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Photosynthetic traits, water use and the yield of maize are influenced by soil water stability

Ge Li^{1,2}, Huaiyu Long^{1*}, Renlian Zhang¹, Aiguo Xu¹ and Li Niu^{1,3*}

Abstract

Background The aim of this study is to investigate the effect of soil water stability on maize (*Zea mays* L.) yield, water use, and its photosynthetic physiological mechanisms, and to innovate the relationship between maize and soil water, which currently only considers soil water content and neglects soil water stability.

Methods An organized water experiment was conducted on maize. The effects of stable soil water (SW) at two water content levels were examined, with fluctuating soil water (FW) as a control. The assessed effects included leaf water, chlorophyll, gas exchange, leaf water use efficiency (WUE), stable carbon isotope ratio ($\delta^{13}\text{C}$), and yield of maize.

Results Soil water stability had a significant effect on maize yield, yet it was slightly smaller than soil water content. Compared with FW, SW increased the maximum net photosynthetic rate, saturated light intensity, stomatal conductance, SPAD, leaf water content, and leaf WUE, and decreased $\delta^{13}\text{C}$, promoting dry matter assimilation and conversion into grain yield, ultimately increasing yield by 100.8%. Under the same soil water stability, 55% FC versus 75% FC weakened photosynthetic capacity and exacerbated stomatal limitation of maize leaves, making them more susceptible to light inhibition, which decreased photoassimilate accumulation, resulting in a significant decrease in yield. And the $\delta^{13}\text{C}$ under 75% FC conditions decreased by 4.7–7.7% compared with 55% FC.

Conclusion In conclusion, SW exhibits a positive effect on maize leaf water content, photosynthetic carbon assimilation, and grain yields, regardless of soil water content. Compared to FW, SW increased leaf WUE and maize yield by enhancing photosynthesis, and SW has stronger discrimination against ^{13}C during photosynthetic CO_2 assimilation, thus decreasing leaf $\delta^{13}\text{C}$. This study fills a gap in understanding how soil water stability influences maize yield and gas exchange, and provides a fresh perspective on how to improve crop yield and WUE by managing soil water stability.

Keywords Soil water stability, Photosynthetic traits, Water use efficiency, Light response curve, Stable carbon isotopes, Maize

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Introduction

Maize (*Zea mays* L.) is one of the most widely cultivated crops, and its production directly influences the development of the food industry and global food security [1]. The overwhelming majority of food production in China depends on irrigation water [2, 3]. Insufficient water cannot sustain normal crop development, and excessive water decreases agricultural yields and depletes groundwater, introduces salts such as nitrates into groundwater, and devastates ecosystems [4, 5]. Improving soil water-maize management strategies can conserve water resources, safeguard food production, and mitigate ecological damage; scientific water management is critical for ensuring future water supply and food security [4, 6].

Soil water is a crucial regulator of crop growth, development, and yield [7, 8]. As soil water information is difficult to obtain in agricultural production, it is frequently defined indirectly by easily accessible irrigation indicators, such as irrigation methods, irrigation amounts, and irrigation frequencies [9–11]. However, there is no accurate correspondence between irrigation indicators and soil water [12–15]. In addition, previous studies on soil water paid more attention to its spatial variability [16–19] but ignored its change in temporal dimension, that is, soil water stability. Although there is always some variation in soil water, it is difficult to maintain absolute stability. For example, Wang et al. (2020) and Niu et al. (2022) used the temporal variation of soil water to quantitatively characterize the soil water stability, and classified the soil water as fluctuating soil water (FW) if the temporal variation was greater than 0.1 and stable soil water (SW) if it was less than or equal to 0.1 [20, 21]. Li et al. (2023) adopted the fluctuation of soil water to quantitatively characterize the soil water stability, and the fluctuation coefficient of 0.01–0.02 was categorized as SW, and the fluctuation coefficient of 0.07–0.10 was called FW [22]. In addition to the quantitative properties of soil water (soil water content, SWC) [23, 24], new studies indicate directly or indirectly that soil water stability has a considerable impact on plant growth and development [20–22, 25]. Wang et al. (2020) suggested that SW conditions were more conducive to the growth and development of maize plants [20]. Li et al. (2023) discovered that SW alleviated water stress and improved the morphogenesis of tomato seedlings [22]. In another study on cherry radish, Li et al. (2024) demonstrated that irrigation with a stable moisture increased radish yield by 35–94% compared to fluctuating moistures [25]. At present, the relationship between maize and soil water stability is very limited, especially in terms of yield, water use efficiency (WUE), photosynthesis, and stable carbon isotope ratio ($\delta^{13}\text{C}$), and the underlying mechanism remains unknown.

Photosynthesis is the fundamental physiological process for producing maize material, which is susceptible

to environmental changes [26]. Severe water stress significantly decreased the leaf area index, relative chlorophyll content, and net photosynthetic rate (Pn) of maize leaves, leading to a reduction in the growth rate and consequently the yield [27]. Meanwhile, excessive SWC was detrimental to maize growth by increasing oxidative damage, reducing photosynthetic ability and chlorophyll concentration, and destroying chloroplast structure and root anatomy [24]. Although many studies have examined the relationships between drought stress and the light response curve [28–31], it is currently unclear how maize plants adapt and self-regulate in response to soil water stability from a photosynthetic physiological perspective. Gas exchange is environmentally responsive and temporally dynamic, which directly reflects the instantaneous state of photosynthesis [32]. Since plant syntheses rely on photosynthetic assimilates, the stable carbon isotope ratio ($\delta^{13}\text{C}$) of leaf dry matter is considered to be a time-integrated measure during tissue growth [33, 34]. The variation of $\delta^{13}\text{C}$ can be used to explain the carbon sequestration process in photosynthesis, which is related to gas exchange and biomass under different water conditions [34, 35]. Extensive research has been conducted on the correlation between leaf $\delta^{13}\text{C}$ and SWC [36–38]. However, little is known regarding the relationship between soil water stability and the leaf $\delta^{13}\text{C}$ of maize.

Our hypothesis argues that leaf gas exchange and the stable carbon isotopic composition of maize may exhibit variations in response to varying soil water conditions. The aim of this study was to investigate the impact of soil water stability on leaf water content, gas exchange characteristics, fitting parameters of light response curves, stable carbon isotopes, and grain yield at various stages of maize.

Materials and methods

Experimental site

The pot experiment was conducted from June to September 2021 in a rainproof shelter located at the Chinese Academy of Agricultural Sciences in Beijing, China (39.6°N, 116.2°E). The study site has a typical continental climate that is characterized as warm-temperate and semi-humid; the annual mean temperature was 10–12 °C and there was an annual frost-free period of 180–220 d. During the test period, Fig. S1 [see Additional file 1] depicts the daily changes in temperature, humidity, and evaporation from a standard reference water surface. The test soil came from 0 to 20 cm cultivated soil in Fangshan District, Beijing, and the soil texture was loam with a: field capacity (FC) of 35% (v/v), total nitrogen content of 0.8 g kg⁻¹, total phosphorus content of 0.6 g kg⁻¹, total potassium content of 12 g kg⁻¹, alkali hydrolyzed nitrogen of 81 mg kg⁻¹, available phosphorus of 14.8 mg kg⁻¹,

available potassium of 125 mg kg^{-1} , organic matter content of 13.3 g kg^{-1} , and pH (soil: water, 1:5) was 8.3.

Experimental device

To achieve precise control over soil water conditions, we implemented a method known as pressure potential difference-crop initiate drawing water device (P-CIDW), namely negative pressure irrigation technology. This method allows for the continuous and stable supply of water to soil-plant systems. It has been successfully utilized in various crop studies, as evidenced by works [22, 39–42]. The application of P-CIDW has facilitated a more accurate examination of the relationship between soil water and maize. The P-CIDW was designed by the Chinese Academy of Agricultural Sciences (Chinese Patents. ZL201110093923.2 and ZL201310554433.7) (Fig. 1), which consisted of a negative pressure controller, a water supply bucket (height: 80 cm, inner radius: 13.1 cm, capacity: 22 L), and an irrigator (porous ceramic pipe). The irrigator was 250 mm long, with an outer diameter of 18 mm and an inner diameter of 10 mm.

Experimental design

The soil water stability factor was set to two levels of stable soil water (abbreviated as “S”) and fluctuating soil water (abbreviated as “F”), and the soil water content factor was set to two levels of 55% FC (low soil water, abbreviated as “L”) and 75% FC (high soil water, abbreviated as “H”), for a total of 4 treatments (SL, SH, FL, and FH) with 5 replicates per treatment. A total of 20 pots, at a spacing of $0.45 \times 0.50 \text{ m}$, were set up. Based on previous experimental results [20], the SL and SH treatments were established by -9 kPa and -3 kPa of P-CIDW, respectively. The FL and FH treatments were established by watering

with the lower and upper limits of irrigation at 40–70% FC and 60–90% FC, respectively. The volumetric SWC was recorded every 30 min during the experiment using the ENVIData-DT soil water monitoring system (ENV-Idata-DT, IMKO, Germany). The SL and SH treatments were irrigated using the P-CIDW system, and the irrigation amount was recorded at 17:00 daily according to the water level pipe. The FL and FH treatments triggered irrigation as soon as the SWC approached or was below the lower limit of irrigation and irrigated to the upper limit of irrigation.

The widely-grown maize cultivar cv. Zhengdan 958 (*Zea mays* L.) used in this experiment was purchased from Beijing Zhongnong Fenglian Technology Development Co., Ltd., China. The pot, which had a height of 35 cm and a radius of 17 cm, was used to grow maize plants. Each pot was filled with 30.0 kg of air-dried soil, and the soil bulk density was 1.4 g cm^{-3} . The fertilizer amount was the same (0.25 g N , $0.13 \text{ g P}_2\text{O}_5$ and $0.13 \text{ g K}_2\text{O}$ per 1 kg of soil) for every replicate. Nitrogen fertilizer was applied in accordance with a base-topdressing ratio of 4:6 (topdressing at the eleven-leaf stage), and phosphorus and potassium fertilizers were used as base fertilizers at one time. Before sowing, the base fertilizers were thoroughly mixed into the soil, and all pots were irrigated to 100% FC. Each pot was sown with three seeds on 1 June in 2021. After emergence, the pots were thinned to one seedling for a follow-up study on 10 June in 2021. The seedling stage was uniformly irrigated to maintain the SWC at 70–80% FC. The water control experiment began on 15 June in 2021 (the three-leaf stage) and ended on 27 September in 2021 (the harvest stage).

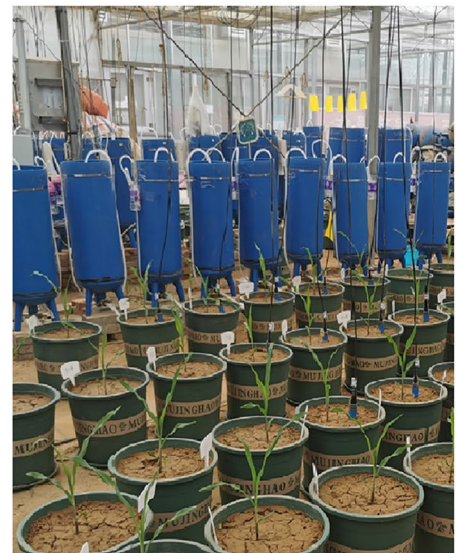
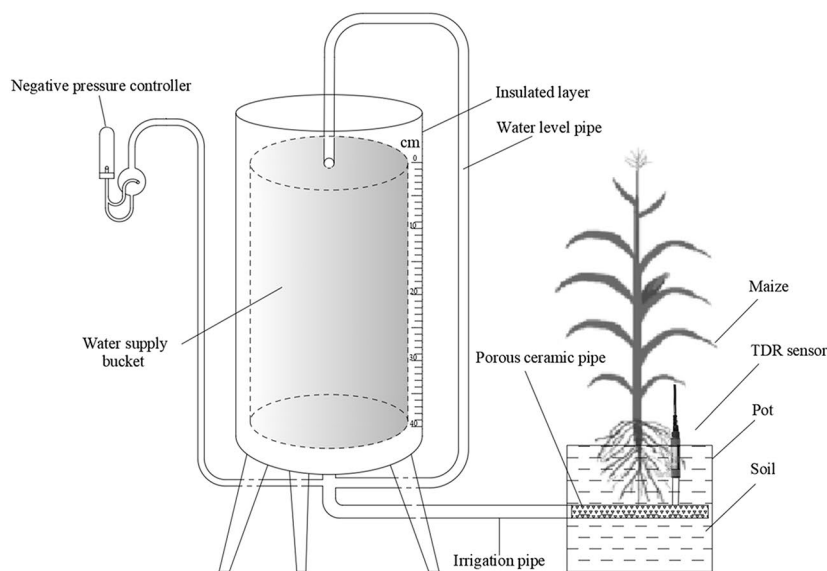


Fig. 1 The schematic diagram and physical photo of the pressure potential difference-crop initiate drawing water device

Sampling and measurements

Determination of soil water stability parameters

The fluctuation coefficient (δ) of soil water was determined using Eq. (1) [20]:

$$\delta = \frac{1}{n-1} \sum \frac{2|\theta_i - \theta_{i-1}|}{\theta_i + \theta_{i-1}} \quad (1)$$

where θ_i is the mean SWC on the i^{th} d, θ_{i-1} is the mean SWC on the $(i-1)^{\text{th}}$ d, and n is the number when SWC was observed. The magnitude of δ reflects the soil water stability, with a smaller value indicating a more stable SWC.

The coefficient of soil water temporal variability (CV) was calculated as follows [20]:

$$CV = SD/\theta \quad (2)$$

where SD is the standard deviation of SWC at different times, and θ is the mean SWC at various periods. If $CV \leq 0.1$, the soil water belongs to weak variability; if $0.1 < CV < 1$, it belongs to medium variability; and if $CV \geq 1$, it belongs to strong variability. The smaller the CV value, the more stable the soil water is.

Determination of leaf relative water content (LRWC) and relative electrical conductivity (LREC)

The latest fully expanded leaf/ear-leaf of maize plants were sampled at the ten-leaf stage (V10), milk stage (R3), and physiological maturity stage (R6) for the determination of $LRWC$ and $LREC$ [43], and the calculation formulas were as follows:

$$LRWC = (W_F - W_D) / (W_T - W_D) \times 100 \quad (3)$$

where W_F is the leaf fresh weight (g), W_D is the leaf dry weight (g), and W_T is the leaf saturated weight (g).

$$LREC = EC_1/EC_2 \times 100 \quad (4)$$

where EC_1 is the initial leaf electrical conductivity ($\mu\text{S cm}^{-1}$) and EC_2 is the final leaf electrical conductivity ($\mu\text{S cm}^{-1}$).

Leaf SPAD measurements

The SPAD value of maize leaves was measured every 7 days after treatment using a SPAD-502 portable chlorophyll meter (Minolta Camera Co. Ltd., Japan). The indicator leaf was the latest fully expanded leaf/ear-leaf, and 6–10 sites were selected at equal intervals throughout the leaf to determine its mean SPAD value.

Determination of gas exchange

At the six-leaf stage (V6), V10, silking stage (R1), R3, and R6 stages of maize, the light response curves were measured by a portable photosynthesis system (Li-6400XT, LI-Cor, NE, USA) on sunny and windless days. The photosynthetically active radiation (PAR) was taken at 2000, 1500, 1000, 700, 500, 300, 200, 100, 50, 20, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and the maximum and minimum waiting times were 200 s and 120 s, respectively. Under each specified PAR, P_n , stomatal conductance (G_s), and transpiration rate (Tr) of the latest fully expanded leaf/ear-leaf were determined. The light response curve was fitted using a modified rectangular hyperbolic model [44], which was depicted as follows:

$$P_n = \alpha \frac{1 - \beta PAR}{1 + \gamma PAR} PAR - R_d \quad (5)$$

where P_n is the net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), α is the initial slope of the light response curve, PAR is the photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), R_d is the dark respiration rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), and β and γ are coefficients.

In the meantime, the saturated light intensity (I_{sat}) and the maximum P_n ($P_{n_{\text{max}}}$) of maize leaves were estimated using the formulas:

$$I_{\text{sat}} = \frac{\sqrt{(\beta + \gamma)/\beta} - 1}{\gamma} \quad (6)$$

$$P_{n_{\text{max}}} = \alpha \left(\frac{\sqrt{\beta + \gamma} - \sqrt{\beta}}{\gamma} \right)^2 - R_d \quad (7)$$

At the leaf level, instantaneous water use efficiency (WUE_{ins}) was calculated as follows [45]:

$$WUE_{\text{ins}} = P_n/Tr \quad (8)$$

where WUE_{ins} is the instantaneous water use efficiency ($\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$), P_n is the net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and Tr is the transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$).

Measurement of stable carbon isotopes

After the leaf samples were ground with a ball mill, the stable carbon isotope ratio ($\delta^{13}\text{C}$) in the samples was determined by a stable isotope ratio mass spectrometer (Thermo Fisher Inc., USA). The $\delta^{13}\text{C}$ value was expressed relative to the Pee Dee Belemnite (PDB) [46].

$$\delta^{13}\text{C} = (R/R_{\text{PDB}} - 1) \times 1000 \quad (9)$$

where $\delta^{13}\text{C}$ is the ratio expressed in parts per thousand (‰), R is the molar abundance ratio of the sample ($^{13}\text{C}/^{12}\text{C}$), and R_{PDB} is the molar abundance ratio of PDB.

Grain yield

At the R6 stage, five maize plants were harvested per treatment, and the grain yield (14% moisture content) was measured [47].

Statistical analysis

Microsoft Excel 2010 software (Microsoft Corp, Redmond, WA, USA) was used for data processing, SAS 9.0 (SAS Institute, Cary, NC, USA) was used for analysis of variance (ANOVA) (two-way ANOVA), and Duncan's multiple-range test was used for multiple comparisons ($P < 0.05$). Origin Pro 2021 software (OriginLab Corporation, Northampton, MA, USA) was used for correlation analysis and graph construction.

Results

Soil water parameters

The average soil water content (SWC) for the SL, SH, FL, and FH treatments were 19.4% (55.5% FC), 25.8% (73.8% FC), 19.1% (54.5% FC), and 25.9% (73.9% FC), respectively. The fluctuation coefficients for these treatments were 0.01, 0.01, 0.06, and 0.08, while the temporal variability coefficients were 0.05, 0.02, 0.16, and 0.12, respectively. The SL and SH treatments could be classified as stable soil water (SW) due to their minimal changes in SWC, very minor fluctuation coefficients observed during the treatment, and temporal variability coefficients below 0.1 (Fig. 2). The FL and FH treatments could be classified as fluctuating soil water (FW) due to their significant changes in SWC, which showed a “sawtooth” pattern. Additionally, these treatments exhibited relatively substantial fluctuation coefficients and temporal variability coefficients exceeding 0.1. The observed SWC

of the SL and FL treatments closely approximated the target value of 55% FC, whereas the observed SWC of the SH and FH treatments closely approximated the target value of 75% FC. These observed values fell within the acceptable margin of error for the experimental design, which was $\pm 2\%$.

Variation of LRWC and LREC

The LRWC and LREC were shown to be highly influenced by soil water stability and water content. Additionally, it was observed that the interaction between these factors had a considerable impact on LRWC during the R6 stage and LREC during the R3 and R6 stages, as depicted in Fig. 3. In comparison to FW, SW showed enhancements in the LRWC at the V10, R3, and R6 stages, with improvements of 3.0, 5.0, and 5.9%, respectively. Conversely, the LREC experienced a drop of 20.3, 18.8, and 23.7% at the same stage. Compared to the low water (LW), the high water (HW) showed an increase in LRWC of 3.4, 8.1, and 10.3% at the V10, R3, and R6 stages, respectively. Conversely, the LREC exhibited a drop of 19.8, 23.8, and 27.8% at the same stages.

Dynamic changes in the leaf SPAD

The observed pattern of variation in maize leaf SPAD remained consistent across different treatments (Fig. 4). The soil water stability and water content exerted a notable influence on the leaf SPAD after a week of water treatment. However, their interaction was found to have a meaningful effect only during the late reproductive growth stages. Overall, the ranking of SPAD could be summarized as follows: SH > FH > SL > FL. The SL increased leaf SPAD by 7.6% compared to the FL. Similarly, the SH increased leaf SPAD by 4.6% compared to the FH. Additionally, the SW exhibited an average increase of 6.1% in leaf SPAD compared to the FW. The SH increased leaf SPAD by 9.5% compared to the SL.

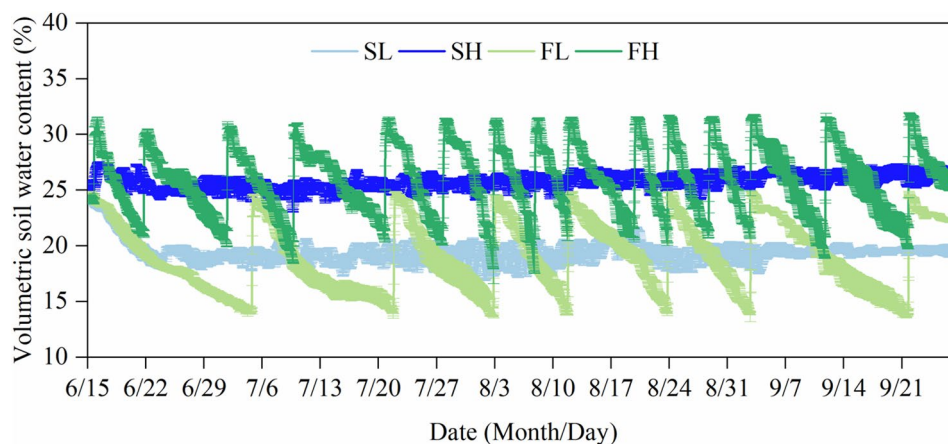


Fig. 2 Changes in volumetric soil water content of different treatments. Values are the mean \pm SD ($n = 4$). SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, and FH: fluctuating soil water with 75% FC

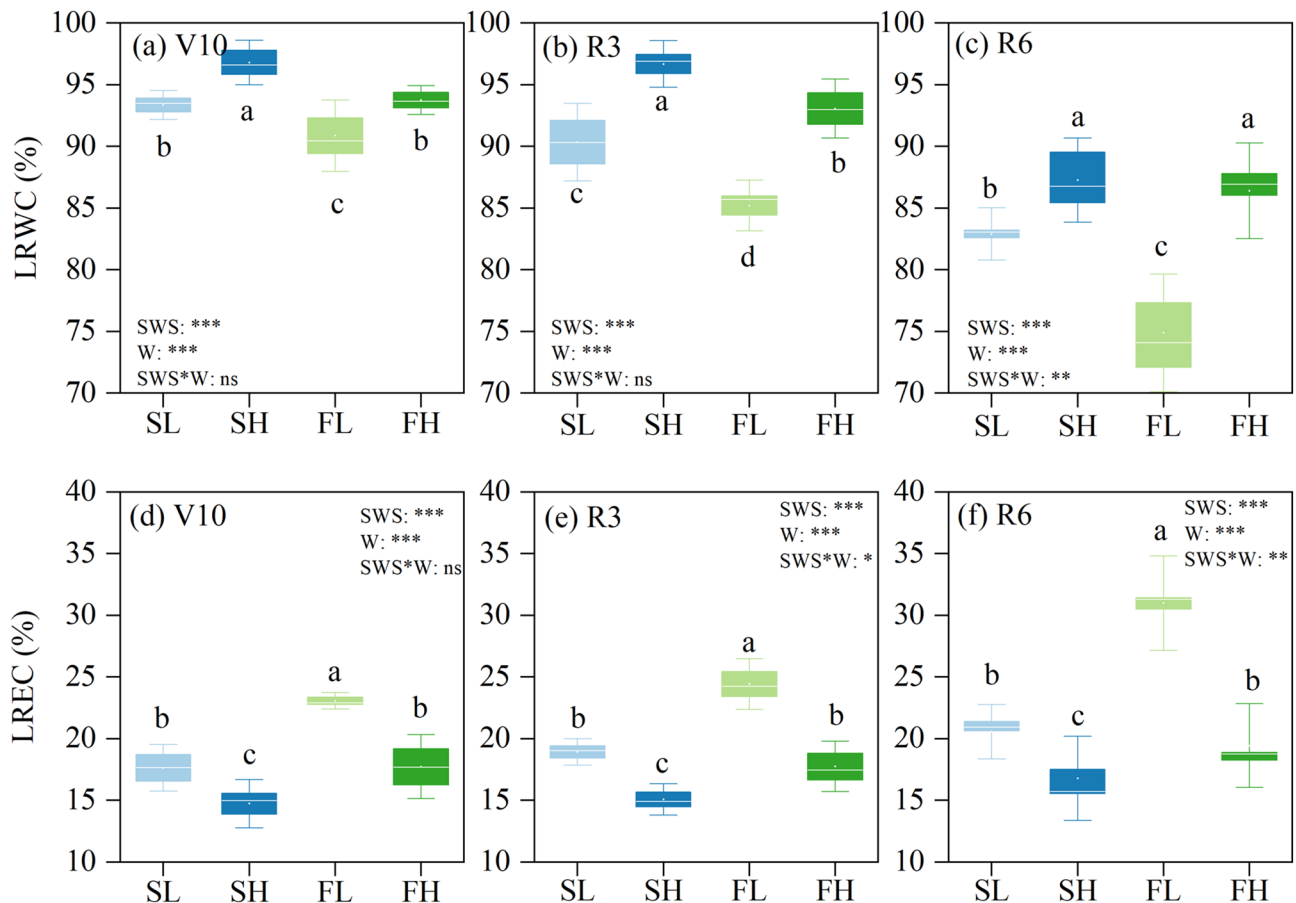


Fig. 3 Dynamic changes in leaf relative water content (LRWC) and relative electrical conductivity (LREC) of maize plants. Values are the mean \pm SD ($n=4-5$). Duncan's multiple-range test was used to test differences among treatments at the $P < 0.05$ level. Different lowercase letters above the columns indicate significant differences among treatments at the same stage. SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, FH: fluctuating soil water with 75% FC, V10: ten-leaf stage, R3: milk stage, R6: physiological maturity stage, SWS: soil water stability, W: soil water content, SWS*W: the interaction between soil water stability and soil water content. *, **, and *** indicate significance levels at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively, and ns indicates that the difference is not significant

Similarly, the FH led to a 12.7% increase in leaf SPAD compared to the FL. Furthermore, the HW showed an average increase of 11.1% in leaf SPAD compared to the LW. The effect of SW on enhancing leaf SPAD was shown to be more significant in situations when SWC was low, whereas the influence of increasing SWC on leaf SPAD was seen to be more prominent under FW conditions.

Response of leaf gas exchange

The order of the P_n at every stage was as follows: SH > FH > SL > FL, as depicted in Fig. 5. The observed trends in the light response curves per treatment at the R1, R3, and R6 stages were largely consistent. There was no significant difference between the SL and FH treatments. Additionally, the P_n showed a declining trend as maize maturity progressed. Under similar SWC, maize plants subjected to SW exhibited higher P_n compared to those subjected to FW. This difference in P_n suggested that the SW created a more favorable environment for

the production of photosynthetic products. Under similar soil water stability, the HW exhibited a greater propensity for enhancing the P_n of maize leaves compared to the LW. Furthermore, the impact of maize growth stages on the effectiveness of the SWC was shown to be negligible.

The G_s curve of maize leaves indicated that the G_s was higher with the SH during the V6 stage. Conversely, the G_s was lower with the FL. However, there was no significant difference between the SL and FH. The study revealed that the G_s under SW conditions exhibited a greater value compared to those under FW, given similar SWC levels. Under similar soil water stability, HW was shown to have a more positive impact on the G_s of maize leaves compared to the LW. At the V10 stage, there was a minimal disparity observed among the SL, SH, FL, and FH treatments. During the R1 stage, there was no apparent distinction observed among the four treatments under weak light conditions. However, when the light

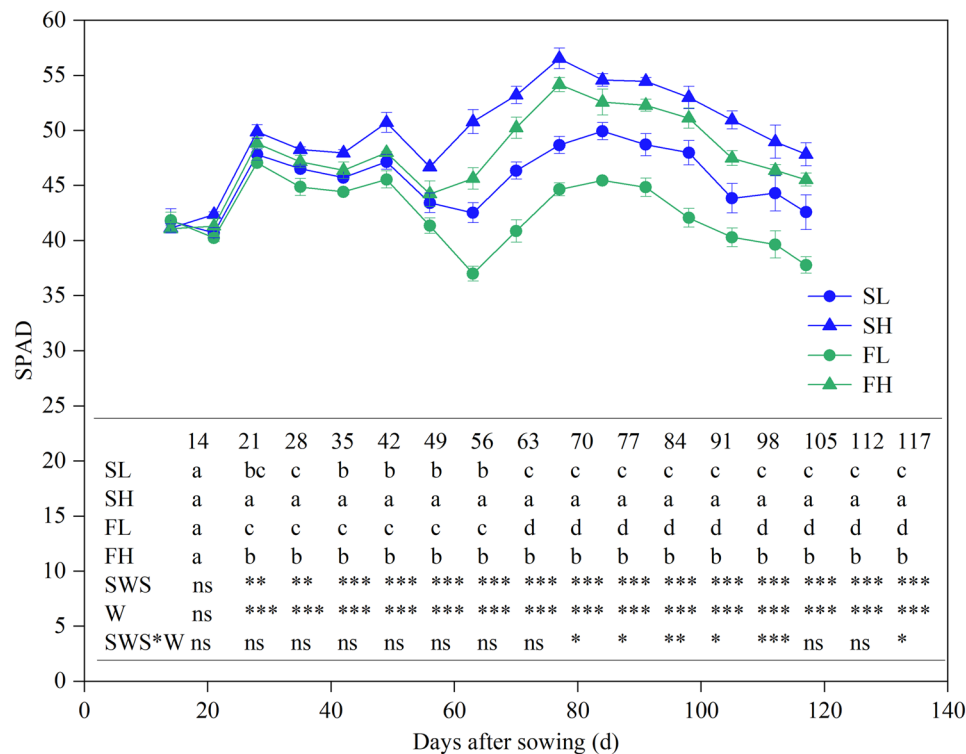


Fig. 4 Dynamic changes in maize leaf SPAD over time under different treatments. Values are the mean \pm SD ($n=4-5$). Duncan's multiple-range test was used to test differences among treatments at the $P < 0.05$ level. Different lowercase letters in the same column indicate significant differences among treatments within the same day. SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, FH: fluctuating soil water with 75% FC, SWS: soil water stability, W: soil water content, SWS*W: the interaction between soil water stability and soil water content. *, **, and *** indicate significance levels at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively, and ns indicates that the difference is not significant

intensity increased, the G_s of maize leaves subjected to the SH exhibited a quick increase, followed by the SL and FH, while the FL showed a slower increase. During the R3 stage, there was a collective decline in the G_s values of the four treatments in comparison to the R1 stage. The variation of G_s in each treatment was similar to that of R1, but the gap between SW and FW increased. During the R6 stage, there was a drop observed in the G_s values as the maize plants matured.

The Tr curve of maize leaves showed that at the V6 stage, the leaf Tr of maize plants under FH treatment was higher than that under SH treatment, while the Tr of SL treatment was higher than that of FL treatment under strong light. At the V10 stage, the Tr of FH treatment was larger and the Tr of SL treatment was minor, while there was no significant difference between SH and FL treatment. At the R1 and R3 stages, the Tr under HW treatment was greater than that under LW treatment, but there was no substantial difference between Tr under stable and fluctuating moisture conditions with the same SWC. At the R6 stage, the ranking of Tr was $FH > SH > FL > SL$ (Fig. 6).

The WUE_{ins} curve of maize leaves indicated that there was no discernible disparity in WUE_{ins} among the treatments throughout the V6 stage. At the V10 stage, the

leaf WUE_{ins} in maize plants of SW were found to be better than those of FW when subjected to identical SWC constitutions. Conversely, HW exhibited lower WUE_{ins} than LW when exposed to equivalent levels of soil water stability. During the R1 stage, the WUE_{ins} of plants subjected to the SL treatment were found to be higher compared to the FL treatment. However, no significant difference in WUE_{ins} was seen between the SH and FH treatments under weak light conditions. Furthermore, the WUE_{ins} of plants exposed to the SH treatment under strong light conditions were found to be higher than those subjected to the FH treatment. During the R3 and R6 stages, the application of SW resulted in an increase in WUE_{ins} when compared to the use of FW. Furthermore, the impact of SW on WUE_{ins} of maize leaves was particularly pronounced under LW conditions.

Maximum net photosynthetic rate, saturated light intensity, light compensation point, and dark respiration rate

The Pn_{max} , I_{sat} , and R_d of maize leaves were strongly influenced by the soil water stability throughout all stages. Additionally, the light compensation point (I_c) during the V6 and R1 stages, as well as the α during the R3 stage, were also affected by the stability of soil water (Table 1).

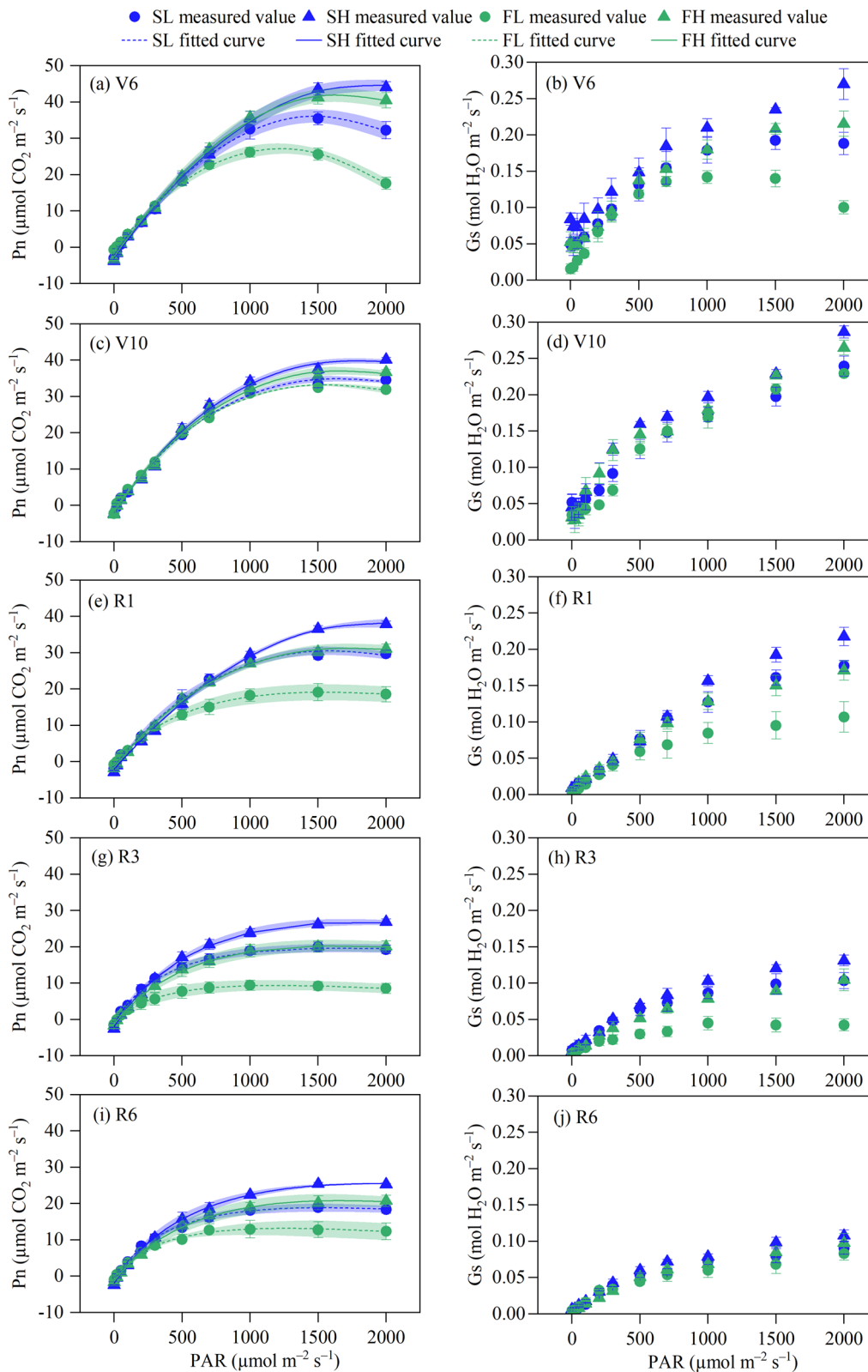


Fig. 5 Dynamic changes in net photosynthetic rate (Pn) and stomatal conductance (Gs) of maize leaves. Values are the mean \pm SD ($n=3$). SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, FH: fluctuating soil water with 75% FC, PAR: photosynthetically active radiation, V6: six-leaf stage, V10: ten-leaf stage, R1: silking stage, R3: milk stage, and R6: physiological maturity stage

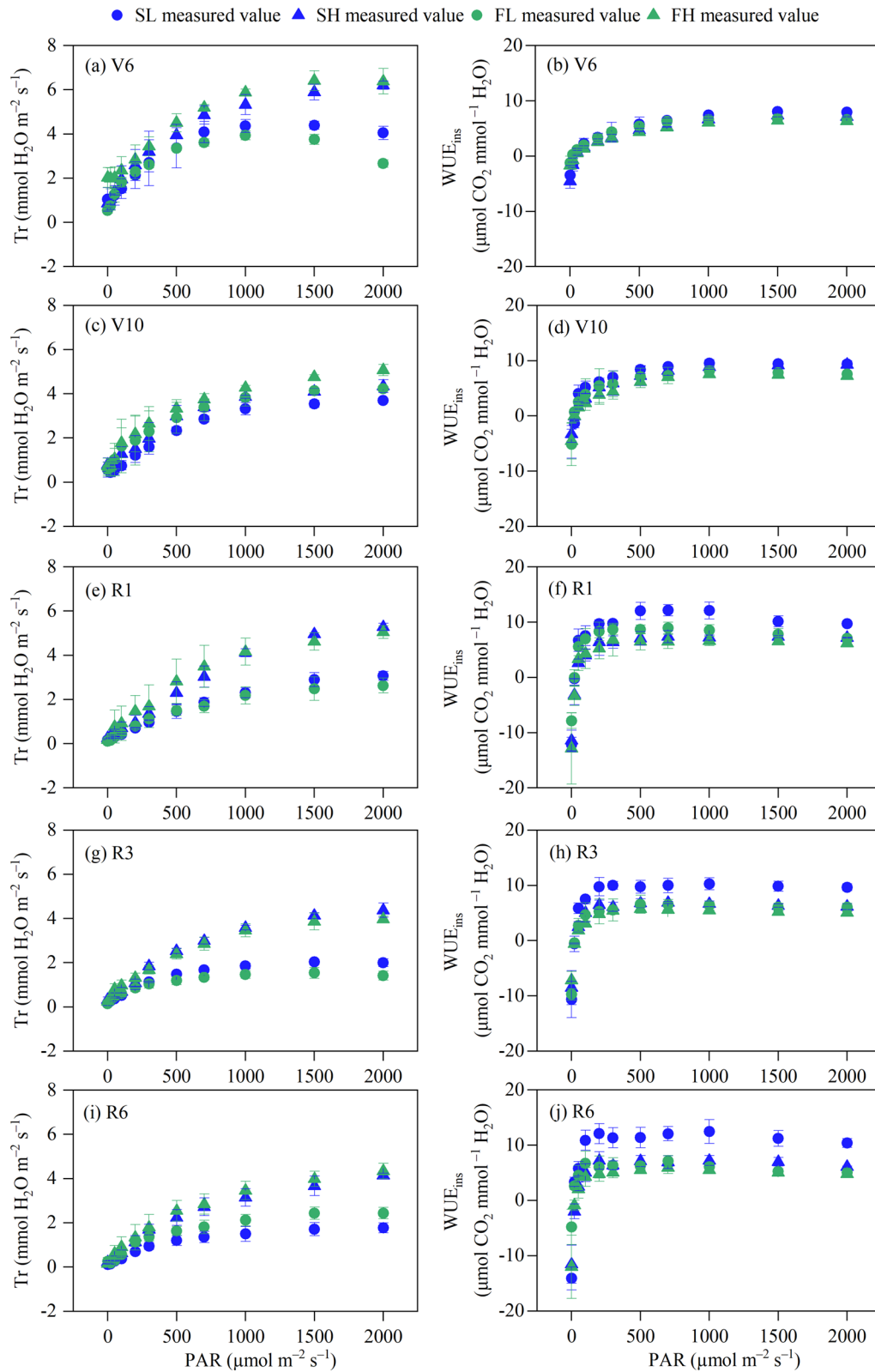


Fig. 6 Dynamic changes in transpiration rate (Tr) and instantaneous water use efficiency (WUE_{ins}) of maize leaves. Values are the mean \pm SD ($n=3$). SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, FH: fluctuating soil water with 75% FC, PAR: photosynthetically active radiation, V6: six-leaf stage, V10: ten-leaf stage, R1: silking stage, R3: milk stage, R6: physiological maturity stage

Table 1 Effects of different treatments on the fitting parameters of light response curves of maize leaves

Stage	Treatment	α	Pn_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	I_{sat} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	I_c ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	R_d ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
V6	SL	0.053a	36.14b	1500c	48.01a	2.45a
	SH	0.051a	44.94a	1877a	56.20a	2.82a
	FL	0.049a	27.10c	1223d	19.69b	0.96b
	FH	0.053a	42.22a	1683b	49.86a	2.62a
V10	SL	0.056a	34.98c	1674bc	33.05a	1.80a
	SH	0.056a	40.00a	1796a	35.39a	1.96a
	FL	0.056a	33.26d	1584c	24.32b	1.34b
	FH	0.056a	37.19b	1698ab	34.23a	1.86a
R1	SL	0.049a	30.61b	1610bc	31.18b	1.48b
	SH	0.042a	38.32a	1924a	50.08a	2.09a
	FL	0.046a	19.10c	1565c	17.87c	0.82c
	FH	0.048a	31.37b	1748b	34.48b	1.64b
R3	SL	0.070a	19.73b	1621b	21.51b	1.42b
	SH	0.060ab	26.89a	1825a	34.87a	2.01a
	FL	0.043b	9.44c	1192c	26.76b	1.03c
	FH	0.050ab	20.34b	1648ab	28.97ab	1.37bc
R6	SL	0.064a	18.85b	1549b	19.84b	1.21bc
	SH	0.059a	25.53a	1949a	35.27a	1.97a
	FL	0.060a	13.23c	1219c	17.63b	0.94c
	FH	0.049a	20.83b	1684ab	30.24a	1.43b
ANOVA (<i>F</i> values)						
V6	SWS	0.05	35.38***	28.40***	11.40**	14.07**
	W	0.37	146.26***	89.60***	13.96**	19.99**
	SWS*W	1.71	10.22*	0.88	4.58	8.13*
V10	SWS	0.01	23.67**	9.46*	4.86	10.45*
	W	0.00	92.26***	14.82**	7.46*	14.87**
	SWS*W	0.06	1.36	0.02	2.85	4.10
R1	SWS	0.33	109.69***	6.26*	49.80***	17.50**
	W	0.57	128.52***	31.54***	75.12***	28.97***
	SWS*W	1.80	6.69*	2.19	0.31	0.68
R3	SWS	6.22*	128.43***	23.83**	0.02	20.08**
	W	0.06	147.65***	28.27***	10.70*	15.95**
	SWS*W	1.28	6.38*	4.14	5.50*	1.20
R6	SWS	1.18	36.55***	1330**	2.55	20.11**
	W	1.42	70.00***	28.17***	38.34***	47.69***
	SWS*W	0.23	0.29	0.16	0.39	2.21

Note: Duncan's multiple-range test was used to test differences among treatments at the $P < 0.05$ level. Different lowercase letters in the same column indicate significant differences among treatments at the same stage. SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, FH: fluctuating soil water with 75% FC, SWS: soil water stability, W: soil water content, SWS*W: the interaction between soil water stability and soil water content, α : the initial slope of the light response curve, Pn_{max} : maximum net photosynthetic rate, I_{sat} : saturated light intensity, I_c : light compensation point, R_d : dark respiration rate, V6: six-leaf stage, V10: ten-leaf stage, R1: silking stage, R3: milk stage, and R6: physiological maturity stage. *, **, and *** indicate significance levels at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

Throughout all stages, the SWC had a notable impact on the Pn_{max} , I_{sat} , I_c , and R_d , but no discernible influence was observed on the α . The interaction between the stability and content of soil water had a notable impact on Pn_{max} and R_d during the V6 stage, Pn_{max} during the R1 stage, and Pn_{max} and I_c during the R3 stage.

At the V6 stage, there was no significant difference in Pn_{max} between the SH and FH treatments; however, it did differ from the Pn_{max} observed in the SL and FL treatments (Table 1). At the V10 stage, there was a small difference observed in the light response curves across all

treatments. However, there was a significant difference in Pn_{max} between the different treatments. There was no significant difference in Pn_{max} between the SL and FH treatments at the R1, R3, and R6 stages. However, this difference was considerably different from the SH and FL treatments.

At all stages, the ranking of I_{sat} of maize leaves was as follows: SH > FH > SL > FL. However, it is pertinent to note that only at the V6 stage did the four treatments exhibit a statistically significant difference. At the V6, V10, R1, R3, and R6 stages, the Pn_{max} of SW increased

by 19.9, 6.4, 41.2, 70.6, and 32.5%, respectively, compared to FW. Additionally, I_{sat} of SW increased by 17.1, 5.7, 6.5, 23.3, and 21.4%, respectively, compared to FW. When comparing the performance of LW at five different stages, it was shown that HW increased Pn_{max} by 40.1, 13.1, 44.7, 75.9, and 46.5%, respectively. Additionally, HW increased I_{sat} by 31.4, 7.2, 15.6, 25.4, and 32.0%, respectively.

The I_c and R_d increased at all stages when the SWC and soil water stability increased, with the exception of the I_c at the R3 stage. Under the similar SWC, SW raised the I_c by 0.4–78.3% and the R_d by 20.0–81.4% compared to FW. Under similar soil water stability, the HW increased I_c by 23.9–85.1% and R_d by 23.6–93.4% compared to the LW.

Stabilize carbon isotopes and grain yield

The soil water stability and water content significantly affected leaf $\delta^{13}\text{C}$ and grain yield of maize, while their interaction had no significant effects on $\delta^{13}\text{C}$ or yield (Table 2). Under similar SWC conditions, compared to FW, the $\delta^{13}\text{C}$ of SW was reduced by 5.3, 8.4, and 10.3% at the V10, R3, and R6 stages, respectively. Under the same soil water stability, compared with LW, the $\delta^{13}\text{C}$ of HW decreased by 4.7, 7.7, and 7.6% at the V10, R3, and R6 stages, respectively. All water treatments showed clear carbon isotope fractionation; more carbon was assimilated when fractionation was stronger in the treatment of SW or HW. The $\delta^{13}\text{C}$ fluctuation trend was consistent across all treatments across the three stages, and the fractionation at the V6 stage was more pronounced, suggesting that the carbon assimilation during this time was stronger than in other periods.

The treatments significantly affected maize yield, following SH>FH>SL>FL. Compared with FL treatment, the yield of SL treatment was increased by 163.3%;

Table 2 Effects of different treatments on leaf $\delta^{13}\text{C}$ and grain yield of maize

Treatment	$\delta^{13}\text{C}$			Grain yield (g plant ⁻¹)
	Ten-leaf stage	Milk stage	Physiological maturity stage	
SL	-11.08b	-10.81b	-11.90b	99.49c
SH	-11.57c	-11.56c	-12.97c	194.45a
FL	-10.49a	-9.91a	-10.93a	37.79d
FH	-11.02b	-10.73b	-11.61ab	140.60b
ANOVA (<i>F</i> values)				
SWS	13.97**	18.93***	19.90***	288.40***
W	11.09**	15.88**	11.08**	844.88***
SWS*W	0.01	0.04	0.54	1.33

Note: Duncan's multiple-range test was used to test differences among treatments at the $P < 0.05$ level. Different lowercase letters in the same column indicate significant differences among treatments at the same stage. SL: stable soil water with 55% FC, SH: stable soil water with 75% FC, FL: fluctuating soil water with 55% FC, FH: fluctuating soil water with 75% FC, SWS: soil water stability, W: soil water content, SWS*W: the interaction between soil water stability and soil water content. *, **, and *** indicate significance levels at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

compared with FH treatment, the yield of SH treatment was increased by 38.3%; SW improved yield by an average of 100.8% compared to FW under similar SWC conditions. Compared with SL treatment, the yield of SH treatment was increased by 95.5%; compared with FL treatment, the yield of FH treatment was increased by 272.1%; HW, compared with LW, increased yield by an average of 183.8% under the same soil water stability.

Discussion

Stable soil water improves the leaf WUE of maize plants by increasing Pn rather than decreasing Tr

The soil water plays a significant role in influencing various aspects of crop growth, yield, and water use efficiency (WUE). Several reports have shown that leaf WUE increased with the decrease of soil water content (SWC) [48, 49], and the same phenomenon was found in our study: lower SWC resulted in lower plant transpiration, thus increasing instantaneous water use efficiency (WUE_{ins}), regardless of being in a stable soil water (SW) or fluctuating soil water (FW) condition. Our study confirms that stable water conditions are beneficial for improving photosynthesis in crops [50]. The gradual decrease in soil water may leave a “memory” for plants. In a prior study, stomatal conductance of maize leaves could not return to the control level following rehydration [51]. Compared with a stable water state, stomate pore length became smaller under fluctuating water conditions, which was a change in anatomical structure, and even if soil water fluctuated to a peak again, the developed stomate pore length could not be changed [52]. These were the reasons why stomatal conductance of maize leaves under SW was greater than that under FW in this study. A study in tomato plants showed that the activities of superoxide dismutase, peroxidase, and catalase increased continuously during the gradual drought, and their activities decreased to close to the control level after rehydration but still higher than the control level [53], resulting in drought memory. It could be inferred that the process of gradually decreasing soil water might affect the antioxidant protection system and thus affect the damage of cell membranes (Fig. 3) and produce memory. Research has indicated that there was a notable decrease in the rate of chlorophyll synthesis in leaves during rehydration [54]. It was observed in this study that the SPAD under FW conditions was, in fact, lower than that under SW conditions (Fig. 4). At 96 h after rehydration, the maximum quantum efficiency, photosystem II operating efficiency, and Rubisco (Ribulose-1,5-bisphosphate carboxylase) activity showed a gradual recovery process [54], but Rubisco activity was slower to recover [55]. As a result, Rubisco activity might not have recovered sufficiently yet and has dropped again. Therefore, Rubisco activity was consistently higher in stable soil water than in fluctuating

soil water (Fig. S3 [see Additional file 1]). Concisely, the combination of steady and elevated stomatal conductance, SPAD value, and Rubisco activity in SW led to an increased photosynthetic rate.

Another important finding was that SW, versus FW, resulted in an increase in the WUE_{ins} of maize leaves, and increasing Pn played a more fundamental role than decreasing Tr in WUE_{ins} improvement (Figs. 5 and 6). Furthermore, the present study demonstrated that FW exacerbated stomatal limitations due to isohydric behavior in response to frequent dry and wet alternations (Figs. 2 and 5), which was aligned with that of Morabito et al. (2022), who found that isohydric behavior protected *Vitis vinifera* from a sudden increase in tension in response to a fast-developing drought [56]. It is widely acknowledged that the parameters of gas exchange in plant leaves have the ability to promptly respond to changes in soil water levels, and there is often a strong relationship between these two variables [48]. Nevertheless, it was found that there was not a good correlation between the Pn and Gs of maize leaves with the instantaneous SWC (Fig. S2 [see Additional file 1]), which might be due to the changed leaf stomatal morphology under FW compared with SW. Xu et al. (2024) showed that when the median value of soil water was the same, the stomate pore length of soil water with larger fluctuation was smaller than that of soil water with smaller fluctuation [52], indicating that Pn and Gs were not only affected by SWC but also affected by stomatal morphological differences. In combination with Fig. 4, it was evident that the relationship between the response of the SPAD and soil water stability, long-term average SWC, and their interaction became increasingly apparent as the growth stage progressed, rather than being influenced by instantaneous SWC. These findings indicated that the observed variations in Pn, Gs, and SPAD of maize leaves were not solely influenced by the instantaneous SWC but rather by the specific water treatment applied. Here, we provide a new perspective for improving leaf WUE through managing soil water stability.

Stable soil water promotes maize yield via enhancing photosynthetic capacity

The process of photosynthesis serves as the foundation for the accumulation of dry matter, while soil water has an important impact on plants photosynthetic activity, growth, and yield [57]. Previous studies have demonstrated that the application of mulching ridges and furrows in maize fields resulted in a notable increase in soil water storage. This improved the light response curve and increased photosynthetic capacity, chlorophyll content, and crop yield [58]. Our study corroborated these findings, showing a suitable SWC level can increase the photosynthetic and grain yield of maize plants. The

most interesting findings were that soil water stability had a significant effect on maize yield; specifically, maize plants grown under SW conditions exhibited considerably higher yields compared to those grown under FW settings, which was confirmed by a two-way ANOVA (Table 2).

In order to further analyze the mechanism of yield variation, we simulated the light response curves of maize leaves subjected to various treatments using a modified rectangular hyperbolic model. According to a study conducted by Xing et al. (2020), an elevation in soil water stress during the maize silking stage resulted in a reduction in Pn_{max} , I_{sat} , and R_d [29]. Here, it was noted that potential photosynthetic capacity of maize leaves was diminished during various growth stages due to low SWC. Based on the observed increase rates of Pn_{max} by HW relative to LW, it could be inferred that SWC exerted varying influences on Pn_{max} at different stages, with the order of impact being $R3 > R6 > R1 > V6 > V10$, which suggested that SWC had stage-dependent effects on Pn_{max} of maize leaves and that the effect of SWC on leaf Pn_{max} during the reproductive growth stage was greater than that during the vegetative growth stage. This was due to the fact that maize plants had considerably more leaf area during their reproductive growth stage than during their vegetative growth stage, together with increased transpiration [59, 60]. Eom et al. (2013) calculated crop water requirements through potential evapotranspiration and crop coefficient and also found that the water requirements in the maize reproductive growth stage were greater than those in the vegetative growth stage [59]. Additionally, during the reproductive growth stage, the SPAD of different SWC treatments varied substantially, but not during the vegetative growth stage (Fig. 4). Lower SWC appeared to have significantly accelerated the degradation of photosynthetic pigments in leaves at the reproductive growth stage. As a result, SWC had a greater effect on Pn_{max} during the reproductive growth stage than the vegetative growth stage. Moreover, it was evident that soil water stability exerted varying influences on Pn_{max} at different growth stages. Specifically, the impact on Pn_{max} followed the order $R3 > R1 > R6 > V6 > V10$. It was worth noting that these findings have not been previously documented in existing literature. These findings will doubtless be much scrutinized, but there are some immediately dependable conclusions that the application of SW, as compared to FW, resulted in a notable enhancement in the Pn_{max} and I_{sat} (Table 1), indicating that SW increased the photosynthetic capacity of maize leaves and expanded the range of available light intensity. The potential reason for this outcome could be attributed to the fact that SW enhanced the Rubisco activity of maize leaves (Fig. S3 [see Additional file 1]). When the soil water returned from its

valleys to its peaks, the recovery of Rubisco activity under FW conditions was comparatively delayed. Previous research revealed that the activity of Rubisco was still significantly below the control level even after one day of rehydration and that some varieties needed eight days to regain the control level [55]. Nevertheless, in this study, the SWC was lower than the SW around 4 days after the FW peaked (Fig. 2). Consequently, Rubisco activity might not have rebounded fully and might have declined once more. Therefore, Rubisco activity under the FW condition was consistently lower than that of SW, and Rubisco significantly enhanced the carbon carboxylation ability of maize leaves and then improved its energy conversion efficiency [61]. Another potential factor may be a long-term variation in soil water levels resulting from the FW treatment, which induced significant water stress in maize plants [21]. Water fluctuation subsequently impaired the leaf photosynthetic efficiency, resulting in a decrease in the capacity for photosynthetic carbon assimilation. Consequently, FW had an adverse impact on the crop biomass accumulation, ultimately leading to a substantial reduction in maize yield.

Additionally, the findings suggested that soil water stability and water content had minimal impact on the photosynthetic capacity of maize leaves under conditions of low light intensity (Table 1), but the growth and development of maize plants in FW were susceptible to inhibition under conditions of high light intensity. In agricultural production, summer maize plants commonly thrive in an area characterized by ample light availability [62]. The results of this study indicated that the potential photosynthetic capacity of maize leaves was improved by managing the SW mode, increasing the tolerance of maize plants to strong light, avoiding photosynthesis inhibition by intense light, and promoting maize plant growth and development, corroborating a previous study [50]. Furthermore, previous research has indicated a strong correlation between the photosynthetic capacity of plants and many anatomical characteristics of plant leaves, including stomatal density, vein density, and palisade tissue thickness [63, 64]. The observed variations in the photosynthetic physiology of maize leaves in response to water treatments at different stages may be attributed to alterations in leaf anatomical traits, and this will be thoroughly and systematically analyzed in future studies.

Stable soil water decreased leaf $\delta^{13}\text{C}$ by altering the maize plants carbon assimilation

Plants discriminate against the heavier isotope, and this discrimination happens mainly during the process of photosynthesis fixing carbon [65]. The $\delta^{13}\text{C}$ reflects the preferential assimilation in C_3 crops of the lighter carbon isotope ^{12}C over ^{13}C [46]. However, C_4 crops have a

more complex process; the Kranz anatomy determined the carbon concentrating mechanism, which spatially separated the initial carbon fixation from the Rubisco-catalyzed carbon assimilation in mesophyll and bundle sheath cells, respectively [65]. The $\delta^{13}\text{C}$ of cotton plants under a limited water supply was higher than in crops grown under well-watered conditions [36]. Similarly, in this study, higher $\delta^{13}\text{C}$ values were usually obtained in the LW treatment relative to the HW treatment (Table 2), indicating that C_3 and C_4 crops have similar responses to SWC. Interestingly, $\delta^{13}\text{C}$ of plant material in SW showed more negative values than that in FW, showing that the discrimination against ^{13}C was stronger for maize plants grown in SW during photosynthetic CO_2 assimilation (Table 2). On the one hand, studies have shown that soil water with a large fluctuation will reduce stomate pore length, which may lead to a decrease in intercellular carbon dioxide concentration [52, 66]. In the process of gradually decreasing soil water content in FW, the decrease in CO_2 conductivity in leaves resulted in a decrease in the availability of the gaseous substrate of Rubisco. In such adverse conditions, $\delta^{13}\text{C}$ increased and leaves' usage ratio of $^{13}\text{CO}_2$ increased (Table 2). On the other hand, along with the ratio of CO_2 assimilation rate and Gs, $\delta^{13}\text{C}$ is determined as an extra contributing component by the leakage of CO_2 from the bundle sheath cells back to the mesophyll [67]. The effectiveness of photosynthesis is reduced by this leakage, which is influenced by the coordination of several photosynthetic enzymes. In the process of decreasing soil water, Rubisco activity also gradually decreased. Research has exhibited that there was a positive correlation between Rubisco activity and chloroplastic CO_2 concentration [68], and the recovery of Rubisco activity was relatively slow after soil water reached the peaks [55], which may be reduced after insufficient recovery. Therefore, lower Rubisco activity and higher $\delta^{13}\text{C}$ were observed in FW treatment, and the two were negatively correlated (Table 2, Figs. S3 and S4 [see Additional file 1]). In addition, soil water stability significantly affected the leaf LRWC and LREC (Fig. 3), which were closely related to proteins, lipids, and sugars in leaves [22, 69], and these substances carried different isotopic signatures. The relative composition of compounds caused by post-photosynthetic fractionations may also contribute to differences in leaf $\delta^{13}\text{C}$ of maize plants grown in SW and FW [65, 70]. Alternatively, $\delta^{13}\text{C}$ was negatively correlated with the leaf relative water content, SPAD, net photosynthetic rate, maximum net photosynthetic rate, saturated light intensity, light compensation point, and dark respiration rate, and positively correlated with the leaf relative conductivity, while the relationship between $\delta^{13}\text{C}$ and leaf WUE varied with the growth of maize plants (Fig. 7). This indicated that $\delta^{13}\text{C}$ may serve as a comprehensive indicator of the water physiology and

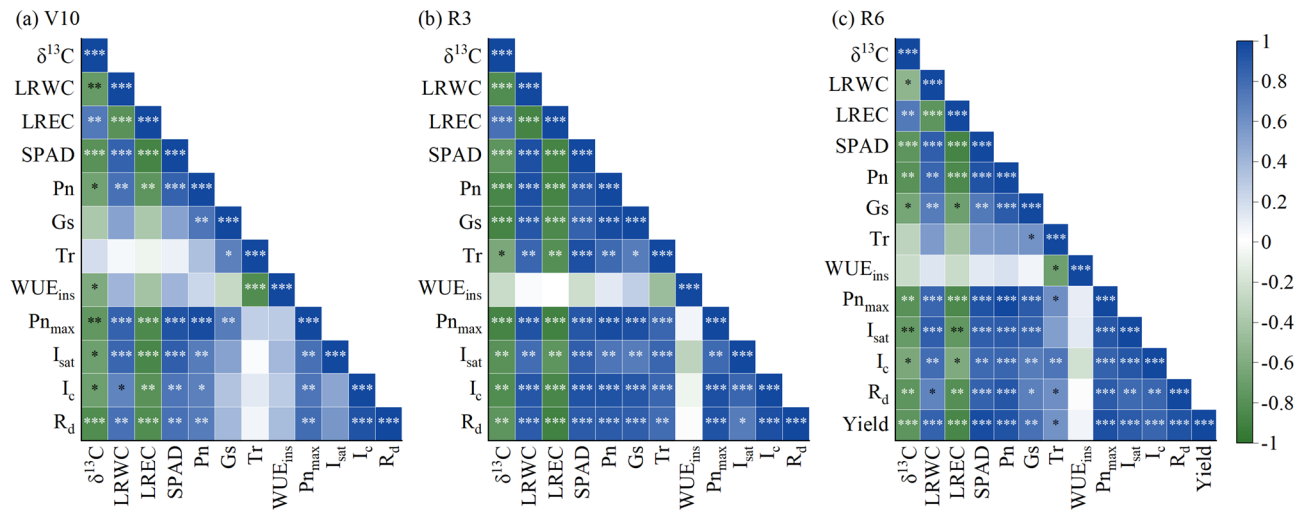


Fig. 7 Relationship between stable carbon isotope ratio ($\delta^{13}\text{C}$), photosynthetic parameters, and water use efficiency of maize plants. LRWC: leaf relative water content, LREC: leaf relative electrical conductivity, SPAD: relative chlorophyll content, Pn: net photosynthetic rate, Gs: stomatal conductance, Tr: transpiration rate, WUE_{ins} : instantaneous water use efficiency, Pn_{max} : maximum net photosynthetic rate, I_{sat} : saturated light intensity, I_c : light compensation point, R_d : dark respiration rate, V10: ten-leaf stage, R3: milk stage, and R6: physiological maturity stage. Pn, Gs, Tr, and WUE_{ins} were the data when photosynthetically active radiation was $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. *, **, and *** indicate significance levels at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively

water status of maize plants. Further research should be undertaken to investigate the influence of soil water stability on the values of fractionation factors, including fractionation during diffusion of CO_2 in the liquid phase, carboxylation of Rubisco, and the combined fractionation of CO_2 dissolution and PEPC carboxylation [34].

Conclusion

In this study, the effects of soil water stability and water content on the leaf water content, SPAD, photosynthetic physiology, leaf water use efficiency, $\delta^{13}\text{C}$, and yield of maize at various stages were studied using a two-factor experimental design. The main results were as follows:

- (1) Both soil water stability and soil water content were shown to have an impact on maize grain yield; however, it was observed that soil water content had a greater impact than soil water stability. Furthermore, their interaction did not have a significant effect on yield. In contrast to the fluctuating soil water, the stable soil water resulted in a significant increase in yield. Specifically, the stable soil water led to a yield increase of 163.3% under 55% FC and 38.3% under 75% FC. When comparing the yield of stable soil water with fluctuating soil water under similar water content, it was shown that the average yield increase was 100.8%.
- (2) Stable soil water improved the maximum net photosynthetic rate, saturated light intensity, stomatal conductance, leaf SPAD, leaf water content, and leaf water use efficiency of maize plants compared to fluctuating soil water, which promoted

the assimilation and conversion of dry matter into grain yield and ultimately increased the maize yield, while its effect depended on soil water content.

- (3) Low soil water content of 55% FC, as opposed to high water content of 75% FC, weakened photosynthetic capacity and exacerbated stomatal limitation of maize leaves, rendering them more susceptible to light inhibition, which decreased photoassimilate accumulation, resulting in a significant decrease in yield.
- (4) The $\delta^{13}\text{C}$ of maize leaves was influenced by soil water stability and water content. The maize leaf $\delta^{13}\text{C}$ under stable soil water decreased by 5.3–10.3% relative to fluctuating soil water with the same water level, indicating that stable soil water has stronger discrimination against ^{13}C during photosynthetic CO_2 assimilation. And the $\delta^{13}\text{C}$ under 75% FC fell by 4.7–7.7% in comparison to that under 55% FC under similar soil water stability.

This work applies a two-dimensional perspective to the stability and content of soil water for understanding the relationship between maize and soil water. It also provides new ideas on how to manage agricultural water resources.

Supplementary Information

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Supplementary Material 1

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Ge Li, Huaiyu Long, and Renlian Zhang. Aiguo Xu and Li Niu supervised the study and contributed to reviewing and editing the manuscript. The first draft of the manuscript was written by Ge Li, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability

All data supporting the findings of this study are available within this article and within its additional files published online.

Declarations**Ethics approval and consent to participate**

Not applicable.

Consent for publication

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Competing interests

The authors declare no competing interests.

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References

- Zilberman D, Lefler J. Biotechnology for African food security. *Nat Food*. 2021;2:79.
- Ministry of water resources of the People's Republic of China. Statistic bulletin on China water activities. Beijing, China: China Water & Power; 2022.
- Kang S, Hao X, Du T, Tong L, Su X, Lu H, et al. Improving agricultural water productivity to ensure food security in China under changing environment: from research to practice. *Agric Water Manag*. 2017;179:5–17.
- Leghari SJ, Hu K, Wei Y, Wang T, Bhutto TA, Buriro M. Modelling water consumption, N fates and maize yield under different water-saving management practices in China and Pakistan. *Agric Water Manag*. 2021;255:107033.
- Bwambale E, Abagale FK, Anornu GK. Smart irrigation monitoring and control strategies for improving water use efficiency in precision agriculture: a review. *Agric Water Manag*. 2022;260:107324.
- Shen Z, Zhang Q, Singh VP, Pokhrel Y, Li J, Xu C-Y, et al. Drying in the low-latitude Atlantic Ocean contributed to terrestrial water storage depletion across Eurasia. *Nat Commun*. 2022;13:1849.
- Nam S, Kang S, Kim J. Maintaining a constant soil moisture level can enhance the growth and phenolic content of sweet basil better than fluctuating irrigation. *Agric Water Manag*. 2020;238:106203.
- Liang J, Liang G, Zhao Y, Zhang Y. A synergic method of Sentinel-1 and Sentinel-2 images for retrieving soil moisture content in agricultural regions. *Comput Electron Agric*. 2021;190:106485.
- Mehmood F, Wang G, Gao Y, Liang Y, Chen J, Si Z, et al. Nitrous oxide emission from winter wheat field as responded to irrigation scheduling and irrigation methods in the North China Plain. *Agric Water Manag*. 2019;222:367–74.
- Siakou M, Bruggeman A, Eliades M, Zoumides C, Djuma H, Kyriacou MC, et al. Effects of deficit irrigation on 'Koroneiki' olive tree growth, physiology and olive oil quality at different harvest dates. *Agric Water Manag*. 2021;258:107200.
- Attia A, El-Hendawy S, Al-Suhaibani N, Alotaibi M, Tahir MU, Kamal KY. Evaluating deficit irrigation scheduling strategies to improve yield and water productivity of maize in arid environment using simulation. *Agric Water Manag*. 2021;249:106812.
- Hokam EM, El-Hendawy SE, Schmidhalter U. Drip irrigation frequency: the effects and their interaction with nitrogen fertilization on maize growth and nitrogen use efficiency under arid conditions. *J Agron Crop Sci*. 2011;197:186–201.
- Sarker KK, Hossain A, Timsina J, Biswas SK, Malone SL, Alam MK, et al. Alternate furrow irrigation can maintain grain yield and nutrient content, and increase crop water productivity in dry season maize in sub-tropical climate of South Asia. *Agric Water Manag*. 2020;238:106229.
- Liu H, Li H, Ning H, Zhang X, Li S, Pang J, et al. Optimizing irrigation frequency and amount to balance yield, fruit quality and water use efficiency of greenhouse tomato. *Agric Water Manag*. 2019;226:105787.
- Shu L, Liu R, Min W, Wang Y, Yu H, Zhu P, et al. Regulation of soil water threshold on tomato plant growth and fruit quality under alternate partial root-zone drip irrigation. *Agric Water Manag*. 2020;238:106200.
- Alliaume F, Echeverria G, Ferrer M, González Barrios P. A study of the multivariate spatial variability of soil properties, and their association with vine vigor growing on a clayish soil. *J Soil Sci Plant Nutr*. 2024.
- Jasse A, Berry A, Alexandre-Tudo JL, Poblete-Echeverria C. Intra-block spatial and temporal variability of plant water status and its effect on grape and wine parameters. *Agric Water Manag*. 2021;246(December 2020):106696.
- Lin X, Wang Z, Li J. Spatial variability of salt content caused by nonuniform distribution of irrigation and soil properties in drip irrigation subunits with different lateral layouts under arid environments. *Agric Water Manag*. 2022;266:107564.
- Lazarovitch N, Kisekka I, Oker TE, Brunetti G, Wöhling T, Xianyue L et al. Modeling of irrigation and related processes with HYDRUS. In: Sparks DLBT-A in A, redakteur. Academic Press; 2023. bl 79–181.
- Wang Z, Zhu G, Long H, Zhang R, Shen Z, Qu X, et al. Effects of temporal variation of soil moisture on the growth and water use efficiency of maize. *J Agric Sci Technol*. 2020;22:153–64.
- Niu L, Wang Z, Zhu G, Yu K, Li G, Long H. Stable soil moisture improves the water use efficiency of maize by alleviating short-term soil water stress. *Front Plant Sci*. 2022;13:1–12.
- Li G, Long H, Zhang R, Drohan PJ, Xu A, Niu L. Stable soil moisture alleviates water stress and improves morphogenesis of tomato seedlings. *Horticulturae*. 2023;9:391.
- Ali S, Jan A, Manzoor, Sohail A, Khan A, Khan MI, et al. Soil amendments strategies to improve water-use efficiency and productivity of maize under different irrigation conditions. *Agric Water Manag*. 2018;210:88–95.
- Guo Q, Huang G, Guo Y, Zhang M, Zhou Y, Duan L. Optimizing irrigation and planting density of spring maize under mulch drip irrigation system in the arid region of Northwest China. *F Crop Res*. 2021;266:108141.
- Li G, Zhu G, Liu J, Wang Z, Long H, Zhang R et al. Effects of stable and fluctuating soil water on the agronomic and biological performance of root vegetables. *Front Plant Sci*. 2024;15.
- Liu J, Wang X, Rong Z, Gao Y, Zhang G, Wang W, et al. Modified non-rectangular hyperbola equation with plant height for photosynthetic light-response curves of *Potentilla anserina* and *Elymus nutans* at various growth phases in the Heihe River Basin, Northwest China. *J Arid Land*. 2019;11:764–73.
- Li G, Zhao B, Dong S, Zhang J, Liu P, Lu W. Controlled-release urea combining with optimal irrigation improved grain yield, nitrogen uptake, and growth of maize. *Agric Water Manag*. 2020;227:105834.
- Ali S, Xu Y, Ma X, Henchiri M, Cai T, Ren X, et al. Cultivation modes and deficit irrigation strategies to improve ¹³C carbon isotope, photosynthesis, and winter wheat productivity in semi-arid regions. *Environ Sci Pollut Res*. 2019;26:5539–53.
- Xing H, Zhou W, Hao W, Li L, Wang C, Ma H, et al. Inhibition of nitrogen increasing on maize growth under water stress. *Chin J Agrometeorol*. 2020;41:240–52.
- Xia JB, Zhang GC, Wang RR, Zhang SY. Effect of soil water availability on photosynthesis in *Ziziphys jujuba* var. *Spinosus* in a sand habitat formed from seashells: comparison of four models. *Photosynthetica*. 2014;52:253–61.
- Moreno-Sotomayor A, Weiss A, Pappozzi ET, Arkebauer TJ. Stability of leaf anatomy and light response curves of field grown maize as a function of age and nitrogen status. *J Plant Physiol*. 2002;159:819–26.
- Medrano H, Tomás M, Martorell S, Flexas J, Hernández E, Rosselló J, et al. From leaf to whole-plant water use efficiency (WUE) in complex canopies: limitations of leaf WUE as a selection target. *Crop J*. 2015;3:220–8.
- Ellsworth PZ, Cousins AB. Carbon isotopes and water use efficiency in C₄ plants. *Curr Opin Plant Biol*. 2016;31:155–61.

34. Ubierna N, Holloway-Phillips M-M, Farquhar GD. Using stable carbon isotopes to study C₃ and C₄ photosynthesis: Models and calculations. In: *Methods in molecular biology* (Clifton, N.J.). United States; 2018. bl 155–96.
35. Twohey RJ, Roberts LM, Studer AJ. Leaf stable carbon isotope composition reflects transpiration efficiency in *Zea mays*. *Plant J*. 2019;97:475–84.
36. Saranga Y, Flash I, Paterson AH, Yakir D. Carbon isotope ratio in cotton varies with growth stage and plant organ. *Plant Sci*. 1999;142:47–56.
37. Dercon G, Clymans E, Diels J, Merckx R, Deckers J. Differential ¹³C isotopic discrimination in maize at varying water stress and at low to high nitrogen availability. *Plant Soil*. 2006;282:313–26.
38. Brück H, Payne WA, Sattelmacher B. Effects of phosphorus and water supply on yield, transpirational water-use efficiency, and carbon isotope discrimination of pearl millet. *Crop Sci*. 2000;40:120–5.
39. Li S, Tan D, Wu X, Degré A, Long H, Zhang S, et al. Negative pressure irrigation increases vegetable water productivity and nitrogen use efficiency by improving soil water and NO₃⁻-N distributions. *Agric Water Manag*. 2021;251:106853.
40. Yang P, Bian Y, Long H, Drohan PJ. Comparison of emitters of ceramic tube and polyvinyl formal under negative pressure irrigation on soil water use efficiency and nutrient uptake of crown daisy. *Agric Water Manag*. 2020;228:105830.
41. Yang P, Bai J, Yang M, Ma E, Yan M, Long H, et al. Negative pressure irrigation for greenhouse crops in China: a review. *Agric Water Manag*. 2022;264:107497. October 2021.
42. Zhang J, Ji J, Wang P, Long H, Wu X. Molecular mechanism of negative pressure irrigation inhibiting root growth and improving water use efficiency in maize. *Plant Soil*. 2022;472:127–43.
43. Challabathula D, Analin B, Mohanan A, Bakka K. Differential modulation of photosynthesis, ROS and antioxidant enzyme activities in stress-sensitive and -tolerant rice cultivars during salinity and drought upon restriction of COX and AOX pathways of mitochondrial oxidative electron transport. *J Plant Physiol*. 2022;268:153583.
44. Ye Z, Yu Q. A coupled model of stomatal conductance and photosynthesis for winter wheat. *Photosynthetica*. 2008;46:637–40.
45. Sun Q, Wang Y, Chen G, Yang H, Du T. Water use efficiency was improved at leaf and yield levels of tomato plants by continuous irrigation using semipermeable membrane. *Agric Water Manag*. 2018;203:430–7.
46. Farquhar G, Richards R. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Funct Plant Biol*. 1984;11:539.
47. Zhang G, Dai R, Ma W, Fan H, Meng W, Han J, et al. Optimizing the ridge-furrow ratio and nitrogen application rate can increase the grain yield and water use efficiency of rain-fed spring maize in the Loess Plateau region of China. *Agric Water Manag*. 2022;262:107430.
48. Guo L, Bornø ML, Niu W, Liu F. Biochar amendment improves shoot biomass of tomato seedlings and sustains water relations and leaf gas exchange rates under different irrigation and nitrogen regimes. *Agric Water Manag*. 2021;245:106580.
49. Pazzagli PT, Weiner J, Liu F. Effects of CO₂ elevation and irrigation regimes on leaf gas exchange, plant water relations, and water use efficiency of two tomato cultivars. *Agric Water Manag*. 2016;169:26–33.
50. Wang Z. Effects of soil moisture temporal variation on growth, physiology and water use efficiency of maize and lettuces. *Chinese Academy of Agricultural Sciences*; 2020.
51. Guo Q, Li X, Niu L, Jameson PE, Zhou W. Transcription-associated metabolomic adjustments in maize occur during combined drought and cold stress. *Plant Physiol*. 2021;186:677–95.
52. Xu S, Huang Y, Zhang R, Niu L, Long H. Appropriate nitrogen application for alleviation of soil moisture-driven growth inhibition of okra (*Abelmoschus esculentus* L. (Moench)). *Horticulturae*. 2024;10:425.
53. Hao S, Cao H, Wang H, Pan X. The physiological responses of tomato to water stress and re-water in different growth periods. *Sci Hortic (Amsterdam)*. 2019;249:143–54.
54. Perez P, Rabnecz G, Laufer Z, Gutierrez D, Tuba Z, Martinez-Carrasco R. Restoration of photosystem II photochemistry and carbon assimilation and related changes in chlorophyll and protein contents during the rehydration of desiccated *Xerophyta scabrada* leaves. *J Exp Bot*. 2011;62:895–905.
55. Calcagno AM, Rivas M, Castrillo M. Structural, physiological and metabolic integrated responses of two tomato (*Solanum lycopersicum* L.) cultivars during leaf rehydration. *Aust J Crop Sci*. 2011;5.
56. Morabito C, Orozco J, Tonel G, Cavalletto S, Meloni GR, Schubert A, et al. Do the ends justify the means? Impact of drought progression rate on stress response and recovery in *Vitis vinifera*. *Physiol Plant*. 2022;174:e13590.
57. Lamptey S, Li L, Xie J, Zhang R, Antille SY. Photosynthetic response of maize to nitrogen fertilization in the semiarid western Loess Plateau of China. *Crop Sci*. 2017;57:2739–52.
58. Fu L, Ren H, Xu S, Hu S, Yang J, Liu C. Planting models and mulching material strategies to reduce bundle sheath cell leakage and improve photosynthetic capacity and maize production in semi-arid climate. *Environ Sci Pollut Res*. 2021;28:2315–27.
59. Eom K, Park S-H, Yoo S-Y. Water requirement of maize according to growth stage. *Korean J Soil Sci Fertil*. 2013;46:16–22.
60. Guo J, Fan J, Xiang Y, Zhang F, Yan S, Zhang X, et al. Maize leaf functional responses to blending urea and slow-release nitrogen fertilizer under various drip irrigation regimes. *Agric Water Manag*. 2022;262:107396.
61. Zhu K, Zuo Q, Liu F, Qin J, Wang A, Zhang J, et al. Divergences in leaf CO₂ diffusion conductance and water use efficiency of soybean coping with water stress and its interaction with N addition. *Environ Exp Bot*. 2024;217:105572.
62. Wu H, Qiao M, Zhang W, Wang K, Li S, Jiang C. Systemic regulation of photosynthetic function in maize plants at grainning stage under a vertically heterogeneous light environment. *J Integr Agric*. 2022;21:666–76.
63. Amitrano C, Arena C, Cirillo V, De Pascale S, De Micco V. Leaf morpho-anatomical traits in *Vigna radiata* L. affect plant photosynthetic acclimation to changing vapor pressure deficit. *Environ Exp Bot*. 2021;186:104453.
64. Gao H, Li N, Li J, Khan A, Ahmad I, Wang Y, et al. Improving boll capsule wall, subtending leaves anatomy and photosynthetic capacity can increase seed cotton yield under limited drip irrigation systems. *Ind Crops Prod*. 2021;161:113214.
65. Eggels S, Blankenagel S, Schön C-C, Avramova V. The carbon isotopic signature of C₄ crops and its applicability in breeding for climate resilience. *Theor Appl Genet*. 2021;134:1663–75.
66. Zhang YJ, Gao H, Li YH, Wang L, Kong DS, Guo YY, et al. Effect of water stress on photosynthesis, chlorophyll fluorescence parameters and water use efficiency of common reed in the Hexi Corridor. *Russ J Plant Physiol*. 2019;66:556–63.
67. Farquhar G. On the nature of carbon isotope discrimination in C₄ species. *Funct Plant Biol*. 1983;10:205.
68. Galmes J, Ribas-Carbo M, Medrano H, Flexas J. Rubisco activity in Mediterranean species is regulated by the chloroplastic CO₂ concentration under water stress. *J Exp Bot*. 2011;62:653–65.
69. Liu F, Jensen CR, Shahanzari A, Andersen MN, Jacobsen S-E. ABA regulated stomatal control and photosynthetic water use efficiency of potato (*Solanum tuberosum* L.) during progressive soil drying. *Plant Sci*. 2005;168:831–6.
70. Cao M, Wu C, Liu J, Jiang Y. Increasing leaf δ¹³C values of woody plants in response to water stress induced by tunnel excavation in a karst trough valley: implication for improving water-use efficiency. *J Hydrol*. 2020;586:124895.

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