Agricultural Water Management 266 (2022) 107603

Contents lists available at ScienceDirect

Agricultural Water Management

journal homepage: www.elsevier.com/locate/agwat

Effects of waterlogging at different stages on growth and ear quality of waxy maize

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ARTICLE INFO

Handling editor - Dr R Thompson

Keywords:
Waxy maize
Waterlogging
Leaf physiological characteristic
Fresh ear yield
Grain quality

ABSTRACT

A waterlogging experiment under a rain shelter was used to investigate the response mechanism of waxy maize plant growth, ear yield, and quality to waterlogging at various growth stages. Waterlogging for 10 d were carried out at V6-VT ($W_{V6\text{-}VT}$), VT-R1 ($W_{VT\text{-}R1}$) and R1-R3 ($W_{R1\text{-}R3}$) stages of waxy maize in lysimeters in 2019 and 2020 seasons, and non-waterlogging was used as control (CK). The results showed that waterlogging at V6-VT had the highest impact on waxy maize growth, fresh ear yield, and grain quality, followed by that at the VT-R1, and finally that at the R1-R3. During the waterlogging at V6-VT, the growth of waxy maize plants was accelerated, while the gas exchange parameters in leaves were decreased, however the plant height, leaf area index (LAI), and gas exchange parameters of the $W_{V6\text{-}VT}$ treatment were significantly lower than those of CK at R3. Compared with CK, the content of malondialdehyde (MDA) and the activities of superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) in leaves increased, whereas the contents of soluble sugar, soluble protein and proline in leaves decreased. As a result, waxy maize ear length, grain number per ear, 100-grain weight, and fresh ear yield fell, and grain quality suffered as well. Total protein and soluble sugar content in grains decreased, but starch and lysine content in grains increased. Principal component analysis (PCA) revealed that when waterlogging for 10 d occurred in waxy maize, it was the first to alter maize growth and physiology, and then affecting grain quality. Waterlogging at V6-VT waxy maize were the most severe, followed by VT-R1 and R1-R3.

1. Introduction

Rainfall in most areas rises and becomes more common with the global warming progresses (IPCC, 2021). According to statistics, excessive rainfall can easily lead to waterlogging, which affects 12% of the world's crop hectare and can result in up to 20% crop losses. (Ren et al., 2016a; Shabala, 2011). Waterlogging first impacts the root activity of crops, and then affects the growth of aboveground plants (Gao et al., 2018). During waterlogging, air in soil pores is replaced by water, resulting in hypoxia of crop roots, suppression of root respiration, stomatal closure, reduction of CO_2 entry, reduction of transpiration rate and photosynthetic rate, and eventually crop yield reduction or failure (Pezeshki, 1994; Tian et al., 2019). Moreover, waterlogging can cause the accumulation of reactive oxygen species (ROS) in plants, which can cause membrane lipid peroxidation, damage membrane homeostasis, and produce superoxide anion radical (O_2^-) and hydrogen peroxide (H_2O_2), as well as the accumulation of malondialdehyde (MDA) and accelerate leaf senescence (Liu et al., 2010; Wang et al., 2021a). The antioxidant enzymes (POD, CAT, and SOD, etc.) can be triggered to alleviate and remove ROS produced by plant cells induced by waterlogging (Gill et al., 2019; Jia et al., 2019; Tang et al., 2010; Wang et al., 2019).

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https://doi.org/10.1016/j.agwat.2022.107603
Received 19 January 2022; Received in revised form 6 March 2022; Accepted 8 March 2022

Studies have shown that waterlogging not only reduces crop yield, but also reduces protein accumulation, protein content and protein components, resulting in lower grain starch and soluble sugar content (Ren et al., 2013; Wu et al., 2013). Waterlogging not only reduces the protein content and its components content of wheat grain, and the ratio of glutenin to gliadin, but also decreases the accumulation of starch, starch content, amylopectin content, and the ratio of amylopectin to amylose (Wang et al., 2015). Zhou et al. (2018) reported that waterlogging after anthesis inhibited the transformation of carbohydrates into starch in wheat grain. Otie et al. (2019) suggested that waterlogging at V3 stage affected nutrient uptake and decreased grain protein content of maize. Ren et al. (2013) found that waterlogging significantly decreased grain protein, starch, total soluble sugar, and amylopectin, while increase amylose of maize (*Zea mays* L.), and that the effect of waterlogging at V3 stage was the most significant, followed by V6 and 10 d after flowering. However, in the study of Wang et al. (2021b), waterlogging stress at grain maturity stage of waxy maize (*Zea mays* L. var. certaina Kulesh) reduced starch content, but increased protein content. Conversely, Yang et al. (2016) reported that waterlogging increased starch content and decreased protein content in waxy maize grain. The different responses of grain quality to waterlogging between waxy maize and common maize maybe the distinct expresses of waxy gene (Wu et al., 2022).

The ear characteristics and grain quality standards for excellent fresh-eating waxy maize are high-demanded. Due to rich nutrient content and good palatability of waxy maize, the planting area of fresh-eating maize in China has now reached 1.34 million hectares (Xu et al., 2010). However, in recent decades, some extreme weather resulted from climate changes occurring more frequently, for example, the heavy precipitation process in July 2016 in our experimental area, 450.2 mm rainwater were given in about 5 days, while the rainfall of 907 mm in about 6 days in July 2021, resulted in serious waterlogging and yield loss. Therefore, the objectives of this study were to (1) determine the effects of waterlogging at different growth stages on growth and grain quality of waxy maize; (2) fully study the tolerance of waxy maize to waterlogging under the current soil texture and organic matter content levels, so as to speed up the planting and promotion of waxy maize in local areas; (3) the study results can provide necessary theoretical basis and basic data support for the determination of local suitable drainage modulus and engineering scale.

2. Materials and methods

2.1. Site description

The experiment was carried out in 2019 and 2020 under a large-scale rain shelter at the Xinxiang Comprehensive Experimental Station of Chinese Academy of Agricultural Sciences, which located in Qiliying Town, Xinxiang, China (35°18′N, 113°54′E), the physical and chemical properties of soil are shown in Table 1. All lysimeters were non-weighing style, made of steel sheets with irrigation and drainage systems, and measured 3.33 m in length× 2.0 m in width× 1.8 m in depth. The bottom layer of 20 cm of each lysimeter was filled with mixed very coarse sands and gravels and acted as a filter layer to prevent soil loss from 150 cm of soil layer above it while permitting normal leakage water through. The top side of the steel outer frame of the lysimeter is 10 cm higher than the soil surface in the lysimeter to prevent runoff during rain or irrigation events. The upper part of the lysimeters is equipped with a mobile rain shelter. The rain shelter is closed during rainfall and opened after rain, which can effectively control the influence of rainfall on waterlogging test.

An automatic weather station was set near the edge of the lysimeters. The changes of temperature and precipitation during the whole growth period of waxy maize in the two experiments years are shown in Fig. 1.

2.2. Experimental design

The experimental variety was "Shenkenuo 602", which was bred by Shanghai Academy of Agricultural Sciences and widely cultivated in China. The experimental planting density was set at 60 000 plants per hectare (row spacing 60 cm, plant spacing 30 cm). Lysimeters were fertilized with 750 kg ha^{-1} of compound fertilizer (contains 18% nitrogen, 10% phosphorus, 6% potassium) during the seed bed preparation and no fertilizer for topdressing application hereafter. Waterlogging was scheduled at V6-VT, VT-R1 and R1-R3 (Table 2), respectively, with suitable irrigation as control (CK), and each treatment had 3 replicates. Table 3 presents the start date of each growth stage. Irrigation was carried out when soil water content reaches the lower limit as shown in Table 2. During waterlogging, the water layer was maintained at 5–8 cm, after 10 d of waterlogging, the drainage valve at the bottom of the pit was opened for drainage. Soil water content during the non-waterlogging stage was managed according to the scheduling of CK (Table 2). Dates of ear growth stage of waxy maize was presented in Table 3, refer to Hanway (1966).

2.3. Measurements set-up

2.3.1. Soil water content

Volumetric soil water content (VSWS, cm^{-3}•cm^{-3}) in the 0–100 cm soil layer was measured once every 7 d by using the Insentek sensor (Oriental Zhigan Technology Ltd., Zhejiang, China) with 10 cm increment. The sensor parameters were shown in Qin et al. (2019).

2.3.2. Plant growth and physiological, biochemical indexes of maize leaves

In each lysimeter, three plants with representative and similar growth status were selected and labeled at start date of the V6 stage of waxy maize. Then at VT, R1 and R3 stages, photosynthesis parameters of each ear leaf on the three labeled plants were measured by Li-6400 portable photosynthesis analyzer (LI-COR, USA) and the average value was applied finally in data analysis. At the same date, the length and largest width of all leaves on the three plants were measured with ruler. Photosynthetic parameters, including net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r) and intercellular CO_2 concentration (C_i), were measured at 9: 00–11: 00 a.m. on sunny days, and the leaf-level water use efficiency (LWUE) was calculated as following (Eq. 1) (Yao et al., 2012), and LAI for each experimental plot

Table 1
Basic soil parameters in lysimeters.

Location	Soil texture	Soil pH	Soil bulk density (g·cm^{-3})	Soil field capacity (cm^{-3}·cm^{-3})	Organic carbon (g·kg^{-1})	Total nitrogen (g·kg^{-1})	Exchangeable potassium (mg·kg^{-1})	Total phosphorus (g·kg^{-1})	Steady infiltration rate (mm·min^{-1})
Xinxiang	Silt loam soil	8.8	1.51	0.31	6.22	0.73	138.96	0.94	0.52

Note: Soil pH was determined in 1:5, soil to CO_2-free water suspension by pH meter (120 P-02A, Thermo Fisher Scientific); soil bulk density was measured by ring knife method; soil field capacity was measured by infiltration method; organic carbon was determined by potassium dichromate volumetric method; total nitrogen was determined by microcalorimetric method; exchangeable potassium was determined by flame photometric method; total phosphorus was determined by perchloric acid-sulfuric acid method; steady infiltration rate was measured by double-loop method.

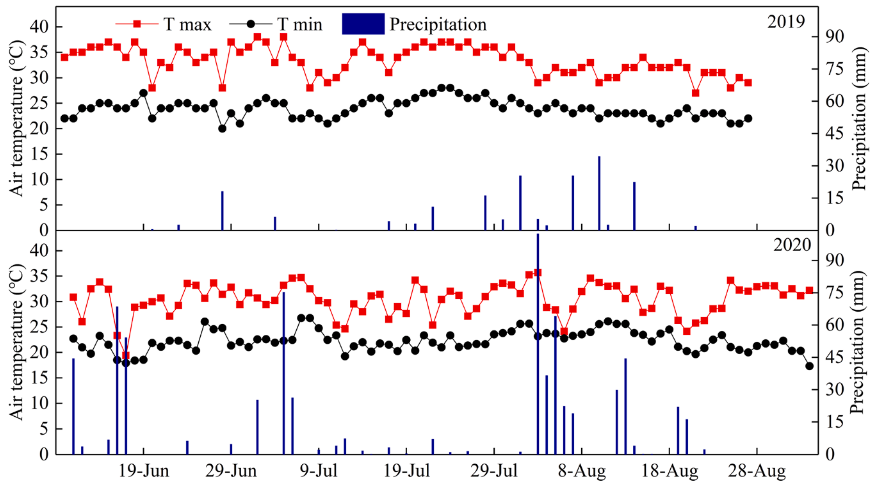

Fig. 1. Air temperature and precipitation during the whole growth period of waxy maize in 2019 and 2020. (Note: T max: maximum temperature of the day; T min: minimum temperature of the day.).

Table 2
Waterlogging experimental design of fresh waxy maize.

Waterlogging	Lower limit of soil moisture control			
	V1-V6	V6-VT	VT-R1	R1-R3
CK (Non-waterlogging)	65	65	65	65
W_{V6-VT} (Waterlogging for 10 d from V6 to VT stage)	65	—	65	65
W_{VT-R1} (Waterlogging for 10 d from VT to R1 stage)	65	65	—	65
W_{R1-R3} (Waterlogging for 10 d from R1 to R3 stage)	65	65	65	—

Note: The values in the table are the lower limit index of soil moisture control, which is the percentage of soil water in field capacity; ' – ' indicates 10 d waterlogging. V1: first leaf; V6: sixth leaf; VT: tasseling; R1: silking; R3: milk stage.

was calculated using (Eq. 2) (Ren et al., 2017).

$$\text{LWUE}(\mu mol\cdot mmol^{-1}) = \frac{P_n(\mu mol\cdot m^{-2}\cdot s^{-1})}{T_r(mmol\cdot m^{-2}\cdot s^{-1})} \quad (1)$$

$$\text{LAI} = 0.75 \times \frac{\sum_{i=1}^{m}\sum_{j=1}^{n}(L_{ij}\times W_{ij})}{m} \times N \Big/ S \quad (2)$$

where, LAI is the leaf area index, L_{ij} is the leaf length (cm) of the j^{th} leaf on i^{th} plant, W_{ij} is the largest width (cm) of the j^{th} leaf on i^{th} plant, m is the measured number of plants, n is the number of leaves per plant, N is the plant numbers of a plots, S is land area of a plot (cm^2).

A SPAD-502 portable chlorophyll meter (Konica Minolta Holdings, Inc., Japan) was used to estimate chlorophyll content (measured in SPAD units on ear leaf of the three labeled plants) of waxy maize ear leaf at VT, R1 and R3 stages, respectively (Padilla et al., 2018). Five other ear leaf samples of each treatment were taken at milk stage, and the soluble protein content in sample leaf was measured by the BCA protein method, soluble sugar by anthrone colorimetry method (Ye et al., 2020), proline by ninhydrin method (Li et al., 2017), MDA by thiobarbituric acid method (Li et al., 2017), CAT by ammonium molybdate method (Anjum et al., 2016), SOD takes the enzyme amount of 50% of NBT photooxidation inhibition as a unit of enzyme activity (Anjum et al., 2016), POD by guaiacol method (Anjum et al., 2016). The specific activities of MDA and CAT, SOD and POD were calculated by protein concentration.

2.3.3. *Fresh grain yield*

At the late milk stage of waxy maize, maize ears were collected with husks, and 20 ears were collected in each lysimeter to measure the fresh ear yield with husks. Then the husks were removed, measured the fresh ear yield, ear length, ear diameter, bald tip length, rows number per ear and grains number per row. The fresh grains were manually removed, and 100 grains were randomly selected to determine the 100-grain weight.

2.3.4. *Grain quality*

After completing yield measurement, all grains were collected and the soluble sugar, total protein, starch and lysine content were measured. The soluble sugar content of grains was determined by the anthrone colorimetric method (Ye et al., 2020), starch content by anthrone-sulfuric acid method (Wang et al., 2021a), and lysine content by ninhydrin chromogenic method (Lu et al., 2021). The total protein content (total protein content = total nitrogen content × 6.25) was calculated by measuring total nitrogen content (Wang et al., 2021b).

2.4. *Statistical*

Data were analyzed using analysis of variance with Excel 2019 (Microsoft, USA) and SPSS version 19.0 (IBM Inc., Chicago, IL, USA), and figures were plotted using Origin 2017 (OriginLab, USA). Principal component analysis was used to determine the comprehensive impact of waterlogging. Means were compared using Duncan's least significance difference (LSD) tests (Table 4). Significance was declared at the probability level of 0.05, unless otherwise stated.

Table 3
Date of per growth stage of waxy maize.

Year	Sowing	V2	V6	VT	R1	R3	Harvest
2019	2019.6.10	2019.6.17	2019.7.10	2019.7.29	2019.8.12	2019.8.24	2019.8.27
2020	2020.6.11	2020.6.18	2020.7.9	2020.7.29	2020.8.14	2020.8.25	2020.9.4

Note: V2: second leaf; V6: sixth leaf; VT: tasseling; R1: silking; R3: milk stage.

Table 4
ANOVA results of relevant maize indices in 2019–2020.

Factor	Year	Plant height	LAI	SPAD	P_n	G_s	C_i	T_r	LWUE	Ear length	Ear diameter	Bald tip length	Grains number per ear	100-grain weight	Fresh ear yield with husk	Fresh ear yield	Total Protein	Grain soluble sugar	Starch	Lysine
Stage	2019	**	ns	ns	**	**	**	**	**	**	**	*	**	**	**	**	**	*	**	**
	2020	**	**	**	**	**	**	**	*	**	**	**	**	**	**	**	**	**	**	**
2 year																				
Stage		**	*	ns	**	**	**	**	**	*	**	ns	ns	**	**	**	**	**	*	**
Year		ns	**	**	ns	*	*	ns	*	**	*	**	**	*	**	*	*	ns	**	ns

Note: LAI: leaf area index; SPAD: leaf chlorophyll content index; P_n: net photosynthetic rate; G_s: stomatal conductance; C_i: intercellular CO_2 concentration; T_r: transpiration rate; LWUE: leaf water use efficiency.
ns No significant. 'Stage' indicated the significant between CK, $W_{V6\text{-}VT}$, $W_{VT\text{-}R1}$ and $W_{R1\text{-}R3}$, 'Year' indicated the significant between 2019 and 2020.
* Significant at $P < 0.05$.
** Significant at $P < 0.01$.

3. Results

3.1. Effects of waterlogging at different growth stages on growth and development of waxy maize

Waterlogging had distinct effects on waxy maize growth at different growth stages, and the alterations in the two growing seasons were essentially the same (Fig. 2; Table 4). Waterlogging at V6-VT stage accelerated early growth of waxy maize. Compared with CK, the plant height and leaf area index (LAI) of $W_{V6\text{-}VT}$ treatment at VT stage increased by 10.0% and 21.6%, respectively ($P < 0.05$), but at R3 stage, the plant height and LAI of $W_{V6\text{-}VT}$ treatment decreased by 11.5% and 15.3%, respectively. Compared with CK, the plant height and LAI of $W_{VT\text{-}R1}$ treatment decreased by 6.4% and 13.9% at R1 stage, and decreased by 4.0% and 11.4% at R3 stage, respectively. LAI of $W_{R1\text{-}R3}$ treatment decreased by 12.5% at R3 stage.

3.2. Effects of waterlogging on the physiological characteristics of waxy maize leaves

3.2.1. MDA and antioxidant enzymes

Waterlogging at different growth stages increased MDA content and antioxidant enzyme activity in waxy maize leaves (Fig. 3) to maintain the dynamic balance of reactive oxygen species, thereby reducing cell membrane peroxidation and triggering SOD, POD and CAT activities, and the activities of SOD, POD and CAT decreased with the delay of waterlogging stage. At the R3 stage of waxy maize, the MDA contents of $W_{V6\text{-}VT}$ and $W_{VT\text{-}R1}$ treatments increased by 35.1% and 16.6% compared with CK ($P < 0.05$), respectively. Compared with CK, the SOD, POD and CAT activities of $W_{V6\text{-}VT}$ treatment increased by 42.9%, 156.3% and 55.6%, respectively ($P < 0.05$), and those of $W_{VT\text{-}R1}$ treatment increased by 40.7%, 89.4% and 41.2%, respectively ($P < 0.05$). Compared with CK, SOD and POD in $W_{R1\text{-}R3}$ treatment decreased by 28.2% and 24.0%, respectively ($P < 0.05$).

3.2.2. Osmotic adjustment substances

Soluble protein, soluble sugar and proline are important osmotic regulators in plant tissues, and when plants are subjected to waterlogging, these substances change to maintain cell water potential balance (Fig. 4). At R3 stage, compared with CK, the soluble sugar, soluble protein and proline of $W_{V6\text{-}VT}$ treatment decreased by 31.9%, 33.0% and 14.3%, respectively ($P < 0.05$), and $W_{VT\text{-}R1}$ treatment decreased by 11.7%, 25.1% and 28.3%, respectively ($P < 0.05$), while the soluble protein of $W_{R1\text{-}R3}$ treatment increased by 35.1% ($P < 0.05$).

3.2.3. Photosynthetic characteristics

Waterlogging stress can lead to stomatal closure of plant leaves, while the photosynthesis of waxy maize almost does not recover after waterlogging at different stages. The changes of SPAD, photosynthetic characteristics in the two growing seasons are basically the same (Fig. 5; Table 4). $W_{V6\text{-}VT}$ and $W_{VT\text{-}R1}$ treatments decreased the SPAD (Fig. 5a) and G_s (Fig. 5c) of waxy maize leaves, resulting in a significant decrease in C_i. The decreased of C_i caused by the decrease of SPAD and G_s eventually led to the decrease of P_n in $W_{V6\text{-}VT}$ and $W_{VT\text{-}R1}$ treatments (Fig. 5b). The decrease of G_s caused by waterlogging also led to the decrease of T_r, and T_r in $W_{V6\text{-}VT}$ and $W_{VT\text{-}R1}$ treatments decreased significantly (Fig. 5e; $P < 0.05$). resulted in differences in LWUE (Fig. 5f), and the LWUE of leaves under drought treatment at different growth stages was $W_{V6\text{-}VT} > W_{VT\text{-}R1} > W_{R1\text{-}R3}$. With the advancement of growth stage, P_n, G_s, C_i and T_r increased, while LWUE decreased.

3.3. Effects of waterlogging on ear traits and yield of waxy maize

Waterlogging stress reduced the ear length, ear diameter, grain number per ear and 100-grain weight of waxy maize, and the changes were consistent in the two growing seasons (Table 4; Table 5). $W_{V6\text{-}VT}$

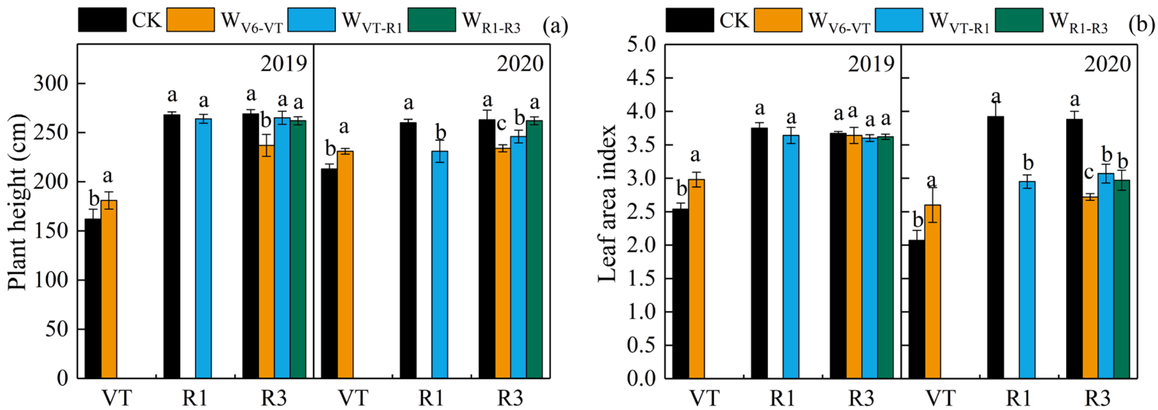

Fig. 2. Difference of plant height and LAI of waxy maize under waterlogging at different stages. (Note: different lowercase letters during the same stage indicated significant at 0.05 level. The X axes are growth stages. CK: non-waterlogging; $W_{V6\text{-}VT}$: waterlogging for 10 d from six leaf stage (V6) to tasseling stage (VT); $W_{VT\text{-}R1}$: waterlogging for 10 d from tasseling stage to silking stage (R1); $W_{R1\text{-}R3}$: waterlogging for 10 d from silking stage to milk stage (R3). VT: tasseling stage; R1: silking stage; R3: milk stage.).

treatment had the greatest influence on ear length, ear diameter, grain number per ear and 100-grain weight of waxy maize, followed by $W_{VT\text{-}R1}$ and $W_{R1\text{-}R3}$. Compared with CK, the ear length, ear diameter, grain number per ear and 100-grain weight of $W_{V6\text{-}VT}$ treatment decreased by 19.9%, 8.4%, 18.3% and 16.2% ($P < 0.05$), and those of $W_{VT\text{-}R1}$ treatment decreased by 12.7%, 6.7%, 14.0% and 7.2% ($P < 0.05$), respectively, while the bald tip length increased significantly under waterlogging at different growth stages. The effect of waterlogging on ear traits eventually led to the decrease of ear yield. Th fresh ear yield with husks (HFY) and fresh ear yield (FY) in $W_{V6\text{-}VT}$ treatment were 34.5% and 35.7% lower than those in CK ($P < 0.05$), respectively. The HFY and FY in $W_{VT\text{-}R1}$ treatment were 18.4% and 17.4% lower than those in CK ($P < 0.05$), respectively, while the effect of $W_{R1\text{-}R3}$ treatment on the yield of waxy maize was the smallest. Due to different waterlogging stages, the maturity of ears at harvest were different, resulting in different grain moisture contents. The grain moisture contents of $W_{V6\text{-}VT}$, $W_{VT\text{-}R1}$ and $W_{R1\text{-}R3}$ treatments were significantly lower than those of CK.

3.4. Effects of waterlogging on grain quality of waxy maize

Waterlogging stress decreased the total protein and soluble sugar content of fresh waxy maize grains, and increased the starch and lysine content of grain (Fig. 6). The effects of waterlogging at different growth stages on grain quality were different, and the change trend of two growing seasons was consistent (Fig. 6; Table 4). The total protein (Fig. 6a) and soluble sugar contents (Fig. 6b) of $W_{V6\text{-}VT}$ treatment were the lowest, which were 19.9% and 30.3% lower than those of CK ($P < 0.05$), followed by $W_{VT\text{-}R1}$ treatment, which decreased by 9.5% and 20.7%, respectively ($P < 0.05$), while the total protein content of $W_{R1\text{-}R3}$ treatment also decreased significantly. The starch content of $W_{V6\text{-}VT}$ treatment increased the most (Fig. 7c), with an increase of 31.9% ($P < 0.05$), followed by $W_{VT\text{-}R1}$ treatment, with an increase of 19.1% ($P < 0.05$), and the starch content of $W_{R1\text{-}R3}$ treatment decreased significantly. $W_{V6\text{-}VT}$ treatment significantly increased lysine content in grain by 30.2%.

As waterlogging at V6-VT stage exhibited the most significant impactions on the total protein and starch content of waxy maize ears (Fig. 6), the changes of amylose, amylopectin and component protein content of waxy maize ears treated with $W_{V6\text{-}VT}$ were compared to further reveal effects of waterlogging on grain quality. As shown in Table 6, compared with CK, the amylose and amylopectin content of waxy maize ears treated with $W_{V6\text{-}VT}$ increased by 26.7% and 32.5%, respectively ($P < 0.05$). The protein content of each component in $W_{V6\text{-}VT}$ treatment was significantly decreased, and the contents of gliadin, glutenin, albumin and globulin were decreased by 31.9%, 8.6%, 32.2% and 39.6%, respectively ($P < 0.05$).

3.5. Principal component analysis

Principal component analysis was performed on all indexes of waxy maize in the two growing seasons. Three principal components (PC1, PC2 and PC3) were extracted from the data of 2019 and 2020 ($\lambda > 1$), and the eigenvalues (λ) of principal component 1 (PC1) in 2019 and 2020 were 21.15 and 14.02, respectively, which explained 81.3% and 73.8% of the total variation, respectively (Table 7). The λ of PC2 in 2019 and 2020 were 3.14 and 3.88, which explained 12.1% and 20.4% of the total variation, respectively. The λ of PC3 in 2019 and 2020 were 1.72 and 1.11, which explained 6.6% and 5.8% of the total variation, respectively (Table 7). The maximum load in 2019 was plant height, followed by proline, C_i, starch and leaf soluble sugar. The largest load variable in 2020 was LWUE, followed by starch, soluble sugar, lysine and SPAD (Fig. 7). This indicated that waterlogging had the greatest impact on the growth and physiology of waxy maize plants, followed by the grain quality of waxy maize. The comprehensive scores of $W_{V6\text{-}VT}$, $W_{VT\text{-}R1}$ and $W_{R1\text{-}R3}$ treatments were lower than those of CK, and the comprehensive scores increased with the waterlogging stage (Fig. 8). Therefore, $W_{V6\text{-}VT}$ treatment had the greatest impact on waxy maize, followed by $W_{VT\text{-}R1}$ and $W_{R1\text{-}R3}$ treatments.

4. Discussion

4.1. Effects of waterlogging on leaf physiological characteristics of waxy maize at different growth stages

In this study, $W_{V6\text{-}VT}$ treatment accelerated the growth of waxy maize, however, plant height and LAI were considerably lower in $W_{V6\text{-}VT}$ treatment than in the CK at the R3 stage. Waterlogging not only inhibits waxy maize growth, but it also causes the accumulation of reactive oxygen species (ROS), membrane lipid peroxidation, and disruption of membrane homeostasis, resulting in increased O_2^-, H_2O_2, and MDA concentrations, and in order to scavenge ROS, SOD, POD, and CAT activities will increase to protect plants from ROS damage (Gill et al., 2019; Jia et al., 2019; Ren et al., 2018; Wang et al., 2021a, 2019). SOD catalyzes the conversion of O_2^- to H_2O_2, while CAT and POD convert H_2O_2 to O_2 and H_2O (Salah et al., 2019a). In this study, $W_{V6\text{-}VT}$ treatment showed the highest increase in leaf MDA content at R3, followed by $W_{VT\text{-}R1}$, and the activities of SOD, POD and CAT increased significantly. Many studies (Mahmood et al., 2021; Salah et al., 2019b; Tang et al., 2010; Wang et al., 2021c) have also shown that waterlogging can

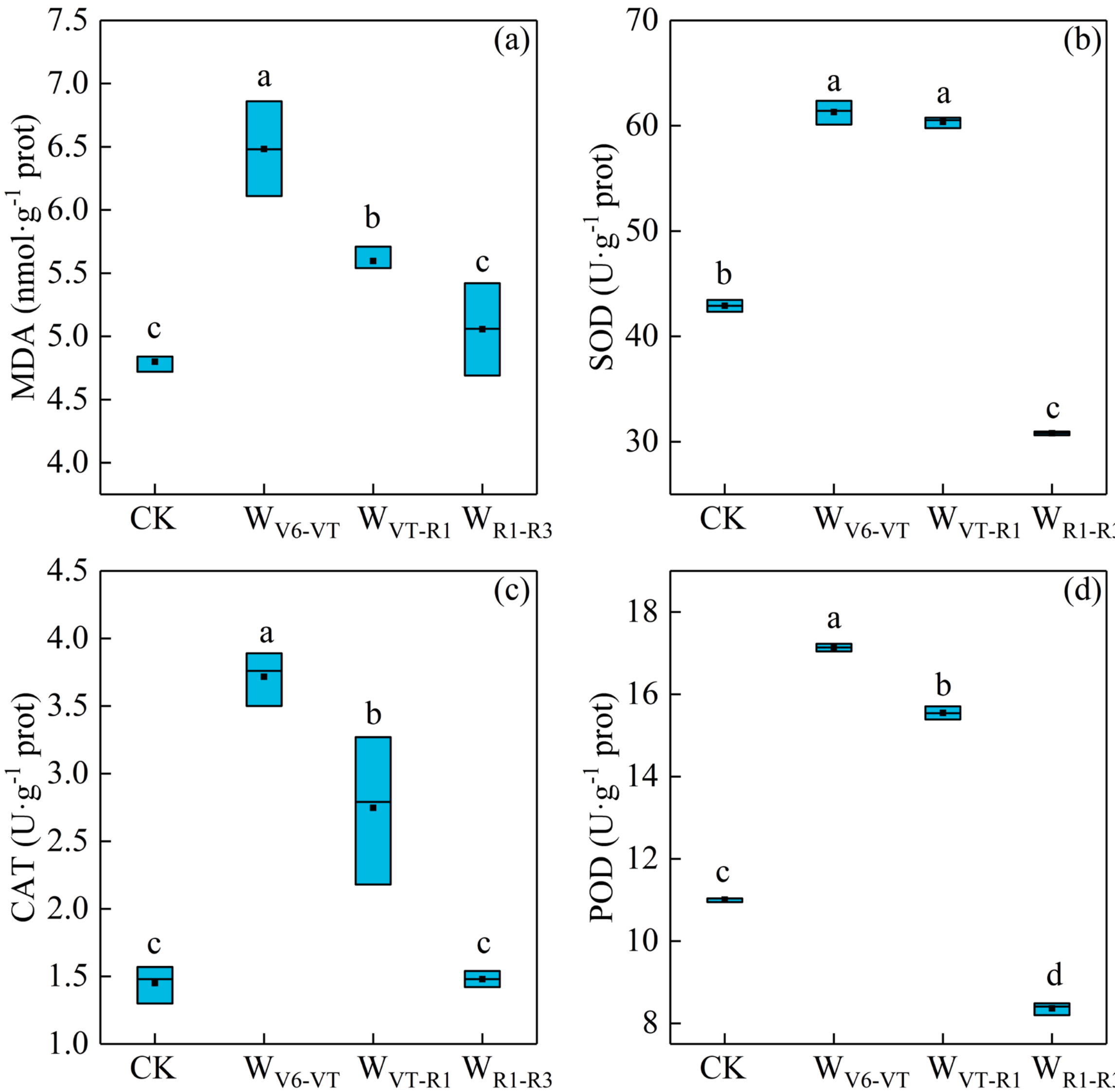

Fig. 3. Changes in MDA and antioxidant enzyme activities of waxy maize leaves under waterlogging at different growth stages in 2019. (Note: lowercase letters indicate the difference of different treatments at 0.05 level; MDA: malonaldehyde; SOD: superoxide dismutase; CAT: catalase; POD: peroxidase. the box from bottom to top indicated the lower quartile, median and upper quartile respectively, and the middle black box indicated the mean value. CK: non-waterlogging; W_{V6-VT}: waterlogging for 10 d from six leaf stage (V6) to tasseling stage (VT); W_{VT-R1}: waterlogging for 10 d from tasseling stage to silking stage (R1); W_{R1-R3}: waterlogging for 10 d from silking stage to milk stage (R3).).

increase SOD, POD and CAT activities due to the up-regulation of antioxidant genes (CAT and POD) expression under waterlogging stress conditions. It may be that excessive water activates the response of non-hydraulic root signal (nHRS) to waterlogging, and under the regulation of nHRS, ROS generation of waxy maize is significantly enhanced, and then the activities of antioxidant enzymes such as POD, CAT and SOD were truly enhanced (Gui et al., 2021; Batool et al., 2019). MDA changes were minimal under W_{R1-R3} treatment, while the highest levels were still found in the W_{V6-VT} treatment at the R3 stage, indicating that the plants recovered poorly after the lifting of waterlogging at the V6-VT stage. This result is similar to Liu et al. (2013), who found that means the compensatory growth capacity of flooded plants was weak at the jointing stage. Waterlogging also leads to the leaf proteins degradation, resulting in a significant decrease in soluble protein (Ren et al., 2014a; Tang et al., 2010), which was significantly reduced in both W_{V6-VT} and W_{VT-R1} treatments, as well as soluble sugars and proline content in our study. The results are similar to the Tang et al. (2010) and Ren et al. (2014a), but soluble protein increased significantly in the W_{R1-R3} treatment. It further indicates that the physiology of waxy maize leaves was also shown to be most affected by V6-VT waterlogging, while it was least affected by R1-R3 waterlogging.

Waterlogging leads to a reduction in leaf area and accelerates leaf senescence, then causes the decrease in photosynthetic characteristics (Ren et al., 2016a). In our study, leaf P_n, G_s, C_i, and T_r were significantly reduced in W_{V6-VT} and W_{VT-R1} treatments at R3 stage, obviously waterlogging affected leaf stomata, resulted in C_i decrease, and reduced photosynthesis and transpiration. This is similar to the findings of Ren et al. (2016a), Ashraf and Habib-ur-Rehman (1999) and Wang et al. (2021c), namely, G_s *of* maize reduced significantly under waterlogging, and P_n, C_i, and T_r decreased significantly, and P_n reduction was mainly affected by stomatal factors (Ren et al., 2018, 2016a; Salah et al., 2019a). In our study, the W_{V6-VT} treatment showed a significant increase in C_i and a significant decrease in P_n at the end of waterlogging at the V6-VT stage in 2019, which indicates that the decrease in photosynthesis was also limited by non-stomatal factors, mainly due to a decrease in the activity of the leaf photosynthetic enzymes ribulose-1, 5-bisphosphate (RuBP) carboxylase and phosphoenolpyruvate (PEP) carboxylase after waterlogging, which in turn limited photosynthesis

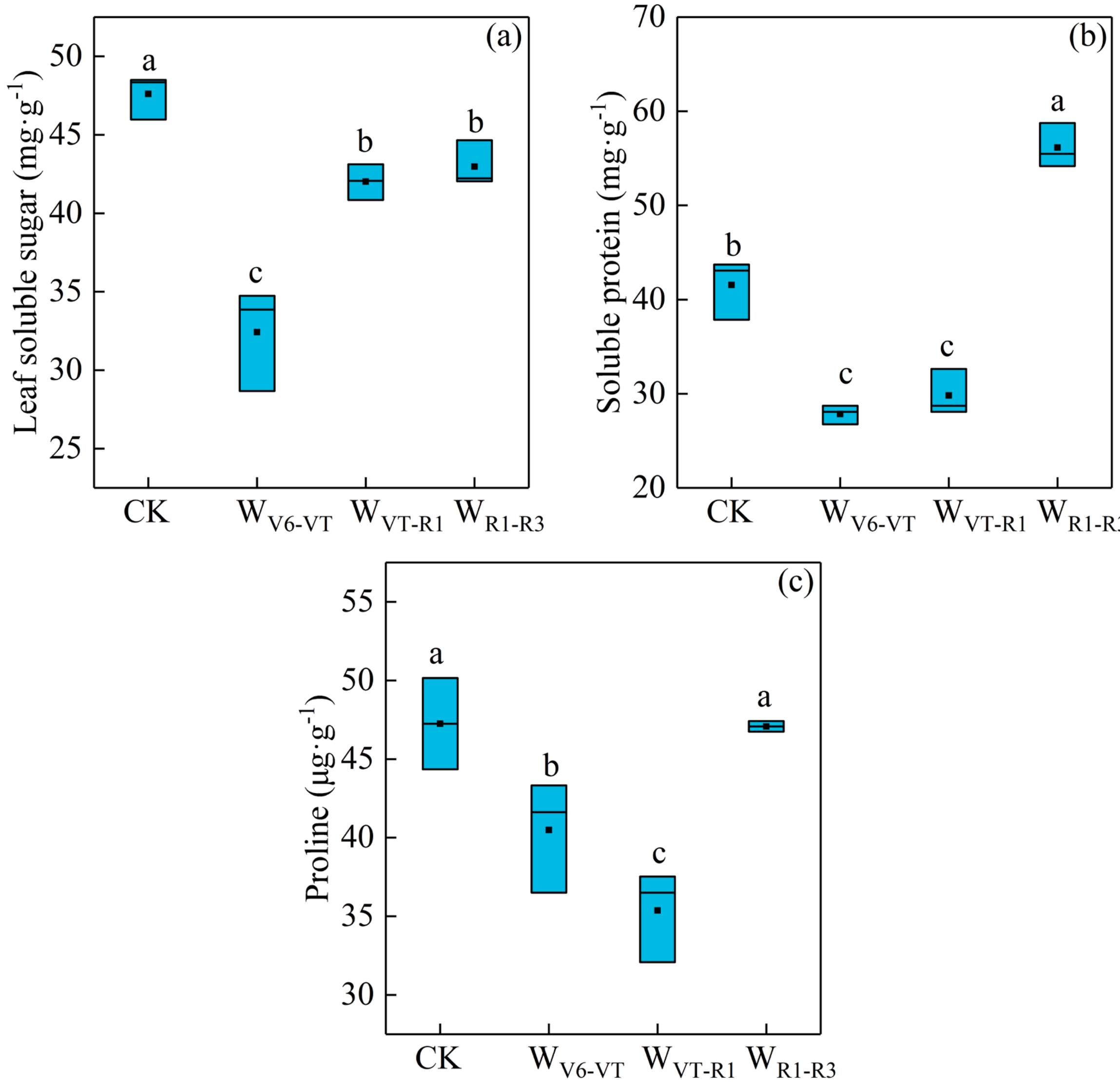

Fig. 4. Changes of osmotic adjustment substances in waxy maize leaves under waterlogging at different growth stages in 2019. (Note: lowercase letters indicate the difference of different treatments at 0.05 level; the box from bottom to top indicated the lower quartile, median and upper quartile respectively, and the middle black box indicated the mean value. CK: non-waterlogging; $W_{V6\text{-}VT}$: waterlogging for 10 d from six leaf stage (V6) to tasseling stage (VT); $W_{VT\text{-}R1}$: waterlogging for 10 d from tasseling stage to silking stage (R1); $W_{R1\text{-}R3}$: waterlogging for 10 d from silking stage to milk stage (R3).).

(Ren et al., 2018, 2014a; Tian et al., 2019). Simultaneously, because waterlogging limits nutrient absorption, nitrogen absorption is reduced, resulted in a drop in chlorophyll and SPAD levels in leaves, reduced photosynthesis (Men et al., 2020; Tuo et al., 2015).

4.2. Effects of waterlogging on yield and yield traits of waxy maize at different growth stages

With the advancement of growth period, the effect of waterlogging on fresh ear yield of waxy maize showed a decreasing trend, with HFY and FY decreasing the most under $W_{v6\text{-}vt}$ treatment, followed by $W_{VT\text{-}R1}$ (Table 5). Previous studies indicated that waterlogging reduced the grain storage capacity, filling rate and filling length of maize (Ren et al., 2016b, 2014b; Shin et al., 2017), thereby reduced maize silage yield and grain yield (Kaur et al., 2020; Ren et al., 2016c), which is similar to our study. In our previous study with common maize, it was also found that waterlogging at the jointing stage had the greatest effect on maize yield and its components, and the yield reduction was mainly affected by the grain number per ear and 100-grain weight (Huang et al., 2022), and waterlogging at V3, V6, flowering and post-flowering stages of maize caused a reduction in the grain number per ear and 100-grain weight, which in turn led to yield reduction. In the present study, the grain number per ear and 100-grain weight of waxy maize were reduced the most in $W_{V6\text{-}VT}$ treatment. Waterlogging at the jointing stage led to a decrease in N concentration in the main stalk of the maize, which in turn limited the nutritional growth of maize, resulting in lower dry matter accumulation and also limited normal flowering and spatulation (Otie et al., 2019; Zaidi et al., 2004), which in turn led to a decrease in the grain number per ear and 100-grain weight. In our study, less dry matter accumulation due to severe leaf senescence and significantly reduced photosynthesis in $W_{V6\text{-}VT}$ treatment, and grain water content was significantly reduced in the $W_{V6\text{-}VT}$ treatment. This was mainly due to the waterlogging at the jointing stage leading to shortening of the filling stage (Ren et al., 2016b), early maturity of the seeds and reduction of water content.

4.3. Effects of waterlogging on grain quality of waxy maize at different growth stages

Waterlogging not only affects nutrient absorption and grain filling of

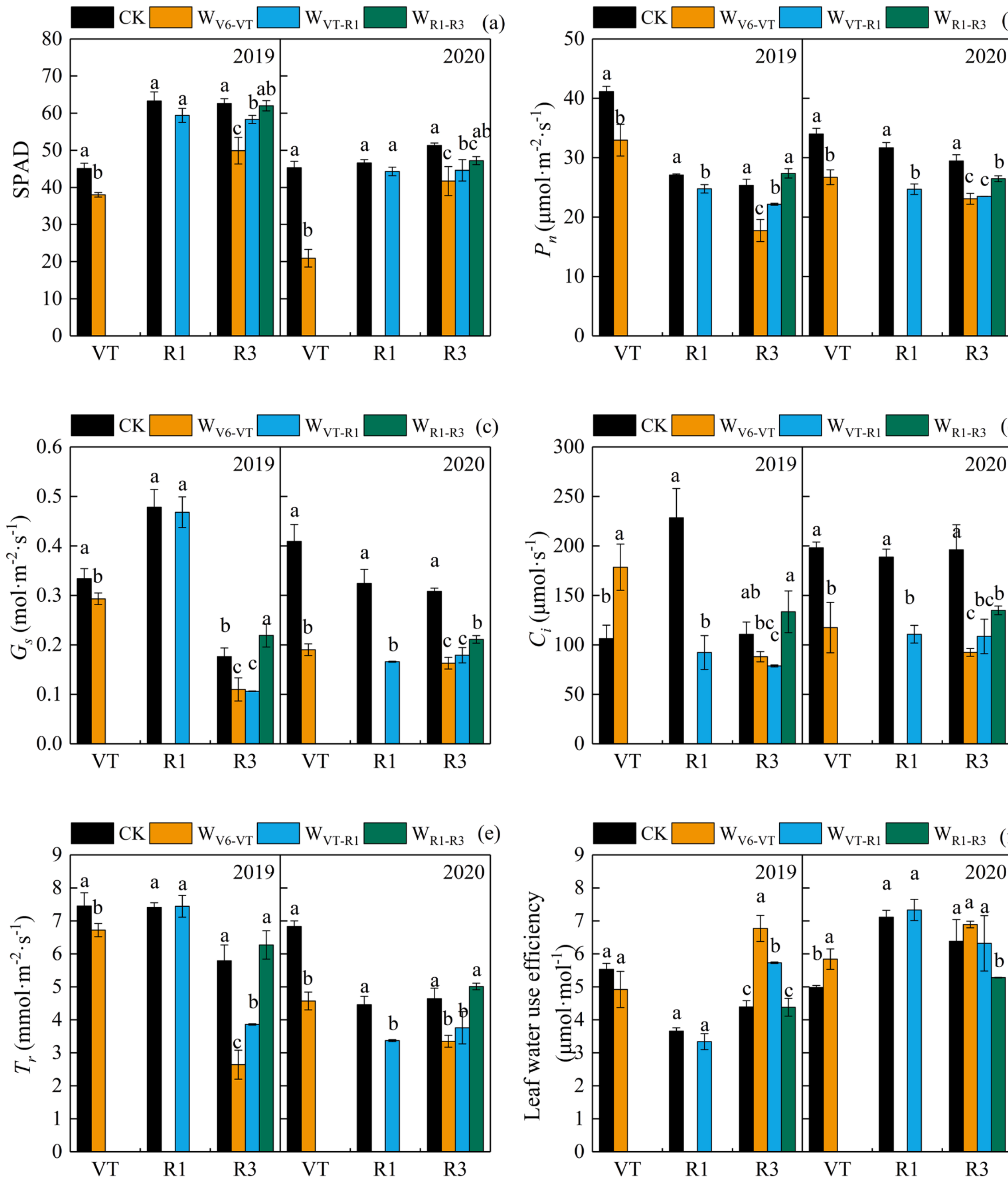

Fig. 5. Photosynthetic characteristics of waxy maize leaves under waterlogging at different growth stages. (Note: different lowercase letters during the same stage indicated significant at 0.05 level. SPAD: leaf chlorophyll content index; P_n: net photosynthetic rate; G_s: stomatal conductance; C_i: intercellular CO_2 concentration; T_r: transpiration rate. The X axes are growth stages. CK: non-waterlogging; $W_{V6\text{-}VT}$: waterlogging for 10 d from six leaf stage (V6) to tasseling stage (VT); $W_{VT\text{-}R1}$: waterlogging for 10 d from tasseling stage to silking stage (R1); $W_{R1\text{-}R3}$: waterlogging for 10 d from silking stage to milk stage (R3). VT: tasseling stage; R1: silking stage; R3: milk stage.).

maize, but also changes grain quality. The nitrogen accumulation in various organs and the nitrogen distribution rate in maize grains decreased as a result of waterlogging (Otie et al., 2019; Ren et al., 2021), resulting in a decrease in total protein content in grains and protein degradation under waterlogging conditions, and then a decrease in protein content (Tang et al., 2010). In the present experiment, waterlogging during various growth stages resulted in varying degrees of total protein loss in grains, with the total protein loss being greatest in the $W_{V6\text{-}VT}$ treatment, and the amounts of gliadin, glutenin, albumin, and globulin all significantly reduced (Table 6). Yang et al. (2016) found that waterlogging at flowering and post-anthesis stages can diminish protein, albumin, and glutenin content in maize kernels, which is similar with the findings of this study. Waterlogging not only reduces grain protein level, but it also reduces starch and soluble sugar content significantly (Ren et al., 2013). While in our study, $W_{V6\text{-}VT}$ and $W_{VT\text{-}R1}$ treatments resulted in an increase in starch content and a decrease in soluble sugar content, as well as an increase in amylopectin and amylose content under $W_{V6\text{-}VT}$ treatment, whereas $W_{R1\text{-}R3}$ treatment resulted in a decrease in starch content. Our results were different from the founding of Ren et al. (2013), because their results were based on mature grains, while the starch content in this study and Yang et al. (2016) were based on data from fresh grain, that is, $W_{V6\text{-}VT}$ treatment significantly reduced

Table 5
Differences in agronomic traits and yield of waxy maize ear under waterlogging at different growth stages.

Year	Treatment	Ear length (cm)	Ear diameter (mm)	Bald tip length (cm)	Grains number per ear	100-grain weight (g)	Fresh ear yield with husk ($t \cdot ha^{-1}$)	Fresh ear yield ($t \cdot ha^{-1}$)	Moisture content of grain (%)
2019	CK	19.3 ± 0.2a	51.93 ± 0.5a	0.1 ± 0.1c	565 ± 1a	44.3 ± 1.2a	16.2 ± 0.4a	12.7 ± 0.4a	49.8 ± 0.5a
	W_{V6-VT}	17.1 ± 0.3c	49.0 ± 0.4b	0.3 ± 0.1a	507 ± 13c	35.5 ± 3.3c	11.9 ± 0.1c	8.7 ± 0.3c	45.4 ± 0.6c
	W_{VT-R1}	18.5 ± 0.3b	48.9 ± 1.8b	0.4 ± 0.1ab	543 ± 5b	40.2 ± 1.0b	15.0 ± 0.7b	11.3 ± 0.1b	45.6 ± 0.4c
	W_{R1-R3}	19.0 ± 0.4ab	53.2 ± 0.7a	0.2 ± 0.0 bc	561 ± 14ab	44.9 ± 1.9a	16.6 ± 0.4a	13.0 ± 0.4a	47.6 ± 0.0b
2020	CK	18.0 ± 0.6a	51.8 ± 0.0a	0.3 ± 0.2c	510 ± 10a	40.2 ± 0.4a	15.9 ± 0.9a	12.5 ± 1.2a	52.4 ± 0.4a
	W_{V6-VT}	12.9 ± 0.2c	46.1 ± 0.1c	2.0 ± 0.6a	376 ± 35c	35.1 ± 0.7c	9.2 ± 0.4c	7.5 ± 0.1c	48.9 ± 0.1c
	W_{VT-R1}	14.2 ± 0.2b	47.9 ± 0.6b	1.3 ± 0.0b	388 ± 22 bc	38.1 ± 0.3b	11.2 ± 0.2b	9.5 ± 0.0b	50.2 ± 0.5b
	W_{R1-R3}	14.5 ± 0.4b	48.3 ± 0.3b	1.4 ± 0.2ab	439 ± 47b	39.0 ± 0.7b	11.3 ± 0.9b	9.0 ± 0.5b	50.4 ± 0.3b

Note: The lowercase letters in the same column are the differences at the 0.05 level in the same year.

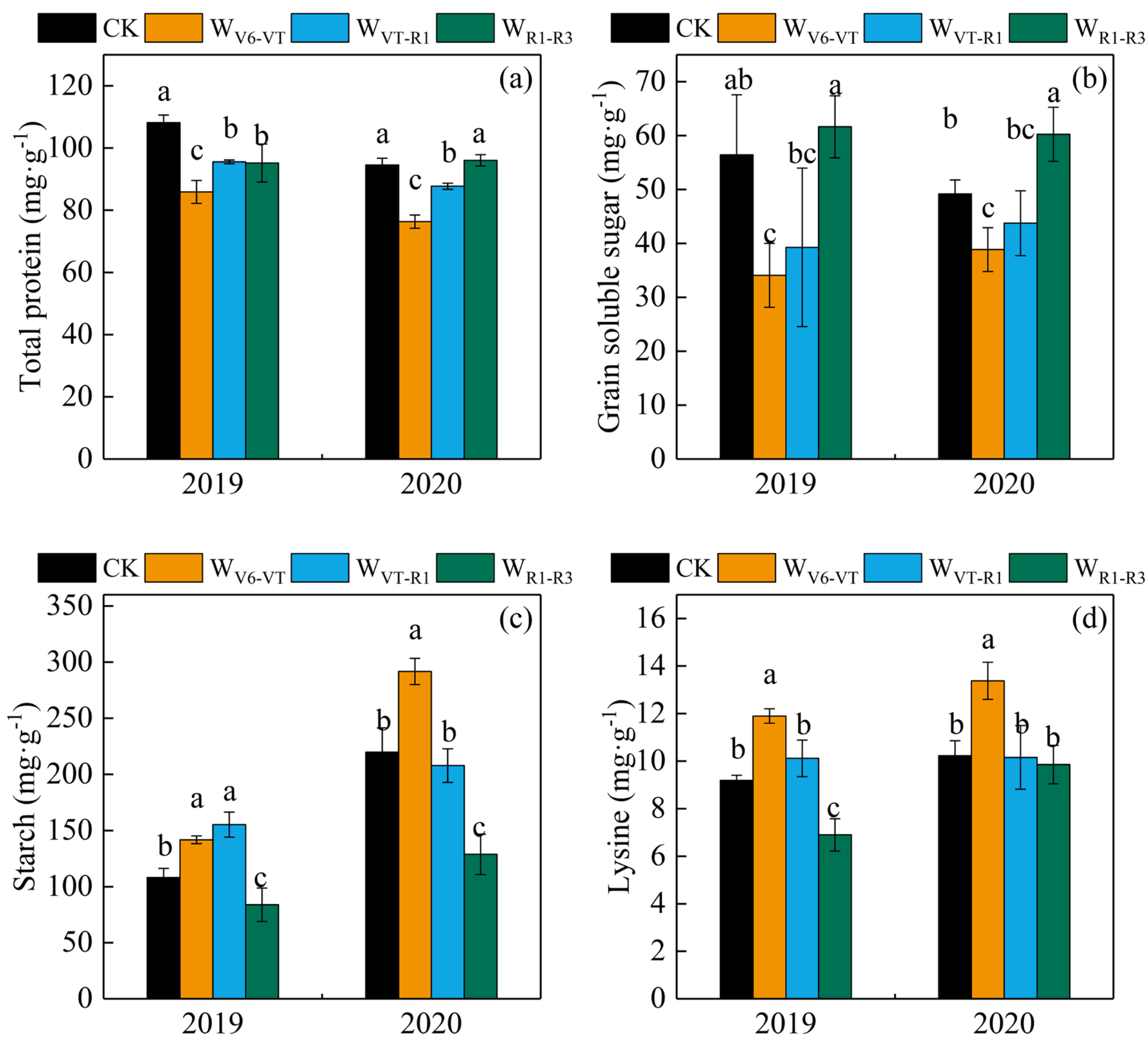

Fig. 6. Grain quality differences of waxy maize under waterlogging at different growth stages. (Note: different lowercase letters during the same year indicated significant at 0.05 level. The CK, W_{V6-VT}, W_{VT-R1}, W_{R1-R3} are different treatments; the X axes are year. CK: non-waterlogging; W_{V6-VT}: waterlogging for 10 d from six leaf stage (V6) to tasseling stage (VT); W_{VT-R1}: waterlogging for 10 d from tasseling stage to silking stage (R1); W_{R1-R3}: waterlogging for 10 d from silking stage to milk stage (R3).).

grain moisture content at R3 stage. ABA content in leaves increased after waterlogging, and ABA increased the activity of key enzymes that transformed soluble sugar into starch (Ren et al., 2018; Zhang et al., 2012), thereby accelerating the maturation of maize grains and accumulating starch in advance, resulting in the decrease of soluble sugar and the increase of starch content in grains at R3 stage, and waterlogging may limit the transfer of soluble sugar in stems to kernels, resulting in the decrease of soluble sugar in grains (Araki et al., 2012). While post-anthesis waterlogging may inhibit the transformation of soluble sugar to starch in grains (Zhou et al., 2018). Our results also showed that W_{V6-VT} and W_{VT-R1} significantly increased grain lysine content.

The results of PCA (Fig. 7) showed that the antioxidant enzymes, gas exchange parameters in leaves and plant growth were first affected when waterlogging occurred in waxy maize, and then affected the grain quality, as well as affected the ear growth, resulting in the decrease of

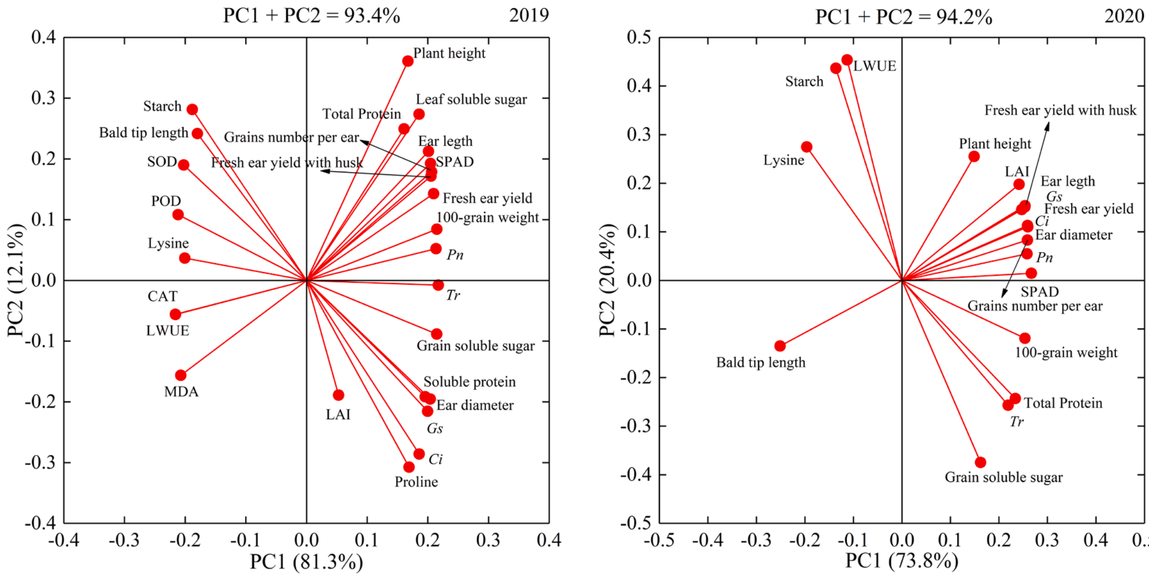

Fig. 7. Loading diagram of principal component analysis. (Note: LAI: leaf area index; MDA: malonaldehyde; SOD: superoxide dismutase; CAT: catalase; POD: peroxidase; SPAD: soil and plant analyzer develotrnent; P_n: net photosynthetic rate; G_s: stomatal conductance; C_i: intercellular CO_2 concentration; T_r: transpiration rate; LWUE: leaf water use efficiency. PCn indicated the extracted principal component.).

Table 6
Effects of waterlogging at jointing stage on starch and protein content in grains of waxy maize.

Year	Treatment	Amylose (mg·g^{-1})	Amylopectin (mg·g^{-1})	Gliadin (mg·g^{-1})	Glutenin (mg·g^{-1})	Albumin (mg·g^{-1})	Globulin (mg·g^{-1})
2019	CK	26.2 ± 4.3b	82.0 ± 9.1b	42.9 ± 0.3a	39.5 ± 0.1a	5.1 ± 0.4a	1.2 ± 0.0a
	W_{V6-VT}	34.9 ± 0.5a	106.9 ± 3.3a	31.8 ± 0.6b	36.8 ± 0.5b	3.5 ± 0.6b	0.8 ± 0.1b
2020	CK	28.6 ± 0.1b	191.2 ± 21.5b	38.3 ± 0.7a	34.1 ± 1.0a	4.3 ± 0.1a	1.3 ± 0.2a
	W_{V6-VT}	34.4 ± 0.0a	257.2 ± 11.7a	23.8 ± 0.2b	30.6 ± 0.3b	2.9 ± 0.0b	0.7 ± 0.0b

Note: The lowercase letters in the same column are the differences at the 0.05 level in the same year.

Table 7
Eigenvalues and variances of principal component analysis.

Year	Principal Component Number	Eigenvalue	Total variation (%)	Cumulative (%)
2019	PC1	21.15	81.3	81.3
	PC2	3.14	12.1	93.4
	PC3	1.72	6.6	100
2020	PC1	14.02	73.8	73.8
	PC2	3.88	20.4	94.2
	PC3	1.11	5.8	100

grain number per ear and 100-grain weight, and decrease in water content in fresh grains due to early maturity of grains, thereby affecting grain yield.

5. Conclusion

Waterlogging imposed at the jointing stage has the greatest impact on waxy maize growth and development, ear yield, and grain quality. It's vital to avoid it at this stage of the waxy maize planting management process. It has little effect on growth and development at the R1-R3 stages, ear yield, and grain total protein, soluble sugar, and starch content because it can mitigate the negative effects of waterlogging in time after waterlogging at the stages. However, the waterlogging duration set in this experiment was 10 d, and the change process of waxy maize growth, physiology and grain quality with the increase of waterlogging duration could not be understood. Thus, further research is needed on this basis, i.e. different waterlogging durations were set to investigate the variations in waxy maize growth, physiology, and grain quality under various waterlogging conditions.

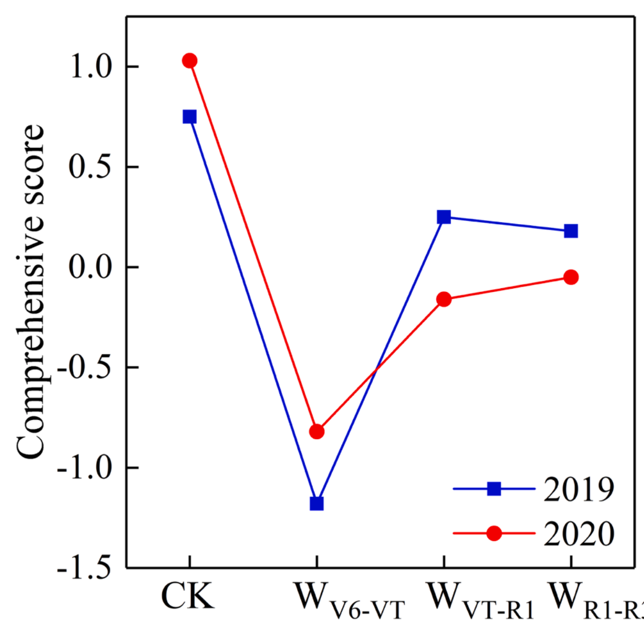

Fig. 8. Comprehensive scores of principal component analysis. (Note: CK: non-waterlogging; W_{V6-VT}: waterlogging for 10 d from six leaf stage (V6) to tasseling stage (VT); W_{VT-R1}: waterlogging for 10 d from tasseling stage to silking stage (R1); W_{R1-R3}: waterlogging for 10 d from silking stage to milk stage (R3).).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was jointly supported by the China Agriculture Research System (CARS-02), the Henan Provincial Natural Science Foundation (202300410553), the Agricultural Science and Technology Innovation Program (ASTIP), the National Natural Science Foundation of China (32101856), and Key Project of Water Conservancy Science and Technology in Henan Province (Key Technology Innovation and Application of Agricultural Intensive and Efficient Water Use in Irrigation Areas).

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