

EFFECTS OF SUMMER PRUNING ON THE GROWTH AND PHOTOSYNTHETIC CHARACTERISTICS OF PEPPER (*Capsicum annuum* L.)

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ABSTRACT

The objective of the study is to investigate the mechanism by which summer pruning enhances the growth of pepper plants, as indicated by growth and fruit appearance indicators, photosynthetic rate and gas exchange parameters, rapid light response and induction kinetics curves and the related chlorophyll fluorescence parameters. The results indicated that the leaf growth rate, the individual pepper fruit weight, and the fruit longitudinal and cross diameters of the pruned group were significantly higher than those of the control. The stomatal conductance (G_s), intercellular CO_2 concentration (C_i) and transpiration rate (T_r) of the pruned group were significantly higher than those of the control. The initial slope of the rapid light response curve, which represents light energy utilisation efficiency (α), the maximum electron transfer rate (J_{max}) and saturated light intensity (PAR_{sat}) were all higher in the summer pruning group than in the control group. The F_0 of the pruned group decreased by 16.83%, F_v/F_0 increased by 23.69%, PI_{abs} increased by 58.33%, and DIO/RC decreased by 22.09% compared to the control group. In summary, summer pruning significantly improves the leaf growth rate and fruit appearance quality of pepper, effectively promotes the photosynthesis of functional leaves, and reduces the degree of stress under adverse environmental conditions.

Key words: chlorophyll fluorescence induction kinetics curves, chlorophyll fluorescence parameters, fruit appearance, gas exchange parameters, rapid light-response curves

INTRODUCTION

Pepper (*Capsicum annuum* L.) is one of the world's most important economically significant solanaceous vegetable crops [Sun et al. 2020, Mao et al. 2023]. Pepper is also widely cultivated in China, and its economic value and cultivated area now have ranked first in the vegetable industry [Lv et al. 2020]. There are about 2 mln hectares of land dedicated to pepper cultivation; the annual production is about 40 mln tons in China [Chen et al. 2021].

Peppers are originally tropical perennial plants characterised by their ability to withstand high and low temperatures. They can tolerate temperatures above freezing if they have at least three true leaves. Peppers have well-developed root systems and strong regenerative abilities. The process of flowering and fruiting in peppers is continuous. The plants can continue to branch and grow if the environmental conditions, such as temperature, light, and humidity, are suitable. Pep-

pers can grow into “pepper trees” in mild climates like Yunnan, China. In the middle and lower reaches of the Yangtze River region in China, traditional pepper production includes open-field cultivation in spring and summer and two seasons of greenhouse cultivation in spring and autumn [He 2016]. Studies have shown that pepper plants grow slowly during the hot and dry summer. After harvesting in July, the pepper plants can be pruned to stimulate new growth, flowering, and fruiting, taking advantage of their strong regenerative ability. It extends the harvesting period from one season to two or even three seasons, saving the cost of replanting and prolonging the growth period of peppers. It also increases the value of greenhouse production, providing a new and vital approach for achieving high yield and efficiency in greenhouse pepper cultivation [Yuan et al. 2015, Shao et al. 2019].

Currently, theoretical research on summer pruning cultivation of pepper is scarce, with most studies focusing on management techniques. There is still a lack of systematic and in-depth research on the regrowth mechanism of pruning, and comprehensive data support the regulatory effects of pruning on the growth and development of pepper plants. In this study, we conducted summer pruning on spring-season pepper plants and measured the growth indicators, fruit appearance indicators, gas exchange parameters, rapid light response curve and chlorophyll fluorescence parameters, as well as the induction kinetics curve and chlorophyll fluorescence parameters in pruned and unpruned plants. The present study aims to elucidate the mechanism of summer pruning in promoting the growth of pepper plants from these indicators. It will provide a theoretical basis for further promoting and developing summer pruning techniques. The research results are summarised as follows.

MATERIALS AND METHODS

Plant materials and growth conditions. The experiment was conducted between 2015 and 2022 at the Vegetable Research Institute of Hunan Province in Changsha, China (28.19 N, 112.98 E). One pepper cultivar, Xingshu-215, was used in the experiment. The typical morphological traits of this variety are mid-maturity, strong continuous fruiting ability, long harvesting period, resistance to bacterial wilt, anthrac-

nose, and viral diseases, and tolerance to high temperature and drought. The soil cultivation experiment was conducted in a plastic greenhouse measuring 30 m in length and 8 m in width. The greenhouse was divided into five beds, measuring 1 m in width and 28 m in length each. In mid and late March, double-row planting was adopted for each bed, with a plant spacing of 60 cm and a row spacing of 60 cm. A total of 92 plants were planted in each bed. Field management was consistent with local conventional practices. As the basal fertiliser, a compound fertiliser (with N, P₂O₅, and K₂O content of 15%) was applied at 450 kg/hm². Seven days after transplanting, urea was applied at 60 kg/hm². During the budding stage, a high-nitrogen water-soluble fertiliser (containing 30% N, 10% P₂O₅, and 10% K₂O) was applied at 60 kg/hm², along with a high-potassium water-soluble fertiliser (containing 10% N, 5% P₂O₅, and 35% K₂O) at 30 kg/hm². During the fruit enlargement stage, a high-nitrogen water-soluble fertiliser was applied at 60 kg/hm² and a high-potassium water-soluble fertiliser at 90 kg/hm². During the fruit harvesting period, three additional fertilisations were applied, each consisting of 45 kg/hm² of high-nitrogen water-soluble fertiliser and 75 kg/hm² of high-potassium water-soluble fertiliser. The growth conditions were consistent for the research conducted in 2015 and 2022.

Experimental design and treatments. According to a randomised block design, the middle adjacent three beds were selected as three experimental groups. Sixty plants in the middle of each row were chosen as the experimental materials. The experiment included two treatments: pruned and unpruned (control) groups; each treatment group consisted of thirty plants. Pruning was performed as follows: 1 cm below the bifurcation of the four main branches of the pepper plant was pruned in mid to late July, with four branches left on the plant (preliminary preparatory experiments indicate that this method has resulted in better pruning effects). The unpruned group was treated as follows: peppers that reached the commercial fruit harvest standard were harvested on the same day as the pruned group.

Measurement of plant growth indicators. From late July to mid-August 2015, ten new leaves randomly selected from the top of the plants in each plot were marked from the seventh day after pruning. The leaf length and width of the marked leaves were measured

every seven days. In early September 2015, the survival rate of plants in each plot was investigated. Additionally, ten plants randomly selected from each plot were measured for plant height, stem thickness, number of fruits per plant, and yield per plant. Ten mature fruits were randomly selected from each plot to measure longitudinal and transverse diameters, individual fruit weight, and pedicel length [Li and Zhang 2006]. The measurements were repeated three times.

Measurement of gas exchange parameters. In early September 2015, on a sunny day, a Li-6400XT photosynthesis system (Li-COR Inc., USA) was used to measure the gas exchange parameters, including net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_r). Photosynthesis chamber conditions were set as follows: light intensity of $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, CO_2 concentration of $400 \mu\text{mol}\cdot\text{mol}^{-1}$, leaf area of 6 cm^2 , airflow of $500 \mu\text{mol}\cdot\text{s}^{-1}$, and temperature of 30°C . Five fully expanded leaves from the top of randomly selected plants from each plot were measured with three replicates.

Measurement of rapid light response curves. In early September 2022, a hand-held chlorophyll fluorescence instrument FluorPen FP100 (Brno, Czech Republic), was used to measure the rapid light response curve of the leaves. The software “Photosynthetic Calculation 4.1.1” and the rectangular hyperbolic correction model [Ye et al. 2013] was used to fit the chlorophyll fluorescence rapid light response curve (RLC_s), and obtain parameters such as initial slope (α), maximum electron transfer efficiency (J_{max}) and saturation light intensity (PAR_{sat}). Two fully expanded leaves from the top of randomly selected plants from each plot were measured with three replicates.

Measurement of chlorophyll fluorescence induction kinetics curves. In early September 2022, a hand-held chlorophyll fluorescence instrument, FluorPen FP100 (Brno, Czech Republic), was used to measure the chlorophyll fluorescence induction kinetics (OJIP) curves of the leaves [Kasampalis et al. 2021]. A total of 27 parameters, including minimum fluorescence (F_0), maximum fluorescence (F_m), maximum photochemical efficiency (F_v/F_m), and photosynthetic performance index (PI_{abs}), were obtained [Kasampalis et al. 2020]. Before measuring, it was necessary to use a leaf clip to mark the leaves and acclimate them to the

dark for 20 minutes. The saturation light intensity was set at $3000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and the actinic light was set at $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Five fully expanded leaves from the top of randomly selected plants were chosen for each plot, with three replicates.

Statistical analyses. Statistical analysis was performed using the statistical software DPS (ver. 7.05), and the differences between the pruned treatment and the control were evaluated by the t -test ($P \leq 0.05$).

RESULT

Effect of summer pruning on the growth of pepper. The summer pruning treatment significantly increased the leaf growth rate of the pepper plants (Fig. 1). The growth rate of plant leaves after summer pruning treatment was significantly faster than that of the control. At seven days after treatment (DAT), leaves of the same size were selected, and at 14 DAT, the leaf length and width were significantly larger than those of the control. Afterwards, they continued to be significantly larger than those of the control. As shown in Table 1, the plant height after summer pruning treatment was significantly lower than that of the control plants. The number of fruits per plant was significantly lower than that of the control. There were no significant differences in stem thickness or individual plant yield. Specifically, regarding the appearance-related indicators of the fruits, the individual fruit weight of peppers treated with summer pruning reached 16.37 g , significantly higher than the control group's average weight of 11.95 g . The longitudinal and transverse diameters of the fruits were also significantly more extensive than those of the control fruits (Fig. 2). However, the two groups had no significant differences in fruit flesh thickness or stem length.

Effect of summer pruning on the gas exchange parameters of pepper. Summer pruning treatment significantly impacted the gas exchange parameters of the functional leaves at the top of the pepper plants (Tab. 2). The pruned plants' G_s , C_i , and T_r were significantly higher than those of the control group. However, the P_n of the pruned plants was $12.72 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while that of the control was $9.21 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; the difference did not reach a significant level.

Effect of summer pruning on pepper's rapid light response curves (RLCs). The trends of the rapid light

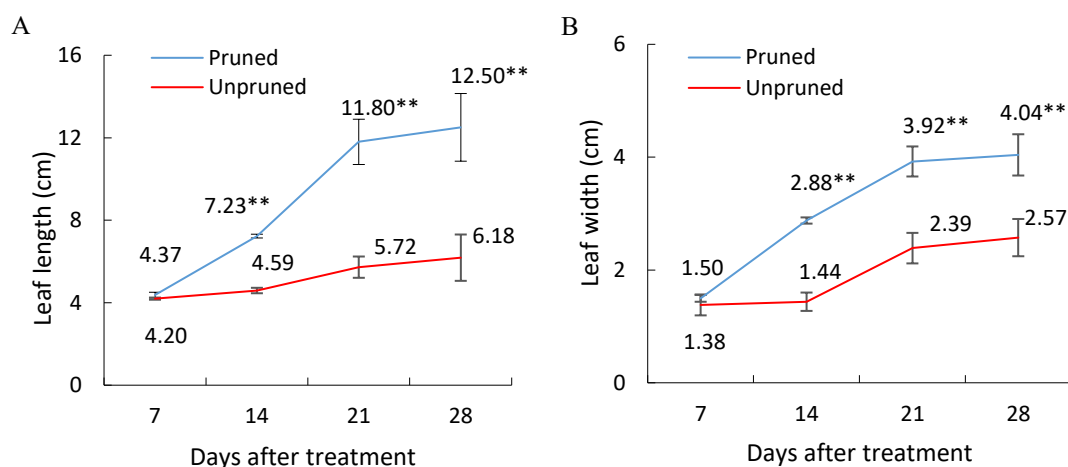


Fig. 1. Effect of summer pruning on leaf length (A) and leaf width (B) in early September 2015. Pruned, the summer pruning treatment group; unpruned, the unpruned control group. In the line chart, the points and vertical bars represent the mean \pm SD (three replicates). * indicates a significant difference between treatments, $P < 0.05$; ** indicates a highly significant difference between treatments, $P < 0.01$

Table 1. Effect of summer pruning treatment on the growth of pepper in early September 2015

Parameter	Pruned	Unpruned
Plant height (cm)	50.75 \pm 1.31	79.70 \pm 0.74**
Stem diameter (cm)	14.25 \pm 0.31	15.56 \pm 0.53
Fruit number per plant	15.83 \pm 0.47	20.10 \pm 1.08**
Yield per plant (g)	228.85 \pm 11.38	234.98 \pm 8.03
Single fruit weight (g)	16.37 \pm 0.82**	11.95 \pm 0.99
Longitudinal diameter (cm)	16.70 \pm 0.33**	13.25 \pm 0.89
Cross diameter (cm)	24.81 \pm 0.84**	21.36 \pm 0.67
Flesh thickness (mm)	2.36 \pm 0.11	2.35 \pm 0.17
Fruit handle length (cm)	4.22 \pm 0.21	3.53 \pm 0.43

Pruned – the summer pruning treatment group; unpruned – the unpruned control group.

* Significant at $P < 0.05$, ** significant at $P < 0.01$.

Table 2. Effect of summer pruning treatment on the gas exchange parameters of pepper in early September 2015

Parameter	Pruned	Unpruned
P_n ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	12.72 \pm 2.34	9.21 \pm 0.97
G_s ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.30 \pm 0.03 **	0.09 \pm 0.02
C_i ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	257.74 \pm 13.32 **	171.11 \pm 23.89
T_r ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	5.90 \pm 0.22 **	2.52 \pm 0.44

Pruned – the summer pruning treatment group; unpruned – the unpruned control group.

* Significant at $P < 0.05$, ** significant at $P < 0.01$.

response curves for the summer pruning treatment and the control group were consistent (Fig. 3). The relative electron transport rate (rETR) increases with increasing light intensity and declines after reaching a certain level. However, the rapid light response curve increase for the pruning treatment was significantly higher than that of the control. At various light intensities, the rETR values of the pruned leaves were higher than those of the control group. The results of fitting the parameters using the hyperbolic curve correction model (Tab. 3) show that the initial slope of the curve, which represents the light energy use efficiency (α), the maximum electron transport rate (J_{max}), and the saturation light intensity (PAR_{sat}) of the summer pruning treatment were higher than those of the control. Among them, the J_{max} of the summer pruning group reached $53.53 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, an increase of 71.41% compared to the control.

Effect of summer pruning on the basic fluorescence parameters calculated from the OJIP curve. The summer pruning treatment significantly impacted the chlorophyll fluorescence parameters of the functional leaves at the top of the pepper plants (Tab. 4). The F_v/F_m of the functional leaves of the control group



Fig. 2. Fruits of the pruned (left) and unpruned peppers (right) in early September 2015

was 0.71, while the F_v/F_m of the pruned plants was 0.75, both lower than the expected value of 0.8. The F_0 of the pruned plants decreased by 16.83%, F_v/F_0 increased by 23.69%, PI_{abs} increased by 58.33%, and DIO/RC decreased by 22.09% compared to the control group.

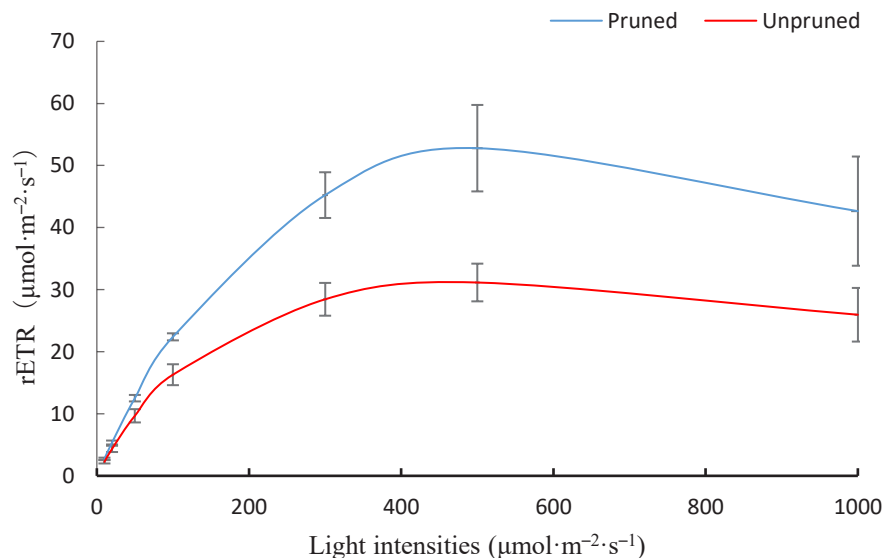


Fig. 3. Effect of summer pruning treatment on the chlorophyll fluorescence-rapid light curve (RLC_s) of pepper in early September 2022. Pruned – the summer pruning treatment group; unpruned – the unpruned control group. In the line chart, the points and vertical bars represent the mean \pm SD (three replicates)

Table 3. Effect of summer pruning on the fitted values of chlorophyll fluorescence characteristics of pepper based on rapid light curves in early September 2022

Parameter	Pruned	Unpruned
α	0.28 ±0.02	0.24 ±0.03
J_{\max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	53.53 ±7.95 *	31.23 ±3.09
PAR_{sat} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	570.63 ±62.48	532.36 ±46.33

Pruned – the summer pruning treatment group; unpruned – the unpruned control group.

* Significant at $P < 0.05$, ** significant at $P < 0.01$.

Table 4. Effect of summer pruning on the basic fluorescence parameters calculated from the OJIP curve in early September 2022

Parameter	Pruned	Unpruned	Increasing degree
F_0	8504.73 ±1080.28	10225.67 ±356.98	–16.83
F_m	33796.07 ±1075.47	35172.40 ±1878.60	–3.91
F_v	25291.33 ±85.90	24946.73 ±1784.00	1.38
F_v/F_0	3.08 ±0.27	2.49 ±0.22	23.69
F_v/F_m	0.75 ±0.02	0.71 ±0.01	5.63
$PsIo$	0.61 ±0.03	0.59 ±0.01	3.39
$PhIEo$	0.46 ±0.03	0.42 ±0.02	9.52
$PhIDo$	0.25 ±0.02	0.29 ±0.01	–13.79
$PhIPav$	930.48 ±6.66	941.81 ±1.77	–1.20
PI_{abs}	2.09 ±0.37	1.32 ±0.25	58.33
ABS/RC	2.61 ±0.16	2.90 ±0.12	–10.00
TRo/RC	1.94 ±0.06	2.04 ±0.06	–4.90
ETo/RC	1.19 ±0.03	1.20 ±0.02	–0.83
DIO/RC	0.67 ±0.10	0.86 ±0.07	–22.09

Pruned – the summer pruning treatment group; unpruned – the unpruned control group.

* Significant at $P < 0.05$, ** significant at $P < 0.01$.

DISCUSSION

Pruning is a crucial technique in plant cultivation management, and it plays a significant role in optimizing the relationship between aboveground growth, leaf area, photosynthesis, and storage capacity to achieve high yield and quality [Demirtas et al. 2010]. Generally, pruning refers to the process of trimming branches to promote nutrition or reproductive growth. Pruning branches can disrupt the balance between plant nutritional and reproductive growth, promote flowering [Zhang et al. 2022], induce reflowering by pruning inflorescences [Zhang et al. 2016], and effectively pro-

long flowering and fruiting time [Peng et al. 2022]. For plants with a long growth period, such as tea, pruning is an essential agronomic measure to maintain tree height [Bora et al. 2022]. Without pruning, developing buds become shorter and thinner, forming a complex canopy, and the overall growth and volume of the plant decrease [Mozumder et al. 2021]. Depending on the season, pruning can essentially be divided into winter-spring and summer-autumn types [Zhang et al. 2018]. Summer pruning can improve fruit illumination, increase fruit size, reduce nutritional growth, and reduce canopy transpiration under high plant density [Albarracín et al. 2017]. It can alleviate the im-

pact of drought on peach trees without additional costs in a climate change scenario [Conesa et al. 2019]. Compared to control and winter pruning, summer pruning increases peaches' average fruit weight and soluble solid content [Ikinci 2014]. Summer pruning of apples can reduce second-year nutritional growth, promote fruit ripening [Mierowska et al. 2002], and help increase soil respiration within two weeks after treatment [Glenn et al. 2011]. Regardless of timing or intensity, summer pruning can increase the vigour of blueberry vegetative growth and decrease the incidence of leaf disease [Kovaleski et al. 2015].

This study found that after pruning, the leaf growth rate of pepper plants significantly increased; summer pruning promoted the growth of pepper plants. Previous studies have reported similar findings on crops such as *Ginkgo biloba* L. [Cao et al. 2022] and *Moringa oleifera* Lam. [Du Toit et al. 2020]. Besides, a more meaningful discovery is that the appearance quality of the fruits improved significantly, with significantly higher fruit weight, longitudinal diameter, and transverse diameter than those of the control group fruit. Similar findings have been reported more frequently in studies on fruits. As the pruning intensity increased, the number of flowers per bud, fruits, and branches per plant of the guava (*Psidium guajava* L.) significantly decreased. Fruit size increased significantly, and fruit weight increased with pruning intensity [Adhikari and Kandel 2015]. Although pruning reduces the number of fruits per blueberry plant, it also increases fruit size, compensating for the final yield per plant [Lee et al. 2016]. Pruning improved the physicochemical qualities of cv. Flordasun peach fruits, including fruit weight and size and total soluble solids (TSS), sugar, and acid contents [Kumar et al. 2010]. Pruning reduces the number of branches and flowers on the plant, decreasing the number of fruits per plant. Therefore, under the same fertilisation and watering conditions, the weight of individual fruits will increase accordingly.

This study also indicated that summer pruning promoted photosynthesis in pepper leaves. After pruning, the net photosynthetic rate of pepper leaves increased by 38.11% compared to the control group. The pepper leaves after summer pruning treatment showed better light energy utilisation efficiency, maximum electron transfer rate, and tolerance to high light intensity compared to the control. Specifically, the J_{\max} of pepper

leaves in the summer pruning treatment increased by 71.41% compared to the control. These findings are consistent with previous research: after pruning Eucalyptus trees by 50% for 19 weeks, the upper canopy J_{\max} significantly increased by 19%, and pruning also significantly increased leaf instantaneous transpiration, nitrogen use efficiency (NUE), phosphorus use efficiency (PUE), and specific leaf area (SLA) while reducing sodium and chlorophyll content [Forrester et al. 2012]. Pruning of the 70% of the crown of *Eucalyptus regnans* F. Muell. trees increased the photosynthetic rate by 40% in contrast to the control trees, and this effect lasted up to 28 weeks after pruning [Lisboa et al. 2014]. Summer pruning increased the overall canopy light penetration, positively correlated with the photosynthetic rate, thereby improving the photosynthetic rate [Bhusal et al. 2017]. Summer pruning promotes photosynthesis in functional leaves because there are many new leaves on the pruned plants, which have more substantial photosynthetic capacity and physiological activity. Likewise, it is possible that after pruning, the “source” organ (leaves) of photosynthetic products decreases, while the “sink” organ (root system) remains almost unchanged. The remaining leaves are relatively stimulated by the pull of the “sink”, increasing their activity and Pn. Additionally, the transpiration area decreases after pruning, while the water absorption area (root surface area) does not decrease significantly, leading to increased water supply to the remaining leaves, stimulating transpiration, and increasing Tr. The generation of new leaves consumes many photosynthetic products, which further strengthens the pull force of the “sink” organ on the “source,” resulting in a further increase in Pn.

In addition to the above, we have also observed that the F_v/F_m values of the control group and the pruned group's functional leaves were lower than the standard value of 0.8. F_v/F_m is an essential photochemical quenching parameter that determines the maximum quantum yield of PSII [Shin et al. 2021]. It is also the most frequently used parameter in chlorophyll fluorescence analysis. Under normal conditions, F_v/F_m shows minimal variation and is not influenced by species or various conditions. It maintains a constant value of around 0.8 in healthy leaves, only decreasing under various stress conditions, such as drought, high temperature, and low temperature [Chiango et

al. 2021], and approximately recovers to the control level in recovery treatments. It indicates that the pepper plants were under adverse conditions during the measurements. Besides that, F_0 and DIo/RC values were lower, while F_v/F_m and PI_{abs} were higher in the pruned group plants than in the control group plants. F_0 , or fixed fluorescence, is the chlorophyll fluorescence yield when the PSII reaction centre is open. The magnitude of F_0 is related to the chlorophyll content of plants, and changes in F_0 can reflect the degree of damage to the PSII reaction centre in photosynthesis. An increase in F_0 indicates that the PSII reaction centre is damaged by light and cannot effectively utilise excess light energy. PI_{abs} is also a commonly used parameter for quantifying nonbiological stress responses and is significant in evaluating photosynthetic performance [Bano et al. 2021, Mendes Bezerra et al. 2021, Sousaraei et al. 2021]. These results suggest that under adverse conditions, the pruned pepper plants had less energy for thermal dissipation, experienced lower stress levels, and exhibited stronger stress resistance. It may be because pruning reduces the number of leaves, resulting in a smaller plant size than the control group. This reduction in leaf area decreases transpiration and reduces water loss, thereby enhancing the plant's tolerance to high temperatures and drought. It could also be due to the newly formed leaves' more vigorous physiological activity and stress resistance. However, further research is needed to determine the specific reasons.

CONCLUSION

Summer pruning significantly improves the leaf growth rate and fruit appearance quality of pepper, effectively promotes the photosynthesis of functional leaves, and reduces the stress degree under adverse environmental conditions. Moreover, more evidence is needed to support the claim that pruning enhances the resistance of plants, and the current research cannot determine whether the stress observed in this experiment is due to high temperature, drought, or both.

SOURCE OF FUNDING

This work was supported by the Natural Science Foundation of Hunan Province (2021JJ40301) and the

Modern Agricultural Technology Industry System of Hunan Province.

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