Critical Leaf Water Content for Maize Photosynthesis under Drought Stress and Its Response to Rewatering

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Abstract: Crop photosynthesis is closely related to leaf water content (LWC), and clarifying the LWC conditions at critical points in crop photosynthesis has great theoretical and practical value for accurately monitoring drought and providing early drought warnings. This experiment was conducted to study the response of LWC to drought and rewatering and to determine the LWC at which maize photosynthesis reaches a maximum and minimum and thus changes from a state of stomatal limitation (SL) to non-stomatal limitation (NSL). The effects of rehydration were different after different levels of drought stress intensity at different growth stages, and the maize LWC recovered after rewatering following different drought stresses at the jointing stage; however, the maize LWC recovered more slowly after rewatering following 43 days and 36 days of drought stress at the tasselling and silking stages, respectively. The LWC when maize photosynthesis changed from SL to NSL was 75.4% ± 0.38%, implying that the maize became rehydrated under physiologically impaired conditions. The LWCs at which the maize $V_{cmax25}$ reached maximum values and zero differed between the drought and rewatering periods. After exposure to drought stress, the maize exhibited enhanced drought stress tolerance, an obviously reduced suitable water range, and significantly weakened photosynthetic capacity. These results provide profound insight into the turning points in maize photosynthesis and their responses to drought and rewatering. They may also help to improve crop water management, which will be useful in coping with the increased frequency of drought and extreme weather events expected under global climate change.

Keywords: maize; leaf water content; critical point of photosynthesis; drought; rewatering

1. Introduction

Drought stress is considered to be one of the major environmental factors limiting crop productivity worldwide [1,2]. The occurrence of global drought disasters is gradually becoming the norm, and the frequency and intensity of extreme drought events show increasing trends under climate change. In addition, drought disasters are becoming stronger and more destructive, which further threatens the security of future food production [3–5]. China is one of the regions of the world that is most seriously affected by drought. Drought-disaster-affected areas and losses account for a large proportion of the total areal extent of and losses caused by all kinds of natural disasters. The area affected by drought disasters accounts for 56.2% of the global area affected by all meteorological disasters [6,7].

Maize is an important food crop worldwide, and the total yield of maize makes up the highest proportion of the total yield of all major food crops [8–10]. Northeast China is part
of the renowned northeastern maize production belt, and the annual yield of maize from this area accounts for 33.8% of the total maize yield in China [11]. With global warming, the increase in extreme rainfall and the uneven distribution of precipitation have often led to frequent drought [12]; accordingly, drought has become the most important factor limiting maize production in the area. Photosynthesis is a vital process by which plants accumulate organic matter with light energy, and it is also the process in plants that is most sensitive to drought stress [13]. Water stress is considered to be the critical abiotic factor affecting plant photosynthesis [14], and can cause damage to plant photosynthetic organs, thereby inhibiting photosynthesis. In maize, drought can reduce stomatal conductance, limit photosynthesis, and ultimately lead to a reduction in yield [15,16]; the annual maize yield reduction caused by drought is approximately 25–30% [17].

In general, stomatal limitation (SL) is the main factor that causes decreased photosynthesis under mild and moderate drought stress. Under severe drought stress, crop photosynthetic organs are destroyed, and non-stomatal limitation (NSL) reduces the crop photosynthetic capacity. The change in crop photosynthesis from being affected by SL to NSL is an important turning point for a crop from mild and moderate drought stress to severe drought stress, and this transition is of great importance in drought disaster identification [18,19]. Carboxylation is an important process in plant photosynthesis, and plays a decisive role in determining the rate of photosynthesis. The maximum carboxylation rate normalized to 25 °C ($V_{cmax25}$) of plants is an important parameter for characterizing plant photosynthetic capacity [20]. Timely and reasonable rewatering can alleviate the adverse effects of drought on crops, restore their photosynthetic capacity, and ultimately improve the utilization efficiency of water resources [21]. In a study by Song et al., plant photosynthetic processes at both the vegetative and reproductive periods were severely reduced, particularly at the late development period and with longer drought stress duration, and the strength of recovery was proportional to the persistence of pre-drought episodes [10]. Besides, drought intensity, drought duration, and the growth stages during which drought occurs are the main factors determining whether the plant photosynthetic capacity will recover to its original level after rewatering under drought stress [22,23].

Accurately identifying the critical point of drought stress for crop photosynthesis is conducive to formulating reasonable irrigation and drought resistance measures. However, there are few indicators that are easy to obtain and monitor to guide scientific and reasonable crop water management to address the adverse effects of drought stress [24–27]. Leaves are the most important organ for plant photosynthesis, and they are the most sensitive plant organs to drought stress. The leaf water content (LWC) represents the actual growth and development state of a crop, and is the optimal indicator of the water retention capacity of the crop [28–30]. Changes in LWC can reflect the crop drought degree to a certain extent, and LWC is easy to observe. Therefore, the LWC is irreplaceable in crop drought identification and remote sensing drought monitoring [31,32]. In our previous study, the first fully expanded leaf was sensitive to water stress, and its water content was obtained when the status of maize photosynthesis changed from SL to NSL [30]. As the drought period continued further, SL was no longer the main factor reducing maize photosynthesis, and NSL damaged photosynthetic organs and decreased the photosynthetic capacity of maize. In this study, we focused on exploring the LWC at critical points for maize photosynthesis during periods of drought and its response to rewatering. The aims were to (1) explore the response of the maize $V_{cmax25}$ to periods of drought and rewatering; (2) determine the LWC at which maize photosynthesis changed from SL to NSL; and (3) determine the LWC when the maize $V_{cmax25}$ reached its maximum and reached zero. Our hypotheses are as follows: (1) the recovery degree of the maize $V_{cmax25}$ after rewatering is different following droughts of different durations that occur at different growth stages; (2) the same relationship exists between the $V_{cmax25}$ and the LWC during the drought and rewatering periods; and (3) the LWCs at which the $V_{cmax25}$ reach a maximum and zero during the drought and rewatering periods are different. We expect that this study will provide a better understanding of the relationship between critical points in maize
photosynthesis and the LWC. We also believe that the findings may provide a reference for crop drought identification and classification, and for developing scientific and reasonable crop water management practices.

2. Materials and Methods

2.1. Climate and Soil Characteristics

The experiment was carried out at Jinzhou Ecology and Agricultural Meteorology Center (41°09'N, 121°12'E and an altitude of 27.4 m asl), Liaoning Province, China. The center is located within the renowned northeastern maize production belt. This region is located in northeastern Eurasia and has a warm-temperate semi-humid monsoon climate. The average annual mean air temperature over the past 30 years was 9.9 °C, with extreme maximum and minimum temperatures of 41.8 °C and −31.3 °C, respectively. The annual precipitation is 568 mm, approximately 60–70% of which occurs in summer. The annual frost-free period is 144–180 days. The soil at the experimental site is a typical brown soil with a pH value of 6.3. The bulk density, field capacity, and wilting coefficient are 1.62 g cm\(^{-3}\), 22.3%, and 6.5% at 0–100 cm, respectively. The soil organic carbon, total nitrogen, phosphorus, and potassium contents are 10.44 g kg\(^{-1}\), 0.69 g kg\(^{-1}\), 0.50 g kg\(^{-1}\), and 22.62 g kg\(^{-1}\), respectively. Maize is the staple food crop in this region.

2.2. Experimental Design

The maize cultivar used in this experiment was Danyu 405, which is commonly planted across Northeast China. The experimental plots were arranged randomly, with three replicates per treatment. Five treatments were established in this experiment: D1, control; D2, water withholding during the jointing to tasselling stages (27 days, 37–64 days after sowing (DAS)); D3, the jointing to anthesis stages (41 days, 37–78 DAS); D4, the tasselling to milking stages (41 days, 51–92 DAS); and D5, the silking to milking stages (34 days, 58–92 DAS). In this setup, each treatment received 261, 188, 138, 136, or 161 mm of irrigation, respectively, over the entire period of plant development. The irrigation regimes are shown in Table 1. Before the treatments began, the soil moisture was measured in each plot, and irrigation was applied to bring the soil moisture in each plot to the same level and to ensure normal maize growth. Suitable soil water conditions were maintained in the control plot throughout the growth period.

| Treatment | DAS (Day after Sowing) | Total |
|-----------|------------------------|-------|
|           | 2   | 8   | 17  | 24  | 31  | 38  | 52  | 59  | 66  | 73  | 80  | 87  | 94  |       |
| D1        | 8.7 | 0.8 | 10  | 10  | 10  | 24  | 24  | 24  | 25  | 25  | 25  | 25  | 25  | 24  | 260.5 |
| D2        | 8.7 | 0.8 | 10  | 10  | 10  | 24  |     |     |     | 25  | 25  | 25  | 25  | 25  | 187.5 |
| D3        | 8.7 | 0.8 | 10  | 10  | 10  | 24  |     |     | Drought | 25  | 25  | 25  | 25  | 24  | 137.5 |
| D4        | 8.7 | 0.8 | 10  | 10  | 10  | 24  | 24  | 24  |     |     |     |     | 24  | 24  | 135.5 |
| D5        | 8.7 | 0.8 | 10  | 10  | 10  | 24  | 24  | 24  | 25  |     |     |     |     | 24  | 160.5 |

2.3. Field Management

A large, electrically powered waterproof shelter was used to keep natural precipitation from falling on the plants. Each plot was 15 m\(^2\) in area (5 m × 3 m), and the plots were surrounded by cement walls extending 0.1 m above the soil surface and 1.9 m below the soil surface in order to prevent water from flowing between the plots. Maize was sown on 23 May 2016, and harvested on 28 September 2016. The plant density was 5.3 plants m\(^{-2}\), which was consistent with local field management practices, and a total of 600 kg ha\(^{-1}\) of a conventional compound fertilizer containing 28%, 11%, and 12% of N, P\(_2\)O\(_5\), and K\(_2\)O, respectively, was applied before sowing. The agronomic management practices applied during the year of the experiment were consistent with local practices.
2.4. Sampling and Measurements

2.4.1. Leaf Gas Exchange

We measured the leaf gas exchange parameters in situ using a portable photosynthesis measurement system (Li-6400; LI-COR Inc., Lincoln, NE, USA) between 9:00 a.m. and 11:00 a.m. on clear days. Three replicates were measured in each plot at intervals of 7–10 days, and the measurements were added during the critical maize growth stages. The first fully expanded leaf on three healthy and uniform maize plants was selected to determine the leaf photosynthetic parameters. The measurements were taken at the middle upper part of the leaf, avoiding the central leaf vein. The photosynthetically active radiation (PAR) in the leaf chamber was set to 1500 µmol m\(^{-2}\) s\(^{-1}\), which is the light saturation point of maize. During the measurement periods, the temperature, relative humidity, and CO\(_2\) concentration inside the leaf chamber were consistent with those of the ambient air, and the flow rate was set to 500 µmol s\(^{-1}\). The SL value (L\(_s\)) was calculated with the following equation:

\[
L_s = 1 - \frac{C_i}{C_a}
\]  

where C\(_i\) is the intercellular CO\(_2\) concentration and C\(_a\) is the ambient CO\(_2\) concentration.

2.4.2. Leaf Water Content

The LWC was assessed on the same leaves used for the gas exchange measurements. The leaves were detached from the plants, weighed, placed into a paper bag, placed into an oven for deactivation at 105 °C for 1 h, dried to constant weight at 80 °C, and weighed to determine their dry weight. The LWC was calculated with the following equation:

\[
\text{Leaf water content (LWC)} = \frac{\text{leaf fresh weight} - \text{leaf dry weight}}{\text{leaf fresh weight}} \times 100
\]  

2.4.3. Maximum Carboxylation Rate at 25 °C (V\(_{\text{cmax25}}\))

Farquhar et al. [33] proposed a photosynthetic biochemical mechanism model for C\(_3\) plants, and Von Caemmerer [34] applied that model to C\(_4\) plants. In these models, the leaf photosynthetic rate (A\(_n\), µmol m\(^{-2}\) s\(^{-1}\)) is considered to be limited mainly by Rubisco enzyme activity, expressed as:

\[
A_n = \frac{V_{\text{cmax}}}{C + k_c(1 + O/k_0)} \left(1 - \frac{\gamma^* O}{C}\right) - R_d
\]  

Massad et al. [35] applied the C\(_4\) plant photosynthesis model to maize and noted that at or near the light saturation point, the level of photosynthetic activity at the Rubisco enzyme activity limit was more sensitive to the temperature in C\(_4\) plants than in C\(_3\) plants, and that photosynthetic activity in C\(_4\) plants was more sensitive to V\(_{\text{cmax}}\) but less sensitive to the Michaelis–Menten constants for CO\(_2\) (K\(_c\)) and O\(_2\) (K\(_o\)). Therefore, the reduction in enzyme activity at high temperature was taken into consideration by applying the Arrhenius equation, and the temperature correction function for V\(_{\text{cmax}}\) was applied as follows:

\[
f(T_k) = \exp \left[ \frac{E_a (T_k - 298)}{(298RT_k)} \right] \frac{1 + \exp \left( \frac{298AS - H_d}{298R} \right)}{1 + \exp \left( \frac{298AS - H_d}{T_kR} \right)}
\]  

which can obtain:

\[
A_n = \frac{C}{C + K_c(1 + O/k_0)} \left(1 - \frac{\gamma^* O}{C}\right) - 0.01]V_{\text{cmax25}} \exp \left[ \frac{E_a(T_k - 298)}{(298RT_k)} \right] \frac{1 + \exp \left( \frac{298AS - H_d}{298R} \right)}{1 + \exp \left( \frac{298AS - H_d}{T_kR} \right)}
\]  

The values and meanings of the parameters in Equations (3)–(5) are shown in Table 2 [35,36]. The Li-6400 fluorescent leaf chamber was used to observe the physiological photosynthetic parameters of the leaves. The light intensity was set at 1500 µmol m\(^{-2}\) s\(^{-1}\), and the temperature, humidity, and CO\(_2\) concentration were all consistent with the ambient environmental
conditions. Maize is a C\textsubscript{4} plant. Under saturating light, temperature is an important environmental factor affecting leaf physiological parameters. The temperature value in the leaf chamber was adjusted to obtain the \( V_{\text{cmax25}} \) according to Equation (5).

Table 2. Summary of C\textsubscript{4} photosynthesis model parameters at 25 °C.

| Parameter              | Description                                      | Value                      |
|------------------------|--------------------------------------------------|----------------------------|
| \( A_n \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) | Net photosynthetic rate                           | Measured                   |
| \( R_d \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) | Leaf mitochondrial respiration                    | 0.01 \( V_{\text{cmax}} \) |
| \( C \) (mbar)         | CO\textsubscript{2} concentration in the bundle sheath | CO\textsubscript{2} concentration in reference room |
| \( O \) (mbar)         | Partial pressure of O\textsubscript{2}           | 210                        |
| \( \gamma^* \) (bar/bar) | Half the reciprocal of Rubisco specificity        | 0.000193                   |
| \( V_{\text{cmax}} \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) | Maximum carboxylation rate                        | /                          |
| \( K_c \) (mbar)       | Michaelis–Menten constant of Rubisco for CO\textsubscript{2} | 650                        |
| \( K_0 \) (mbar)       | Michaelis–Menten constant of Rubisco for O\textsubscript{2} | 450                        |
| \( f(T_k) \)           | Temperature correction function                   | /                          |
| \( T_k \) (K)          | Leaf temperature                                 | Measured                   |
| \( E_a \) (kJ mol\textsuperscript{-1}) | Activation energy                                | 58.52                      |
| \( R \) (JK\textsuperscript{-1} mol\textsuperscript{-1}) | Gas constant                                    | 8.31                       |
| \( \Delta S \) (JK\textsuperscript{-1} mol\textsuperscript{-1}) | Entropy term                                    | 710                        |
| \( H_d \) (KJ mol\textsuperscript{-1}) | Deactivation energy                              | 220                        |

Notes: the detailed descriptions about the parameters in this table can be found in Massad et al. [35] and Carmo-Silva et al. [36].

2.5. Statistical Analyses

SPSS v.21.0 statistical software (SPSS Inc., Chicago, IL, USA) was used to perform the statistical analysis. One-way ANOVA with Duncan’s multiple comparison test was used to test the significance of the differences in the LWC and \( V_{\text{cmax25}} \) between treatments at the 0.05 significance level. Data fitting and figure generation were performed in Origin Pro 2016 (Origin Lab, IL, USA). The relationships between LWC and \( V_{\text{cmax25}} \) were determined using polynomial regression analyses.

3. Results

3.1. Response of Maize Leaf Water Content to Drought and Rewatering

As shown in Figure 1, the maize LWC showed a decreasing trend as the growth period progressed. The LWC of D2 was lower than that of the control treatment (D1) during the water-withholding period. The drought period led to a decline in LWC in D2 to a minimum of 75.7%. Significant differences in LWC were not found between the D1 and D2 treatments (\( p < 0.05 \), Table 3). The LWCs of the D1 and D2 treatments after rewetting were 76.7% and 76.4%, respectively, and there was no significant difference in this value between the treatments. The LWC of D2 was slightly higher than that of D1 8 days after rewetting, indicating that the LWC of the D2 treatment recovered to its original level after a 27-day drought period in the jointing-tasselling stages. The response of LWC to drought and rewetting in the D3 treatment was similar to that in the D2 treatment. The LWC for the D3 treatment marked a decreasing trend, and reached its lowest level of 72.1% during the drought period, which was significantly lower than that in the D1 treatment (76.7%). After rewetting, the LWC values were 72.5% and 73.9% in the D1 and D3 treatments, respectively, and significant differences could not be found between the D1 and D3 treatments (\( p < 0.05 \), Table 3), indicating that the LWC of the D3 treatment recovered after rewetting. The LWC in the D4 and D5 treatments always markedly decreased, even though it remained a low and stable level after rewetting, and the rewetting had no obvious effect on the LWC of D4 and D5 treatments.
D2 treatments (p < 0.05, Table 3). The LWCs of the D1 and D2 treatments after rewatering were 76.7% and 76.4%, respectively, and there was no significant difference in this value between the treatments. The LWC of D2 was slightly higher than that of D1 8 days after rewatering, indicating that the LWC of the D2 treatment recovered to its original level after a 27-day drought period in the jointing-tasselling stages. The response of LWC to drought and rewatering in the D3 treatment was similar to that in the D2 treatment. The LWC for the D3 treatment marked a decreasing trend, and reached its lowest level of 72.1% during the drought period, which was significantly lower than that in the D1 treatment (76.7%). After rewatering, the LWC values were 72.5% and 73.9% in the D1 and D3 treatments, respectively, and significant differences could not be found between the D1 and D3 treatments (p < 0.05, Table 3), indicating that the LWC of the D3 treatment recovered after rewatering. The LWC in the D4 and D5 treatments always markedly decreased, even though it remained a low and stable level after rewatering, and the rewatering had no obvious effect on the LWC of D4 and D5 treatments.

Figure 1. Response of leaf water content to drought and rewatering. Notes: data in the figure are the average of 3 single values obtained during the drying and rewatering process.

Table 3. Effects of drought and rewatering on leaf water content (%).

| Treatments | DAS (Day after Sowing) | 53 | 67 | 74 | 80 | 95 |
|------------|------------------------|----|----|----|----|----|
| D1         | 76.5a                  | 76.7a | 73.5ab | 72.5a | 71.4a |
| D2         | 75.7ab                 | 76.4a | 74.9a | 72.3a | 69.8a |
| D3         | 75.0b                  | 73.7b | 72.1b | 73.9a | 70.1a |
| D4         | 75.2b                  | 75.8a | 73.8ab | 72.9a | 71.0a |
| D5         | 75.2b                  | 76.2a | 74.5a | 73.6a | 70.8a |

Notes: the means within a column followed by the same letters are not significantly different at 5% level (Duncan’s one-way ANOVA). Data present in table are the average of 3 single values.

3.2. Leaf Water Content at Which Maize Photosynthesis Changed from Stomatal Limitation to Non-Stomatal Limitation

The change in photosynthesis from SL to NSL is a sign of the transformation of plants from environmental restriction to physiological and ecological damage. The changes in the intercellular CO$_2$ concentration ($C_i$) and the $L_s$ value are the key to determining whether crop photosynthesis is affected by SL or NSL [30]. The changes in the $C_i$ occurred at 52, 57, 60, and 72 DAS in the D2, D3, D4, and D5 treatments, respectively, while changes in the $L_s$ occurred at 51, 52, 60, and 72 DAS in the D2, D3, D4, and D5 treatments, respectively (Figure 2; Table 4). Moreover, the changes in LWC during the drought periods were analyzed (Figure 3). The DAS on which $C_i$ and $L_s$ changed were substituted into the formula for the changes in LWC with DAS (Figure 3; Table 4) in order to determine the LWC values when maize photosynthesis changed from being affected by SL to NSL. The LWC values when $C_i$ changed were 75.8%, 75.2%, 75.1%, and 75.2% in the D2–D5 treatments, respectively, while the LWC values when $L_s$ changed were 75.9%, 76.0%, 75.2%, and 75.2% in the D2–D5 treatments, respectively.
at 52, 57, 60, and 72 DAS in the D2, D3, D4, and D5 treatments, respectively, while changes in the Ls occurred at 51, 52, 60, and 72 DAS in the D2, D3, D4, and D5 treatments, respectively (Figure 2; Table 4). Moreover, the changes in LWC during the drought periods were analyzed (Figure 3). The DAS on which Cᵢ and Ls changed were substituted into the formula for the changes in LWC with DAS (Figure 3; Table 4) in order to determine the LWC values when maize photosynthesis changed from being affected by SL to NSL. The LWC values when Cᵢ changed were 75.8%, 75.2%, 75.1%,  and 75.2% in the D2–D5 treatments, respectively, while the LWC values when Ls changed were 75.9%, 76.0%, 75.2%, and 75.2% in the D2–D5 treatments, respectively.

Figure 2. Changes of Cᵢ and Ls during the drying process. Notes: Cᵢ, intercellular CO₂ concentration; Ls, stomatal limitation value.

Table 4. Regression equation between Cᵢ and Ls and day after sowing (DAS) during the drying process.

| Treatment | Parameter | Regression Equation | R²  |
|-----------|-----------|---------------------|-----|
| D2        | Cᵢ        | y = 0.4817 x² − 50.367 x + 1390.4 | 0.810 |
|           | Ls        | y = −0.0013 x² + 0.1338 x − 2.6914 | 0.811 |
| D3        | Cᵢ        | y = 0.145 x² − 16.405 x + 554.14 | 0.294 |
|           | Ls        | y = −0.0004 x² + 0.0415 x − 0.4152 | 0.260 |
| D4        | Cᵢ        | y = 0.3721 x² − 44.882 x + 1498.2 | 0.514 |
|           | Ls        | y = −0.0009 x² + 0.1071 x − 2.5226 | 0.523 |
| D5        | Cᵢ        | y = 1.6631 x² − 238.25 x + 8696 | 0.344 |
|           | Ls        | y = −0.0044 x² + 0.6333 x − 22.067 | 0.360 |

Notes: Cᵢ, intercellular CO₂ concentration; Ls, stomatal limitation value.

3.3. Response of Maize V<sub>cmax25</sub> to Drought and Rewatering

As drought continues, SL is replaced as the main factor limiting crop photosynthesis, and NSL leads to a reduction in photosynthetic capacity. V<sub>cmax25</sub> is the optimal parameter for characterizing plant photosynthetic capacity. As shown in Figure 4, the V<sub>cmax25</sub> of D1 increased during early maize development, reaching a maximum of 65.4 µmol m<sup>−2</sup> s<sup>−1</sup> at 46 DAS and then sharply decreasing until reaching a minimum of 24.9 µmol m<sup>−2</sup> s<sup>−1</sup> at 95 DAS.

In the D2 treatment, V<sub>cmax25</sub> continuously decreased during the drought period (Figure 4) to a minimum of 35.5 µmol m<sup>−2</sup> s<sup>−1</sup>, which was lower than that in the D1 treatment (37.7 µmol m<sup>−2</sup> s<sup>−1</sup>) before rewatering. Significant differences in the V<sub>cmax25</sub> before rewatering were not found between the D2 and D1 treatments (p < 0.05, Table 5). The V<sub>cmax25</sub> in the D2 treatment increased rapidly to 48.5 µmol m<sup>−2</sup> s<sup>−1</sup>, which was slightly lower than that in the D1 treatment (48.7 µmol m<sup>−2</sup> s<sup>−1</sup>) after rewatering. Significant differences in the V<sub>cmax25</sub> after rewatering were not found between the D2 and D1 treatments (p < 0.05, Table 5). Upon re-irrigating, the V<sub>cmax25</sub> for the D2 treatment (48.5 µmol m<sup>−2</sup> s<sup>−1</sup>) almost
reached the level of control at the same stage, with a maximum of 48.7 μmol m$^{-2}$ s$^{-1}$ for the control plant. This indicated that a 27 day episodic drought from jointing to tasseling significantly inhibited photosynthetic capacity, while the capacity recovered when subsequent rewatering occurred. The changes in the $V_{cmax25}$ in the D3 treatment exhibited a similar change pattern to those in the D2 treatment (Figure 4). $V_{cmax25}$ for D3 treatment showed a decreasing trend, while it increased to the level of 46.6 μmol m$^{-2}$ s$^{-1}$ upon rewatering, which was lower than the D1 treatment of 48.7 μmol m$^{-2}$ s$^{-1}$, and significant differences were not found ($p < 0.05$, Table 5), indicating that episodic drought significantly inhibited photosynthetic capacity and that it recovered only partially following rewatering. The $V_{cmax25}$ in the D4 treatment continuously decreased during drought from the tasselling to milking stages and remained at a low and stable level after rewatering. The $V_{cmax25}$ in the D5 treatment continuously decreased to a minimum of 21.3 μmol m$^{-2}$ s$^{-1}$ and remained a low level after rewatering.

Figure 3. Changes of leaf water content during the drying process. Note: * $p < 0.01$, ** $p < 0.05$.

Figure 4. Response of $V_{cmax25}$ to drought and rewatering. Notes: data present in figure are the average of 3 single values.
Table 5. Effects of drought and rewatering on $V_{cmax25}$ ($\mu$mol m$^{-2}$ s$^{-1}$).

| Treatments | DAS (Days after Sowing) |
|------------|-------------------------|
|            | 53         | 67         | 74         | 80         | 95         |
| D1         | 58.6a      | 37.7bc     | 48.7a      | 48.4a      | 24.9a      |
| D2         | 45.8c      | 35.5c      | 48.5a      | 33.3c      | 12.3c      |
| D3         | 43.6c      | 40.8b      | 32.1c      | 46.6a      | 22.2ab     |
| D4         | 58.4a      | 48.4a      | 33.3c      | 23.6d      | 20.5b      |
| D5         | 57.3a      | 45.6a      | 40.2b      | 40.9b      | 21.3ab     |

Notes: the means within a column followed by the same letters are not significantly different at the 5% level (Duncan’s one-way ANOVA). Data present in table are the average of 3 single values.

The adverse effects of drought can be alleviated by timely and reasonable rewatering. The LWC for the D2 treatment was 75.7% when rewatering, which was the LWC when maize photosynthesis changed from SL to NSL; a partial recovery of maize photosynthetic capacity was achieved after rewatering. The LWC values were 72.1%, 72.9%, and 73.6% in the D3, D4, and D5 treatments, respectively, which were lower than the LWC values when photosynthesis changed from SL to NSL. The drought periods in the D3, D4, and D5 treatments destroyed photosynthetic organs and significantly inhibited the photosynthetic capacity of maize, which did not recover to its original level after rewatering.

3.4. Critical Water Conditions for Maize Photosynthetic Capacity during Drought

The $V_{cmax25}$ levels decreased significantly under the drought periods imposed in this study. As drought stress continues, the $V_{cmax25}$ decreases to zero, resulting in the total loss of photosynthetic capacity in crops. The relationships between the LWC and $V_{cmax25}$ were analyzed during drying process (Figure 5). There was a parabolic relationship between LWC and $V_{cmax25}$. The $V_{cmax25}$ reached a maximum of 51.5 $\mu$mol m$^{-2}$ s$^{-1}$ when the LWC was 77.2%, which is the optimal LWC for maize photosynthesis. The $V_{cmax25}$ reached its lowest level (zero) when the LWC was 70.8% or 83.7%. The LWC of 70.8% indicated that the maize was experiencing extreme drought, and when the LWC fell below 70.8%, the maize lost its photosynthetic capacity.

![Figure 5. Relationship between leaf water content and $V_{cmax25}$ during the drying process. Notes: data presented in the figure are the average of 3 single values obtained during the drying process. Note: *** p < 0.001.](image)

3.5. Critical Water Conditions for Maize Photosynthetic Capacity during Rewatering

Suitable rehydration measures can relieve the adverse effects of drought stress on crops and alleviate the yield losses caused by drought stress. LWC is an effective indicator of the
Appropriate rewatering can compensate for the plant growth inhibition caused by drought, and has compensatory or even super compensatory effects on plant growth. The response of maize to drought stress and rewatering is short-term rapid growth after the stress is relieved, to partially compensate for the lost growth due to drought [37]. Luo et al. found that water deficit reduced the water potential of cotton leaves, but the water potential recovered quickly to a level that was equal to or higher than the control level after rewatering [38]. The present results indicated that drought for 27 days and 41 days during the jointing period impacted the maize LWC, but that the LWC recovered after rewatering. In contrast, drought for 43 days during the tasselling period and for 36 days during the silking period had severe effects on the LWC, which did not fully recover after rewatering. Nevertheless, compensatory plant growth after rewatering following drought stress is not guaranteed. As reported, the degree and rate of recovery through rehydration may be related to the duration and severity of the predrought [39]. After a short period of drought stress, rewatering restored the photosynthetic rate of wheat to the control level, but after long-term drought stress, it recovered to only 80% of the control level [40]. In this study, the maize photosynthetic capacity was almost restored by rewatering after 27 days of drought at the jointing stage, while it was only partially restored by rewatering after 41 days of drought. This result is consistent with our hypothesis that the “the recovery degree of the maize Vcmax25 after rewatering would be different following droughts of...
different durations that occurred at different growth stages”. The drought intensity has a strong impact on the recovery degree of crops after drought stress. Compared with severe (relative soil water content of 45–50%) drought stress, moderate (relative soil water content of 60–65%) drought stress led to a greater compensation effect for the physiological and ecological indicators of soybean after rewatering in [41]. In the current study, the LWC when maize photosynthesis changed from being affected by SL to NSL was the critical water condition required for the complete restoration of maize photosynthetic capacity.

Drought stress is the primary limiting factor for crop photosynthesis. In the early stage of drought, the drought conditions cause the crop leaf stomata to close, and the amount of CO$_2$ entering the stomata decreases to below the amount required for photosynthesis. Ultimately, this leads to a decrease in crop photosynthesis. SL is the major factor limiting crop photosynthesis at this stage, and the photosynthetic capacity of the crop can be restored to its original level by timely rewatering [42]. The change in crop photosynthesis from SL to NSL is an important indicator of the transition from mild and moderate drought stress to severe drought stress. The LWC when maize photosynthesis changed from being affected by SL to NSL was shown to be between 75 ± 1.5% and 75 ± 1.3% in [30]; this is similar to the results of this study, in which the LWC was 75.4% when maize photosynthesis changed from being affected by SL to NSL.

As drought continues, it causes damage to plant photosynthetic organs, and NSL factors lead to a reduction in the plant photosynthetic capacity. The V$_{\text{cmax25}}$ is an important parameter that characterizes crop photosynthetic capacity. It determines the crop maximum net photosynthetic rate, mitochondrial respiration in light, photorespiration, and other important physiological processes, and plays a decisive role in crop photosynthesis [33,43]. Water is an important environmental factor that impacts the V$_{\text{cmax25}}$. In the dry season, the V$_{\text{cmax25}}$ decreases with decreasing soil moisture, and the soil moisture can explain 61–64% of the variation in V$_{\text{cmax25}}$ [44]. The results of this study indicate that the V$_{\text{cmax25}}$ decreased gradually as the drought period continued, and only partially recovered after rewatering. Vaz et al. [45] found that the maximum carboxylation rate of plant leaves exhibited an obvious threshold response to water stress and that a relative soil water content of 58–62% was the critical water condition for the maize gas exchange parameters [46]. A decrease in LWC from 75% to 70% was found to be an important turning point for the photosynthetic physiological activity of wheat leaves in [47]. Our results showed that the LWC was 77.2% when the maize V$_{\text{cmax25}}$ reached its highest point of 51.5 μmol m$^{-2}$ s$^{-1}$ and that the LWC values were 70.8% and 83.7% when the maize V$_{\text{cmax25}}$ decreased to zero. As previously reported, the crop V$_{\text{cmax25}}$ has a certain degree of adaptability and plasticity, and can adjust to adapt to the external environment when external environmental conditions change [45]. These adjustments led to the difference in the maximum V$_{\text{cmax25}}$ during the drought (51.5 μmol m$^{-2}$ s$^{-1}$) and rewatering (44.0 μmol m$^{-2}$ s$^{-1}$) processes in this study. The changes in V$_{\text{cmax25}}$ indicate that maize photosynthesis began to transition from SL to NSL during rewatering. Moreover, drought damaged the maize photosynthetic organs, which led to the reduction of the maize V$_{\text{cmax25}}$ in response to the adverse external conditions. As a result, the maximum V$_{\text{cmax25}}$ during the rewatering process was lower than that during the drought period. Appropriate water stress improves the ability of plants to adapt to drought, thus allowing them to better resist drought [38–50]; however, studies have also shown that plants that experience drought stress do not continue to improve their ability to resist drought when they encounter drought again [51–53]. The present study indicated that the LWC when the maize V$_{\text{cmax25}}$ reached zero during rewatering was lower than that during drought. This result suggests that drought stress improved the adaptability and resistance of maize to drought stress, but also caused a reduction in the suitable water range for maize and caused a reduction in the photosynthetic capacity of maize. The determination of a suitable rewatering time is of great significance for rehydration recovery after drought. This study verified that an LWC of less than 75.4% caused damage to the photosynthetic organs and reduced the photosynthetic capacity of maize; as a result, rehydration could not restore the maize photosynthetic capacity to its original level.
Under mild and moderate drought stress, reductions in crop photosynthesis are mainly caused by SL, and timely rehydration will lead to the recovery of photosynthesis to its original level. As drought progresses, its effects decrease the crop photosynthetic capacity, and the reductions in crop photosynthesis are caused mainly by NSL, and rehydration will only partly recover the plant photosynthetic capacity [8,18,54]. LWC is the best indicator reflecting crop water conservation; changes in LWC effectively reflect crop drought degree, and LWC is easy to measure. Moreover, it is important in crop drought monitoring with remote sensing. The $V_{\text{cmax}25}$ reflects the crop photosynthetic capacity [55], and it has different thresholds (maximum, minimum, and optimal values) under different environmental conditions. Determining these $V_{\text{cmax}25}$ thresholds in response to LWC under drought and rewatering has great practical significance for improving crop productivity, and can also provide a technical basis for dealing with extreme weather and climate events and making relevant agronomic decisions. In this study, the LWC values at which maize photosynthesis changed from being affected by SL to NSL and at which the maize $V_{\text{cmax}25}$ reached its thresholds were determined under drought and rewatering conditions. The lowest LWC at which maize photosynthesis still occurred was also determined. These results provide a reference for the identification and the classification of crop drought stress and the formulation of scientific and reasonable crop water management measures. Future research should be expanded to the canopy scale to provide a theoretical basis for global drought identification, classification, and monitoring.

5. Conclusions

The present study indicates that the LWC recovered after rewatering following different intensities of drought stress at the jointing stage, but did not recover after rewatering following 43 days and 36 days of drought stress at the tasselling stage and silking stage, respectively. These results suggest that drought during the reproductive stages, particularly the late developmental stage, had severe effects on the LWC. Maize photosynthesis changed from being determined by SL to NSL when the LWC was 77.2%, which was the critical water condition required for the complete recovery of the photosynthetic capacity of maize. The values of LWC at which the maize $V_{\text{cmax}25}$ reached its maximum value and zero differed between the drought and rewatering periods. The drought periods improved the drought resistance ability of maize; however, its suitable LWC range was reduced, and its photosynthetic capacity was significantly weakened. The findings of this study provide new insight into a better understanding of crop drought stress as well as a basis for the scientific management of crop drought resistance and avoidance.

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