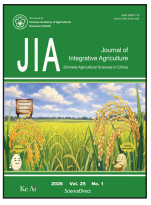
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RESEARCH ARTICLE

Shading and waterlogging interactions exacerbate summer maize yield losses by reducing assimilate accumulation and remobilization processes

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Highlights

- Shading, waterlogging, and their combination reduced leaf photosynthetic assimilation and inhibited lignin biosynthesis.
- Under shading, waterlogging, and their combination, stem vascular system was disrupted, reducing the remobilization capacity of dry matter to the ear.
- Impact of waterlogging and combined stress occurred at the third leaf growth stage, while shading had the greatest impact at tasseling growth stage.

Abstract

Persistent overcast rain was an essential limiting factor for summer maize production, of which immediate impact was the dual pressure of waterlogging and shading. However, the mechanisms underlying independent and combined effects of waterlogging and shading on maize yield losses remain understudied, particularly across different growth stages. Denghai 605 (DH605) was selected to be subjected shading, waterlogging, and their combined stress at the 3rd leaf stage (V3), the 6th leaf stage (V6), and tasseling stage (VT). Results showed that shading, waterlogging and their combination significantly restricted leaf area expansion, reduced leaf net photosynthetic rate (P_n) and net assimilation rate (NAR), thereby decreasing the crop growth rate (CGR) and biomass accumulation. Additionally, compared to control, the process of lignin synthesis was inhibited under stressed treatment, resulting in diminished stem mechanical strength and impaired vascular system development, which substantially reduced assimilate remobilization efficiency to the ear and ultimate grain yield. Waterlogging and combined stresses exhibited maximum impact at the V3 stage, followed by V6 and VT stages, while shading effects were most pronounced at the VT stage, followed by V6 and V3 stages. Moreover, the compound stress exacerbated the damage brought about by a single stress. As climate change is projected to increase the frequency of multiple abiotic stress occurrences, these findings provide valuable insights for future summer maize breeding research under persistent rainfall conditions.

Keywords: maize, abiotic stress combination, photosynthetic capacity, stem development, yield

1. Introduction

Maize is the highest-yielding cereal crop in the world, is essential for human consumption, animal feed, and industrial materials, with its production intrinsically connected to global food security (Zhao *et al.* 2018; Cui *et al.* 2020). In the context of global warming, surface temperatures have increased by 1.1°C above pre-industrial levels (IPCC 2023), resulting in more frequent and intense heavy rainfall in agricultural regions worldwide, leading to increased flooding events (Kaur *et al.* 2021). Additionally, since precipitation

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typically coincides with cloudy conditions and elevated aerosol concentrations, shading and waterlogging often occur simultaneously under field conditions, making it challenging to predict their distribution based on physiological responses to individual stress factors (Najeeb *et al.* 2016; Liu S *et al.* 2019). In the Huang-Huai-Hai region of China, persistent monsoon rainfall coincides with the summer maize growing season, exposing crops to both waterlogging and low light availability, significantly constraining maize production in this area.

Photosynthesis is the material basis for crop yield formation, contributes to over 90% of crop biomass, and photosynthetic efficiency is a critical determinant for high yield output, particularly in C_4 crops like maize (Cheng and Shen 2020). Higher leaf area facilitates superior canopy construction, increasing the effective light energy interception rate and thereby improving crop population photosynthetic capacity and assimilate production (Wu *et al*. 2022). Additionally, stems play a vital role in yield formation, serving as substantial carbohydrate reservoirs and essential conduits for photosynthate transport from source to sink organs (Liu *et al.* 2021; Xu *et al.* 2021). Stem development and functional formation partially depend on photosynthate supply. Light, as a prerequisite for photosynthesis, significantly influences stem development. Research indicates that shading reduces leaf area extension, disrupts chloroplast ultrastructure and function (Du *et al.* 2011; Gao *et al.* 2018), and decreases key photosynthetic enzyme activity (Jia *et al.* 2010), resulting in the inhibition of photosynthetic capacity and photosynthate production (e.g., sucrose). While sucrose as the substrate for structural carbohydrate can boost cell wall thickening and increase thestem strength, of these change are the key dimensions thataffecting the stem development under shading stress (Wu *et al.* 2017). At the same time, shading as an environmental factor, induces longitudinal stem internode elongation ensuring that the plant competes for more light resources, but synergistically brings about a reduction in stem thickness as well as a weaker mechanical strength (Keuskamp *et al.* 2010; Shi *et al.* 2018).

In contrast to shading, waterlogging stress initially decreases soil oxygen content, inhibits root aerobic respiration, and resulted in ethanol and carbon dioxide accumulation in root cells (Shabala 2011; Pan *et al.* 2021). Furthermore, waterlogging intensifies soil microbial activity, accelerating soil organic matter decomposition and toxic substance accumulation (Setter *et al.* 2009), collectively reducing root system dry weight and absorption capacity, ultimately affecting aboveground organ growth (Wang *et al.* 2020). Waterlogging damages leaf antioxidant systems, disrupts the balance between reactive oxygen species (ROS) production and neutralization (Ren *et al.* 2018; Anee *et al.* 2019), and increases leaf ethylene and polyamine concentrations (Chen *et al.* 2014), promoting leaf senescence and chlorophyll degradation (Ren *et al.* 2020). Additionally, waterlogging triggers stomatal closure, restricting CO_2 supply to leaves, thereby reducing net photosynthetic rate and affecting photosynthetic product accumulation and stem transport (Ashraf 2012; Rahayuningsih *et al.* 2017). Which caused a significant reduction in stem dry matter accumulation, as well as poor development of xylem and phloem, especially on the third base internode (Dong *et al.* 2010; Li *et al.* 2019).

The process of crop yield formation fundamentally results from interactions within the “source, sink, flow” system (Mason and Maskell 1928). The vascular system in the stem serves the “flow” function, acting as a transport channel for water and nutrients between crop organs and playing a crucial role in transporting post-flowering assimilates to the ear (Sowiński *et al.* 1999). The efficiency of the “flow” directly affects the rate and quantity of assimilate transport, thereby enhancing assimilate supply to the “sink” and promoting the production potential of the “source” (Liang *et al.* 2019). Previous research has shown that both shading (Cui *et al.* 2012) and waterlogging (Ren *et al.* 2013; Tian *et al.* 2020) decrease the number and area of vascular bundles, affecting assimilate transport to the ear, resulting in excessive dry matter retention in the stem and insufficient grain filling. Furthermore, lignin, a prominent stem constituent, facilitates water and solute transport through the vascular system (Boerjan *et al.* 2003). As a hard aromatic polymer in vascular plants, lignin provides mechanical strength to the stem and plays a vital role in protecting plants against environmental stress (Zhang *et al.* 2014; Hussain *et al.* 2019). It has been suggested that lignin biosynthesis is influenced by genotype and environment (Koyama *et al.* 2012), but studies have not definitively determined its response under combined shading and waterlogging stress.

Previous studies mainly focus the effects of single shading or waterlogging on maize physiological characteristics and grain yield varied with stress stages (Irfan *et al.* 2009; Cui *et al.* 2014; Gao *et al.* 2017; Tian *et al.* 2021). Notably, shading and waterlogging frequently occur simultaneously under field conditions, and their interactions require further investigation. This study examines photosynthetic characteristics and stem development to explore the impact of individual and combined shading and waterlogging on assimilate accumulation and remobilization in summer maize. The results can filling some knowledge gaps for the stress-resistant cultivation techniques under simultaneous shading and waterlogging stresses.

2. Materials and methods

2.1. Field experimental conditions and plant materials

This field experiment was conducted from 2019 to 2020, summer maize hybrid Denghai 605 (DH605) was used as the material in Huang-Huai-Hai Maize Center (36.09°N, 117.09°E), Shandong Province, China. Seeds were sown on June 15 in 2019 and June10 in 2020 in bottomless pools (2.5 m×2.5 m) separated by concrete walls at a planting density of 67,500 plants ha^{-1}. The soil type was sandy loam. Field management, including fertilization, pest control, and chemical control, followed high-yielding field protocols. The climatic conditions during 2019 and 2020 are shown in Appendix A.

2.2. Stress treatment and experimental design

Three stress treatments — shading (S), waterlogging (W),

and simultaneous stress of shading and waterlogging (S–W) were applied at the 3rd leaf stage (V3), the 6th leaf stage (V6), and tasseling stage (VT). The control consisted of non-stressed plants under natural sunlight and normal water management. Each treatment period lasted 6 days. Treatment details are described in Appendix B. The experiment utilized a randomized complete block design with three replications per treatment. For shading treatment, plants were covered with a black polyethylene net providing 60% shading rate, over a removable shade shelter built on a steel frame. The shade net was positioned 2 m above the maize canopy to maintain microclimate conditions similar to the control. For waterlogging treatment, plots were piped and over-irrigated to maintain a 2–3 cm water layer on the soil surface. The compound stress treatment was carried out using a combination of shading and waterlogging treatment methods, with field management detailed in Appendix C. During treatment, light intensity was recorded 30 cm above the canopy from 5:00 to 18:00 using a TES-1332A digital illuminance meter (TES Electrical Electronic Corp, Taibei, Taiwan, China). Temperature and relative humidity were measured every 60 min at 30 cm above the maize canopy using a GSP-6 temperature and humidity recorder (Elitech Instrument Co., Suzhou, Jiangsu, China). Results are shown in Appendix D. After treatment, the shade net was removed, and surface water was pumped out on the sixth night. Soil moisture returned to control levels within a few days by evaporation.

2.3. Data acquisition

Plant growth and biomass At V6, 9th leaf stage (V9), 12th leaf stage (V12), VT, R3, and physiological maturity stage (R6), three representative plants were selected from each treatment. Samples were divided into leaves and stems at V6, V9, V12, and VT, divided into leaves, stems, grains and cobs at R3 and R6, placed in the oven at 105°C for 30 min, dried at 80°C until reaching constant weight, then weighed. The dry matter distribution ratio of each part was calculated at R6. Crop growth rate (CGR) was calculated according to the method described by Liu *et al.* (2014) based on the dry matter weight at each growth stage.

$$CGR\ (g\ m^{-2}\ d^{-1})=(W2–W1)/(T2–T1)$$

where T2–T1 represents the interval between two measurements, derived from the recorded data on the course of fertility (Appendix E). W2–W1 represents the dry matter growth of plants per square metre of land area between two measurement times.

Photosynthetic properties At V6, V9, V12, VT, R3, and R6, ten representative and uniformly growing plants were tagged. The length and maximum width of each leaf were measured, and the leaf area index (LAI) was calculated as follows (Zhang B *et al.* 2007):

$$Leaf\ area=Leaf\ length\times Leaf\ width\times 0.75$$

$$LAI=(Leaf\ area\ per\ plant\times Plant\ number\ per\ plot)/Plot\ area$$

The net assimilation rate (NAR) was calculated using the following formula (Ghosh 2004):

$$NAR\ (g\ m^{-2}\ d^{-1})=(LnL2–LnL1)/(L2–L1)\times(W2–W1)/(T2–T1)$$

where T2–T1 represents the interval between two measurements, L1 and L2 are leaf areas at T1 and T2, W2–W1 represents the difference in dry matter weight between the two measurement times.

At VT, R3 and the next day after treatment, five plants were selected. The net photosynthetic rate (P_n) of the functional leaf was measured between 10:00 a.m. and 12:00 a.m. using CIRAS-3 Portable Photosynthesis Measurement System (CIRASIII, PP System, Hansatech, UK).

Stem development 1) Stem morphology and puncture strength. At R3, five plants were selected, and the internode length and stem thickness of the third base internode were measured using vernier calipers. The stem puncture strength was measured using a YYD-1 stem strength tester (Topo Instrument Co., Hangzhou, Zhejiang, China). 2) Stem microstructure. At R3, three plants were selected from each treatment. Approximately 2 cm of the third base internode of each treatment was resected, preserved in FAA fixative (90 mL of 70% ethanol, 5 mL formaldehyde, 5 mL glacial acetic acid), and rinsed in 70% ethanol. Freehand sections were stained with safranin solution and the internal vascular bundle structure of the stems was observed using an OLYMPUSBX51 fluorescence microscope (Olympus, Tokyo, Japan) and photographed. The number of vascular bundles was recorded, and the vascular bundle area, cortical thickness and thick-walled tissue thickness were measured using the measurement tool included in the system. 3) Lignin metabolism characteristics. At R3, three representative and uniformly growing plants were selected from each treatment plot, and approximately 2 cm of the third stem node above ground was ground to powder with liquid nitrogen. Lignin content was determined following the method of Flavia (Moreira-Vilar *et al.* 2014). A spectrophotometer (UV-2450, Shimadzu, Kyoto, JPN) was used to determine the absorbance value of the extraction at 280 nm. Lignin content was expressed as the absorbance value at 280 nm per millilitre of solution per gram of fresh sample ($OD_{280}\ mL^{-1}\ g^{-1}$ FW).

An Enzyme-linked Immunoassay (ELISA) Kit (MIbio, Shanghai, China) was used to determine the activities of lignin synthesis-related enzymes phenylalanine ammonia-lyase (PAL), 4-coumarate: CoA ligase (4CL), and cinnamyl alcohol dehydrogenase (CAD). The assays were performed according to the manufacturer's instructions, and the absorbance was measured at 450 nm using an enzyme standardizer. The enzyme activities were calculated in U mg^{-1} FW.

Yield At R6 stage, 30 ears harvested from the three intermediate rows of each treatment plot were evaluated for ear characteristics (ear length and width, 1,000-grain weight, grains per ear, bald tip length) and yield (at 14% moisture content).

2.4. Data analysis

Data organization was performed using Microsoft Excel 2003 (Microsoft, Redmond, WA, USA), charts were generated with Sigmaplot 12 (Systat Software, Inc., Richmond, CA, USA), and statistical and correlation analyses were conducted using IBM SPSS Statistics 21.0 (IBM Corporation, Armonk,

NY, USA). Statistical comparisons between groups were performed using ANOVA with least significant differences (LSD) tests at the 0.05 significance level.

3. Results

3.1. Photosynthetic parameters

On the day following the end of treatment, significant reductions in P_n were observed across all three periods of shading, waterlogging, and their combination. During V3 and V6 stages, waterlogging caused greater reduction in P_n compared to shading, with the effect being more pronounced in V6. Conversely, during VT stage, shading stress exhibited a greater impact on P_n than waterlogging. Combined stress demonstrated the most significant effect regardless of growth stage. Although P_n showed partial recovery at VT and R3 stages for all treatments, values remained below control levels (Fig. 1).

At V3 and V6 stages, shading, waterlogging, and their combination significantly reduced leaf area expansion in summer maize, with waterlogging showing greater impact than shading. At VT stage (largest LAI was reached), waterlogging treatments at V3 and V6 decreased LAI by 27.3 and 24.9%, while shading treatments reduced it by 7.0 and 11.7%, respectively, compared to control. However, during VT stage, shading demonstrated greater impact on LAI than waterlogging. At R3, VT-S and VT-W treatments showed LAI decreases of 13.2 and 8.9%, while at R6, decreases were 26.0 and 16.8%, respectively, compared to control. Furthermore, compound stress produced more pronounced reductions compared to single stress treatments (Fig. 2).

Additionally, shading, waterlogging and their combination decreased the NAR at all growth stages. During V9–VT stages, waterlogging and combined stress at V3 and V6 stages significantly reduced NAR compared to control, with these treatments showing significant differences from shading stress, but no significant difference between waterlogging and combined stress, indicate that waterlogging stress played a predominant role under compound stress before VT stage. During reproductive growth (VT–R6), the NAR difference between stressed and control treatments decreased but remained below control levels. Notably, during V6–V9 stages, V6-W showed lower NAR than V3-W, while this pattern reversed during V9–V12 stages, indicating stronger impact of V3 waterlogging. No significant differences were observed in waterlogging effects on NAR between V12–VT stages (Fig. 3).

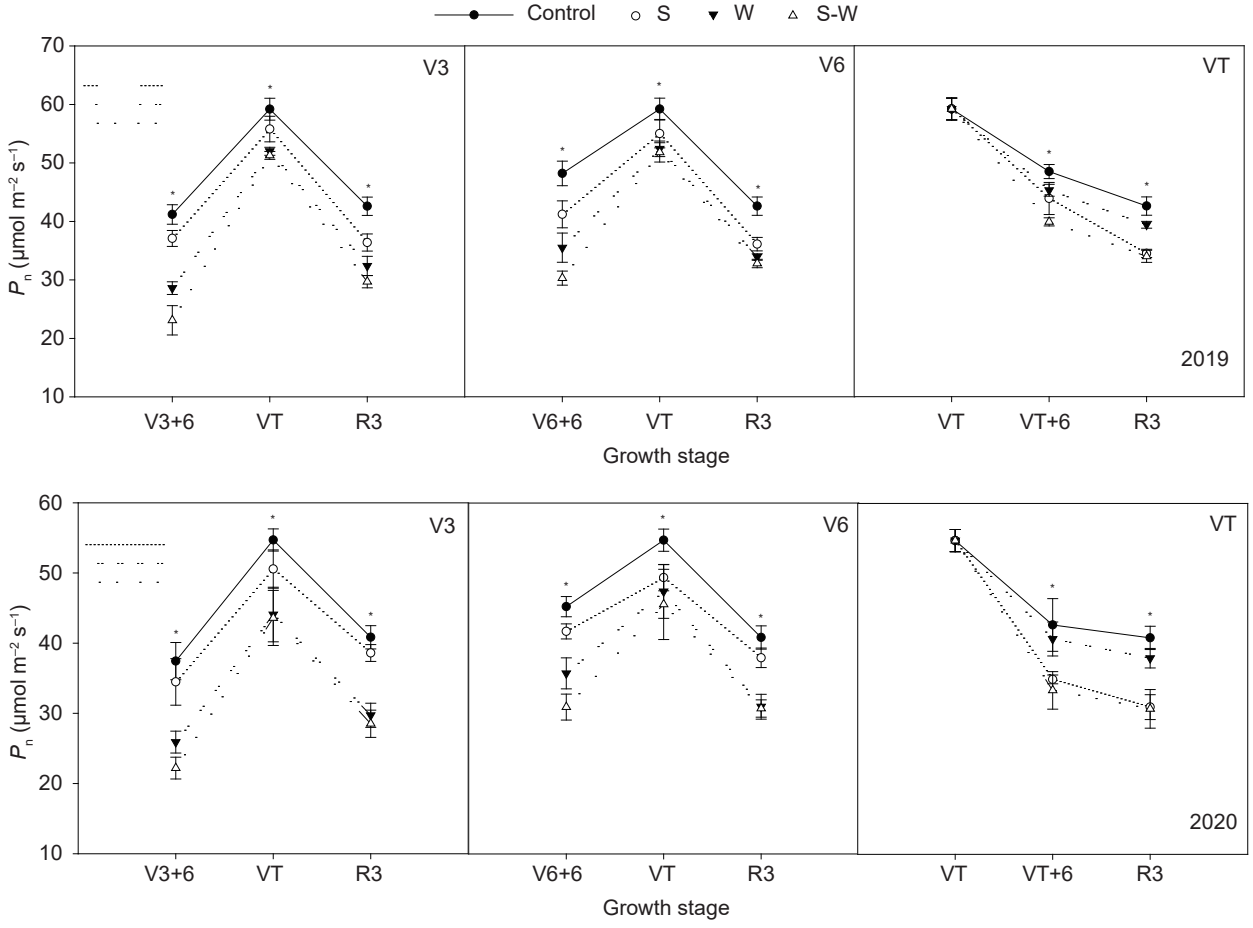


Fig. 1 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on leaf net photosynthetic rate (P_n) of summer maize. V3, V6, VT and R3 represent the 3rd leaf, 6th leaf, tasseling, and milk stages, respectively. V3+6, V6+6 and VT+6 indicate the end of shading, waterlogging and combined stress at V3, V6 and VT after 6 days of treatment. Bars mean SE (n=5). *, significant difference at P<0.05 by LSD test.

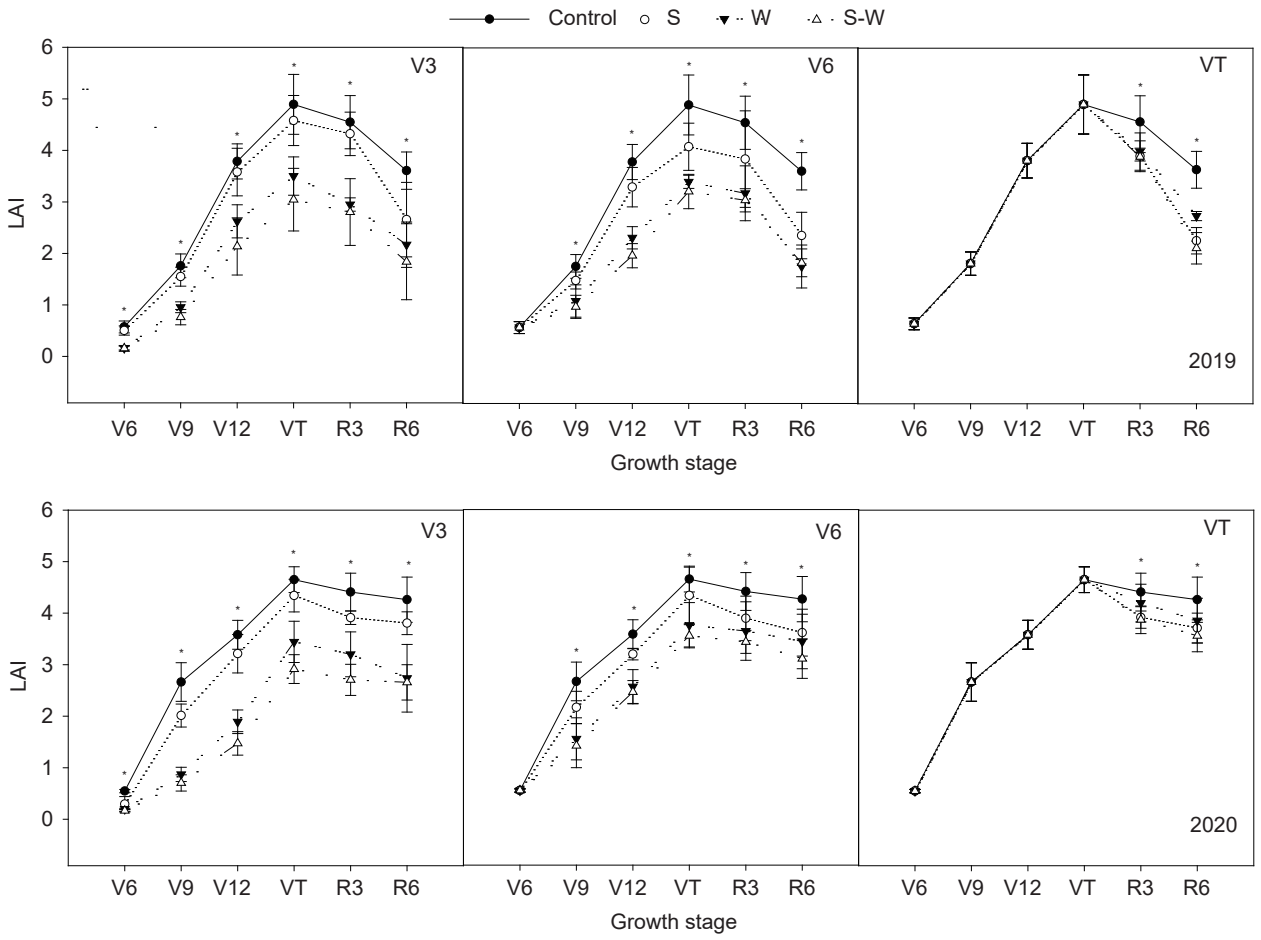


Fig. 2 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on leaf area index (LAI) of summer maize. V3, V6, V9, V12, VT, R3, and R6 represent the 3rd leaf, 6th leaf, 9th leaf, 12th leaf, tasseling, milk, and maturity stages, respectively. Bars mean SE (n=10). *, significant difference at P<0.05 by LSD test.

3.2. Stem development

Morphology and puncture intensity Shading, waterlogging, and their combination treatments at different growth stages resulted in thinner and shorter third base internodes with reduced puncture intensity (Table 1). Combined stress showed maximum impact at V3 stage, decreasing stem thickness, node length, and puncture intensity by 24.1, 26.3 and 22.7%, respectively, compared to control, with diminishing effects at V6 and VT stages. Waterlogging effects paralleled combined stress, showing reductions of 21.6, 22.4 and 19.6% (V3 stage), 10.4, 21.1 and 16.5% (V6 stage), and 3.4, 8.5 and 9.6% (VT stage) in stem thickness, node length and puncture intensity, respectively, compared to control. Shading demonstrated lesser effects on these parameters. Significant differences between shading and waterlogging effects were observed at V3 and V6 stages, but not at VT stage.

Stem microstructure Cortical thickness, sclerenchyma thickness, number and area of small and large vascular bundles decreased under shading, waterlogging, and their combined conditions. The arrangement of vascular bundles became dispersed after stress treatments (Appendix F; Table 2). Cortical thickness decreased by 5.5% (S), 29.0% (W), and 30.5% (S-W) at V3, by 3.6% (S), 21.7% (W), and 25.4% (S-W) at V6, and by 2.3% (S), 0.8% (W), and 4.0% (S-W) at VT, respectively, while sclerenchyma thickness decreased by 10.2% (S), 24.1% (W) and 27.1% (S-W) at V3, 5.7% (S), 21.1% (W) and 22.0% (S-W) at V6, 9.9% (S), 9.9% (W) and 11.6% (S-W) at VT, respectively, compared with control. These results indicate that shading and waterlogging at V3 and V6 stages had greater effects on cortical and sclerenchyma thickness than at VT stage. Conversely, shading's effect on vascular bundle number and area was more pronounced at VT stage than at V3 and V6 stages, establishing shading as the primary factor affecting stem microstructure during VT stage. Furthermore, the reduction in stem microstructure caused by combined stress exceeded that of individual shading or waterlogging treatments.

Lignin accumulation and lignin synthetic enzymatic activities Lignin content of the third base internode decreased under shading, waterlogging and their combination at three stages (Fig. 4). The reduction in lignin content under combined treatment significantly exceeded that of single stress treatments. Lignin content in V3-S, V3-W, and V3-S-W treatments decreased by 16.3, 31.5, and 38.5%, respectively, while V6-S, V6-W, and V6-S-W treatments showed

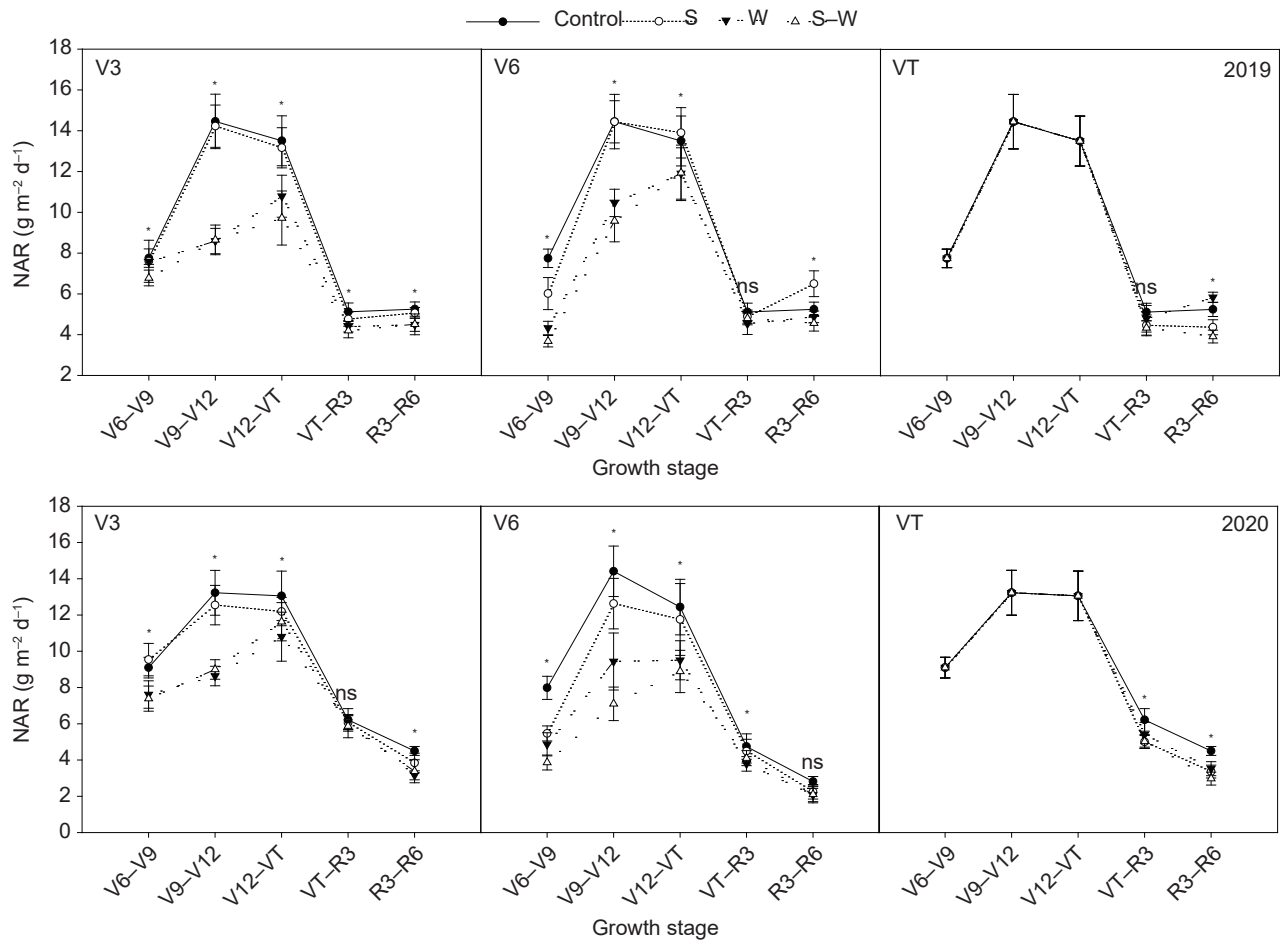


Fig. 3 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on net assimilation rate (NAR) of summer maize. V3, V6, V9, V12, VT, R3, and R6 represent the 3rd leaf, 6th leaf, 9th leaf, 12th leaf, tasseling, milk, and maturity stages, respectively. Bars mean SD SE (n=3). ns, no significant; *, significant difference by LSD test.

Table 1 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on morphology and puncture intensity of the third base internode of summer maize

Treatment[1)]	2019			2020		
	Puncture intensity (N mm^{-2})	Stem diameter (mm)	Stem node length (cm)	Puncture intensity (N mm^{-2})	Stem diameter (mm)	Stem node length (cm)
Control	73 a	24.0 a	11.9 a	72 a	22.0 a	12.1 a
V3-S	70 b	19.1 c	11.3 ab	68 a	19.4 c	11.9 ab
V3-W	58 e	17.6 e	9.7 e	59 d	18.0 e	9.1 e
V3-S-W	55 e	16.7 f	9.1 f	57 d	17.1 f	9.1 e
V6-S	71 ab	21.1 b	11.3 ab	69 a	21.7 ab	11.7 ab
V6-W	63 d	19.9 c	10.8 c	62 c	21.0 b	10.7 d
V6-S-W	64 c	18.5 d	10.5 cd	64 c	18.1 e	10.9 c
VT-S	68 bc	21.0 b	11.3 b	67 ab	21.0 b	11.2 b
VT-W	67 bc	20.8 b	11.5 ab	66 b	21.0 b	11.7 ab
VT-S-W	65 c	18.5 d	10.9 c	66 b	18.9 d	10.8 cd
ANOVA						
S	*	**	**	ns	*	**
W	**	*	**	**	**	**
S-W	**	**	**	**	*	**

[1)] V3, V6, and VT represent the 3rd leaf, 6th leaf, and tasseling stages, respectively.
Different lowercase letters within the same column indicate significant differences at P<0.05 according to the LSD test. Treatment differences were calculated within hybrids for each specific year. ns indicates not significant; * and ** indicate significance at the 0.05 and 0.01 probability levels, respectively.

Table 2 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on stem microstructure of summer maize

Year	Treatment[1)]	Big vascular bundle area (μm)	Small vascular bundle area (μm)	Number of vascular bundles	Cortex thicklness (μm)	Sclerenchyma thickness (μm)
2019	Control	115,977 a	93,873 a	459 a	71.5 a	1,303 a
	V3-S	104,932 c	86,971 b	421 c	69.5 b	1,143 c
	V3-W	65,824 f	45,781 f	320 f	51.4 e	897 f
	V3-S-W	66,101 f	45,133 f	308 f	49.5 e	887 f
	V6-S	112,514 b	86,535 b	425 c	69.1 b	1,204 b
	V6-W	87,105 e	49,426 e	348 e	53.3 d	912 e
	V6-S-W	89,958 e	56,431 d	344 e	54.5 d	901 e
	VT-S	94,529 d	85,214 c	398 d	69.9 b	1,082 d
	VT-W	104,878 c	91,412 a	441 b	71.1 a	1,074 d
	VT-S-W	92,515 d	86,545 c	398 d	67.3 c	1,054 d
2020	Control	109,847 a	90,674 a	490 a	69.5 a	1,003 a
	V3-S	99,432 b	83,456 c	457 d	65.4 cd	951 bc
	V3-W	71,475 d	44,156 e	351 g	48.7 g	831 e
	V3-S-W	69,569 e	44,050 e	330 g	48.5 g	779 f
	V6-S	105,815 a	86,547 b	462 d	66.2 c	965 b
	V6-W	74,705 c	60,354 d	389 e	55.1 e	881 d
	V6-S-W	70,358 e	61,458 d	367 f	50.9 f	872 d
	VT-S	98,936 b	85,141 c	474 c	67.8 b	975 b
	VT-W	10,0041 a	88,625 b	481 b	68.9 b	981 a
	VT-S-W	97,956 b	84,963 c	467 c	68.1 b	961 b
ANOVA						
S		**	*	**	**	ns
W		*	**	**	*	**
S-W		**	ns	*	**	*

[1)] V3, V6, and VT represent the 3rd leaf, 6th leaf, and tasseling stages, respectively.
Different lowercase letters within the same column indicate significant differences at $P<0.05$ according to the LSD test. Treatment differences were calculated within hybrids for each specific year. ns indicates not significant; * and ** indicate significance at the 0.05 and 0.01 probability levels, respectively.

decreases of 12.3, 21.4, and 26.8%, respectively, compared to control. Furthermore, PAL and CAD activities decreased significantly after shading, waterlogging and their combined stresses. Waterlogging exhibited greater effects on PAL and CAD activity at V3 and V6 stages compared to shading, while shading showed stronger effects at the VT stage.

3.3. Plant growth, biomass and grain yield

The CGR pattern shows gradual increases from V6–VT stages followed by gradual decreases after VT stage. All stress treatments resulted in significant CGR decreases compared to control across all stages from V6 to R6. During V6-VT stage, waterlogging's impact on CGR exceeded that of shading, while during VT–R6 stage, particularly R3-R6, shading's impact was greater. Notably, at V6–V9 stages, V6-W treatment showed greater CGR effects than V3-W, with this pattern reversing during V9–VT stages, suggesting V6-W treatment's gradual recovery and superiority over V3-W treatment post-V9 stage. This indicates waterlogging's greater impact during V3 stage compared to V6 stage, further evidenced by total biomass accumulation from VT stage (Table 3; Appendix G).

Shading, waterlogging and their combination significantly decreased the accumulation and distribution of dry matter to grains at R6 stage, resulting in a significant yield decrease (Appendix H; Fig. 5). The dry matter weight of V3-S-W, V6-S-W and VT-S-W treatments was decreased by 46.0, 36.3 and 21.9%, respectively, compared to control. Earlier waterlogging caused greater dry matter accumulation reduction than later treatment, while later shading decreased accumulation more than earlier shading. Additionally, later-stage shading increased stem dry matter accumulation. Regarding dry matter distribution, grain allocation percentage decreased under all stress treatments compared to control, while stem, leaf and cob proportions increased. Grain yield decreased by 6.4% (S), 34.4% (W), and 39.3% (S-W) at V3, by 10.2% (S), 28.8% (W), and 31.9% (S-W) at V6, and by 27.1% (S), 9.4% (W), and 28.9% (S-W) at VT, respectively, compared to control. Combined treatment caused greater reductions in dry matter accumulation, distribution, and overall production than individual stress treatments.

3.4. Correlation analysis between yield and parameters related to photosynthesis and stem development

The correlation analysis showed that photosynthesis properties and stem development indicators demonstrated positive correlations with yield. The lignin content, vascular bundle number and area, cortex thickness, and sclerenchyma thickness exhibited positive correlations with puncture intensity, and these parameters also correlated positively with photosynthesis property indicators. Furthermore, lignin content showed positive correlations with PAL, 4CL, and CAD enzyme activities (Fig. 6).

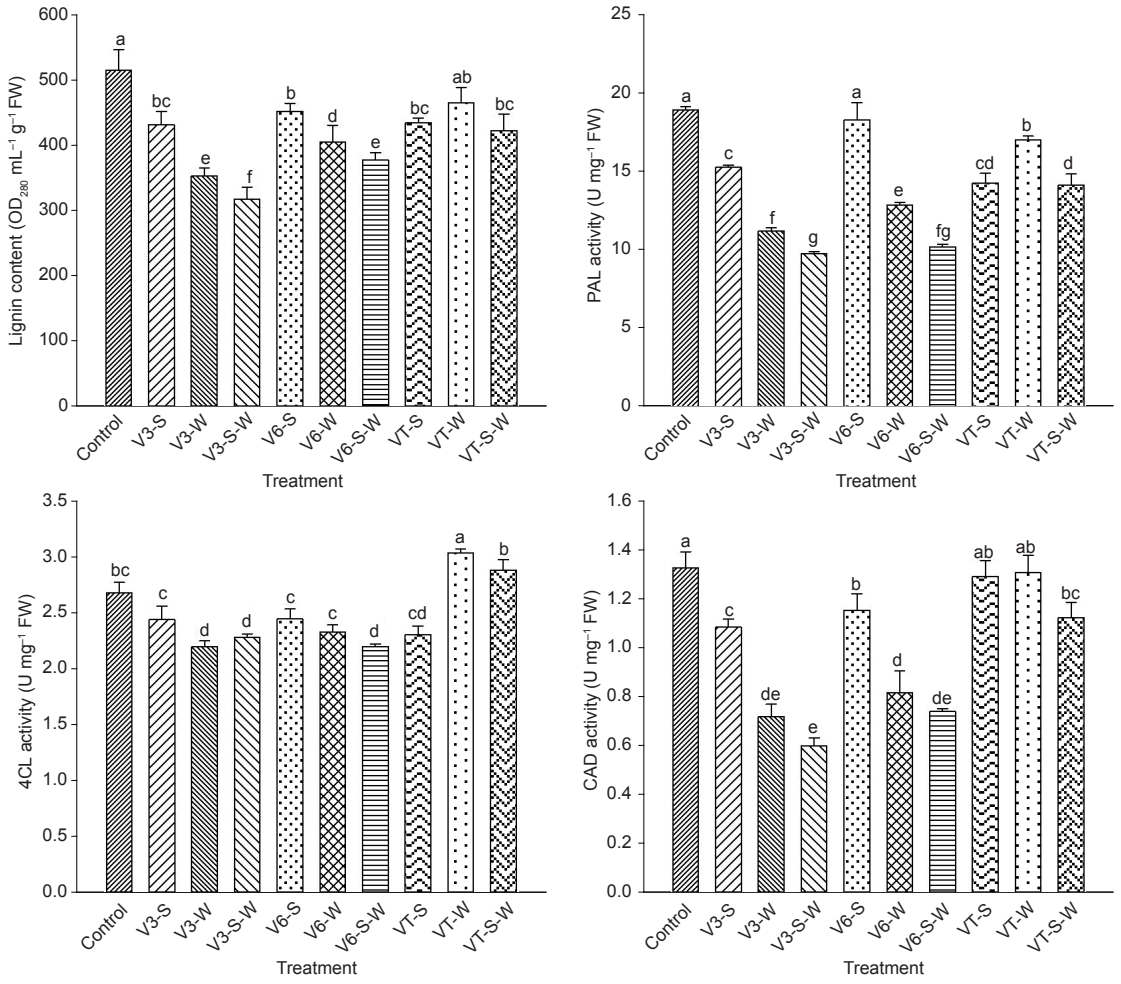


Fig. 4 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on lignin content and lignin synthetic activity in summer maize. V3, V6, and VT represent the 3rd leaf, 6th leaf, and tasseling stages, respectively. Bars mean SE (n=3). Different lowercase letters within the same column indicate significant differences at P<0.05 according to LSD test.

4. Discussion

4.1. Shading and waterlogging interactions altered stem morphology and microstructure and decreased mechanical strength

Since stem collapse frequently occurs below the ears, the basal internode characteristics (particularly the third base internode) serve as the primary site for evaluating stem strength (Zuber and Grogan 1961; Martín and Russell 1984). Stem thickness, cortical thickness, and mechanical tissues contribute to stem mechanical strength formation (Sekhon *et al.* 2020; Xue *et al.* 2020; Xu *et al.* 2022), while puncture intensity directly reflects stem mechanical strength (Feng *et al.* 2010). Our experimental correlation analysis demonstrated that puncture intensity positively correlated with all stem morphology and anatomical structure indicators (P<0.01), suggesting that enhanced stem morphology and anatomical structure was the basis of high puncture intensity. Previous studies have shown that both shading and waterlogging reduced the thickness and length of the third base internode in summer maize, decreased cortex thickness, diminished vascular bundle numbers and area, resulting in lower puncture intensity and negatively impacting stem development and lodging resistance (Cui *et al.* 2012; Ren *et al.* 2013). In the present study, we found that the combined stress aggravated the effect on stem morphology and anatomical structure, leading to reduced stem strength. Additionally, early waterlogging stress and compound stress exhibited more pronounced effects on stem development, while the effects of either single or compound stress on stem development were smaller at VT stage, indicating that nutritional growth completion at flowering stage and basic stem development completion resulted in reduced stress impact on stem strength.

4.2. Shading and waterlogging interactions reduced lignin synthesis driving abnormal stem development

Beyond developed mechanical tissues, stem mechanical strength primarily depends on carbohydrate composition. While non-structural carbohydrates readily transfer to ears during grain filling, plant mechanical strength is largely determined by structural carbohydrates, particularly lignin, in the stem (Zhang *et al.* 2014). Lignin serves as a crucial structural component of plant cell walls and plays a key

Table 3 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on crop growth rate of summer maize (g m^{-2} d^{-1})[1)]

Year	Treatment	Growth stage				
		V6–V9	V9–V12	V12–VT	VT–R3	R3–R6
2019	Control	8.20 a	38.24 a	58.29 a	24.17 a	21.33 a
	V3-S	7.31 b	34.51 ab	53.82 b	21.42 b	19.33 b
	V3-W	4.50 d	15.01 d	45.24 c	13.91 d	11.39 d
	V3-S-W	3.88 de	14.35 d	42.91 c	14.89 d	11.27 d
	V6-S	5.68 c	32.96 b	55.66 a	20.75 b	19.67 b
	V6-W	3.48 e	17.01 c	53.05 b	16.86 c	12.10 c
	V6-S-W	2.79 f	14.38 d	46.83 c	16.77 c	13.86 c
	VT-S				19.54 bc	13.12 c
	VT-W				21.14 b	19.23 b
	VT-S-W				20.14 b	11.62 d
2020	Control	9.13 a	33.06 a	47.62 a	28.90 a	19.50 a
	V3-S	8.36 a	27.49 b	45.69 a	28.14 a	12.55 c
	V3-W	4.93 c	12.57 d	33.35 c	20.20 cd	9.36 e
	V3-S-W	4.67 c	11.47 d	33.93 c	16.49 e	9.29 e
	V6-S	6.12 b	31.80 a	46.46 a	24.58 b	14.98 b
	V6-W	4.62 c	16.87 c	32.58 c	20.89 cd	14.48 b
	V6-S-W	3.89 cd	12.99 d	39.04 b	19.70 d	12.64 c
	VT-S				21.37 c	12.82 c
	VT-W				26.22 ab	11.92 c
	VT-S-W				21.34 c	11.04 d
ANOVA						
S					ns	*
W					**	**
S×W					*	**

[1)] V3, V6, V9, V12, VT, R3, and R6 represent the 3rd leaf, 6th leaf, 9th leaf, 12th leaf, tasseling, milk, and maturity stages, respectively.

Different lowercase letters within the same column indicate significant differences at $P<0.05$ according to the LSD test. Treatment differences were calculated within hybrids for each specific year. ns indicates not significant; * and ** indicate significances at the 0.05 and 0.01 probability levels, respectively.

role in establishing stem morphology and toughness (Li *et al.* 2009; Wang *et al.* 2014). Studies have demonstrated strong correlations between lignin accumulation and stem mechanical strength in wheat (Nguyen *et al.* 2016), rice (Zhang *et al.* 2014), and soybean (Liu W *et al.* 2019). Furthermore, PAL, 4CL, and CAD are essential enzymes that regulate lignin synthesis in stems (Eudes *et al.* 2014; Hussain *et al.* 2019). In the present study, correlation analysis suggested that stem puncture intensity was positively correlated with lignin content (R^2=0.53**), and lignin content was positively correlated with PAL (R^2=0.67**), 4CL (R^2=0.65**) and CAD (R^2=0.58**) activities. Research indicates that lignin, a phenolic compound, exhibits high sensitivity to light conditions (Koyama *et al.* 2012). Wu *et al.* (2017) reported that shading stress significantly reduced lignin synthesis-related gene expression, impeding lignin biosynthesis in rice stems, while Liu W *et al.* (2019) observed reduced lignin content and synthase activity in shaded soybean stems. Similar effects were observed in wheat under waterlogging stress (Nguyen *et al.* 2016). The increased demand for soluble sugars following waterlogging directs pyruvate toward glycolysis rather than phenylalanine production through the mangiferous acid pathway. This reduction in phenylalanine, a critical lignin synthesis precursor, impedes stem lignin synthesis (Vanholme *et al.* 2012). Additionally, photosynthesis provides carbon sources for lignin synthesis (Rogers *et al.* 2005). In the present study, we observed shading, waterlogging, and their combined stresses at all growth stage reduced leaf net photosynthetic rate and decreased stem lignin synthase activity, resulting in reduced lignin content, particularly at V3 and V6 stages. Moreover, combined stress produced significantly lower lignin content compared to individual stresses, indicating more severe inhibition of lignin biosynthesis. Consequently, combined stress demonstrated greater impact on stem strength than individual waterlogging or shading treatments.

4.3. Shading and waterlogging interactions blocked dry matter accumulation and remobilization and decreased yield

Many studies have established the impact of shading and waterlogging periods on crop yield. Waterlogging during V3 demonstrated the most significant effect on summer maize yield, followed by V6, while waterlogging during the 10th day after flowering showed reduced impact on yield (Ren *et al.* 2014). Conversely, shading at the flowering stage exhibited the strongest effect on maize yield, followed by ear stage and seedling stage (Zhang J *et al.* 2007). The combined effect of shading and waterlogging on cotton yield demonstrated greater impact during early growth compared to late growth stages (Najeeb *et al.* 2016). Research indicates that dry matter accumulation in vegetative organs and its distribution to reproductive organs are crucial determinants of maize yield (Hou *et al.* 2020), while enhancing dry matter production capacity and maximizing grain allocation represent essential conditions for yield improvement (Ding *et al.* 2005). These processes are integrally connected to leaf photosynthetic capacity and stem transport capability. Leaf area indicates plant canopy photosynthetic capacity, showing linear positive correlation with radiation interception (Gallo *et al.* 1993), while developed vascular tissues regulate carbon and nitrogen metabolism, facilitate nutrient storage during vegetative periods, and control assimilate distribution across organs during reproductive growth (Housley and Peterson 1982; Sowiński 1999). Our results demonstrated positive correlations between yield and number (R^2=0.86**) and area of big (R^2=0.73**) and small (R^2=0.73**) vascular bundles. In this study, shading, waterlogging, and their combination during V3 and V6 inhibited leaf area expansion and decreased radiation interception capacity, leading to reduced net assimilation rate during nutritional growth and disrupted vascular system development. This resulted in diminished crop growth rate at V6–VT, reduced biomass accumulation at VT stage, and significantly decreased dry matter remobilization from stem to ear. Consequently, the crop growth rate of VT–R6 decreased substantially with reduced ear weight, increasing the proportion retained in stems and leaves at maturity, significantly impacting grain yield reduction (Fig. 7). Waterlogging at V3 and V6 stages had a greater effect on dry matter accumulation in stem and leaf and the development of vascular system, resulting in insufficient grain filling during reproductive growth. The compound stress pattern

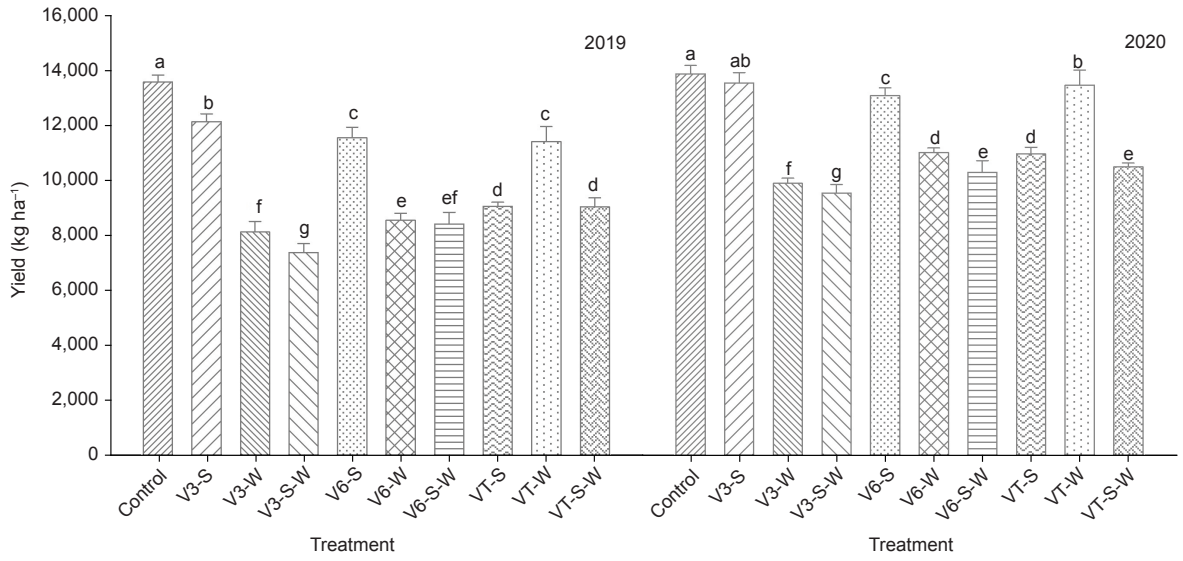


Fig. 5 Effects of shading (S), waterlogging (W) and their combined treatment (S-W) on grain yield in summer maize. V3, V6, and VT represent the 3rd leaf, 6th leaf, and tasseling stages, respectively. Bars mean SE (n=3). Different lowercase letters in the same column indicate significant differences at P<0.05 according to the LSD test.

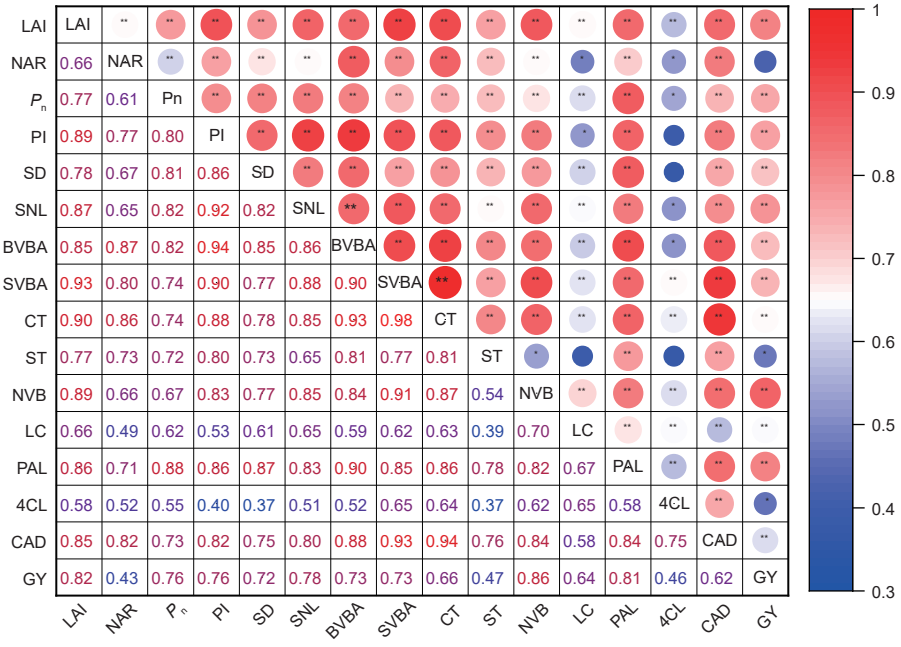


Fig. 6 Correlation analysis. LAI, leaf area index; NAR, net assimilation rate; P_n, net photosynthetic rate; PI, puncture intensity; SD, stem diameter; SNL, stem node length; BVBA, big vascular bundle area; SVBA, small vascular bundle area; CT, cortex thickness; ST, sclerenchyma thickness; NVB, number of vascular bundles; LC, lignin content; PAL, phenylalanine ammonia-lyase; 4CL, 4-coumarate: CoA ligase; CAD, cinnamyl alcohol: dehydrogenase; GY, grain yield. * and **, significant at the 0.05 and 0.01 probability levels, respectively.

aligned with waterlogging stress patterns, intensifying single stress effects on yield. Notably, as crop yield formation is mediated by source–sink interactions (Mason and Maskell 1928), sink development partially constrains source–flow coordination, particularly during late grain filling (Franck *et al.* 2006, Damatta *et al.* 2008). Additionally, at VT stage, the ear represents a secondary sink compared to the tassel. Under stress conditions, the ear experiences greater impact than other plant organs (Andrade *et al.* 1999). According to previous studies (Zhou *et al.* 2013; Cui *et al.* 2014), VT stage shading significantly restricted silk growth and fertility rate, reducing kernels per spike (grain sink size) (Appendix I). Therefore, anthesis shading stress minimally affected leaf area and vascular bundles, maintaining source and flow intensity similar to control conditions and high population growth rate at VT–R3 stage. However, limited sink capacity

restricted dry matter transport during late grain filling (R3–R6), leading to stem dry matter accumulation at R6 stage, significantly affecting yield formation.

4.4. Future directions for research on combined stress to address global complex climate change

Currently, crop survival, growth, and yield face severe challenges from global warming and climate change, resulting in increased abiotic impacts including droughts, extreme temperatures, and floods, frequently leading to multifactorial combinations of adverse conditions (Zandalinas *et al.* 2022). Our experiment represents the first investigation using artificially simulated conditions of combined shading and waterlogging stresses to examine summer maize photosynthetic capacity and stem development responses, clarifying yield loss mechanisms. The author suggests addressing these future research priorities regarding combined stress: (i) The effects of combined stresses demonstrate non-additive properties, with maize exhibiting certain regulatory capabilities under compound stress through unclear mechanisms; (ii) single stress effects on crop physiological processes vary (directly or indirectly), with stress dominance differing across growth stages, necessitating synergistic consideration of their constraints.

Previous studies have demonstrated that spike differentiation before the reproductive stage and fertilization processes in maize were affected by shading, waterlogging, and their combined stress (Hu *et al.* 2021). These factors were determining elements in the decline of grain numbers and yield. Additionally, the reduction in grain numbers may lead to decreased ear sink capacity which, according to the feedback inhibition hypothesis, could limit leaf photosynthesis and assimilate transport (Pan *et al.* 2017). Some studies suggest that low sink demand does not affect assimilate retranslocation (Fan *et al.* 2010), while Zhang *et al.* (2013) proposed that leaf source intensity should be evaluated alongside sink size when determining whether sink size limits assimilate transport to grain. Consequently, further investigation is needed to determine whether restricted assimilate transport to grains is limited by the vascular system in our experiment.

5. Conclusion

This study demonstrates that shading, waterlogging, and their combined stresses negatively impacted yield through multiple mechanisms: they suppressed leaf photosynthetic capacity (e.g., LAI, P_n, and NAR), leading to reduced dry matter accumulation; decreased lignin metabolism and impaired stem development resulted in hindered remobilization of assimilates from nutrient organs to the ears, collectively limiting carbon supply to grains during grain filling. Waterlogging and combined stress effects were most pronounced at V3, followed by V6 and VT, while shading effects were most significant at VT, followed by V6 and V3. Combined stresses caused greater yield losses compared to single stresses. This research provides a foundation for future studies examining how maize responds to shading and waterlogging stress across different growth stages. Furthermore, our findings regarding lignin metabolism and vascular phylogeny's contribution to yield may offer potential targets for developing stress-resistant maize varieties and gene editing technologies.

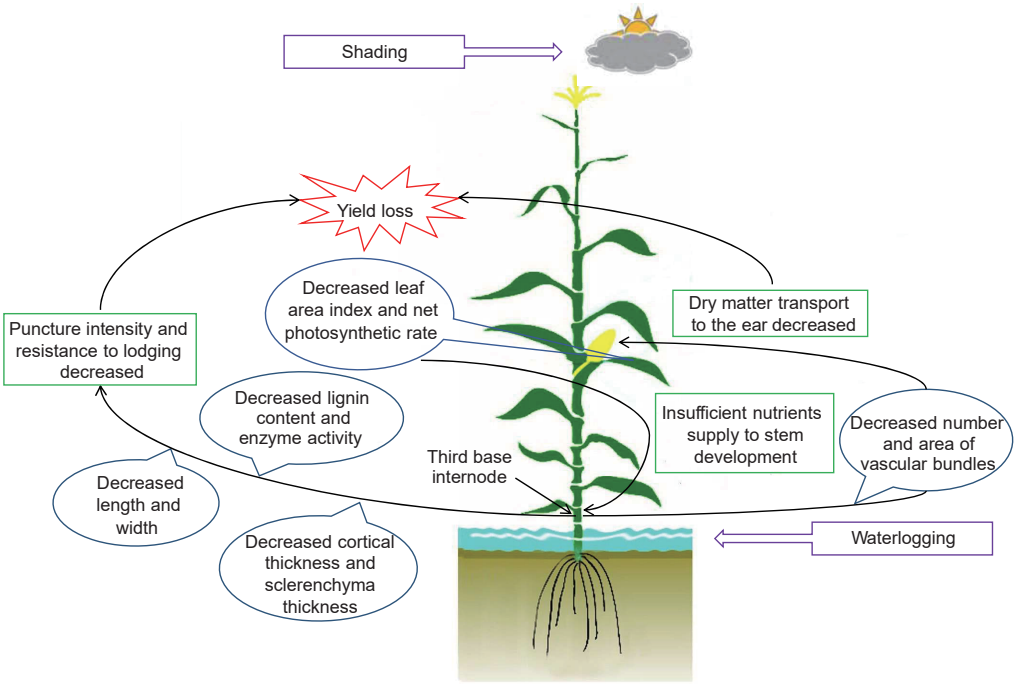


Fig. 7 Mechanism of yield loss in summer maize under combined shading and waterlogging stress. Combined effects of shading and waterlogging diminished leaf photosynthetic capacity, which led to decreased lignin synthesis and impaired stem development, consequently reducing stem strength. Additionally, the deterioration of the vascular bundle system limited assimilate transport to the ear, ultimately resulting in yield reduction.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

Data availability

Data will be made available on request.

Appendices associated with this paper are available at https://doi.org/10.1016/j.jia.2024.03.046

References

Andrade F, Vega C, Uhart S, Cirilo A, Cantarero M, Valentinuz O. 1999. Kernel number determination in maize. *Crop Science*, **39**, 453–459.

Anee T, Nahar K, Rahman A, Mahmud J, Bhuiyan T, Alam M, Fujita M, Hasanuzzaman M. 2019. Oxidative damage and antioxidant defense in *Sesamum indicum* after different waterlogging durations. *Plants*, **8**, 196.

Ashraf M. 2012. Waterlogging stress in plants: A review. *African Journal of Agricultural Research*, **7**, 1976–1981.

Boerjan W, Ralph J, Baucher M. 2003. Lignin biosynthesis. *Annual Review of Plant Biology*, **54**, 519–546.

Chen Y, Chen X, Wang H, Bao Y, Zhang W. 2014. Examination of the leaf proteome during flooding stress and the induction of programmed cell death in maize. *Proteome Science*, **12**, 33.

Cheng J, Shen Y. 2010. My humble opinions on high photosynthetic efficiency of crop. *Acta Agronomica Sinica*, **36**, 1235–1247. (in Chinese)

Cui A, Zhang J, Zhang H, Shan H, Chen W. 2020. Preliminary exploration on current situation and development of maize production in China. *Journal of Agricultural Science and Technology*, **22**, 10–19.

Cui H, Ji L, Li B, Zhang J, Dong S, Liu P. 2012. Effects of shading on stalks morphology, structure and lodging of summer maize in field. *Scientia Agricultura Sinica*, **45**, 3497–3505. (in Chinese)

Cui H, Jin L, Li B, Dong S, Liu P, Zhao B, Zhang J. 2014. Effects of shading on endogenous hormones regulation in kernel development of summer maize in the field. *Chinese Journal of Applied Ecology*, **25**, 1373–1379. (in Chinese)

Damatta F, Cunha R, Antunes W, Martins S, Araújo W, Fernie A, Moraes G. 2008. In field-grown coffee trees source–sink manipulation alters photosynthetic rates, independently of carbon metabolism, *via* alterations in stomatal function. *The New Phytologist*, **178**, 348–357.

Ding L, Wang K, Jiang G, Liu M, Niu S, Gao L. 2005. Post-anthesis changes in photosynthetic traits of maize hybrids released in different years. *Field Crops Research*, **93**, 108–115.

Dong H, Li H, Li A, Yan X. 2010. Relationships between spike and stem growth and female spike differentiation under different densities. *Maize Science*, **18**, 65–71, 75. (in Chinese)

Du C, Li C, Liu T, Zhao Y. 2011. Response of anatomical structure and photosynthetic characteristics to low light stress in leaves of different maize genotypes. *Acta Ecologica Sinica*, **31**, 6633–6640. (in Chinese)

Eudes A, Liang Y, Mitra P, Loqué D. 2014. Lignin bioengineering. *Current Opinion in Biotechnology*, **26**, 189–198.

Fan P, Li L, Duan W, Li W, Li S. 2010. Photosynthesis of young apple trees in response to low sink demand under different air temperatures. *Tree Physiology*, **30**, 313–325.

Feng G, Liu Z, Wu Y, Li Y, Huang C. 2010. Primary study on correlation between corn variety lodging resistances and its stem puncture-pull strength. *Crop Science*, **18**, 19–23.

Franck N, Vaast P, Génard M, Dauzat J. 2006. Soluble sugars mediate sink feedback down-regulation of leaf photosynthesis in field-grown *Coffea arabica*. *Tree Physiology*, **26**, 517–525.

Gallo K, Daughtry C, Wiegand C. 1993. Errors in measuring absorbed radiation and computing crop radiation use efficiency. *Agronomy Journal*, **85**, 1222–1228.

Gao J, Cui H, Shi J, Dong S, Liu P, Zhao B, Zhang J. 2018. Effects of light intensities after anthesis on the photosynthetic characteristics and chloroplast ultrastructure in mesophyll cell of summer maize *(Zea mays* L.). *Chinese Journal of Applied Ecology*, **29**, 883–890. (in Chinese)

Gao J, Shi J, Dong S, Liu P, Zhao B, Zhang J. 2017. Grain yield and root characteristics of summer maize (*Zea mays* L.) under shade stress conditions. *Journal of Agronomy and Crop Science*, **203**, 562–573.

Ghosh P. 2004. Growth, yield, competition and economics of groundnut/cerealfodder intercropping systems in the semi-arid tropics of India. *Field Crops Research*, **88**, 227–237.

Hou P, Liu Y, Liu W, Liu G, Xie R, Wang K, Ming B, Wang Y, Zhao R, Zhang W, Wang Y, Bian S, Ren H, Zhao X, Liu P, Chang J, Zhang G, Liu J, Yuan L, Zhao H, *et al.* 2020. How to increase maize production without extra nitrogen input. *Resources Conservation and Recycling*, **160**, 104913.

Housley T, Peterson D. 1982. Oat stem vascular size in relation to kernel number and weight. I. Controlled environment. *Crop Science*, **22**, 259–263.

Hu J, Ren B, Dong S, Liu P, Zhao B, Zhang J. 2021. Poor development of spike differentiation triggered by lower photosynthesis and carbon partitioning reduces summer maize yield after waterlogging. *Crop Journal*, **10**, 478–489.

Hussain S, Iqbal N, Pang T, Naeem M, Liu W, Yang W. 2019. Weak stem under shade reveals the lignin reduction behavior. *Journal of Integrative Agriculture*, **18**, 496–505.

IPCC. 2023. AR6 Synthesis Report: Climate Change 2023. [2023-10-20]. https://www.ipcc.ch/report/sixth-assessment-report-cycle/

Irfan M, Hayat S, Hayat Q, Afroz S, Ahmad A. 2009. Physiological and biochemical changes in plants under waterlogging. *Protoplasma*, **241**, 3–17.

Jia S, Li C, Dong S, Zhang J. 2010. Physiological mechanism of shading stress on photosynthetic efficiency in summer maize (*Zea mays*). *Chinese Journal of Plant Ecology*, **34**, 1439–1447. (in Chinese)

Kaur G, Vikal Y, Kaur L, Kalia A, Mittal A, Kaur D, Yadav I S. 2021. Elucidating the morpho-physiological adaptations and molecular responses under long-term waterlogging stress in maize through gene expression analysis. *Plant Science*, **304**, 110823.

Keuskamp D, Sasidharan, Pierik R. 2010. Physiological regulation and functional significance of shade avoidance responses to neighbors. *Plant Signaling & Behavior*, **5**, 655–662.

Koyama K, Ikeda H, Poudel P, Goto-Yamamoto N. 2012. Light quality affects flavonoid biosynthesis in young berries of Cabernet Sauvignon grape. *Phytochemistry*, **78**, 54–64.

Li C, Jia C, Tao Z, Yang J, Liu J, Zhao M. 2019. Effects of waterlogging at jointing stage on grain yield, plant morphology and dry matter production in different plant height of summer maize. *Maize Science*, **27**, 62–67. (in Chinese)

Li X, Yang Y, Yao J, Chen G, Li X, Zhang Q, Wu C. 2009. FLEXIBLE CULM 1 encoding a cinnamyl-alcohol dehydrogenase controls culm mechanical strength in rice. *Plant Molecular Biology*, **69**, 685–697.

Liang X, Gao Z, Zhang L, Shen S, Zhao X, Liu Y, Zhou L, Pual M, Zhou S. 2019. Seasonal and diurnal patterns of non-structural carbohydrates in source and sink tissues in field maize. *BMC Plant Biology*, **19**, 508.

Liu S, Xing J, Zhao B, Wang J, Wang S, Zhang X, Ding A. 2019. Understanding of aerosol–climate interactions in China: Aerosol impacts on solar radiation, temperature, cloud, and precipitation and its changes under future climate and emission scenarios. *Current Pollution Reports*, **5**, 36–51.

Liu W, Hussain S, Liu T, Zou J, Ren M, Zhou T, Liu J, Yang F, Yang W. 2019. Shade stress decreases stem strength of soybean through restraining lignin biosynthesis. *Journal of Integrative Agriculture*, **18**, 43–53.

Liu X, Gu W, Li C, Li J, Wei S. 2021. Effects of nitrogen fertilizer and chemical regulation on spring maize lodging characteristics, grain filling and yield formation under high planting density in Heilongjiang Province, China. *Journal of Integrative Agriculture*, **20**, 511–526.

Liu X, Yong T, Su B, Liu W, Zhou L, Song C, Yang F, Wang X, Yang W. 2014. Effect of reduced N application on crop yield in maize–soybean intercropping system. *Acta Agronomica Sinica*, **40**, 1629–1638. (in Chinese)

Martín M, Russell W. 1984. Correlated responses of yield and other agronomic traits to recurrent selection for stalk quality in a maize synthetic. *Crop Science*, **24**, 746–750.

Mason T, Maskell E. 1928. Studies on the transport of carbohydrates in the cotton plantii. the factors determining the rate and the direction of movement of sugars. *Annals of Botany*, **42**, 571–636.

Moreira-Vilar F, Siqueira-Soares R, Finger-Teixeira A, Oliveira D, Ferro A, Rocha G, Ferrarese M, dos Santos W D, Ferrarese-Filho O. 2014. The acetyl bromide method is faster, simpler and presents best recovery of lignin in different herbaceous tissues than klason and thioglycolic acid methods. *PLoS ONE*, **9**, e110000.

Najeeb U, Bange M, Atwell B, Tan D. 2016. Low incident light combined with partial waterlogging impairs photosynthesis and imposes a yield penalty in cotton. *Journal of Agronomy and Crop Science*, **202**, 331–341.

Nguyen N, Son S, Jordan M, Levin D, Ayele B. 2016. Lignin biosynthesis in wheat (*Triticum aestivum* L.): Its response to waterlogging and association with hormonal levels. *BMC Plant Biology*, **16**, 28.

Pan J, Sharif R, Xu X, Chen X. 2021. Mechanisms of waterlogging tolerance in plants: Research progress and prospects. *Frontiers in Plant Science*, **11**, 627331.

Pan Y, Lu Z, Lu J, Li X, Cong R, Ren T. 2017. Effects of low sink demand on leaf photosynthesis under potassium deficiency. *Plant Physiology and Biochemistry*, **113**, 110–121.

Rahayuningsih S, Indradewa D, Sulistyaningsih E, Maas A. 2017. The tolerance of photosynthesis of summer maize cultivars (*Zea mays* L.) to waterlogging at different stages of growth. *International Journal of Advances in Engineering Sciences and Applied Mathematics*, **7**, 1296–1301.

Ren B, Hu J, Zhang J, Dong S, Liu P, Zhao B. 2020. Effects of urea mixed with nitrapyrin on leaf photosynthetic and senescence characteristics of summer maize (*Zea mays* L.) waterlogged in the field. *Journal of Integrative Agriculture*, **19**, 1586–1595.

Ren B, Zhang J, Dong S, Liu P, Zhao B. 2018. Responses of carbon metabolism and antioxidant system of summer maize to waterlogging at different stages. *Journal of Agronomy and Crop Science*, **204**, 505–514.

Ren B, Zhang J, Li X, Fan X, Dong S, Liu P, Zhao B. 2013. Effects of waterlogging on stem lodging resistance of summer maize under field conditions. *Scientia Agricultura Sinica*, **46**, 2440–2448. (in Chinese)

Ren B, Zhang J, Li X, Fan X, Dong S, Liu P, Zhao B. 2014. Effects of waterlogging on the yield and growth of summer maize under field conditions. *Canadian Journal of Plant Science*, **94**, 23–31.

Rogers L, Dubos C, Cullis I, Surman C, Poole M, Willment J, Mansfield S, Campbell M. 2005. Light, the circadian clock, and sugar perception in the control of lignin biosynthesis. *Journal of Experimental Botany*, **56**, 1651–1663.

Sekhon R, Joyner C, Ackerman A, McMahan C, Cook D, Robertson D. 2020. Stalk bending strength is strongly associated with maize stalk lodging incidence across multiple environments. *Field Crops Research*, **249**, 107737.

Setter T, Waters I, Sharma S, Singh K, Kulshreshtha N, Yaduvanshi N, Ram P, Singh B, Rane J, McDonald G, Khabaz-Saberi H, Biddulph T, Wilson R, Barclay I, McLean R, Cakir M. 2009. Review of wheat improvement for waterlogging tolerance in Australia and India: The importance of anaerobiosis and element toxicities associated with different soils. *Annals of Botany*, **103**, 221–235.

Shabala S. 2011. Physiological and cellular aspects of phytotoxicity tolerance in plants: The role of membrane transporters and implications for crop breeding for waterlogging tolerance. *The New Phytologist*, **190**, 289–298.

Shi Q, Kong F, Zhang H, Jiang Y, Heng S, Liang R, Liu J, Lu X, Li P, Li G. 2018. Molecular mechanisms governing shade responses in maize. *Biochemical and Biophysical Research Communications*, **516**, 112–119.

Sowiński P. 1999. Transport of photoassimilates in plants under unfavourable environmental conditions. *Acta Physiologiae Plantarum*, **21**, 75–85.

Tian L, Bi W, Ren X, Li W, Sun L, Li J. 2020. Flooding has more adverse effects on the stem structure and yield of spring maize (*Zea mays* L.) than waterlogging in Northeast China. *European Journal of Agronomy*, **117**, 126054.

Tian L, Zhang Y, Chen P, Zhang F, Li J, Yan F, Dong Y, Feng B. 2021. How does the waterlogging regime affect crop yield? A global meta-analysis. *Frontiers in Plant Science*, **12**, 634898.

Vanholme R, Storme V, Vanholme B, Sundin L, Christensen J, Goeminne G, Halpin C, Rohde A, Morreel K, Boerjan W. 2012. A systems biology view of responses to lignin biosynthesis perturbations in *Arabidopsis*. *Plant Cell*, **24**, 3506–3529.

Wang C, Ruan R, Yuan X, Hu D, Yang H, Li Y, Yi Z. 2014. Relationship between lignin metabolism and lodging resistance of culm in buckwheat. *The Journal of Agricultural Science*, **6**, 29.

Wang Q, Zhao X, Liu D, Yan Z, Li H, Dong P, Li C. 2020. Root morphological, physiological traits and yield of maize under waterlogging and low light stress. *Scientia Agricultura Sinica*, **53**, 3479–3495. (in Chinese)

Wu H, Qiao M, Zhang W, Wang K, Li S, Jiang C. 2022. Systemic regulation of photosynthetic function in maize plants at graining stage under a vertically heterogeneous light environment. *Journal of Integrative Agriculture*, **21**, 666–676.

Wu L, Zhang W, Ding Y, Zhang J, Cambula E, Weng F, Liu Z, Ding C, Tang S, Chen L, Wang S, Li G. 2017. Shading contributes to the reduction of stem mechanical strength by decreasing cell wall synthesis in *japonica* rice (*Oryza sativa* L.). *Frontiers in Plant Science*, **8**, 881.

Xu C, Zhang P, Wang Y, Luo N, Tian B, Liu X, Wang P, Huang S. 2022. Grain yield and grain moisture associations with leaf, stem and root characteristics in maize. *Journal of Integrative Agriculture*, **21**, 1941–1951.

Xu H, Wang Z, Xiao F, Yang L, Li G, Ding Y, Paul M J, Li W, Liu Z. 2020. Dynamics of dry matter accumulation in internodes indicates source and sink relations during grain-filling stage of *japonica* rice. *Field Crops Research*, **263**, 108009.

Xue J, Gao S, Fan Y, Li L, Ming B, Wang K, Xie R, Hou P, Li S. 2020. Traits of plant morphology, stalk mechanical strength, and biomass accumulation in the selection of lodging-resistant maize cultivars. *European Journal of Agronomy*, **117**, 126073.

Zandalinas S, Balfagón D, Gómez-Cádenas A, Mittler R. 2022. Responses of plants to climate change: Metabolic changes during abiotic stress combination in plants. *Journal of Experimental Botany*, **73**, 3339–3354.

Zhang B, Zhao M, Dong Z, Li J, Chen C, Sun R. 2007. Establishment and test of LAI dynamic Simulation model for high yield population. *Acta Agronomica Sinica*, **4**, 612–619. (in Chinese)

Zhang J, Dong S, Wang K, Hu C, Liu P. 2007. Effects of shading in field on photosynthetic characteristics in summer corn. *Acta Agronomica Sinica*, **33**, 216–222. (in Chinese)

Zhang J, Li G, Song Y, Liu Z, Yang C, Tang S, Zheng C, Wang S, Ding Y. 2014. Lodging resistance characteristics of high-yielding rice populations. *Field Crops Research*, **161**, 64–74.

Zhang W, Fu X, Peng L, Ling L, Cao L, Ma X, Xie F, Li C. 2013. Effects of sink demand and nutrient status on leaf photosynthesis of spring-cycle shoot in 'Newhall' navel orange under natural field conditions. *Scientia Horticulturae*, **150**, 80–85.

Zhao J, Wang S, Li M, Lu H, Wang D, Wei X, Yang W. 2018. Current status and perspective of maize breeding. *Journal of Plant Genetic Resources*, **19**, 435–446. (in Chinese)

Zhou W, Wang X, Mu X, Li C. 2013. Effects of low-light stress on male and female flower development and pollin-ation and fructification ability of different maize (*Zea mays* L.) genotypes. *Acta Agronomica Sinica*, **39**, 2065–2073. (in Chinese)

Zuber M, Grogan C. 1961. A new technique for measuring stalk strength in corn. *Crop Science*, **1**, 378–380.

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