

Review

# Drought–Rewatering Dynamics in Chinese Cropping Systems: A Meta-Analysis of Yield Loss Mitigation, Water Use Efficiency, and Compensatory Physiological Response

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**Abstract:** Drought stress, being a crucial abiotic stress factor, and its recovery mechanism after rehydration are important in regulating crop production. This meta-analysis investigates the effects of drought stress followed by rewatering (DSRW) on crop productivity and water use efficiency (WUE) in Chinese cropping systems, synthesizing data from 90 studies (1997–2023) encompassing 2606 experimental observations. Results indicate that DSRW significantly reduced crop yield (CY) across plant types, with monocots (20.31% decline) outperforming dicots (23.64%) and woody plants (19.98% decline) showing greater resilience than herbaceous species (21.52%). WUE improved in woody plants (+7.81%) but declined in herbaceous crops (−9.44%), with notable increases in *Chenopodiaceae* (+59.39%) and *Malvaceae* (+11.35%). Mild drought stress (>65% field capacity) followed by short-term rewatering during early growth stages minimized CY losses (−19.60%) and WUE reduction (−6.89%), outperforming moderate or severe stress. Physiological analyses revealed DSRW-induced declines in photosynthetic parameters (e.g., net photosynthetic rate: −11.54%) but enhanced antioxidant enzyme activities (CAT: +18.21%, SOD: +10.23%) and osmoregulatory substance accumulation (proline: +16.22%). The study highlights the compensatory potential of strategic rewatering timing and intensity, advocating for early-stage, mild drought interventions to mitigate yield losses, which provide a practical value for promoting the sustainable development of water-saving agriculture. Future research should address regional climatic variability and crop quality responses to DSRW, advancing climate-resilient agricultural practices.

**Keywords:** drought–rewatering; Chinese cropping systems; meta-analysis; water use efficiency



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## 1. Introduction

Water scarcity has emerged as a critical global challenge, exacerbated by the increasing frequency of extreme droughts due to climate change. Analysis of the past decade indicates that drought-related economic losses in crop production alone have exceeded USD 30 billion [1]. Meanwhile, demographic projections suggest that the global population will reach 10 billion by 2050 [2], which will necessitate a doubling of agricultural water demand

to ensure food security. Paradoxically, climate models predict a 50% reduction in accessible freshwater resources during this period [3]. This looming resource disparity underscores the urgent need to implement climate-smart agricultural practices that can simultaneously enhance crop yields (CYs) and optimize water use efficiency (WUE), which are fundamental prerequisites for the sustainable intensification of food production systems.

The impact of drought on agriculture depends on the intensities and durations of reduced precipitation, soil water content, plant types, and developmental stages [4]. Plant drought stress primarily results from insufficient soil and/or air water content and/or high plant transpiration rates, which make it difficult for the root system to obtain adequate water [5]. Drought stress can reduce crop productivity by altering plant growth and development and inhibiting physiological and biochemical processes [6]. Currently, the land area of arid regions globally accounts for about 43 percent of all cultivated land [7], and arid and semi-arid regions in China account for more than half of the cultivated land [8]. Yield losses in the field under drought are usually in the range of 30–90% [9,10]. Specifically, drought stress leads to decreased plant water content, stomatal closure, reduced photosynthetic efficiency, slow growth and development, plant wilting, and ultimately, reduced or even lost yields [11]. Numerous studies have shown that drought stress reduces plant height, stem thickness, and leaf area while increasing the activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), as well as the content of malondialdehyde (MDA). These changes weaken the source–sink strength of plants, ultimately resulting in a decreased yield [12–15].

Under non-irrigated conditions, crops are often irrigated by deficits in drought and rewatering cycles during growth [16]. Deficit irrigation is an irrigation practice that reduces water supply below the maximum level and allows slight stress with minimal impact on yield [17,18]. An interesting phenomenon discovered in long-term drought research is that plants exhibit compensatory responses in physiological, biochemical, and growth aspects when they are re-watered after experiencing a certain degree of drought stress, thereby making up for the losses caused by the water deficit [19,20]. Studies have shown that drought stress followed by rewatering (DSRW) leads to a rapid increase in compensatory growth, such as plant height, leaf area, and dry matter accumulation [21–23]. In plants, high levels of SOD, POD, and CAT activities rapidly clear reactive oxygen species (ROS). Meanwhile, the cellular content of osmoregulatory substances, such as proline (Pro), soluble sugars (SSs), and soluble proteins (SPs), is rapidly reduced, while malondialdehyde (MDA) content also decreases, producing a compensatory effect [24].

In summary, DSRW affects crops in various ways. However, most previous studies were limited to independent point studies, lacking a comprehensive assessment of DSRW's effects on crop productivity across China. To address this gap, we collected and synthesized published literature from both domestic and international scholars spanning the period from 1997 to 2023. Using normal irrigation as a control, we applied meta-analysis to quantify the impact of DSRW on crop productivity in China. This study analyzed the effects of stress intensity, stress duration, and stress timing on crop productivity through group analysis, aiming to elucidate the impact of drought stress on crop productivity. Additionally, group analysis was employed to quantitatively assess the effects of DSRW on the growth, physiological, and photosynthetic characteristics of crops. This approach helps clarify the effectiveness of DSRW and its influencing factors, providing a scientific basis and technical support for the future popularization and application of rewatering after drought stress.

## 2. Materials and Methods

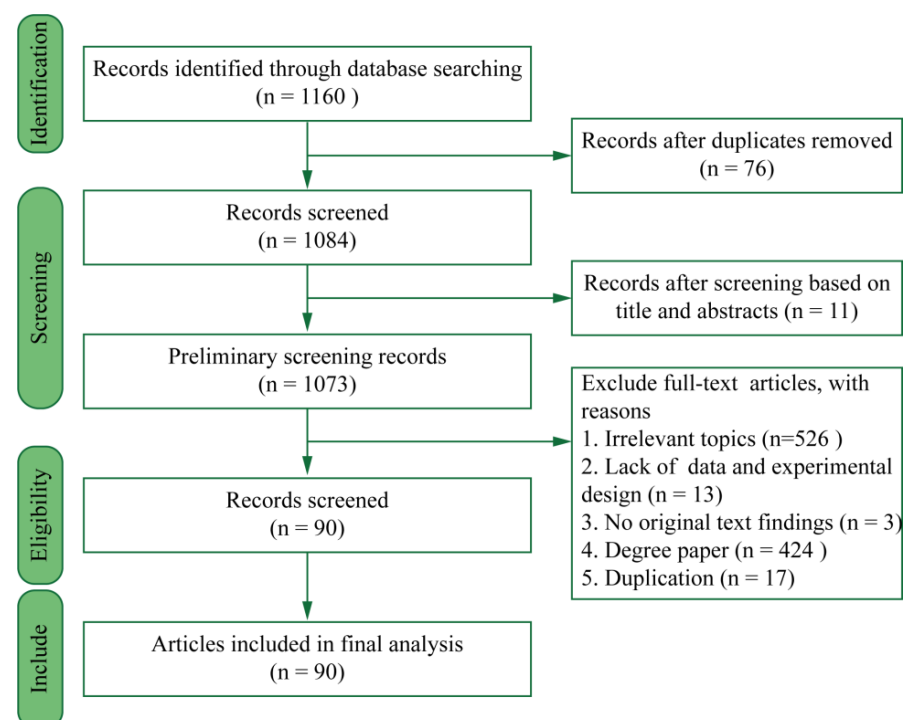
### 2.1. Literature Retrieval and Selection

We conducted a comprehensive literature search through 20 February 2024, across six major databases: Web of Science (<https://webofscience.clarivate.cn/>, accessed on 20 February 2024), PubMed (<https://pubmed.ncbi.nlm.nih.gov/>, accessed on 20 February 2024), CNKI (<https://www.cnki.net/>, accessed on 20 February 2024), ScienceDirect (<https://www.sciencedirect.com/>, accessed on 20 February 2024), China Science and Technology Journal Database (<https://www.cqvip.com/>, accessed on 20 February 2024), and Wanfang Data (<https://www.wanfangdata.com.cn/>, accessed on 20 February 2024). The search strategy employed controlled vocabulary (MeSH/Entrée terms) combined with free-text keywords, with database-specific search syntax detailed in Supplementary Files S1 and S2.

To establish rigorous inclusion criteria for literature selection, we implemented a six-stage screening protocol as follows:

- (1) Empirical studies must report field trial data specifically conducted within China's agricultural regions;
- (2) The literature should include both DSRW and normal irrigation;
- (3) Essential experimental parameters, including geographical coordinates, soil classification, and experimental duration (year/month), must be documented;
- (4) Multi-year trials must be temporally disaggregated, with each cultivation cycle analyzed as an independent observation;
- (5) Full methodological disclosure is required, with quantifiable outcome metrics (e.g., yield components, water use efficiency indices) reported;
- (6) Duplicate datasets are excluded, with corrigenda documenting substantive data corrections retained.

Through the systematic screening of 1160 candidate publications, 90 articles containing 2606 independent experimental observations met all inclusion criteria (Figure 1). The hierarchical elimination process and the complete literature inventory are detailed in Supplementary File S3.



**Figure 1.** Literature search flowchart for meta-analysis studies.

Data regarding stress intensities, stress durations, and stress periods that impacted the treatment effect values were collected in this study. Rewatering is a return to normal irrigation levels after drought stress. The grouping of each effector included in the meta-analysis is elaborated in Table 1.

**Table 1.** Subgroup classification of factors affecting crop productivity.

Influence Factors	Sub-Group		
	Preceding periods	Mid periods	Later periods
Stress Periods	Jointing stage, Rejuvenation stage, Seedling stage, Tillering stage, Trifoliolate stage, Vigorous growing stage	Boll opening stage, Booting stage, Branching stage, Bud stage, Canopy Development, Filling stage, Flowering stage, Heading stage, Leaf cluster stage, Panicle primordium differentiation stage, Stage of grouting, Pollen formation stage, Prime flowering stage, Stamen extraction stage, Tasseling stage, The first flowering stage, The flowering bell stage, The flowering stage, Tuber forming stage	Dilatation stage, Fruiting stage, Maturity stage, Pod-bearing stage, Starch accumulation stage, Storage root development, The flowering pod stage, The stage of silk production, Tuber expansion stage, Tympanic stage
Stress Intensities	Mild stress >65% FC, >−20 kPa	Medium stress 46%~65% FC, <−20 kPa~−40 kPa	Heavy stress <46% FC, <−41 kPa
Stress Durations	Short-term coercion <20 d	Medium-term stress 21 d~40 d	Long-term stress >41 d

## 2.2. Data Extraction and Analysis

An Excel database was created to extract valid data from the paper. The extracted data included the mean ( $\bar{X}$ ), standard deviation (SD), number of replications, and experimental description information (Table S1). Data in the form of images were accurately extracted using the online tool Web Plot Digitizer (<https://automeris.io/WebPlotDigitizer/> accessed on 27 March 2024).

The standard error (SE) of each treatment was extracted, and the SD was calculated as:

$$SD = SE \times \sqrt{n} \quad (1)$$

where  $n$  is the number of repetitions.

Meta-analysis is a quantitative statistical method used to summarize the results of independent studies. In this study, the effect ratio (R) was used to quantify the impact of rewatering on crops following drought stress. The natural logarithm of the effect ratio ( $\ln R$ ) was calculated based on the mean values of the treatment ( $X_t$ ) and control ( $X_c$ ) groups [25]:

$$R = \frac{X_t}{X_c} \quad (2)$$

$$\ln R = \ln \left( \frac{X_t}{X_c} \right) = \ln X_t - \ln X_c \quad (3)$$

$\ln R$  is a unitless coefficient that can take positive or negative values. If the 95% confidence interval (CI) of  $\ln R$  includes zero, it indicates that the effect is not significantly different from drought stress. If the lower bound of the 95% CI is greater than zero, it suggests that the effect is significantly positive, indicating an increase due to drought

stress. Conversely, if the upper bound of the 95% CI is less than zero, it suggests that the effect is significantly negative, indicating a decrease due to drought stress [26]. To better characterize the magnitude of no-tillage effects on yield, this study converted the effect value  $\ln R$  to effect size (E) [27].

$$E = (\exp(\ln R) - 1) \times 100\% \quad (4)$$

### 2.3. Meta-Analysis

The meta-analysis was conducted using R software (4.4.2), with  $\ln R$  selected as the effect size metric. The effect size and combined effect value were calculated accordingly [28]. In cases where heterogeneity was detected ( $p < 0.05$ ), a random effects model was employed; otherwise, a fixed effects model was used [29]. Data analysis was performed using a 95% confidence interval [30]. A normal distribution test was performed using the Shapiro–Wilk test method and SPSS 26.0 software [31]. The forest plot was generated using GraphPad Prism 9.5.1 software.

### 2.4. Meta-Regression

Regression analysis in meta-analysis is employed to examine the relationship between study characteristics and effects across different studies [32]:

$$Y_i = aX_i + b \quad (5)$$

where  $Y_i$  is the effect size of study  $i$ ,  $a$  is the slope coefficient,  $b$  is the intercept, and  $X_i$  is the independent variable. Linear regression effect modeling was conducted using the “lme4” package in the R language, with restricted maximum likelihood estimation [33].

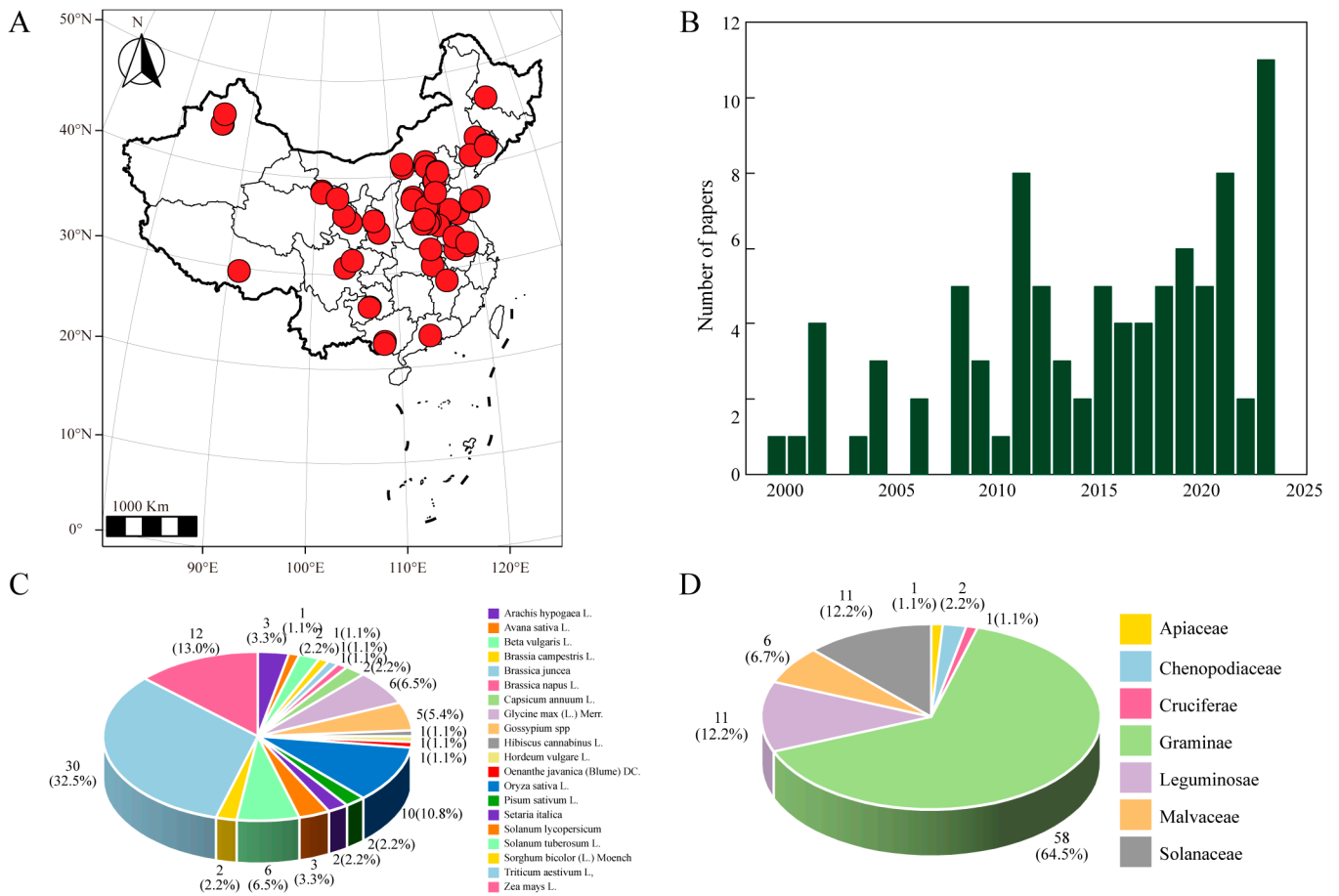
## 3. Results

### 3.1. Data Overview

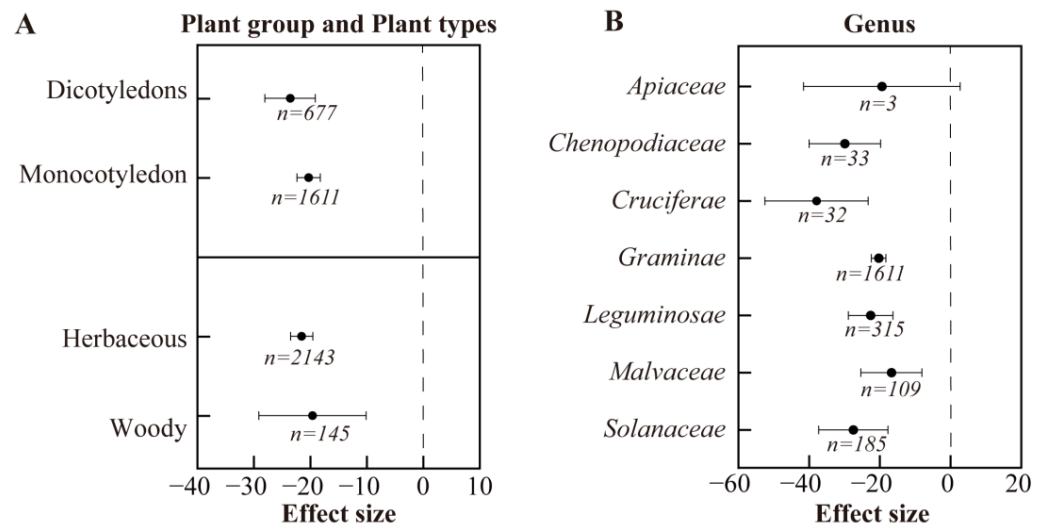
In this study, 90 studies on DSRW published between 1997 and 2023 were collected (Figure 2A,B). The normal distribution test found that the data conformed to a normal distribution and could be analyzed subsequently (Figure S1). A total of 20 crops were included, with *Triticum aestivum* L., *Zea mays* L., *Oryza sativa* L., *Glycine max* (L.) Merr., and *Solanum tuberosum* L. are the most extensively studied, accounting for 32.61%, 13.04%, 10.87%, 6.52%, and 6.52% of the studies, respectively (Figure 2C and Table S2). These crops were distributed across seven genera, with *Gramineae* having the largest proportion (64.44%), followed by *Leguminosae* (12.22%), *Solanaceae* (12.22%), and *Malvaceae* (6.67%) (Figure 2D and Table S3). A total of 2567 independent studies were obtained for subsequent analysis.

### 3.2. Effect of Drought Stress on CY in Different Types of Plants

DSRW suppressed CY across different plant types (Figure 3). CY was significantly reduced by 23.64% ( $n = 677$ ) in dicotyledons and by 20.31% ( $n = 1611$ ) in monocotyledons ( $p < 0.05$ ). Additionally, CY was 3.33% higher in monocotyledonous plants compared to dicotyledonous plants. For herbaceous and woody plants, CY was significantly reduced by 21.52% ( $n = 2143$ ) and 19.98% ( $n = 145$ ), respectively. The CY was 1.54% higher in woody plants than in herbaceous plants. In terms of plant families, CY in *Apiaceae* decreased by 21.42% ( $n = 3$ ), although the difference was not significant. CY was significantly reduced in *Chenopodiaceae*, *Cruciferae*, *Graminae*, *Leguminosae*, *Malvaceae*, and *Solanaceae* by 30.32% ( $n = 33$ ), 38.99% ( $n = 32$ ), 20.31% ( $n = 1611$ ), 22.71% ( $n = 315$ ), 16.98% ( $n = 109$ ), and 27.86% ( $n = 185$ ), respectively. The *Apiaceae* were more stable under DSRW.



**Figure 2.** Distribution, number, species classification, and family classification. (A) Distribution of test sites; (B) number of papers published per year during 1997–2023; (C) percentage of all plants studied; (D) ratio of all plants studied in different families.



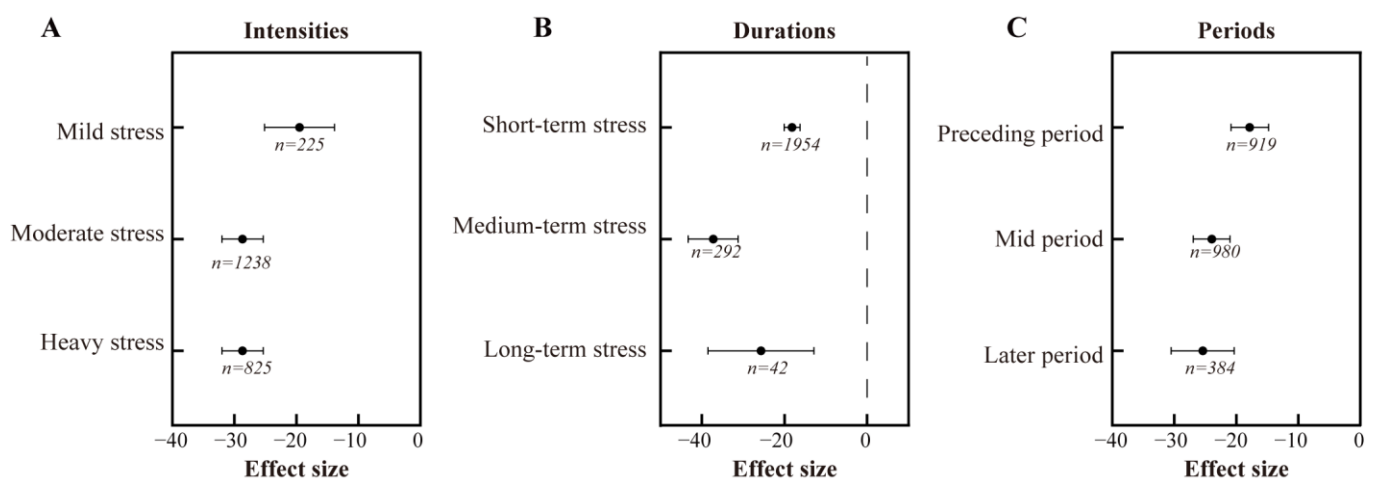
**Figure 3.** Subgroup analysis of rewatering after drought stress on the yield of different crops. Forest plot for combined effect values (lnR) ± 95% CI, n indicates the number of independent studies. (A) Plant group and plant type, (B) Genus. Confidence intervals do not overlap with the dashed line, indicating a significant difference between treatment and control groups.

### 3.3. Effects of Different Intensities of Drought Stress on CY

DSRW at different stress intensities and periods significantly reduced CY (Figure 4). Specifically, rewatering after mild, moderate, and severe stress reduced CY by 19.60%



( $n = 225$ ), 28.72% ( $n = 1238$ ), and 28.72% ( $n = 825$ ), respectively. Compared to rewatering after moderate stress, CY increased by 9.12% for rewatering after mild stress. Similarly, CY increased by 9.12% for rewatering after mild stress compared to rewatering after severe stress. Furthermore, rewatering after short-term, medium-term, and long-term stress reduced CY by 18.16% ( $n = 1954$ ), 37.44% ( $n = 292$ ), and 26.38% ( $n = 42$ ), respectively. The CY of rewatering after short-term stress was 19.28% higher than that after medium-term stress and 8.22% higher than that after long-term stress. Additionally, rewatering after preceding, mid, and later drought stress reduced CY by 17.85% ( $n = 919$ ), 23.99% ( $n = 980$ ), and 25.51% ( $n = 389$ ), respectively. The CY of rewatering after preceding stress was 6.14% higher than that after mid-stress and 7.66% higher than that after later stress. Rewatering after a short-term period of mild drought stress during the preceding period can alleviate the decline in CY caused by drought.



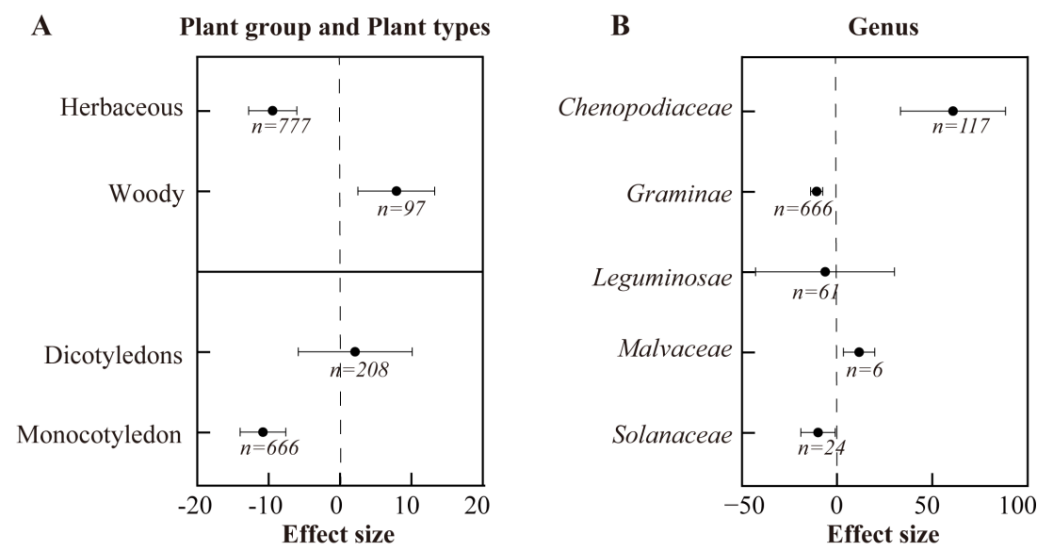
**Figure 4.** Subgroup analysis of rewatering after drought stress on CY for different intensities. (A) Different intensities, (B) different durations, and (C) different periods.

The above study found that CY decreased significantly in different types of plants, and dicotyledons were more susceptible than monocotyledons. The CY of herbaceous plants decreased by 21.52%, while that of woody plants decreased by 19.98%. The *Apiaceae* plants remained stable under DSRW conditions. The intensity and duration of stress had a significant effect on CY: moderate and heavy stress caused a comparable decrease in CY ( $\sim -28.72\%$ ), which exceeded the effect of mild stress. Rewatering after short-term stress mitigated the loss of CY ( $-18.16\%$ ), superior to medium and long-term recovery. The best preservation of CY ( $-17.85\%$ ) was observed if watering was reintroduced preceding drought stress, suggesting that early intervention of mild short-term stress during the initial growth phase could mitigate drought-induced CY decline.

### 3.4. Effect of Drought Stress on Crop WUE in Different Types of Plants

The WUE of the herbaceous plant's DSRW was significantly reduced by 9.44% ( $n = 777$ ), whereas the WUE of the woody plant's DSRW was significantly increased by 7.81% ( $n = 97$ ) (Figure 5). The WUE of DSRW was significantly increased by 17.25% in woody compared to herbaceous plants. The WUE of monocotyledonous plants DSRW was significantly reduced by 10.82% ( $n = 666$ ), whereas the WUE of dicotyledonous plant's DSRW was increased by 1.93% ( $n = 208$ ), but the difference was not significant. DSRW in dicotyledonous plants significantly increased WUE by 12.75% compared to monocotyledonous plants. The WUE significantly increased by 59.39% ( $n = 24$ ) and 11.35% ( $n = 61$ ) for DSRW in *Chenopodiaceae* and *Malvaceae*. The WUE significantly decreased by 10.82% ( $n = 666$ ) and 10.21% ( $n = 117$ ) for DSRW in *Graminae* and *Solanaceae*. The WUE decreased by 11.05% ( $n = 6$ ) of DSRW in

*Leguminosae*, but the difference was not significant. The WUE of DSRW was significantly increased by 70.21%, 70.44%, 48.04%, and 69.60% in *Chenopodiaceae* compared to *Graminae*, *Leguminosae*, *Malvaceae*, and *Solanaceae*, respectively.



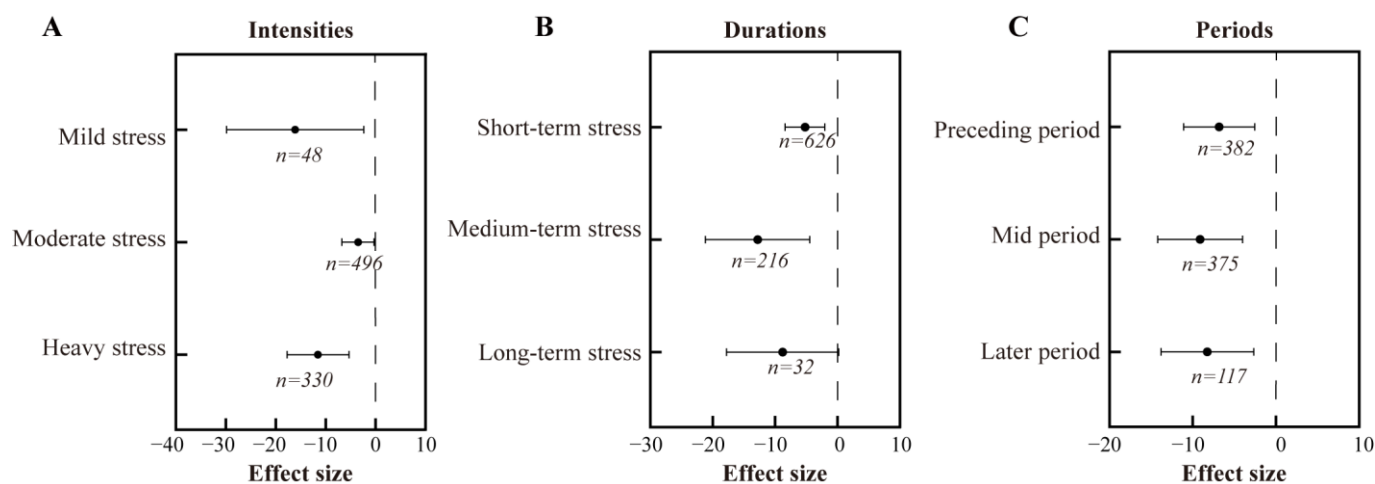
**Figure 5.** Subgroup analysis of rewatering after drought stress on water use efficiency of different crops. (A) Plant group and plant type, (B) genus.

### 3.5. Effects of Different Intensities of Drought Stress on Crop WUE

The WUE was reduced by rewatering after different intensities of drought stress (Figure 6). Rewatering after mild stress, moderate stress, and heavy stress significantly decreased by 16.84% ( $n = 48$ ), 3.53% ( $n = 496$ ), and 11.65% ( $n = 330$ ), respectively. The WUE of rewatering after moderate stress was 13.31% and 5.19% higher than that of rewatering after mild and heavy stress, respectively. The WUE was significantly reduced by 5.22% ( $n = 626$ ) and 13.06% ( $n = 216$ ) by rewatering after short-term and medium-term stress, respectively. Long-term stress followed by rewatering reduced water use efficiency by 9.06% ( $n = 32$ ); the difference was not significant. The WUE of rewatering after short-term stress was 7.84% and 3.84% higher than that of rewatering after medium-term and long-term stress, respectively. DSRW at different stress intensities reduced WUE. The WUE was significantly reduced by 6.89% ( $n = 382$ ), 9.20% ( $n = 375$ ), and 8.34% ( $n = 117$ ) for rewatering after preceding, mid, and later drought stress, respectively. Rewatering after preceding stress increased WUE by 2.31% and 1.45% compared to rewatering after mid and later stress, respectively. Therefore, rewatering preceding periods of moderate and short-term stress can inhibit the decrease in WUE caused by drought stress.

The above study found a significant increase in the WUE of woody plants (+7.81%) while herbaceous plants showed a significant decrease, with woody plants being 17.25% higher than herbaceous plants. Similarly, the WUE of dicotyledonous plants increased insignificantly but exceeded that of monocotyledonous plants by 12.75%. Taxonomically, WUE increased significantly in *Chenopodiaceae* and *Malvaceae* plants (+59.39% and +11.35%, respectively). WUE recovery was higher with moderate stress rewatering compared to mild or heavy stress. Short-term stress rewatering was more effective than the medium and long-term stress. Notably, rewatering during the preceding drought period (−6.89%) was more effective in maintaining WUE compared to rewatering during the mid- to later-stress period.

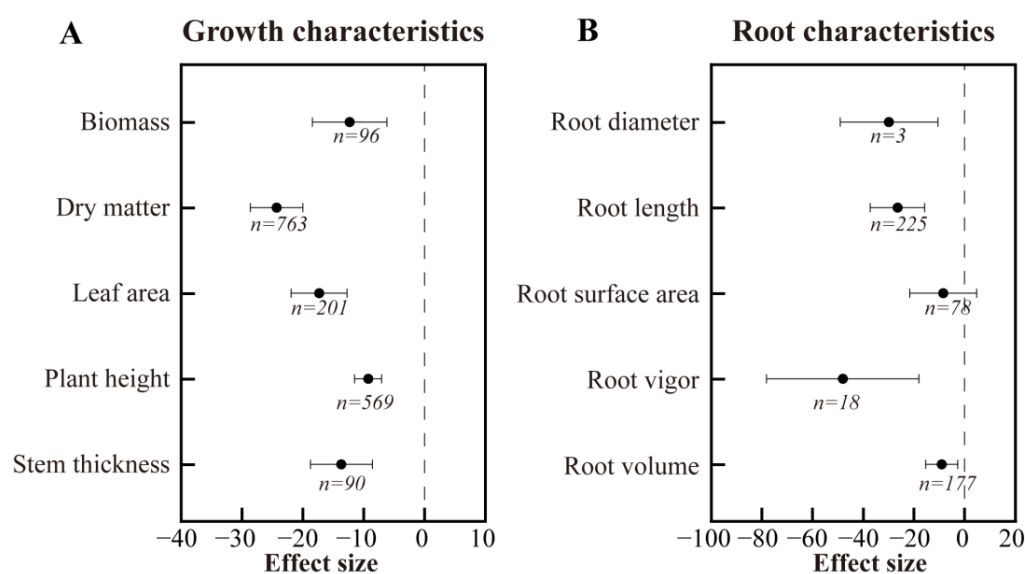




**Figure 6.** Subgroup analysis of rewatering after drought stress on crop WUE for different intensities. (A) Different intensities, (B) different durations, and (C) different periods.

### 3.6. Effect of Drought Stress on Growth Characteristics of Crops

Drought stress severely affected crop growth. DSRW significantly reduced biomass, dry matter, leaf area, plant height, and stem thickness by 12.42% ( $n = 96$ ), 24.37% ( $n = 763$ ), 17.37% ( $n = 201$ ), 9.25% ( $n = 569$ ), and 13.74% ( $n = 90$ ), respectively (Figure 7). Additionally, DSRW significantly decreased root diameter, root length, root vigor, and root volume by 31.58% ( $n = 3$ ), 27.02% ( $n = 225$ ), 53.85% ( $n = 18$ ), and 9.15% ( $n = 177$ ), respectively. DSRW also reduced root surface area by 9.06% ( $n = 78$ ).

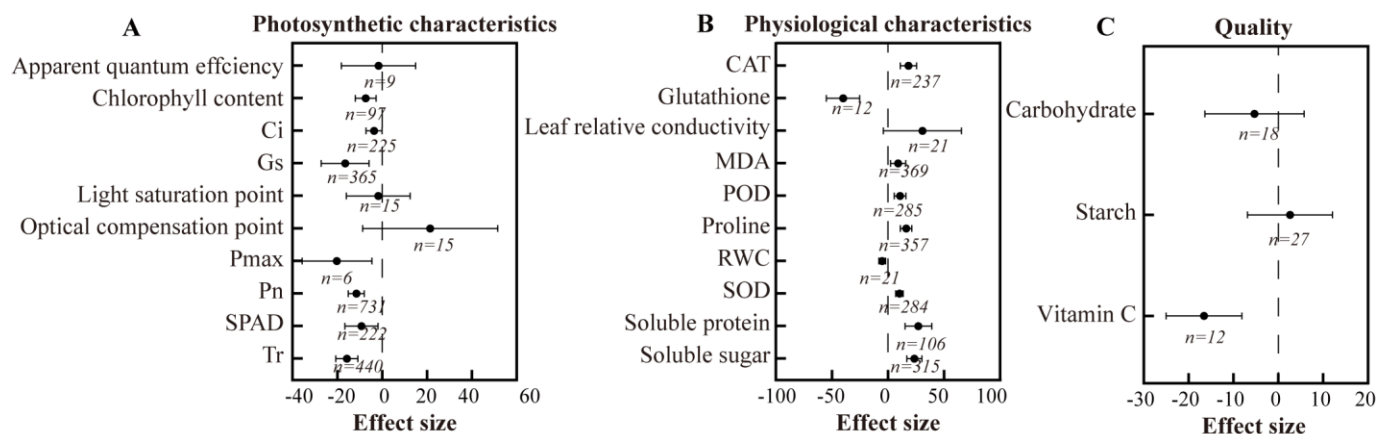


**Figure 7.** Subgroup analysis of rewatering after drought stress on plant growth and root characteristics. (A) Growth characteristics, (B) root characteristics.

### 3.7. Effect of Drought Stress on Physiological Characteristics of Crops

DSRW significantly reduced chlorophyll content, intercellular carbon dioxide concentration ( $C_i$ ), stomatal conductance ( $G_s$ ), maximum net photosynthetic rate ( $P_{max}$ ), net photosynthetic rate ( $P_n$ ), SPAD (Soil plant analysis development), and transpiration rate ( $Tr$ ) by 7.36% ( $n = 97$ ), 3.66% ( $n = 225$ ), 16.94% ( $n = 365$ ), 21.15% ( $n = 6$ ), 11.54% ( $n = 731$ ), 9.35% ( $n = 222$ ), and 15.84% ( $n = 440$ ), respectively (Figure 8). DSRW decreased apparent quantum efficiency and light saturation point by 2.55% ( $n = 9$ ) and 2.38% ( $n = 15$ ), respectively, but

these differences were not significant. DSRW increased the light compensation point by 18.90% ( $n = 15$ ), but this difference was not significant.



**Figure 8.** Subgroup analysis of rewatering after drought stress on plant physiological and photosynthetic characteristics. (A) Photosynthetic characteristics, (B) physiological characteristics, (C) quality.

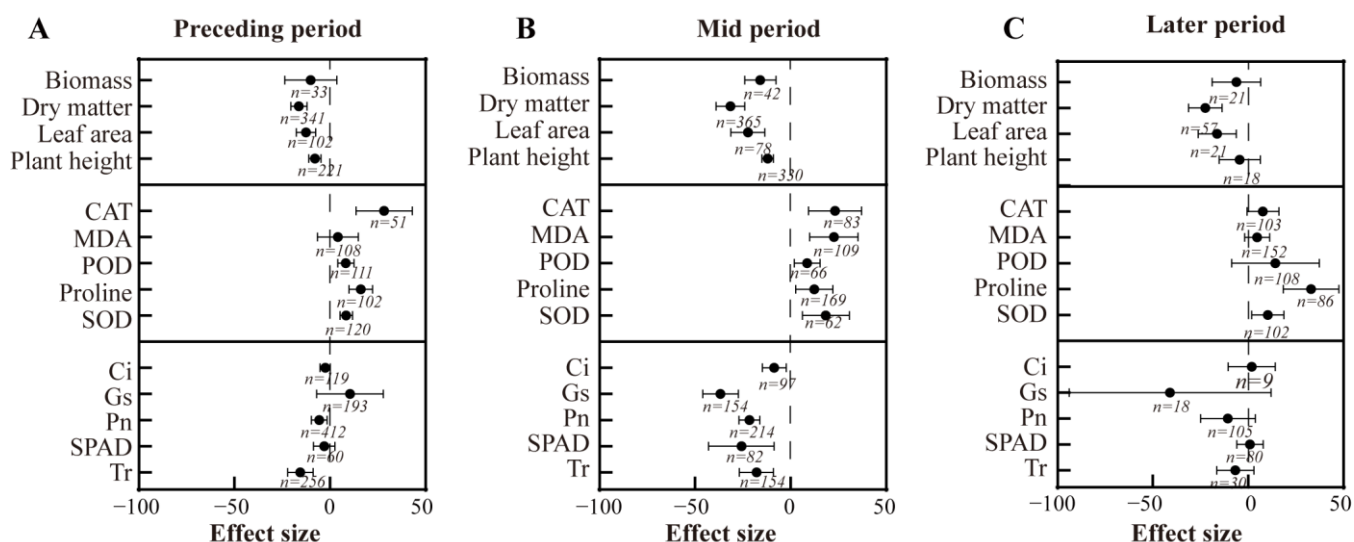
DSRW significantly increased CAT, MDA, POD, Pro, SOD, SPs, and SSs by 18.21% ( $n = 237$ ), 8.97% ( $n = 369$ ), 10.84% ( $n = 285$ ), 16.22% ( $n = 357$ ), 10.23% ( $n = 284$ ), 26.83% ( $n = 106$ ), and 23.52% ( $n = 315$ ), respectively. Glutathione and RWC decreased significantly by 41.15% ( $n = 12$ ) and 5.18% ( $n = 21$ ), respectively, in DSRW. Leaf relative conductivity increased by 27.66% in DSRW, but the difference was not significant.

Vitamin C decreased significantly by 16.81% ( $n = 12$ ) in DSRW. Carbohydrates decreased by 5.71% ( $n = 18$ ) in DSRW, but the difference was not significant. Starch increased by 2.35% ( $n = 27$ ) in DSRW, but the difference was not significant.

The above study found that DSRW severely affected crop growth and physiological functions. Biomass, dry matter, leaf area, plant height, and stem thickness were reduced by  $-9.25\% \sim -24.37\%$ , respectively, and root traits, including root diameter ( $-31.58\%$ ) and root vigour ( $-53.85\%$ ), were also significantly reduced. Photosynthetic efficiency was severely affected, with chlorophyll content, stomatal conductance (Gs), and net photosynthetic rate (Pn) decreasing by  $-7.36\% \sim -16.94$ , respectively. DSRW induced oxidative stress and increased antioxidant enzymes (CAT:  $+18.21\%$ , SOD:  $+10.23\%$ ) and osmolytes (proline:  $+16.22\%$ ), whereas glutathione and RWC decreased significantly by  $-41.15\%$  and  $-5.18\%$ , respectively. It is noteworthy that vitamin C decreased by  $-16.81\%$ , but starch and carbohydrates did not change significantly.

### 3.8. Effects of Drought Stress on Crops at Different Periods

Rewatering after preceding drought stress significantly reduced dry matter, leaf area, plant height, net photosynthetic rate (Pn), and transpiration rate (Tr) by 16.30% ( $n = 341$ ), 12.69% ( $n = 102$ ), 7.86% ( $n = 221$ ), 5.59% ( $n = 412$ ), and 15.66% ( $n = 256$ ), respectively (Figure 9). Additionally, rewatering significantly increased catalase (CAT), peroxidase (POD), proline, and superoxide dismutase (SOD) by 27.88% ( $n = 51$ ), 8.32% ( $n = 111$ ), 16.07% ( $n = 102$ ), and 8.50% ( $n = 120$ ), respectively. Rewatering also reduced biomass, intercellular CO<sub>2</sub> concentration (Ci), and SPAD values by 10.73% ( $n = 33$ ), 2.52% ( $n = 119$ ), and 3.06% ( $n = 60$ ), respectively, but these differences were not significant. Similarly, rewatering reduced stomatal conductance (Gs) and malondialdehyde (MDA) content by 9.64% ( $n = 193$ ) and 3.77% ( $n = 108$ ), respectively, but these reductions were also not significant.



**Figure 9.** Subgroup analysis of rewatering after drought stress at different periods. (A) Preceding periods, (B) mid periods, (C) later periods.

After rewatering following mid-period drought stress, significant changes were observed in various physiological and growth parameters. Specifically, biomass, intercellular CO<sub>2</sub> concentration (Ci), dry matter, stomatal conductance (Gs), leaf area, plant height, net photosynthetic rate (Pn), chlorophyll content (SPAD), and transpiration rate (Tr) were significantly reduced by 16.10% ( $n = 42$ ), 8.69% ( $n = 97$ ), 31.74% ( $n = 365$ ), 37.12% ( $n = 154$ ), 22.67% ( $n = 78$ ), 11.97% ( $n = 330$ ), 21.66% ( $n = 214$ ), 27.06% ( $n = 82$ ), and 18.19% ( $n = 154$ ), respectively. In contrast, rewatering significantly increased the activities of catalase (CAT), malondialdehyde (MDA), peroxidase (POD), proline (Pro), and superoxide dismutase (SOD) by 22.70% ( $n = 83$ ), 22.21% ( $n = 109$ ), 8.50% ( $n = 66$ ), 12.13% ( $n = 169$ ), and 18.05% ( $n = 62$ ), respectively.

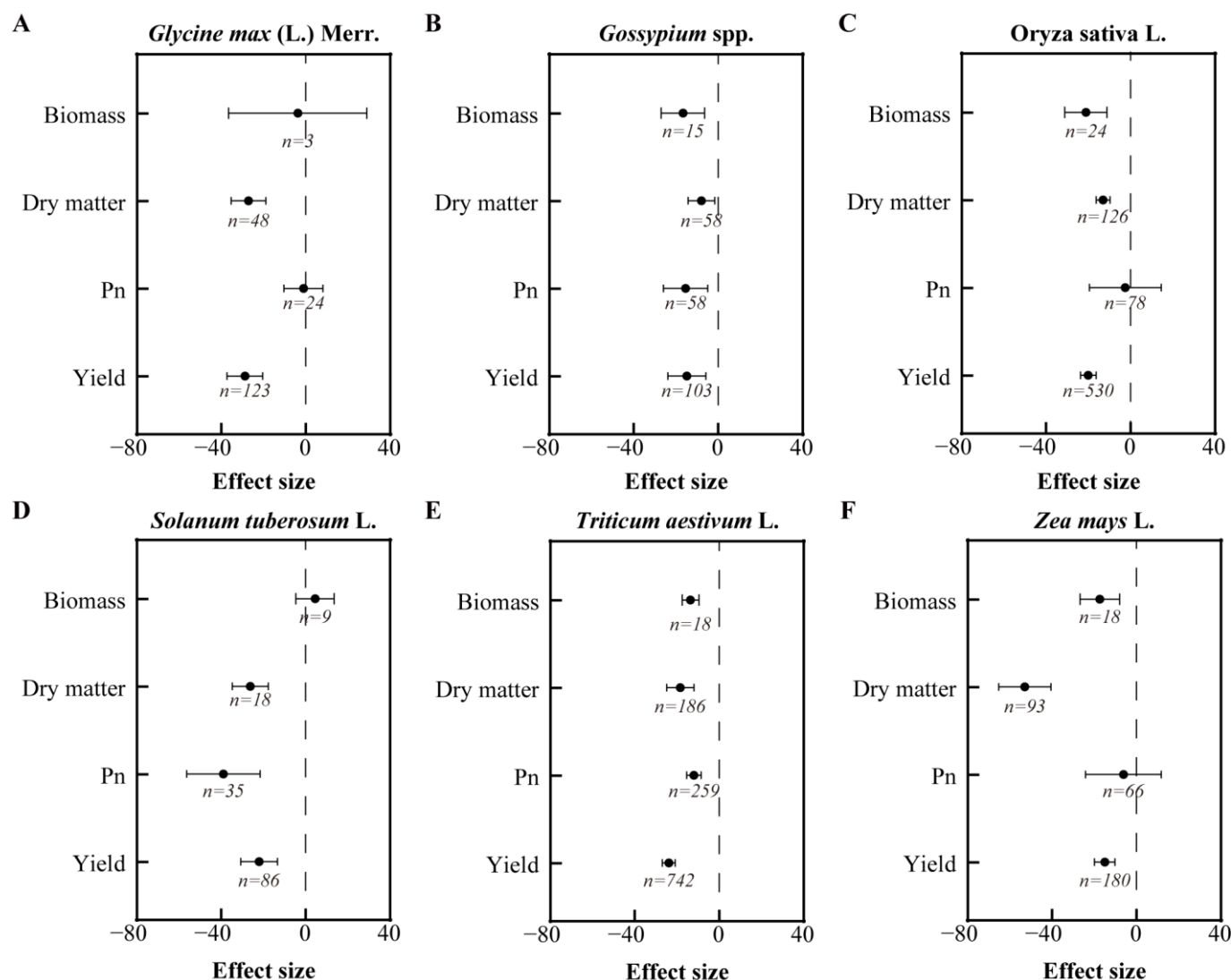
After periods of drought stress, rewatering significantly decreased dry matter and leaf area by 22.83% ( $n = 57$ ) and 16.61% ( $n = 21$ ), respectively. It also significantly increased proline and SOD by 32.45% ( $n = 86$ ) and 10.14% ( $n = 102$ ), respectively. However, rewatering had non-significant effects on biomass, Gs, plant height, Pn, and Tr, reducing them by 6.80% ( $n = 21$ ), 56.79% ( $n = 18$ ), 4.84% ( $n = 18$ ), 11.37% ( $n = 105$ ), and 7.08% ( $n = 30$ ), respectively. Similarly, rewatering increased CAT, Ci, MDA, POD, and SPAD values by 7.56% ( $n = 103$ ), 1.44% ( $n = 9$ ), 4.61% ( $n = 152$ ), 12.78% ( $n = 108$ ), and 0.83% ( $n = 80$ ), respectively, but these changes were not statistically significant.

The dry matter content, Gs, and Pn after rewatering following preceding periods of drought stress significantly increased by 15.44%, 46.76%, and 16.07%, respectively, compared with those after rewatering following mid-periods of drought stress. The SPAD value after rewatering following mid-periods of drought stress significantly decreased by 27.89% compared with that after rewatering following later periods of drought stress.

### 3.9. Effects of Drought Stress on Different Crops

To further understand the effect of DSRW on different crops, we analyzed the common metrics biomass, dry matter, Pn, and yield of *Glycine max* (L.) Merr., *Gossypium* spp., *Oryza sativa* L., *Solanum tuberosum* L., *Triticum aestivum* L., and *Zea mays* L. (Figure 10). *Glycine max* (L.) Merr. and *Solanum tuberosum* L. showed no significant difference in biomass under DSRW (−7.51% and +4.22%). *Gossypium* spp., *Oryza sativa* L., *Triticum aestivum* L., and *Zea mays* L. showed a significant decrease in biomass under DSRW at −17.10% ( $n = 15$ ), −21.57% ( $n = 24$ ), −13.64% ( $n = 18$ ), and −17.70% ( $n = 18$ ), respectively. *Glycine max* (L.) Merr., *Gossypium* spp., *Oryza sativa* L., *Solanum tuberosum* L., *Triticum aestivum* L., and

*Zea mays* L. showed a significant decrease in dry matter under DSRW at  $-27.41\%$  ( $n = 48$ ),  $-8.08\%$  ( $n = 58$ ),  $-13.02\%$  ( $n = 126$ ),  $-26.59\%$  ( $n = 18$ ),  $-18.62\%$  ( $n = 186$ ), and  $-53.93\%$  ( $n = 93$ ), respectively. *Glycine max* (L.) Merr., *Oryza sativa* L., and *Zea mays* L. showed no significant difference in Pn under DSRW ( $-1.38\%$ ,  $-3.46\%$ , and  $-7.32\%$ ). *Gossypium* spp., *Solanum tuberosum* L., and *Triticum aestivum* L. showed a significant decrease in Pn under DSRW at  $-15.81\%$  ( $n = 58$ ),  $-40.60\%$  ( $n = 35$ ), and  $-12.01\%$  ( $n = 259$ ), respectively. *Glycine max* (L.) Merr., *Gossypium* spp., *Oryza sativa* L., *Solanum tuberosum* L., *Triticum aestivum* L., and *Zea mays* L. showed a significant decrease in CY under DSRW at  $-29.15\%$  ( $n = 123$ ),  $-15.12\%$  ( $n = 103$ ),  $-20.08\%$  ( $n = 530$ ),  $-22.34\%$  ( $n = 86$ ),  $-23.89\%$  ( $n = 742$ ), and  $-15.11\%$  ( $n = 180$ ), respectively.



**Figure 10.** Subgroup analysis of rewatering after drought stress at different crop. (A) *Glycine max* (L.) Merr., (B) *Gossypium* spp., (C) *Oryza sativa* L., (D) *Solanum tuberosum* L., (E) *Triticum aestivum* L., (F) *Zea mays* L.

The above study found that DSRW negatively affected dry matter accumulation and yield in all the study crops, with *Zea mays* L. showing the most severe dry matter reduction ( $-53.93\%$ ). Biomass and Pn responses were crop-specific: *Glycine max* (L.) Merr. and *Solanum tuberosum* L. maintained biomass stability under DSRW, while *Solanum tuberosum* L. and *Gossypium* spp. experienced pronounced Pn suppression. Yield losses ranged from  $15.11\%$  (*Zea mays* L.) to  $29.15\%$  (*Glycine max* (L.) Merr.), highlighting differential crop

vulnerability to DSRW stress. These findings underscore the need for tailored mitigation strategies based on species-specific physiological sensitivities.

### 3.10. Relationships Between Different Intensities of Drought Stress and CY and WUE

Linear regression analysis showed that crop yield was significantly and positively correlated with durations of stress ( $p < 0.01$ ). Crop water utilization efficiency was positively correlated with the degree of stress. Crop water utilization efficiency was negatively correlated with durations of stress. Crop yield was negatively correlated with degree of stress (Figure S2). Further multifactorial regression analysis was used to calculate the optimum CY and WUE under different periods, intensities, and durations (Figure 11). It was found that CY was highest under 90% drought stress for 3 d in the preceding period. The highest WUE was found under 30% drought stress for 67.51 d in the late period.

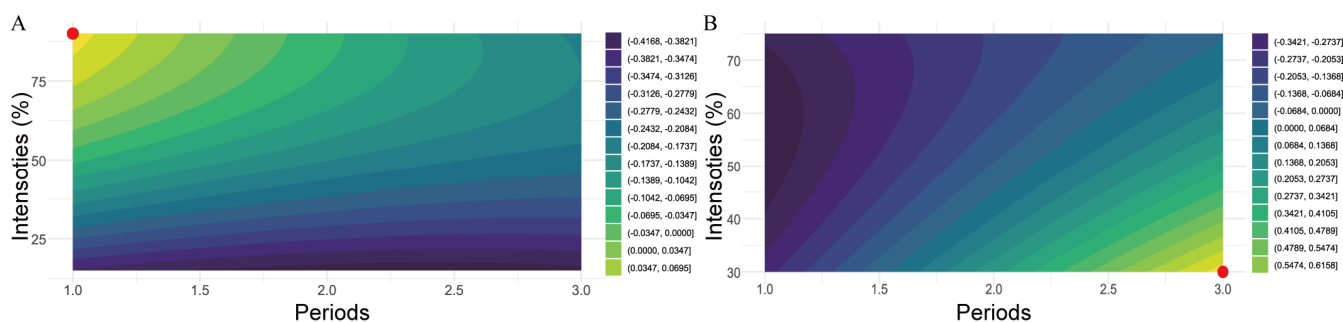


Figure 11. Multifactor regression analysis plot. (A) CY. (B) WUE. Fixed durations for plotting.

## 4. Discussion

Drought stress is one of the most important abiotic stresses, severely limiting crop development and yield [34]. Therefore, exploring methods to improve crop drought tolerance and elucidating the mechanisms that enhance drought tolerance are among the top research priorities in this field. Studies have shown that drought stress followed by rewatering (DSRW) can produce a compensatory effect that significantly promotes crop productivity [35–37]. However, in a large number of studies, the conclusions regarding rewatering after drought stress vary due to differences in stress periods, stress intensities, and stress durations [38,39]. Moreover, many studies have focused on single experiments, which do not provide a comprehensive understanding of the effects of DSRW on crop yield (CY), water use efficiency (WUE), growth characteristics, and physiological characteristics. This study aims to provide a more accurate understanding of the effects of DSRW on crop drought tolerance through a meta-analysis.

### 4.1. Effect of DSRW on Crop Yield

Drought stress affects crop growth and development, ultimately reducing CY [40]. Yield is also the primary basis for evaluating the drought tolerance of crops [41]. Therefore, reducing CY decline under drought stress is the ultimate goal of drought research. The present study showed that DSRW reduced CY. Further subgroup analyses revealed that CY was higher in DSRW monocotyledonous plants than in dicotyledonous plants, and woody plants than in herbaceous plants (Figure 3). DSRW significantly inhibited the CY of *Chenopodiaceae*, *Cruciferae*, *Graminae*, *Leguminosae*, *Malvaceae*, and *Solanaceae*. DSRW was especially not recommended for *Chenopodiaceae* and *Cruciferae*, which may be related to the characteristics of these plants. However, the specific drought resistance mechanisms require further research. We analyzed subgroups of the top six crops and found that both *Glycine max* (L.) Merr., *Gossypium* spp., *Oryza sativa* L., *Solanum tuberosum* L.,



*Triticum aestivum* L., and *Zea mays* L. yields decrease under DSRW conditions, with *Gossypium* spp. and *Zea mays* L. having smaller yield decreases.

Some studies have found that drought stress reduces both the vegetative and reproductive growth of crops. Drought stress at the seedling stage decreases seedling emergence and diminishes photosynthesis. Drought stress during flowering reduces the number of seeds in wheat [42]. Drought stress during seed development reduces fruiting rates [43]. Our subgroup analyses showed that rewatering after the early stages of stress resulted in higher CY than rewatering after mid-periods and later periods of stress. Rewatering after mild stress resulted in higher CY than rewatering after moderate and severe stress (Figure 4). Rewatering after short-term stress significantly increased CY more than rewatering after medium-term stress. This indicates that different stress intensities, durations, and timing of stress have varying effects on CY. Rewatering after short-term stress in the early stages is beneficial for maintaining CY. Further multifactorial regression analysis was carried out, and it was found that maximum CY could be achieved at 90% level of stress for 3 d of the crop preceding period.

#### 4.2. Effect of DSRW on WUE

WUE is related to a plant's ability to maintain high photosynthetic rates and limit water loss by controlling stomatal aperture and closure [44]. Previous studies have shown that drought stress can increase crop WUE [45,46], but excessive drought stress inhibits crop growth, reduces photosynthetic capacity, and decreases CY [47,48]. In the present study, DSRW increased WUE to some extent. Further subgroup analysis revealed that DSRW significantly increased WUE in dicotyledons compared to monocotyledons. Additionally, DSRW significantly increased WUE in woody plants compared to herbaceous plants (Figure 5). DSRW also promoted WUE significantly in *Chenopodiaceae* and *Malvaceae*, while it had a significant inhibitory effect on WUE in *Graminae* and *Solanaceae*. This suggests that different plants respond differently to DSRW, with *Chenopodiaceae* showing a particularly strong positive response. Our subgroup analysis also showed that rewatering after moderate stress resulted in higher WUE than rewatering after mild or heavy stress (Figure 6). Rewatering after short-term stress resulted in higher WUE compared to rewatering after medium-term or long-term stress. Similarly, rewatering after stress in the early stages resulted in higher WUE than rewatering after stress in the middle or later stages. These findings indicate that different stress intensities, durations, and timing have distinct effects on crop WUE. Watering after short periods of stress in the early stages is beneficial for increasing CY. Further multifactorial regression analysis was carried out, and it was found that maximum WUE could be achieved at 30% level of stress for 67.51 d of the crop later period.

#### 4.3. Effect of DSRW on Crop Growth Characteristics

Plant height, root length, and biomass are among the most accurate and direct indicators of plant growth. Drought stress inhibits crop growth, primarily in terms of plant height, root length, and both dry and fresh weights [5,49,50]. For example, studies have shown that deficit irrigation during the seedling and spike stages of winter wheat (*Triticum aestivum* L.) can lead to significant compensatory growth in plant height and leaf area [51]. Similarly, research on soybeans (*Glycine max* (L.) Merr.) has demonstrated that deficit irrigation results in significant compensatory growth in plant height and leaf area [52]. However, deficit irrigation had no significant effect on root surface area (Figure 7). DSRW can significantly reduce biomass, dry matter, leaf area, plant height, stem thickness, root diameter, root length, root vigor, and root volume. Among these, the greatest effects were observed on



leaf area, root diameter, root length, and root vigor, with reductions ranging from 24.37% to 53.85%.

#### 4.4. Effect of DSRW on Crop Physiological Characteristics

It is well established that drought stress induces cellular damage in plants, accelerates the accumulation of superoxide radicals, and triggers the activation of both enzymatic and non-enzymatic systems, the accumulation of osmoregulatory substances, and a reduction in photosynthesis [6]. It has been found that DSRW elicits a series of physiological compensatory responses. For instance, the leaf water potential is rapidly restored after rewatering following drought stress. The activities of osmoregulatory substances such as SOD, APX, and CAT, as well as the contents of Pro, SS, and MDA, which are maintained at high levels in plants under drought stress, are significantly reduced after rewatering. These changes collectively help to mitigate the excessive damage caused by drought stress to the plants [53–57]. In this study, we demonstrated that the contents of CAT, POD, and SOD were significantly elevated in DSRW, which is consistent with findings described above that crops scavenge ROS through high levels of antioxidant enzyme activities to reduce injury. Meanwhile, our analysis revealed that the contents of MDA, Pro, SP, and SS in plants also increased significantly under DSRW, which is inconsistent with earlier studies. This discrepancy may be attributed to severe drought stress, which leads to an increase in osmoregulatory substances in crops to maintain water content. The rewatering period was short, and the levels of these osmoregulatory substances had not yet decreased. Gas exchange parameters, including  $G_s$ ,  $P_{max}$ ,  $P_n$ , and  $T_r$ , were significantly reduced by DSRW. DSRW may reduce  $C_i$  by closing stomata, thereby decreasing  $P_n$  and  $T_r$ . A similar phenomenon has also been observed under salt stress. Rewatering after the early and mid-periods of drought stress significantly decreased  $C_i$ ,  $P_n$ , and  $T_r$  and significantly increased CAT. In contrast, rewatering after the early and late periods of drought stress did not significantly affect photosynthetic properties. This may be due to the strong recovery capacity of crops in the early stages, which allows for rapid restoration of photosynthetic ability after rewatering. However, this hypothesis needs to be further verified in future studies.

Although this study has minimized the influence of environmental factors during the literature collection process, it is challenging to eliminate the impact of natural factors on the experiment due to China's vast territory and the significant differences in climatic characteristics across regions. For instance, variations in soil properties, air temperature, and humidity in different regions can introduce some errors in the experiment. Meanwhile, the lack of sufficient data makes it difficult to refine the effects of DSRW on crop quality. Therefore, to address these limitations, further exploration is needed in future research.

## 5. Conclusions

This meta-analysis quantitatively synthesized 2567 studies from 90 publications to systematically evaluate the impacts of DSRW on crop performance. Key findings demonstrated that *Apiaceae* plants exhibited exceptional capacity in maintaining CY, while *Chenopodiaceae* and *Malvoaceae* showed significant improvements in WUE by 59.39% and 11.35% ( $p < 0.05$ ), respectively, under short-term water-saving irrigation. Multifactorial regression analysis revealed that the maximum CY (0.79%) was achieved under 90% drought stress during the early 3-day phase, whereas the peak WUE (0.12%) occurred under 30% drought stress during the late 67.51-day phase. Notably, drought stress universally impaired dry matter accumulation across studied crops, with *Zea mays* L. exhibiting the most severe reduction (−53.93%). Yield losses ranged from 15.11% in *Glycine max* (L.) Merr. to 29.15% in *Zea mays* L. Physiological mechanisms involved dual responses; drought stress simultaneously suppressed growth parameters and photosynthetic capacity while activat-

ing antioxidant defense systems and promoting osmolyte accumulation. These findings provide multidimensional mechanistic insights into crop drought resilience dynamics, emphasizing the necessity of optimizing stress timing and intensity to enhance agricultural stress resistance. This study establishes a theoretical foundation for improving crop productivity and advancing green-efficient agricultural production systems.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/agronomy15040911/s1>, Supplementary S1. Meta-analysis search terms; Supplementary S2. Search formulas for different databases; Supplementary S3. List of papers used for meta-analysis data extraction; Table S1. Literature data used for meta-analysis; Table S2. Species used for meta-analysis; Table S3. Genera used for meta-analysis; Table S4. Meta-analysis of the number of relevant indicators and effect size; Table S5. Multifactor regression analysis of optimal values. Figure S1. Plot of normal distribution of data; Figure S2. Meta-regression analysis between different intensities.

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## Abbreviations

The following abbreviations are used in this manuscript:

CAT	Catalase
Ci	Intercellular carbon dioxide concentration
CY	Crop yield
DSRW	Drought stress followed by rewatering
FC	Field water holding capacity
Gs	Stomatal conductance
MDA	Malondialdehyde
Pmax	Maximum net photosynthetic rate
Pn	Net photosynthetic rate
POD	Peroxidase
Pro	Proline
ROS	Reactive oxygen species
RWC	Relative leaf water content
SOD	Superoxide dismutase
SP	Soluble proteins
SPAD	Soil plant analysis development

SS	Soluble sugars
Tr	Transpiration rate
WUE	Water use efficiency

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