Physiological Responses of Peanut Seedlings to Repeated Drought Stress (Postprint)

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Abstract

A pot experiment was conducted in a rain shelter with three treatments: control (Control, 75% field capacity), drought stress (D, 35% field capacity), and repeated drought stress (DD, 35% field capacity) to investigate the adaptive and memory responses of peanut seedlings to pre-drought stress and to analyze the physiological role of pre-drought in alleviating damage from repeated drought stress. The results showed that, compared with the drought stress treatment, repeated drought stress increased leaf relative water content, reduced proline accumulation, and decreased MDA and O_2^- contents; the activities of antioxidant enzymes SOD and CAT decreased, with POD activity showing the most significant reduction, which recovered to the same level as or below that of the control after rewatering. Compared with the control under normal water conditions, drought stress significantly reduced leaf photosynthetic rate (PN), maximum photosynthetic potential (PC), and maximum quantum yield (YQ), but the repeated drought treatment exhibited higher PN, PC, and YQ than the drought treatment during both the repeated drought stress period and after rewatering. Pre-drought stress increased the hysteresis area and hysteresis rate (HP and Hg) of photosynthesis and stomatal conductance; after pre-drought stress, repeated drought significantly reduced the hysteresis area and hysteresis rate of photosynthesis and stomatal conductance. Pre-drought stress improved leaf water content in plants under repeated drought stress, alleviated physiological damage caused by repeated drought, enhanced the capacity to resist repeated drought in terms of photosynthesis, and enabled rapid recovery to the growth level of plants under normal water conditions after rewatering, thereby reducing the adverse effects of drought on plants. Therefore, pre-drought stress enables peanut seedlings to develop the capacity to adapt to or memorize the initial stress, exhibiting more rapid and robust physiological defense and rapid physiological recovery mechanisms under repeated drought stress.

Full Text

Preamble

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Physiological Responses of Peanut Seedlings to Recurrent Drought Stress

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Abstract

A pot experiment was conducted in a rain shelter to investigate the potential physiological responses and roles of pre-drought priming in alleviating damage from subsequent severe drought stress in peanut seedlings. Three treatments were designed: control (75% of field water capacity), drought stress without pre-drought treatment (D, 35%), and subsequent drought stress with pre-drought treatment (DD, 35%). Compared with the D treatment, pre-drought priming increased leaf relative water content and reduced proline accumulation in the DD treatment when seedlings experienced subsequent drought stress. In addition, MDA and O_2^- contents and activities of antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) decreased in response to the DD treatment and recovered to the level of the control, or lower, following rewatering. Drought decreased photosynthetic rate (P), photosynthetic capacity (C), and maximum quantum yield of PSII (Q). However, Q in the DD treatment was higher than that in the D treatment when seedlings experienced a second drought stress. The hysteresis area and hysteresis rate of leaf photosynthesis (P) and stomatal conductance (g) decreased significantly in response to the DD treatment following repetitive drought and rewatering. In conclusion, pre-drought priming increased leaf relative water content during subsequent drought stress, reduced physiological damage caused by subsequent drought stress, and enhanced resistance to drought stress. The seedlings that experienced drought priming had the capacity to recover quickly to the growth level observed under normal soil water conditions. Therefore, peanut seedlings can adapt to or 'recognize' the initial stressor from a previous exposure to drought stress, and displayed a more rapid and stronger physiological defense to the second drought stress using a fast physiological recovery mechanism.

Keywords: recurrent drought stress; photosynthetic hysteresis; peanut; antioxidant enzymes; stomatal conductance hysteresis; stress memory

Introduction

Plants cannot quickly escape harsh environmental conditions such as intense light or drought stress, which severely affects their growth and development and causes significant crop yield losses. Environmental variations in nature are diverse, repetitive, or alternating, and single environmental stress events can cause severe damage to plants. During their life cycle, plants often experience multiple environmental stresses of varying degrees, typically resulting in cellular dehydration, membrane system disruption, affected enzyme activities, disordered cell metabolism, inhibited plant growth, and consequently reduced yield. Through long-term evolution, plants have developed self-regulatory mechanisms such as stress sensing and rapid response to environmental changes to resist future stresses. Studying plant adaptation to recurrent and variable environmental changes has important guiding significance for crop production.

In recent years, domestic and international research has proposed the concept of "stress memory" to explain plant self-regulation and adaptation to variable, repetitive, or alternating environmental stresses [1-6]. Plant neurobiology suggests that plants can recognize and memorize previous stress events, displaying more rapid and intense physiological defense when re-exposed to biotic or abiotic stress, thereby increasing survival chances. In arid and semi-arid regions, recurrent drought severely affects crop economic yield and quality. Peanut is an important oil and economic crop known for drought resistance and tolerance to poor soil conditions; however, approximately 70% of yield losses are caused by drought, and plants frequently encounter drought stress during the seedling stage in different cultivation years.

Most studies on peanut drought or water deficit have focused on single drought events, whereas in actual production, drought or water-deficit environments occur repeatedly. The previous drought stress may serve as acclimation for subsequent drought or other stresses. While peanut seedling drought hardening can improve yield as confirmed in practice [21], the specific mechanisms remain unclear. This study focused on pre-drought treatment during the peanut seedling stage to investigate changes in physiological responses under subsequent drought stress and the adaptation mechanisms to initial drought, aiming to provide a theoretical basis for guiding peanut production.

1. Experimental Materials and Design

The peanut variety used was "Huayu 20" . A pot experiment was conducted in a rain shelter at the Shandong Peanut Research Institute in 2015-2016. The soil was sandy loam. Uniform peanut seeds were selected and sown in pots (18 cm height, 3 kg soil). After emergence, seedlings were thinned to retain three plants with similar growth per pot.

The experiment consisted of three treatments: 1) Control (75% field water capacity); 2) Drought stress without pre-drought treatment (D, 35% field water capacity); and 3) Recurrent drought stress with pre-drought treatment (DD,

35% field water capacity). The experiment used a single-factor randomized design.

Pre-drought treatment began one week after peanut emergence and lasted for 5 days, after which plants were rewatered for normal growth. The pre-drought treated seedlings then underwent recurrent drought stress, while seedlings without pre-drought treatment were subjected to drought stress. Both drought treatments lasted 5 days, followed by rewatering to normal growth conditions. Based on the drought treatment timeline, the experiment was divided into three stages: Stage I (pre-drought treatment), Stage II (recurrent drought stress), and Stage III (post-drought rewatering). Soil water content at different stages was controlled using the weighing method.

Experimental treatments showing soil relative water content (percentage of field water capacity) during different stages.

2. Measurement Methods

2.1 Leaf Relative Water Content Determination

Leaf relative water content (LRWC) was measured at Stage I, Stage II, and Stage III. Mixed leaf samples were taken on day 5 of each treatment stage, with three replicates per treatment. LRWC was calculated as: LRWC (%) = (fresh weight - dry weight) / (saturated fresh weight - dry weight) × 100.

2.2 Photosynthetic Response Curves and Photosynthetic Hysteresis Determination

Photosynthetic response curves were measured using a CIRAS-2 portable photosynthesis system (PP Systems, USA). At Stage I, Stage II, and Stage III, photosynthetic rates were measured at light intensities of 0, 200, 500, 800, 1200, 1600, and 2000 mol m^{-2} s^{-1}. The average of three measurements at each light intensity was used to construct light response curves. The curve formula was P = C(1 - e^(-KI)), where P is net photosynthetic rate, C is maximum photosynthetic capacity, K is the half-time constant, and I is light intensity.

Photosynthetic hysteresis was determined following the method of Qin et al. [23]. The photosynthetic rate curve f_1 was measured while increasing light intensity from 0 to 2000 mol m^{-2} s^{-1}, then curve f_2 was measured while decreasing light intensity from 2000 to 0 mol m^{-2} s^{-1}. The definite integral of the area between the two curves was calculated as photosynthetic hysteresis.

2.3 Stomatal Conductance and Stomatal Conductance Hysteresis Determination

Stomatal conductance was measured simultaneously with photosynthetic rate. The light-stomatal conductance curve formula was g = αC(1 - e^(-βI)), where g

is stomatal conductance, α is a constant related to stomatal aperture, β is a constant, C is maximum stomatal conductance, and I is light intensity. Stomatal conductance hysteresis was calculated using the same method as for photosynthetic hysteresis.

2.4 Proline Determination

Proline was determined using the acidic ninhydrin method of Bates et al. [24] and Marin et al. [25]. Mixed leaf samples (0.3 g) were extracted with 5 mL of 3% sulfosalicylic acid. After adding acidic ninhydrin (1:1:1 ratio), the mixture was boiled for 10 minutes, then the reaction was terminated in an ice bath. Absorbance was measured at 520 nm.

2.5 Superoxide Anion and MDA Determination

Superoxide anion (O_2^-) was determined using the hydroxylamine oxidation method of Bissenbaev et al. [26]. Malondialdehyde (MDA) was determined using the thiobarbituric acid method [27].

2.6 Antioxidant Enzyme Activity Determination

Antioxidant enzyme extraction followed the Bradford method [28]. SOD activity was determined using the method of Beyer and Fridovich [29] and Chakrabarty et al. [30]. CAT activity was measured using the Beers and Sizer method [31], and POD activity using the guaiacol oxidation method of Khalil et al. [32]. Mixed leaf samples (0.4 g) were taken from three peanut seedlings per treatment, collecting fully expanded leaves below the heart leaf. Samples were taken at Stage I, Stage II, and Stage III. Absorbance was measured using an Ultraspec 2100 pro visible spectrophotometer (Amersham Biosciences).

2.7 Data Analysis

Data were organized and plotted using Origin 7.5 software. Statistical analysis was performed using SAS 8.0 software. Differences were tested for significance.

3. Results

3.1 Recurrent Drought Increased Leaf Relative Water Content

Pre-drought stress affected seedling growth, showing obvious drought characteristics with stunted shoots. Leaf relative water content decreased to 53.34%. When peanut seedlings were subjected to recurrent drought stress, the DD treatment showed less leaf wilting than the D treatment. DD plants were less stunted than D plants, and leaf relative water content in DD (64.82%) was significantly higher than in D (53.34%). Pre-drought stress significantly increased leaf relative water content under recurrent drought stress to 67.30% (DD), which was significantly higher than the control.

[Figure 1: see original paper] Leaf relative water content. Lowercase letters indicate significant differences between treatments ($P < 0.05$); uppercase letters indicate extremely significant differences ($P < 0.01$).

3.2 Recurrent Drought Reduced Proline Accumulation

Peanut seedlings rapidly accumulated large amounts of proline after pre-drought stress at Stage I. During the recurrent drought stress period (Stage II), proline content in D treatment leaves exceeded 3500 g/g, while proline accumulation in DD treatment leaves was only about 1/3 of D (1312.68 g/g), showing extremely significant differences. After rewatering (Stage III), proline content in all treatments decreased sharply. Proline content in DD treatment leaves decreased to 150.42 g/g, while D treatment leaves still maintained 471.71 g/g, about three times the control level (422.75 g/g).

[Figure 2: see original paper] Proline content in peanut seedling leaves. Uppercase letters indicate extremely significant differences between treatments ($P < 0.01$).

3.3 Recurrent Drought Reduced MDA and O_2^- Accumulation

Drought stress can cause reactive oxygen species accumulation, leading to membrane lipid peroxidation and membrane system damage. Pre-drought stress increased MDA and O_2^- contents in peanut seedling leaves. At Stage I, MDA content in DD treatment leaves was 38.19% higher than control, and O_2^- content was 107.94% of control, though not reaching extremely significant differences. During recurrent drought stress (Stage II), D treatment caused massive accumulation of MDA and O_2^- in seedling leaves, with MDA content 40.56% higher than control and O_2^- content significantly lower than control. After rewatering (Stage III), MDA and O_2^- contents decreased sharply due to drought relief, but DD treatment still showed significantly lower MDA and O_2^- contents than D treatment, even lower than control.

[Figure 3: see original paper] MDA and O_2^- contents in peanut seedling leaves. Uppercase letters indicate extremely significant differences between treatments ($P < 0.01$).

3.4 Recurrent Drought Reduced Antioxidant Enzyme Activities

Pre-drought stress activated the antioxidant enzyme protection system in peanut seedlings. This study measured SOD, CAT, and POD activities. At Stage I (pre-drought), SOD and CAT activities increased but were not significantly different from control. POD activity was significantly higher than control. During recurrent drought stress (Stage II), DD treatment showed SOD, CAT, and POD activities significantly lower than D treatment, with POD activity decreasing most significantly (56.43% of control). At Stage III (rewatering), SOD and CAT activities in both treatments were lower than control but not significantly dif-

ferent, while POD activity in DD treatment was extremely significantly lower than control and D treatment.

[Figure 4: see original paper] Antioxidant enzyme activities in peanut seedling leaves. Uppercase letters indicate extremely significant differences between treatments ($P < 0.01$).

3.5 Photosynthetic Response Curves

Pre-drought stress inhibited photosynthesis in peanut seedling leaves, reducing photosynthetic rate at each light intensity. During recurrent drought stress (Stage II), photosynthetic rates in both treatments approached zero due to drought stress effects. However, DD treatment leaf photosynthetic rates were slightly higher than D treatment, and at 500 mol m^{-2} s^{-1} light intensity, DD photosynthetic rate was significantly higher than D. After rewatering (Stage III), both treatments were lower than control.

From the photosynthetic curve parameters: At Stage I, pre-drought stress significantly reduced maximum photosynthetic capacity (C) and maximum quantum yield (Q), enhanced dark respiration rate (D), and increased half-time constant (K). C was only 39.5% of control (0.03646 mol/mol), and K (7.58×10^{-3}) was extremely significantly greater than control. At Stage II, DD treatment significantly improved Q but C was significantly lower than control, only 12.9% of control (4.8 mol m^{-2} s^{-1}), and K value decreased. At Stage III, C in DD treatment (32.8 mol m^{-2} s^{-1}) was significantly higher than control (25.1 mol m^{-2} s^{-1}) with no significant difference in K.

[Figure 5: see original paper] Photosynthetic response curves in peanut seedling leaves.

Parameters from the analysis of photosynthetic light response curves showing maximum photosynthetic capacity (C), dark respiration (D), half-time constant (K), and maximum quantum yield (Q) across stages and treatments.

3.6 Photosynthetic Hysteresis

At Stage I, when measuring photosynthetic rates under pre-drought stress while increasing light intensity from 0 to 2000 mol m^{-2} s^{-1}, the simulated photosynthetic curve showed that for the same treatment, the area between the curve obtained when light intensity increased from 0 to 2000 mol m^{-2} s^{-1} and the curve when light intensity decreased from 2000 to 0 mol m^{-2} s^{-1} differed. At the same light intensity, photosynthetic rates were not consistent—this phenomenon is called photosynthetic hysteresis [23].

At Stage I, pre-drought treatment showed extremely significantly greater photosynthetic hysteresis area and rate than control. At Stage II (recurrent drought), D treatment showed extremely significantly higher photosynthetic hysteresis area than control. However, due to extremely low photosynthetic rates under drought stress, the two photosynthetic curves overlapped well, resulting in DD

treatment having extremely significantly lower photosynthetic hysteresis area (2805.36) and hysteresis rate (H) than control and D treatment. At Stage III (rewatering), DD treatment showed the lowest hysteresis area (4333.13) and hysteresis rate among all treatments, with no significant difference from control.

[Figure 6: see original paper] Photosynthetic hysteresis in peanut seedling leaves. Solid markers represent data measured with light intensity increasing from 0 to 2000 mol m^{-2} s^{-1}; hollow markers represent data measured with light intensity decreasing from 2000 to 0 mol m^{-2} s^{-1}.

Parameters from photosynthetic hysteresis analysis showing definite integrals, integral mean, hysteresis mean, and photosynthetic hysteresis rate (H) across stages and treatments.

3.7 Stomatal Conductance

Drought and water deficit caused leaf water loss in peanut seedlings, affecting stomatal opening and closing. Stomatal conductance was measured simultaneously with photosynthesis across all treatment stages.

At Stage I (pre-drought), stomatal conductance of both control and pre-drought treated seedlings followed a natural exponential pattern, increasing with light intensity similar to photosynthetic curves. Pre-drought treated leaves showed g significantly lower than control at each light intensity. Maximum stomatal conductance (g max) in pre-drought treatment (0.203 mol m^{-2} s^{-1}) was significantly lower than control (0.495 mol m^{-2} s^{-1}).

At Stage II (recurrent drought), the light-stomatal conductance curves of both treatments did not follow the expected negative exponential pattern. Instead, g gradually decreased from 0.126 to 0.093 mol m^{-2} s^{-1} as light intensity increased, showing an opposite trend to control. At Stage III (rewatering), g in both treatments remained below control, consistent with stomatal conductance curve results.

[Figure 7: see original paper] Stomatal conductance in peanut seedling leaves.

Parameters from stomatal conductance analysis showing maximum stomatal conductance (g max), stomatal conductance at 0 light intensity (g_0), and related constants across stages and treatments.

3.8 Stomatal Conductance Hysteresis

Stomatal conductance hysteresis curves were similar to photosynthetic hysteresis curves. At Stage II (recurrent drought), D treatment showed stomatal conductance values when light intensity increased from 0 to 2000 mol m^{-2} s^{-1} that were lower than when light intensity decreased.

Results showed that at Stage I, pre-drought treatment had greater stomatal conductance hysteresis area and rate than control. At Stage II and Stage III,

DD treatment showed extremely significantly lower hysteresis area and integral mean than control, while hysteresis rate values indicated drought adaptation.

[Figure 8: see original paper] Stomatal conductance hysteresis in peanut seedling leaves. Solid markers represent data measured with light intensity increasing from 0 to 2000 mol m^{-2} s^{-1}; hollow markers represent data measured with light intensity decreasing from 2000 to 0 mol m^{-2} s^{-1}.

Parameters from stomatal conductance hysteresis analysis showing definite integrals, integral mean, hysteresis mean, and stomatal conductance hysteresis rate (S) across stages and treatments.

4. Discussion

Leaf water loss is the most intuitive response when plants encounter drought. Plants can enhance root growth to better absorb soil water for drought adaptation [33]. Under drought conditions, biomass is preferentially allocated to roots. Initial pre-drought stress enabled peanut leaves to maintain higher water content during recurrent drought. Some studies have reported opposite results, which may be explained by root water uptake mechanisms [34]. This result may be related to root systems not being significantly affected by recurrent drought, as roots could maintain higher water uptake capacity after pre-drought rewatering.

Proline accumulation is a rapid stress response in plants encountering stress. As an osmotic adjustment substance, proline increases cellular osmotic pressure, reduces water potential, enables cells to absorb extracellular water under low osmotic conditions, and serves as a signaling molecule that activates antioxidant enzyme systems and induces expression of resistance genes [35]. Initial stress induces proline accumulation as an osmotic regulator, and when encountering subsequent stress, plants can maintain higher proline levels to regulate physiological metabolism and acquire resistance to later stress [36]. In this study, pre-drought stress caused massive proline accumulation, but during recurrent drought, proline content was far lower than that under single drought stress and could rapidly recover to control levels after rewatering. MDA and O_2^- contents and antioxidant enzyme activities showed similar results, indicating that pre-drought stress enabled peanut seedlings to develop certain adaptive or imprinting capacity. When encountering drought stress again, the antioxidant enzyme system could regulate physiological defense functions more quickly and effectively, scavenging reactive oxygen species and reducing cellular peroxidation damage, which helped peanut seedlings maintain higher resistance under subsequent drought stress.

Photosynthetic responses to multiple stress events show different results. Regardless of whether initial stress is moderate or severe, recurrent drought can significantly increase photosynthetic parameters such as transpiration rate, intercellular CO_2 concentration, net photosynthetic rate, and apparent quantum efficiency [37]. Some experiments show that recurrent drought reduces net photosynthetic rate. This study indicates that pre-drought stress significantly in-

creased net photosynthetic rate, maximum quantum efficiency, and maximum fluorescence value in peanut plants under recurrent drought [34]. Pre-drought stress treatment caused significant increases in stomatal and photosynthetic hysteresis. Drought stress damages photochemical systems and enzymes involved in photosynthetic light reactions. However, pre-drought stress significantly reduced stomatal conductance and photosynthetic rate hysteresis. One reason for photosynthetic hysteresis is that light induction of enzyme activation and feedback inhibition by photosynthetic intermediate products and acceptor proliferation require time to reach stability when light intensity changes from weak to strong; another reason is that stomatal aperture lag affects gas conduction [38-39]. Photosynthetic hysteresis reflects the activity of leaf photosystem photochemical reaction enzymes and indirectly indicates plant adaptability to environmental changes [22]. Under normal conditions, when plants grow well, photosynthetic curves obtained by increasing and decreasing light intensity basically coincide. Photosynthetic hysteresis typically occurs in senescing or stressed plants, where stomata are harder to fully open than under normal conditions. More severe hysteresis indicates greater stress impact. In this study, reduced leaf stomatal and photosynthetic hysteresis rates indicate that pre-drought stress improved plant adaptation or resistance to recurrent drought stress, showing enhanced photoprotection.

Plants can develop imprints from initial stress that affect responses to secondary stress [1]. Although pre-drought stress affected plant height and biomass, it improved resistance to secondary drought stress in terms of photosynthesis [36]. The degree of resistance and recovery after recurrent stress may be related to the degree and duration of previous stress [34, 40]. Most studies suggest that plants can recover quickly after recurrent stress, even to pre-stress levels [34, 41], while some indicate that severe stress cannot compensate for growth disadvantages, and more intense or frequent stress does not improve plant resistance but causes productivity loss [34, 37, 43]. The rapid recovery of antioxidant enzyme activities, photosynthesis, and stomatal conductance after rewatering indicates that peanut plants have strong physiological recovery capacity after recurrent drought. Although plant adaptation to multiple stresses has received widespread attention and application in production practice, the underlying mechanisms remain unclear. Pre-drought stress can alleviate physiological damage from recurrent drought stress. Bouslama et al. [44] proposed that after initial stress, plants can develop cross-adaptation to improve resistance to subsequent stresses. Recent research suggests that plant self-defense to recurrent stress at physiological and biochemical levels may be related to transcription factor accumulation and tolerance gene transcription [1]. After perceiving subsequent stress, plants increase expression of defense genes [45-46]. Studies on recurrent drought stress have identified memory genes in addition to drought response genes, with four types of drought stress memory genes functioning during recurrent drought stress, including initial response genes, memory genes, late response genes, and post-response genes. Another mechanism explanation is that stress-induced methylation causes epigenetic imprinting that is heritable

[1, 5-6, 8]. Future research will further explain adaptation and memory response mechanisms to recurrent stress at molecular and biochemical levels.

5. Conclusion

Pre-drought stress during the peanut seedling stage increased leaf water content under recurrent drought stress, reduced physiological damage caused by recurrent drought, and enhanced drought resistance in terms of photosynthesis. Plants recovered quickly to normal growth levels after rewatering. Peanut plants can imprint physiological responses to pre-drought stress and display more rapid and intense physiological defense and fast recovery mechanisms when re-exposed to drought stress. In production practice, this stress memory mechanism can be utilized for drought hardening.

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Note: Figure translations are in progress. See original paper for figures.