme Activity in Cotton

POD enzymes are widely found in a variety of animals, plants and microorganisms, and they directly oxidize phenolic or amine compounds with H_2O_2 as an electron acceptor [16]. With the advancement of cotton development, the peroxidase activity level showed an upward trend, which is the inevitable result of cotton development and senescence [17]. Different intensities of defoliation affect the activity of POD enzymes in cotton leaves. The changes in peroxidase activity under different intensities of defoliation treatment at the bud stage are shown in Figure 2A. As the defoliation intensity increased, so did the POD enzyme activity level. When less than 75% of the leaf area was lost, the peroxidase activity level in the cotton leaves first increased and then decreased, and when 100% was removed, the peroxidase activity level showed an increasing trend. After 8 weeks of treatment, the POD activity levels were higher than that of the control, which were 5.88%, 5% and 11.63%, respectively. This is related to the metabolic adjustment and peroxide removal in cotton after the loss of leaves.

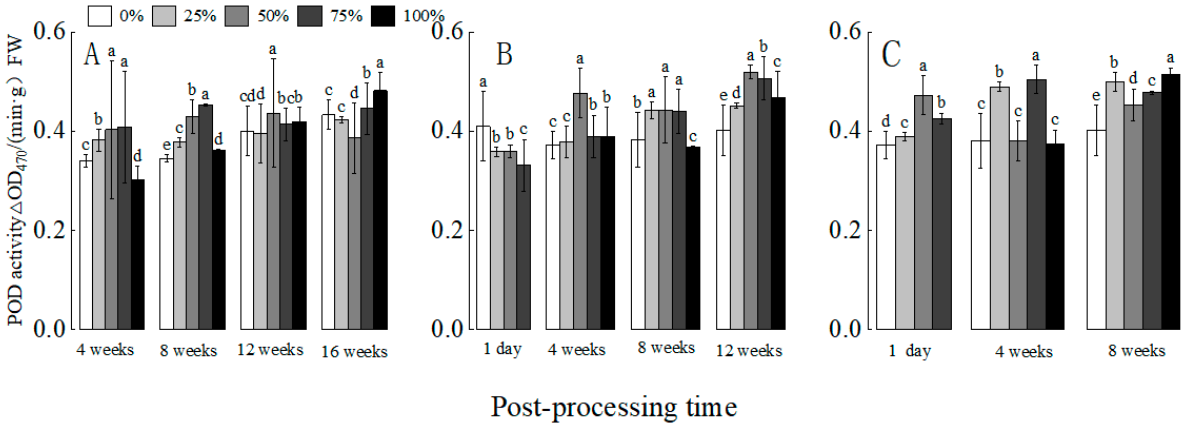

Figure 2. Differential analysis of POD enzyme activity in cotton leaves with different defoliation intensities at bud gestation (**A**), full bud (**B**) and flowering boll stages (**C**). Note: Different lowercase letters indicate that the difference between different treatments of the same index is significant ($p < 0.05$).

3.3.2. Effect of Defoliation at Full Bud Stage on POD Enzyme Activity in Cotton

The changes in peroxidase activity under different intensities of defoliation at the full bud stage are shown in Figure 2B. One day after the treatment, with the increase in defoliation intensity, the peroxidase activity levels decreased continuously, which were 12.2%, 12.2% and 19.51% less than that of the control, respectively. With the advancement of cotton fertility, the peroxidase activity level with different defoliation intensities showed an increasing trend. After 4 weeks of treatment, the peroxidase activity levels of all the intensities of defoliation were higher than that of the control. Four weeks after the treatment, the POD activity levels of each intensity treatment were 1.61%, 29.73%, 5.41% and 5.41% higher than that of the control, respectively. Eight weeks after the treatment, the POD activity levels of each intensity treatment were 15.4%, 15.67% and 14.88% higher than that of the control, respectively. Twelve weeks after the treatment, the POD activity levels of each intensity treatment were 12.5%, 29.75% and 26.75%/17.5% higher than that of the control, respectively. The peroxidase activity level of the 50% defoliation treatment was higher than that of all the other treatments.

3.3.3. Effect of Defoliation at Flowering Stage on POD Enzyme Activity in Cotton

The changes in peroxidase activity at the flowering boll stage are shown in Figure 2C. After 1 day of treatment with different intensities, the peroxidase activity levels were 5.41%, 27.02% and 16.22% higher than that of the control, respectively. As the plants became more fertile, the peroxidase activity level of the treatment group was variably higher than that of the control. The peroxidase activity level at less than 75% defoliation intensity first increased and then decreased. The peroxidase activity level with a defoliation intensity greater than 75% continued to increase.

3.4. Effect of Defoliation at Different Stages on the Activity of Cotton SOD Enzyme

3.4.1. Effect of Defoliation at the Gestation Bud Stage on the Activity of Cotton SOD Enzyme

Different intensities of defoliation affected peroxide dismutase activity in the cotton leaves. The changes in the peroxidase activity of the different intensities of defoliation during the bud stage are shown in Figure 3A. With the increase in defoliation intensity, the SOD enzyme activity level also changed, and as the plants became more fertile, the SOD activity level showed a trend of first increasing, and then decreasing and increasing. Four weeks after the treatment, the peroxide dismutase activity levels were 22.16%, 16.16%, 25% and 6.25% lower than that of the control, respectively. Eight weeks after the treatment, the peroxide dismutase activity levels in the less-than-50%-defoliation treatment group increased by 4.54% and 8.20%, respectively. Twelve weeks after the treatment, the peroxide dismutase activity level in the less-than-75%-defoliation treatment group was lower than that of the control, and the 100% defoliation treatment caused increases of 5.09% and 4.94%, respectively.

3.4.2. Effect of Defoliation on Cotton SOD Enzyme Activity at Full Bud Stage

The changes in the peroxidase activity level at different intensities of defoliation at the full bud stage are shown in Figure 3B. With the increase in defoliation intensity, the activity levels of the SOD enzymes also changed, and as the plants became fertile, it first decreased and then increased and decreased. One day after the treatment, the peroxide dismutase activity levels of the defoliation treatment were higher than that of the control, which were 21.15%, 13.79% and 24.48%, respectively. Four weeks after the treatment, the SOD enzyme activity level of each treatment was significantly lower than that of the control, and with the increase in defoliation intensity, this decreased by 18.95%, 15.24%, 10.65% and 7.36%, respectively. Eight weeks after the treatment, the SOD enzyme activity level in each treatment group was higher than that of the control, and for the 50% defoliation treatment, it was the highest, increasing by 7.59%, 24.63%, 5.04% and 5.49%, respectively. Twelve weeks after defoliation, there were little differences in the activity levels of the SOD

enzyme among the treatments, which were 1.11%, 2%, 7.74% and 6.41% lower than that of the control, respectively.

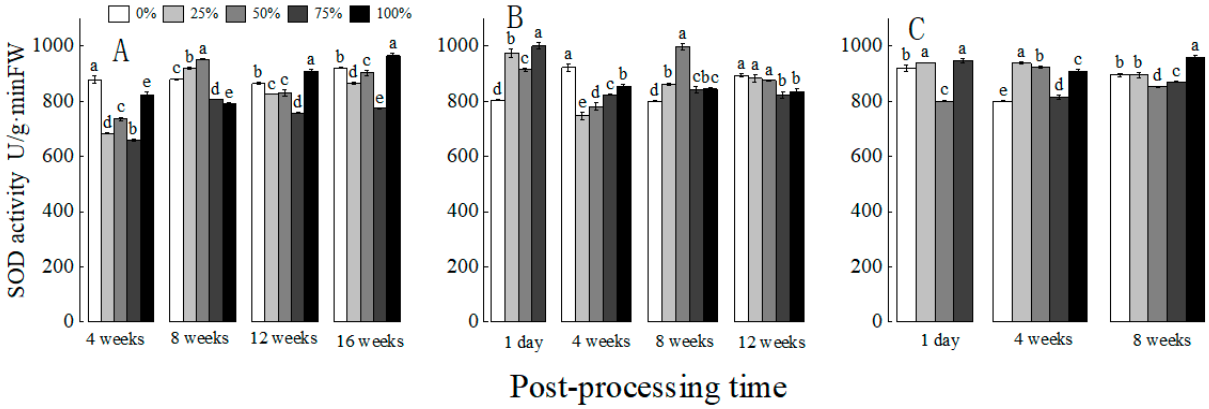

Figure 3. Differential analysis of SOD enzyme activity in cotton leaves with different defoliation intensities at bud gestation (**A**), full bud (**B**) and flowering stages (**C**). Note: Different lowercase letters indicate that the difference between different treatments of the same index is significant ($p < 0.05$).

3.4.3. Effect of Defoliation at Flowering Stage on SOD Enzyme Activity in Cotton

The changes in peroxidase activity at the flowering boll stage are shown in Figure 3C for different intensities of defoliation. As they grew, the SOD enzyme activity level of the normal plants first decreased and then increased, and that of the 25% and 50% defoliation treatments first increased and then decreased. The performance of the plants with 75% defoliated areas was consistent with that of the control, showing a trend of first decreasing and then increasing. Four weeks after the treatment, the SOD enzyme activity levels of each treatment were 17.16%, 15.26%, 1.7% and 13.21% higher than that of the control, respectively. After the 100% defoliation treatment, the activity of the SOD enzyme increased as the plants became more fertile.

3.5. Effects of Defoliation at Different Growth Stages on MDA Content in Cotton Leaves

3.5.1. Effect of Defoliation on MDA Content in Cotton during Pregnancy Bud Stage

Different intensities of defoliation treatments affected the MDA content in the cotton leaves. The changes in MDA content after different intensities of defoliation during the bud pregnancy stage are shown in Figure 4A. As the fertility process increases, so does the MDA content. Four weeks after the treatment, the MDA contents were higher than that of the control, which were 12.05%, 7.1%, 10.96% and 8.93%, respectively. As the plants grew, when the leaf area loss exceeded 75%, the MDA contents increased significantly after 12 weeks of treatment and were 11.64% and 1.5% higher than that of the control, respectively. The MDA contents of the different defoliation treatments were 9.72%, 7.5%, 31.42% and 35.64% higher than that of the control, respectively.

3.5.2. Effect of Defoliation on MDA Content in Cotton at Full Bud Stage

The changes in malondialdehyde content are shown in Figure 4B after different intensities of defoliation at the full bud stage. As the plants became more fertile, the MDA content gradually decreased. With the increase in defoliation intensity, the MDA contents of the 75% smaller leaves were the highest among all the treatments. They were 1.09%, 10.39%, 15.66% and 28.17% higher than that of the control, respectively. Twelve weeks after the treatment, the MDA contents of the different leaves were 0.76%, 7.56%, 28.17% and 18.78% higher than that of the control, respectively.

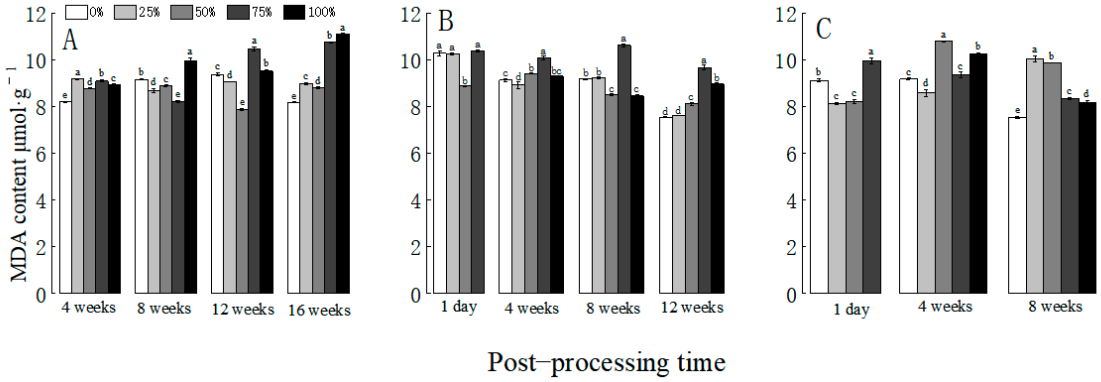

Figure 4. Differences in MDA content in cotton leaves with different defoliation intensities at bud gestation (**A**), full bud (**B**) and flowering boll stages (**C**). Note: Different lowercase letters indicate that the difference between different treatments of the same index is significant ($p < 0.05$).

3.5.3. Effect of Defoliation at Flowering Boll Stage on MDA Content in Cotton

The changes in malondialdehyde content at the flowering stage are shown in Figure 4C after different intensities of defoliation. As the plants grew, the MDA contents of the normal plants decreased, while those of the different groups first increased and then decreased. Compared with the control, the MDA contents increased by 9.18%, 1.91% and 10.76%, respectively, for the more-than-75%-smaller leaves. Four weeks after the treatment, the MDA contents of the more-than-50%-smaller leaves were 17.42%, 31.03% and 11.50% higher than that of the control, respectively. Eight weeks after the treatment, the MDA contents of each treatment were 33.28%, 31.03%, 10.76% and 8.44% higher than that of the control, respectively.

3.6. Effect of Defoliation at Different Times on Cotton Yield

Damage to cotton leaves ultimately affects the cotton yields, with the reduction increasing with the degree of damage. As shown in Table 4, it is clear that there was no significant difference in the number of boll sets per plant among the treatments at the gestational bud stage, and the yield of the plants that underwent 100 percent defoliation was 17.63 percent lower than that of the control. There were significant differences in yield among the treatments, with 3.02, 5.30, 14.21 and 20.01 percent reductions in yield, respectively. Significant differences in the number of boll sets and yield were observed among the treatments at the full bud stage; the number of boll sets per plant increased by 14.99 percent, and the yield increased by 6.39 percent in the plants that underwent 50 percent defoliation as compared to the control. The number of boll sets on a single plant that underwent 25% defoliation was not significantly different from that of the control, but after more than 50% defoliation, this number and the yield were significantly reduced, with 100% defoliation causing 51.72% and 58.20% reductions compared to that of the control. Both the number of boll sets per plant and yield decreased significantly with increasing intensity of defoliation during the bolling stage. There were highly significant differences in the yield between the treatments, with the numbers of boll sets per plant decreasing by 21.74, 31.93, 43.33 and 65.07 percent, and the yields decreasing by 23.14, 35.17, 46.21 and 68.28 percent with increasing intensity of defoliation.

Two-factor ANOVA was utilized to study the relationship between treatment period and defoliation intensity on yield, as can be seen from the table below (Table 5). The treatment period showed significance (F = 1723.441, $p = 0.00$), indicating that the main effect exists and that the treatment period produces a differential relationship on yield. The intensity of defoliation showed significance (F = 2383.006, $p = 0.00$), indicating that the effect was present and treatment defoliation intensity would have a differential relationship on yield. Their interaction also showed significance (F = 287.826, $p = 0.00$) indicating the

presence of interaction effect and that treatment period and defoliation intensity would have a differential relationship on yield.

Table 4. Effect of leaf cutting at different periods on cotton yield.

Defoliation Intensity	Gestational Bud Period		Blooming Bud Period		Cotton Bolling Stage	
	Number of Bells	Yield/(kg·hm^{-2})	Number of Bells	Yield/(kg·hm^{-2})	Number of Bells	Yield/(kg·hm^{-2})
0%	6.67 a	7427.93 a	6.67 a	7429.34 a	6.67 a	7427.93 a
25%	6.78 a	7204.31 b	6.33 a	6927.11 b	5.22 b	5708.95 b
50%	6.67 a	7034.86 c	7.67 a	7904.38 c	4.54 bc	4815.43 c
75%	6.44 a	6372.78 d	5.00 b	5212.83 d	3.78 c	3995.57 d
100%	6.33 a	5938.72 e	3.22 c	3105.56 e	2.33 d	2355.80 e

Note: Different lowercase letters indicate that the difference between different treatments of the same index is significant ($p < 0.05$).

Table 5. Two-factor ANOVA results.

Source of Variation	Square Sum	*df*	Mean Square	*F*	*p*
Intercept	1,586,441,219	1	1,586,441,219	199,475.844	0.00 **
Phase	27,413,222.92	2	13,706,611.46	1723.441	0.00 **
Deal with	75,808,650.32	4	18,952,162.58	2383.006	0.00 **
Phase * Deal with	18,312,750.71	8	2,289,093.839	287.826	0.00 **
Residual	238,591.479	30	7953.049		

R2: 0.997 * $p < 0.05$ ** $p < 0.01$.

4. Discussion

During the growth and development of crops, obtaining a high yield is reliant on the source and reservoirs [18], and ultimately, they reach a state of equilibrium. Leaves predominantly facilitate cotton growth, as they are the "source" of energy for photosynthesis; thus, leaves are essential [19]. The results of this study showed that dry matter accumulation, bud boll shedding, the single boll weight and the number of bolls per plant of cotton were affected by different intensities of defoliation at three different periods. When the leaf area is reduced, the photosynthetic production capacity and dry matter accumulation of cotton are reduced, which ultimately leads to a reduction in cotton yield due to an insufficient material supply.

Among the defoliation treatments, defoliation at the full bud stage had the most pronounced effect on the dry matter accumulation and yield of cotton, which is a period of concurrent nutritive and reproductive growth [20]. At this time, the cotton is damaged, which will cause slow plant growth, dry matter accumulation and leaf area large reduction. When removing 25% of the leaf area, the dry matter biomass of cotton, the number of bolls per plant and yield did not differ significantly from those of the control, but when removing 50% of the leaf area, the nutrient organ dry matter of cotton increased compared with that of the control, and its number of bolls per plant increased by 14.99%, which is the same as the results of Li Yueqiang et al. [20]. These authors simulated the degree of leaf-feeding damage caused by field pests during the full bud stage; a 50% defoliation treatment increased the number of cotton bolls by 24.4%, which resulted in overcompensation.

The defoliation treatments at the boll stage had a large impact on the cotton leaf area and dry matter biomass, resulting in a significant reduction in yield [21]. The excessive loss of leaves during the cotton bolling period affects plant photosynthesis and accelerates the growth of nutrient organs, but it does not favour the increase in yield organs at the later stage, resulting in an increase in the number of buds and bells shed per plant and the rate of shedding, as well as a decrease in the number of bells and yield per plant. This is consistent with the results of Mukhtar Maihmuti et al. [22], who simulated the yield compensatory capacity after the boll stage damage of cotton.

The chlorophyll fluorescence parameters of plants are extremely sensitive to external stresses, and the chlorophyll fluorescence parameters of cotton leaves change with the environment [23]. φPo represents the maximum photochemical efficiency of the photosynthetic capacity of PSII reaction plants, and Fv/Fm decreases when the plants are under stress [24]. In the experiment on the effects of low-temperature stress at the bud stage on growth and development, photosynthetic and chlorophyll fluorescence characteristics of cotton, Zhong Xinxin [25] found that the basic fluorescence parameters Fo, Fm and Fv changed quickly, and there were great differences among the different varieties. Xing et al. [26] studied the changes in the chlorophyll fluorescence kinetic parameters of different genotypes of cotton under high-temperature stress and found that as the intensity increased, the chlorophyll fluorescence kinetic parameters also changed accordingly, which also had a large impact on the high-temperature tolerance between the varieties. The fluorescence kinetic parameters of all the plants were analysed at the cotton budding and flowering boll stages, and the results showed that the values of Mo, Vj and φDo first decreased and then increased with the increase in defoliation intensity at the different stages, and the values of Mo, Vj and φDo were the lowest for the 50% leaf treatment at the bud stage. φpo, ψo and φEo were the highest for the 50% defoliation treatment at the bud stage, while the values of the control were the smallest. The Mo and Vj values of the different defoliation treatments at the full bud stage first decreased and then increased with the increase in defoliation intensity, and the values of ψo and φEo were the highest for the 25% defoliation treatment. The values of Mo and Vj for the different defoliation treatments at the flowering boll stage first increased and then decreased with the increase in defoliation intensity, while the values of φpo, ψo and φEo first decreased and then increased with the increase in defoliation intensity, and the values of the 25% defoliation treatment were the smallest. The defoliation treatment disrupted the cotton PSII reaction center. The values of Mo, Vj and φpo decreased over time, reaching a maximum in the early and middle stages. They were significantly lower than those of the control at the later stage, indicating that the tolerance of cotton to defoliation stress gradually adapted over time. However, the values of Mo, Vj and φDo were higher than those of the control at certain periods and intensities, and the destruction or reversible inactivation of the PSII reaction center caused an increase in Fo [14], indicating that defoliation stress destroyed the PSII reaction center of cotton, which was consistent with the results of the research on Flaveriabidentis [27].

POD is a plant antioxidant enzyme, which can catalyse the redox of various substances in H_2O_2 and resist and eliminate ROS under various stresses, such as drought and disease resistance [28]. In this study, it was found that the peroxidase activity level in the leaves of each treatment was higher than that of the control 4 weeks after the defoliation treatment. The results indicated that artificial defoliation simulated damage to the cotton leaves, and the treated plants activated the protein protective enzymes to protect the plants from peroxidation and eliminate possible further damage. The activity level of the POD enzyme increased in the three different periods of defoliation, and its activity level was the highest in the full bud and flower boll stages, which embody overcompensation. In particular, 4 weeks after the treatment, at the post-fertilized bud bud and full bud stages, the peroxidase activity level of the 50% defoliation treatment was the highest. Peroxidase activity is not only an accurate measure of plant damage, but also a manifestation of the transfer of plant nutrients and hormones to the boll, stimulating boll fruit ripening [29].

When plants are subjected to various stresses, many ROS are produced in the body beyond the normal metabolic level, and if the ROS are not removed in time, they will cause some harmful biochemical reactions [30]. Deleafing produces much ROS in cotton, and the level of SOD enzyme activity reflects the strength of peroxide activity in the plants [31]. When the defoliation intensity exceeded 75%, the cotton produced excessive superoxide radicals to damage the plant cell membrane, which unbalanced the enzyme system and made the enzyme activity level lower than that of the other treatment groups, which is consistent with the fact that the SOD enzyme activity levels of grape [32] and maize [33] are lower than that of the control group. When the leaves are stressed, more SOD enzymes

are produced to scavenge the superoxide radicals produced in the cotton [34]. The SOD enzyme activity level in the plants increased rapidly one day after the treatment. The SOD enzyme activity level increased with the increase in defoliation intensity. The SOD enzyme activity levels during defoliation at the post-fertilized bud bud and the full bud stages first increased and then decreased, weakening the cotton plants. The defoliation of cotton caused it to weaken at the flowering stage.

Malondialdehyde (MDA) is the end product of membrane lipid peroxidation, and its content reflects the degree of damage to the biofilm [35]. With the increase in defoliation intensity, the content of MDA tended to increase, which may be due to the severe damage to biofilms, both the free radicals, an intermediate product of membrane lipid peroxidation, and the final product, MDA [36]. After 4 weeks of treatment at the gestation and full bud stages, the MDA content was the highest in the plants with 75% of the leaf area damaged. This suggests that if the enzyme that scavenges free radicals in the plants is strong enough to control the accumulation of free radical harmful substances, then the membrane lipid peroxidation reaction can be controlled accordingly, and if the balance of this enzyme system is broken, the biofilm damage will be aggravated [35]. Therefore, the MDA content can be used as a physiological and biochemical indicator of cotton stress resistance.

In summary, when plants feel the stimulation of external stress, they will send out specific signals and begin to conduct processes, which change the chlorophyll fluorescence kinetic parameters in the plant and prompt the plant to produce antioxidant enzymes and antioxidants, such as SOD, CAT, POD, etc., [37] to a certain extent, remove excess ROS from the body, maintain the metabolic balance of ROS, protect the membrane structure and resist external stress. Through the changes in the chlorophyll fluorescence kinetic parameters of cotton, the photosynthetic physiological response of cotton to defoliation stress is understood, which provides a scientific theoretical basis for the later field management of damaged cotton. The aim was to clarify the changes in POD and SOD enzyme activities and MDA content under defoliation stress and to reveal the physiological mechanism of the stress growth of hailstorm-damaged cotton, so as to provide a theoretical basis for future research on the efficient production mechanism of hail-damaged cotton.

5. Conclusions

In summary, the results of the simulated hailstorm defoliation test conducted at the post-fertilized bud bud, full bud and boll stages showed that with the reduction of leaf area, the photosynthetic production capacity and dry matter accumulation of cotton will decline, and ultimately lead to the reduction of cotton yield due to the lack of material supply. Leaf removal at the full bud stage had the most pronounced effect on dry matter accumulation and yield of cotton, when 50% of the leaf area was removed, the dry matter mass of the nutrient organs of cotton increased compared to the control, and its number of bolls per plant increased by 14.99%, which occurred as an overcompensation phenomenon. The values of Mo, Vj and φDo of different defoliation treatments measured at the full bloom stage tended to decrease and then increase with the increase in defoliation intensity, and the results measured at the bolling stage showed that the values of Mo, Vj and φDo of the defoliation treatments at the post-fertilized bud bud stage tended to decrease and then increase with the increase in defoliation intensity, while the defoliation treatments at the full bloom stage and the bolling stage tended to increase and then decrease, and the fluorescent parameters of cotton, such as Mo, Vj and φDo, could be used to judge the time period and the degree of the cotton's stress. The POD enzyme activity was elevated in the defoliation treatments at all three different periods, with the highest POD enzyme activity at 50% defoliation at full bud and boll stage, which is a reflection of its supercompensation. SOD enzyme activity tended to increase with defoliation intensity, and defoliation at the post-fertilized bud and full bud stages first increased and then decreased the stress on cotton plants. The stress of defoliation on cotton plants was weakened at the boll stage. The content of MDA showed a gradual increase with increasing intensity of defoliation. The changes of chlorophyll fluorescence kinetic parameters of cotton were used

to understand the photosynthetic physiological response of cotton to defoliation stress and to provide a scientific theoretical basis for the late field management of damaged cotton. To clarify the changes of defoliation stress on POD, SOD enzyme activity and MDA content, to reveal the physiological mechanism of stress growth in hail-damaged cotton, and to provide theoretical basis for further research on the mechanism of efficient production of hail-damaged cotton.

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