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RESEARCH ARTICLE

# Elevated $CO_2$ alleviates adverse effects of drought on plant water relations and photosynthesis: A global meta-analysis

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## Abstract

1. The elevated $CO_2$ concentration (e$CO_2$) is expected to improve plant water relations and carbon (C) uptakes, with a potential to mitigate drought stress. However, the interactive effects of e$CO_2$ and drought on plant physiology and growth are not clear.
2. We performed a meta-analysis on the interactive effects of e$CO_2$ and drought on plant water relations, photosynthesis, biomass production and allocation.
3. We found that e$CO_2$ did not lead to the conservation of soil water, but improved leaf water status under drought conditions as evidenced by a higher leaf relative water content (LRWC) and a less negative midday leaf water potential, resulting from reduced stomatal conductance ($g_s$) and increased root to shoot ratio. Elevated $CO_2$ retarded the response of $g_s$ to drought, which may be mediated by the decrease in leaf abscisic acid concentration under e$CO_2$ and drought. Drought imposed stomatal limitations on photosynthesis ($A$), which was alleviated by e$CO_2$ via increasing intercellular $CO_2$ concentration ($C_i$). This led to a stronger $A$ response to e$CO_2$ under drought, supporting the 'low $C_i$ effect'. However, no interaction of e$CO_2$ and drought was detected on plant biomass production. Intrinsic water use efficiency (iWUE) increased proportionally with e$CO_2$, while plant-scale WUE was less responsive to e$CO_2$. $C_3$ plants had advantages over $C_4$ plants in terms of $A$ and biomass production under e$CO_2$ and well-watered conditions rather than under e$CO_2$ and drought conditions. Drought caused a greater reduction in biomass for woody plants than for herbs. Plants growing in pots showed greater decreases in the physiology and biomass under drought than those growing in field.
4. *Synthesis*. These findings suggest that e$CO_2$ can alleviate the adverse impacts of drought on plant water relations and C sequestration, and are of significance in the prediction of plant growth and ecosystem productivity under global changes.

KEYWORDS
biomass, drought, elevated $CO_2$, gas exchange, global change ecology, water potential, water use efficiency

## 1 | INTRODUCTION

The concentration of atmospheric carbon dioxide ($CO_2$), which accounts for approximately 80% of the greenhouse trace gases, plays an important role in global climate regulation (Lashof & Ahuja, 1990). Elevated $CO_2$ ($eCO_2$) would inevitably cause climate warming, inducing more frequent and intense drought events (Dai, 2013; Spinoni et al., 2020). Elevated $CO_2$ and drought stress interactively affect plant physiology and growth in different ways, but the combined effects are far from clear (Becklin et al., 2017; Pan et al., 2022), which introduce uncertainty in the assessment of plant responses in future global change scenarios.

Drought stress has various effects on plant physiology. One immediate response of plants to drought stress is the reduction in stomatal conductance ($g_s$) to prevent water loss (Buckley, 2019). It is well known that stomatal closure during drought is a consequence of negative feedbacks such as hydraulic and chemical signalling [e.g. abscisic acid (ABA); Buckley, 2019; Flexas & Medrano, 2002]. The decrease in $CO_2$ availability at the level of the chloroplast due to the smaller $g_s$ under drought would inevitably inhibit photosynthesis ($A$). In addition, there are non-stomatal limitations that restrict $A$ in the face of water deficit (Flexas & Medrano, 2002). The drought-induced decrease in $A$ may cause carbon (C) limitation to plant growth (McDowell et al., 2008). In contrast, it is suggested that plant growth and $A$ are decoupled in water-limited environments because plant growth is sink-limited under drought (Muller et al., 2011).

On the other hand, $eCO_2$ may interact with drought stress through the 'water saving effect' and/or the 'low intercellular $CO_2$ concentration ($C_i$) effect'. The 'water saving effect' depicts that a lower $g_s$ under $eCO_2$ reduces plant transpiration, resulting in a higher soil water content (SWC; Duursma & Medlyn, 2012), which has been observed in both grasslands and forests (Leuzinger & Körner, 2007; Morgan et al., 2004). For example, Niklaus et al. (1998) showed that $eCO_2$ increased SWC, which would delay the onset of drought stress. However, Paudel et al. (2018) showed that SWC under $eCO_2$ was typically higher than that under ambient $CO_2$ concentration ($aCO_2$), but the difference diminished when exposed to drought. There is also evidence that $eCO_2$ slowed down the rate of soil drying in the shorter term but not in the longer term (Parvin, Uddin, Tausz-Posch, et al., 2019). These discrepancies may suggest that the net effect of $eCO_2$ on SWC depends on the relative importance of the reduction in $g_s$ and the increases in leaf area and leaf temperatures (Gray et al., 2016; Jiang et al., 2021). A meta-analysis is needed to synthesize whether and under what conditions a positive effect of $eCO_2$ on SWC occurs.

Another potential mechanism underlying the interaction between $eCO_2$ and drought is the 'low $C_i$ effect' (Duursma & Medlyn, 2012; Kelly et al., 2016). It states that the drought-induced reduction in $C_i$ makes $A$ operate on the steep initial linear phase of the $A$-$CO_2$ curve (Ellsworth et al., 2012), and thus the relative response of $A$ to $eCO_2$ would become more pronounced under water-limited conditions (Duursma & Medlyn, 2012; Idso & Idso, 1994; Kelly et al., 2016). The enhanced $A$ under $eCO_2$, together with the potential 'water saving effect', is expected to amplify the relative response of biomass to $eCO_2$ under drought conditions (Duursma & Medlyn, 2012; Kelly et al., 2016); but the experimental evidence for this expectation is equivocal, with some experiments for it (Morgan et al., 2004; Ottman et al., 2001) while others against it (Gray et al., 2016; Kelly et al., 2016).

By reducing $g_s$ and increasing $A$, $eCO_2$ induces a proportional increase in the intrinsic water use efficiency (iWUE; Medlyn et al., 2011; Walker et al., 2021; Wang & Wang, 2021). Evidence from tree rings also suggests that iWUE increased with $eCO_2$ (van der Sleen et al., 2015). The higher iWUE under $eCO_2$ slows the rate of soil moisture depletion (Peñuelas et al., 2011), which may enhance the ability of plant drought resistance (Blum, 2009). However, it is unclear whether such phenomena would maintain under drought conditions. For example, an intercomparison study (De Kauwe et al., 2013) showed that ecosystem models disagreed with one another in how drought affected the proportional relationship between iWUE and $eCO_2$. In addition, it is also controversial whether the $eCO_2$-induced enhancement in iWUE is scale dependent. For example, Barton et al. (2012) reported that the WUE of a *Eucalyptus saligna* forest was enhanced equally at both leaf scale and canopy scale, whereas Kelly et al. (2016) showed that the whole-plant WUE of *Eucalyptus* seedlings was less responsive to $eCO_2$ than the leaf-scale WUE. Therefore, it is needed to determine whether drought would modulate the response of iWUE to $eCO_2$ and how the sensitivity of WUE would change from the leaf level to the plant level.

Decades of experiments manipulating $CO_2$ and water availability provide evidence that the magnitude and direction of plant responses may depend on plant functional groups as well as experimental factors. Plants with different photosynthetic pathways are demonstrated to have different responses of $A$ to $eCO_2$ under ample soil-water supply (Hasegawa et al., 2018; Leakey et al., 2006; Leakey et al., 2009). Specifically, $eCO_2$ stimulates the $A$ of $C_3$ plants regardless of water availability, whereas it does not stimulate the $A$ of $C_4$ plants until the onset of drought stress. This discrepancy is because $C_3$ plants and $C_4$ plants have different mechanisms to concentrate $CO_2$ (Wand et al., 1999). Similarly, previous meta-analyses have shown that woody plants are more responsive to $eCO_2$ than herbaceous plants (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007). Recently, Pan et al. (2022) reported that the above-ground net primary productivity of woody systems showed a stronger enhancement than that of grasslands under $eCO_2$.

With regard to experimental factors, whether plants are grown in pots or in field may affect $A$ response to $eCO_2$, because pot size may restrict root sink strength, leading to a photosynthetic acclimation (Arp, 1991). Experimental duration also affects growth responses to $eCO_2$ probably due to declining nitrogen (N) availability as experiments progress (Norby et al., 2010). Experimental protocols [e.g. free-air $CO_2$ enrichment (FACE), open-top chamber (OTC)] have been demonstrated to influence the above-ground biomass response to $eCO_2$ (de Graaff et al., 2006). Furthermore, drought treatments (e.g. withholding watering, imposing drying–rewetting cycles and keeping a constantly lower SWC) may affect plant responses to drought and their interaction with $eCO_2$ (He & Dijkstra, 2014). Generalizing the patterns associated the variation in plant responses and testing whether they can be explained by functional groups and/or experimental factors can enhance the predictive power in global change scenarios (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007).

To comprehensively assess the interactive effects of $eCO_2$ and drought on plant physiology and growth, we performed a meta-analysis based on 226 papers published from 1983 to 2022 worldwide to evaluate the effects of $eCO_2$, drought and their interaction on plant water status, photosynthesis, WUE, biomass production and allocation. We hypothesized that $eCO_2$ would result in higher SWC due to its negative effect on $g_s$ (H1); drought would reduce $A$ due to stomatal limitation, whereas $eCO_2$ would stimulate $A$ by increasing $C_i$, leading to a greater increase in $A$ in drought treatment than in well-watered treatment (H2); iWUE would increase in response to $eCO_2$, which would not differ between different watering treatments, but it would decrease when scaled to the plant level (H3); the responses of $C_4$ plants to $eCO_2$ would be more strongly modulated by drought than those of $C_3$ plants (H4); woody plants would show a greater response to the drought × $eCO_2$ interaction than herbs (H5); and pot experiments would be more restricted by drought, and less responsive to $eCO_2$ than field experiments (H6).

## 2 | MATERIALS AND METHODS

### 2.1 | Literature searching and data compiling

We searched the Web of Science and China National Knowledge Infrastructure using the following key words: "elevated $CO_2$" or "$CO_2$ enrichment" or "increasing $CO_2$" + "drought" or "water stress" or "reduced precipitation" + "plant responses". The studies had to meet the following criteria for selection: (1) Factorial experiments had four treatments: $aCO_2$ and well-watered treatment; $aCO_2$ and drought treatment; $eCO_2$ and well-watered treatment; $eCO_2$ and drought treatment. (2) Experimental and control plots were established within the same site, that is, same microclimate, vegetation and soil among the treatments. And (3) observations that received other treatments (e.g. warming) were excluded (Figure S1). In total, 226 papers worldwide published from 1983 to 2022 met the criteria and were included in this synthesis (Figure S2; Reference S1). The dataset included 166 plant species from 45 families, among which there were 145 $C_3$ species from 42 families, 18 $C_4$ species from 2 families and 3 CAM species from 2 families. Most sites were located in Europe (77 studies), followed by North America (65 studies), Asia (45 studies), Oceania (27 studies), South America (9 studies) and Africa (2 studies; Figure S2).

The response variables extracted included the following: leaf relative water content (LRWC, %), predawn leaf water potential ($\Psi_{predawn}$, MPa), midday leaf water potential ($\Psi_{midday}$, MPa), WUE at the plant level ($WUE_{plant}$, mg/g and g/L), SWC (%), stomatal conductance ($g_s$, mol $H_2O$ $m^{-2}$ $s^{-1}$), photosynthesis ($A$, μmol $CO_2$ $m^{-2}$ $s^{-1}$), intrinsic WUE [iWUE = $A/g_s$, μmol $CO_2$ (mol $H_2O)^{-1}$], intercellular $CO_2$ concentration ($C_i$, μmol $mol^{-1}$), ratio of $C_i$ to atmospheric $CO_2$ concentration ($C_i$:$C_a$), leaf ABA concentration (mg/g), above-ground biomass (g), below-ground biomass (g), total plant biomass (g), root to shoot ratio (R/S) and leaf area ($cm^2$). Above-ground biomass and below-ground biomass were directly obtained from the original papers or derived from R/S and plant biomass, and vice versa. Notably, to maximize the power of this meta-analysis, we included both volumetric and gravimetric SWC from both field and pot experiments. For the field experiments, the measurements of SWC were taken at 0–1.8 m depths (Albert et al., 2011; Manderscheid et al., 2014; Wall et al., 2001).

The mean and standard deviation (SD) of each treatment were extracted from the tables or figures of the original papers using GetData Graph Digitizer 2.26. If a mean and a standard error (SE) were given, the SD was calculated as:

$$SD = SE\sqrt{n}, \tag{1}$$

where $n$ is the sample size. If a mean and a confidence interval (CI) were available, the SD was calculated as:

$$SD = \left(CI_u - CI_l\right)\sqrt{n} / 2Z_{\alpha/2}, \tag{2}$$

where $CI_u$ and $CI_l$ are the upper and lower limits of 95% CI, respectively; and $Z_{\alpha/2}$ is the $Z$ score at $\alpha = 0.05$. In the cases that there were no SE, SD or CI, SDs were assigned as 1/10 of the means (Luo et al., 2006).

The information on species and experimental factors was also collected wherever possible. If the response variables were reported over time, only the observations over the longest treatment duration were collected. However, the last points of some variables were almost zero in some studies; in these cases, the points before the zero points were used. For studies where same plant species had multiple $eCO_2$ levels and/or drought intensities, we considered them as separate observations. Therefore, the dataset contained some repeated data entries from the same study, and corresponding multiple $eCO_2$ or drought treatments with the same $aCO_2$ or well-watered treatments. The non-independent observations were tackled using the 'shifting the unit of analysis' approach (Cheung, 2015; Liang et al., 2020) in Section 2.3. In our database, species were categorized by photosynthetic pathways ($C_3$ plant and $C_4$ plant, $C_3$ herb and $C_4$ herb, $C_3$ grass and $C_4$ grass, and $C_3$ crop and $C_4$ crop) and plant growth forms (woody plant and $C_3$ herb, tree and shrub, and $C_3$ grass and $C_3$ forb).

We also assessed the effects of experimental protocol (e.g. FACE, growth chamber and OTC), growth condition (in pot vs. in field), pot size [small (≤10 L) vs. big (>10 L)], drought duration [short-term (0–30 days), medium-term (31–90 days) and long-term (>90 days) treatments] and drought manipulation type on plant responses to $eCO_2$ and drought. However, multiple individuals were planted in one pot in some experiments, which were excluded from the analysis of the effect of pot size on plant responses.

Experiments using growth chamber, greenhouse and glasshouse were all lumped into growth chamber. Drought manipulation was grouped into three types: keeping a constant SWC throughout the experimental duration (Type I), undergoing drying–rewetting cycles (Type II) and withholding water supply and allowing SWC decreasing over time (Type III).

## 2.2 | Meta-analysis

The $aCO_2$ and well-watered treatments were considered as the baselines for the $eCO_2$ and drought treatments, respectively. The respective response ratios to $CO_2$ and water manipulation ($r_c$ and $r_w$, respectively) were calculated as:

$$\text{for } eCO_2 \text{ effect in well-watered treatment: } r_c^W = \frac{\overline{X}_{C_eW}}{\overline{X}_{C_aW}}; \tag{3}$$

$$\text{for } eCO_2 \text{ effect in drought treatment: } r_c^D = \frac{\overline{X}_{C_eD}}{\overline{X}_{C_aD}}; \tag{4}$$

$$\text{for drought effect in } aCO_2 \text{ treatment: } r_w^{aCO_2} = \frac{\overline{X}_{C_aD}}{\overline{X}_{C_aW}}; \tag{5}$$

$$\text{for drought effect in } eCO_2 \text{ treatment: } r_w^{eCO_2} = \frac{\overline{X}_{C_eD}}{\overline{X}_{C_eW}}; \tag{6}$$

where $\overline{X}$ represents the mean, $C_e$ and $C_a$ represents $eCO_2$ and $aCO_2$ treatments, and W and D represents well-watered and drought treatments, respectively. Following Jiang et al. (2020), the interactive response ratio to $eCO_2$ and drought ($r$, i.e. the interactive effect of drought and $eCO_2$) was calculated as:

$$r = \frac{\overline{X}_{C_eD}}{\overline{X}_{C_aD}} \Big/ \frac{\overline{X}_{C_eW}}{\overline{X}_{C_aW}}, \tag{7}$$

which was linearized as:

$$\ln(r) = \ln\left(\frac{\overline{X}_{C_eD}}{\overline{X}_{C_aD}}\right) - \ln\left(\frac{\overline{X}_{C_eW}}{\overline{X}_{C_aW}}\right). \tag{8}$$

This interaction term is equivalent to the difference between the log $eCO_2$ response ratio at drought treatment and the log $eCO_2$ response ratio at well-watered treatment. The variance of $r$ ($v$) was calculated as:

$$v = \frac{SD^2{}_{C_eD}}{n_{C_eD}\overline{X}^2{}_{C_eD}} + \frac{SD^2{}_{C_eW}}{n_{C_eW}\overline{X}^2{}_{C_eW}} + \frac{SD^2{}_{C_aD}}{n_{C_aD}\overline{X}^2{}_{C_aD}} + \frac{SD^2{}_{C_aW}}{n_{C_aW}\overline{X}^2{}_{C_aW}}, \tag{9}$$

where $n_{C_eD}$, $n_{C_eW}$, $n_{C_aD}$, and $n_{C_aW}$ are the sample sizes of $eCO_2$ and drought treatment, $eCO_2$ and well-watered treatment, $aCO_2$ and drought treatment, and $aCO_2$ and well-watered treatment, respectively.

To check how normalizing plant responses to $eCO_2$ with the magnitude of the $CO_2$ treatments influences the results of the response ratio, we also calculated a $\beta$-factor for each response variable following previous meta-analyses (Walker et al., 2021; Wang & Wang, 2021). Specifically, the $\beta$-factor was calculated as:

$$\beta = \ln\left(\overline{X_t} / \overline{X_c}\right) / \ln\left(eCO_2 / aCO_2\right), \tag{10}$$

where $\overline{X_t}$ and $\overline{X_c}$ are means of a concerned variable in the treatment and control groups, respectively. The variance of the $\beta$-factor ($v_\beta$) was calculated as:

$$v_\beta = \left(\frac{S_t^2}{n_t\overline{X_t^2}} + \frac{S_c^2}{n_c\overline{X_c^2}}\right) / \left(\ln\left(eCO_2/aCO_2\right)\right)^2. \tag{11}$$

Comparing the results of the $\beta$-factor and those of the response ratio (Figures S13–S17; Table S13), we found that the $\beta$-factors of $eCO_2$ for almost all the 16 response variables at both well-watered and drought treatments were consistently 38.8%–42.0% greater than the corresponding response ratios (Table S13), except for the R/S ratio and ABA concentration at well-watered treatments (they were not significantly affected by $eCO_2$). Considering (1) the normalization of plant responses to drought was impossible because the degree of drought treatments in some studies cannot be determined; (2) the $\beta$-factors and response ratios had the same direction but with relatively consistent differences in the magnitude, which maintained the conclusions; and (3) a clarity of presentation, we only reported the response ratios in the main text, and kept the $\beta$-factors in the supporting information.

## 2.3 | Independence and weights

The 'shifting the unit of analysis' approach (Cheung, 2015) was used to tackle the non-independent observations described above. The initial weight ($w$) of each observation was calculated as:

$$w = 1 / v. \tag{12}$$

The weight of non-independent $r$ ($w'$) was adjusted by the total number ($n'$) of a given variable of the same species from the same study (Liang et al., 2020):

$$w' = w / n'. \tag{13}$$

A random effect model was applied to estimate the mean and the 95% CI of the log-transformed response ratios for each variable, which were weighted by the variance of individual studies. Significant responses were recognized if the 95% CI did not overlap with zero. The between-group heterogeneity was compared by the omnibus test, with the effects of moderators considered being significant for $p < 0.05$. The meta-analysis was conducted with the *Metafor* function in R package.

We checked possible publication bias and data quality using the funnel plots and leave-one-out function. The variables were largely independent of the influence of publication bias and outliers (Figures S3 and S4).

## 3 | RESULTS

### 3.1 | Responses of plant water relations

Drought treatment reduced LRWC (−24.7% to −18.0%) and $\Psi_{midday}$ (−45.0% to −37.2%; Figure 1a), while $eCO_2$ stimulated LRWC (7.9%) and $\Psi_{midday}$ (16%) under drought conditions rather than under well-watered conditions (Figure 1b). The drought × $eCO_2$ interaction on LRWC (8.6%) and $\Psi_{midday}$ (9.5%) were positive (Figure 1c). Drought treatment reduced $\Psi_{predawn}$ (−59.5% to −57.6%) and SWC (−57.4% to −55.6%; Figure 1a), while $eCO_2$ had no significant effect on $\Psi_{predawn}$ and SWC (Figure 1b). Both drought treatment (10.9%–16.5%; Figure 1a) and $eCO_2$ (37.6%–43.4%) enhanced $WUE_{plant}$ (Figure 1b). There were no significant interactions between drought and $eCO_2$ on $\Psi_{predawn}$, SWC and $WUE_{plant}$ (Figure 1c).

### 3.2 | Responses of leaf gas exchanges

Overall, drought and $eCO_2$ decreased $g_s$ by 55.9%–61.1% (Figure 2a) and 19.7%–29.2% (Figure 2b), respectively. However, the drought × $eCO_2$ interaction increased $g_s$ by 10.7% (Figure 2c). Drought reduced *A* by 38.2%–42.2% (Figure 2a), whereas $eCO_2$ increased *A* by 37.2%–46.3% (Figure 2b); and their interaction increased *A* by 7.1% (Figure 2c). Drought increased iWUE (22.5%–26.0%), but decreased $C_i$ (−14.5% to −10.9%) and $C_i$:$C_a$ (−9.8% to −9.2%; Figure 2a). $eCO_2$ enhanced iWUE (84.2%–88.9%) and $C_i$ (59.0%–65.8%), but had no significant effect on $C_i$:$C_a$ (Figure 2b). The drought × $eCO_2$ interaction had no significant effect on iWUE, $C_i$ and $C_i$:$C_a$ (Figure 2c). $eCO_2$ increased iWUE proportionally at both well-watered ($\beta = 1.06$) and drought ($\beta = 1.03$) treatments (Figure S13; Table S13). Drought treatment enhanced leaf ABA concentration by 180.3% and 62.5% under $aCO_2$ and $eCO_2$, respectively (Figure 2a), whereas $eCO_2$ had no significant effect on leaf ABA concentration under well-watered conditions but decreased it under drought conditions (−38.4%; Figure 2b). The drought × $eCO_2$ interaction decreased leaf ABA concentration by 38.7% (Figure 2c).

### 3.3 | Responses of biomass production and allocation

Drought treatment decreased above-ground biomass (−48.1% to −46.2%), below-ground biomass (−38.2% to −35.2%) and total plant biomass (−43.4% to −43.0%; Figure 3a), whereas $eCO_2$ increased above-ground biomass (29.1%–33.4%), below-ground biomass (33.1%–39.8%) and total plant biomass (31.7%–33.8%; Figure 3b). The drought × $eCO_2$ interaction was neutral for above-ground biomass and total plant biomass, but was positive for below-ground biomass (5.6%; Figure 3c). Drought treatment stimulated R/S (20.8%–27.0%), while $eCO_2$ stimulated it under drought conditions (5.4%) but not under well-watered conditions (Figure 3a). The effect of drought and $eCO_2$ interaction was positive on R/S (6.0%; Figure 3c). Drought treatment decreased leaf area (−42.1% to −41.0%), whereas $eCO_2$ increased it (18.6%–19.8%; Figure 3b). The drought × $eCO_2$ interaction was neutral on leaf area (Figure 3c).

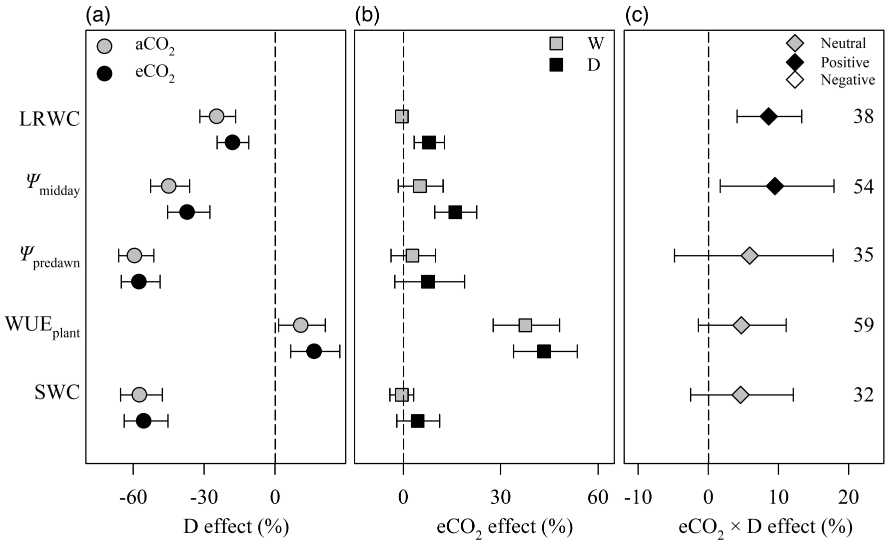

**FIGURE 1** Effects of elevated $CO_2$ ($eCO_2$) and drought (D) on plant water relations. (a) The effect of D at ambient $CO_2$ ($aCO_2$) and $eCO_2$. (b) The effect of $eCO_2$ at well-watered treatment (W) and D. (c) The interactive effect of $eCO_2$ and D. Response variables are: leaf relative water content (LRWC), predawn leaf water potential ($\Psi_{predawn}$), midday leaf water potential ($\Psi_{midday}$), water-use efficiency at the plant level ($WUE_{plant}$), and soil water content (SWC). The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The numbers on the right represent the numbers of observations included

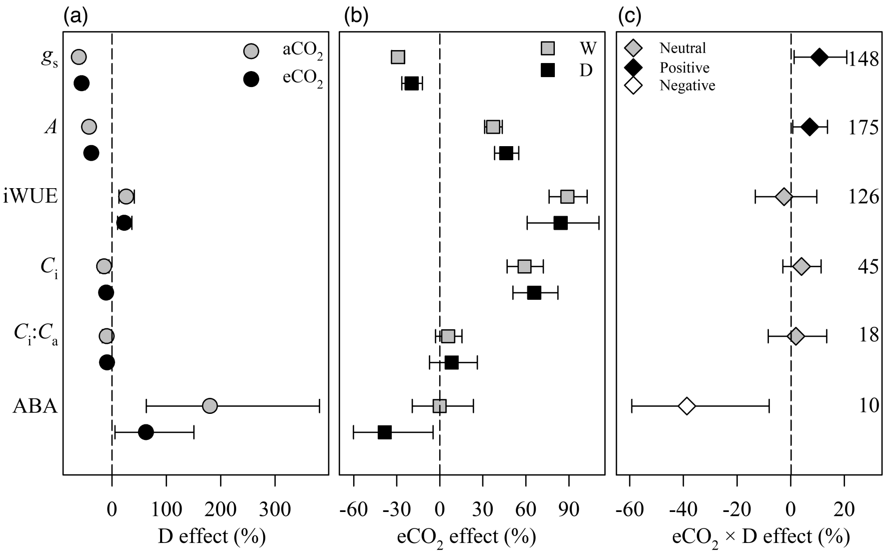

**FIGURE 2** Effects of elevated $CO_2$ ($eCO_2$) and drought (D) on plant leaf gas exchanges. (a) The effect of D at ambient $CO_2$ ($aCO_2$) and $eCO_2$. (b) The effect of $eCO_2$ at well-watered (W) and D. (c) The interactive effect of $eCO_2$ and D. Response variables are: stomatal conductance ($g_s$), photosynthesis ($A$), intrinsic water-use efficiency (iWUE = $A/g_s$), intercellular $CO_2$ concentration ($C_i$), the ratio of $C_i$ to atmospheric $CO_2$ concentration ($C_i$:$C_a$) and leaf abscisic acid concentration (ABA). The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The numbers on the right represent the numbers of observations included

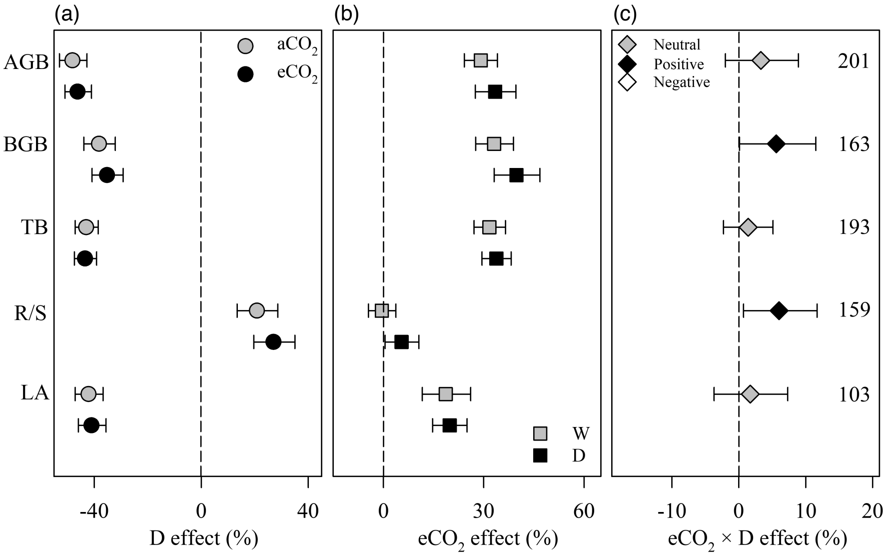

**FIGURE 3** Effects of elevated $CO_2$ ($eCO_2$) and drought (D) on plant biomass production and allocation. (a) The effect of D at ambient $CO_2$ ($aCO_2$) and $eCO_2$. (b) The effect of $eCO_2$ at well-watered treatment (W) and D. (c) The interactive effect of $eCO_2$ and D. Response variables are: above-ground biomass (AGB), below-ground biomass (BGB), total plant biomass (TB), root to shoot ratio (R/S) and leaf area (LA). The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The numbers on the right represent the numbers of observations included

## 3.4 | The effect of $C_3$ and $C_4$ photosynthetic pathway on plant responses

The positive effect of $eCO_2$ on $\Psi_{midday}$ was stronger for $C_4$ plants than for $C_3$ plants at the drought treatment ($p$ = 0.05; Figure 4b; Table S1). The $eCO_2$-induced increase in $WUE_{plant}$ in $C_4$ plants was significantly smaller than that in $C_3$ plants under well-watered conditions ($p < 0.001$; Figure 4a), but was similar to under drought conditions ($p > 0.05$; Figure 4b); drought treatment had a positive effect on the $WUE_{plant}$ response to $eCO_2$ for $C_4$ plants instead of $C_3$ plants ($p$ = 0.01; Figure 4c; Table S1). Under well-watered conditions, the effects of $eCO_2$ on $A$ ($p$ = 0.005), above-ground biomass ($p < 0.001$), below-ground biomass ($p$ = 0.03), total plant biomass ($p$ = 0.02) and leaf area ($p$ = 0.01) were positive for $C_3$ plants but not for $C_4$ plants (Figure 4a), whereas under drought conditions, comparable positive effects of $eCO_2$ were observed for $C_3$ plants and $C_4$ plants ($p > 0.05$; Figure 4b); the interactions between $eCO_2$ and drought on $A$ ($p$ = 0.04), above-ground biomass ($p$ = 0.006) and leaf area ($p$ = 0.05) were positive for $C_4$ plants rather than for $C_3$ plants, with the difference being significant (Figure 4c; Table S1). Additionally, the responses of $C_3$ herbs and $C_4$ herbs (Figure S5; Table S2), $C_3$ grass and $C_4$ grass (Figure S6; Table S3) and $C_3$ crop and $C_4$ crop (Figure S7; Table S4) to $eCO_2$ and drought generally mirrored those of $C_3$ plants and $C_4$ plants.

## 3.5 | The effect of plant growth form on plant responses

Within $C_3$ functional groups, plants showed different responses to drought and $eCO_2$. Decreases in $\Psi_{midday}$ caused by drought were greater for herbs than for woody plants at both $aCO_2$ ($p$ = 0.04; Figure 5a; Table S5) and $eCO_2$ treatments ($p$ = 0.02; Figure 5b; Table S5). The drought-induced reductions in $g_s$ ($p$ = 0.04) and $C_i$ ($p$ = 0.04) were significantly greater for herbs than for woody plants

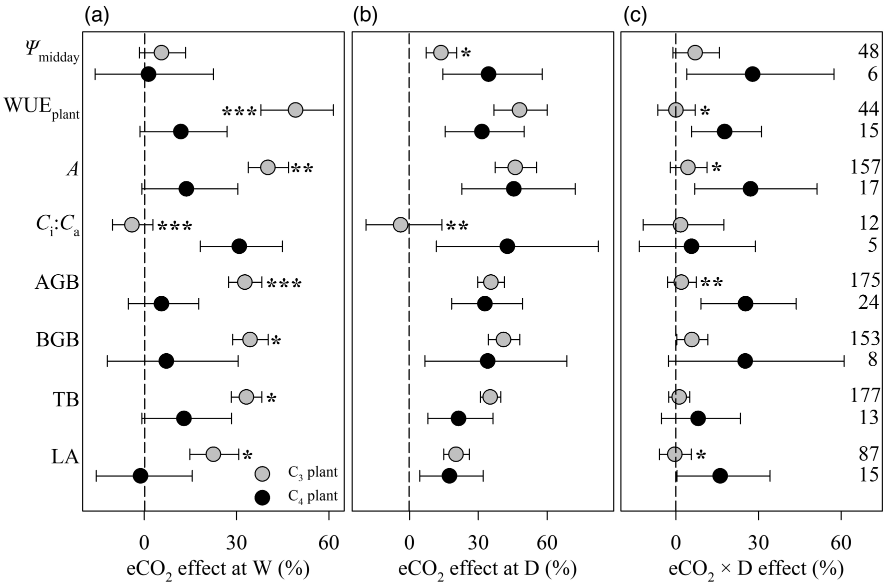

**FIGURE 4** Comparisons of the responses of $C_3$ plants and $C_4$ plants to elevated $CO_2$ ($eCO_2$) and its interaction with drought (D). (a) The effect of $eCO_2$ at well-watered treatment (W). (b) The effect of $eCO_2$ at D. (c) The interactive effect of $eCO_2$ and D. The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The asterisks indicate significant differences in the responses between $C_3$ plants and $C_4$ plants (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The numbers on the right represent the numbers of observations included. Refer to Figures 1–3 for the abbreviations

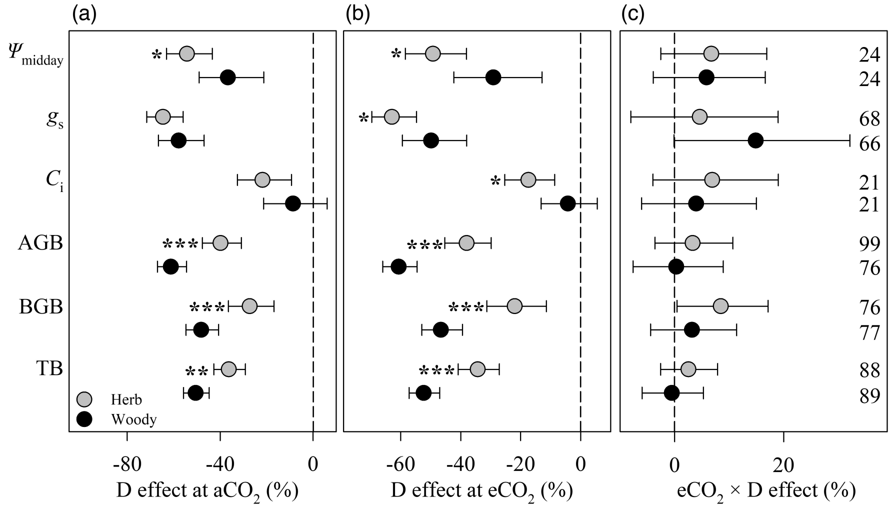

**FIGURE 5** Comparisons of the responses of $C_3$ herbs and woody plants to drought (D) and its interaction with elevated $CO_2$ ($eCO_2$). (a) The effect of D at ambient $CO_2$ ($aCO_2$). (b) The effect of D at $eCO_2$. (c) The interactive effect of $eCO_2$ and D. The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The asterisks indicate significant differences in the responses between herbs and woody plants (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The numbers on the right represent the numbers of observations included. Refer to Figures 1–3 for the abbreviations

at $eCO_2$ (Figure 5b; Table S5). The decreases in above-ground biomass, below-ground biomass and total plant biomass in response to drought were stronger for woody plants than for herbs regardless of $CO_2$ treatments ($p < 0.05$; Figure 5a and b; Table S5). Compared with herbs, $A$ of woody plants showed a larger response to $eCO_2$ ($p = 0.04$; Table S5). However, woody plants and herbs showed no significant differences in their responses to the combination of drought and $eCO_2$ ($p > 0.05$; Figure 5c; Table S5). Under well-watered conditions, no significant difference in $g_s$ response to $eCO_2$ was detected between grass and forbs ($p > 0.05$; Figure S8a; Table S6); however, under drought conditions, a decrease in $g_s$ was observed for forbs but not for grass, although the difference was insignificant ($p = 0.1$; Figure S8b; Table S6). The drought × $eCO_2$ interaction was positive on $g_s$ for grass but was neutral for forbs ($p = 0.005$; Figure S8c; Table S6). There was a positive interaction between drought and $eCO_2$ on $g_s$ for shrubs rather than for trees, with the difference being significant ($P = 0.05$; Figure S9c; Table S7).

## 3.6 | The effect of experimental factors on plant responses

Experimental factors influenced the individual effects of drought and $eCO_2$ rather than their interactive effects on plants. Specifically, drought duration significantly affected the responses of $\Psi_{predawn}$, $WUE_{plant}$, $A$, above-ground biomass, below-ground biomass, total plant biomass and leaf area (Figure 6; Table S8). The negative effect of drought duration on $\Psi_{predawn}$ at $aCO_2$ treatment weakened with increasing drought durations ($p = 0.04$; Figure 6a; Table S8). Similar patterns were observed for $A$ at

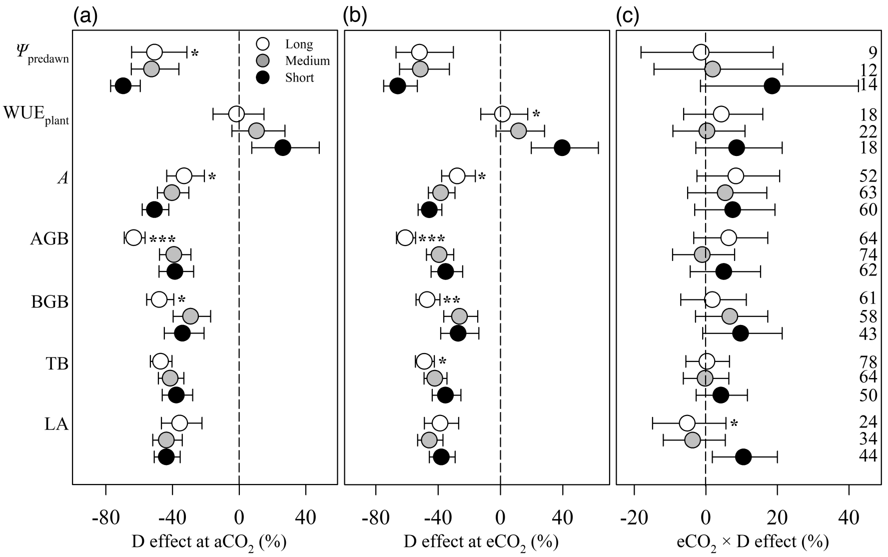

**FIGURE 6** Effects of drought durations on plant responses to drought (D) and its interaction with elevated $CO_2$ ($eCO_2$). (a) The effect of D at ambient $CO_2$ ($aCO_2$). (b) The effect of D at $eCO_2$. (c) The interactive effect of $eCO_2$ and D. The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The asterisks indicate significant differences in the responses among the drought durations (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The numbers on the right represent the numbers of observations included. Refer to Figures 1–3 for the abbreviations

both $aCO_2$ ($p = 0.03$; Figure 6b; Table S8) and $eCO_2$ ($p = 0.02$; Figure 6b; Table S8). The drought-induced increase in $WUE_{plant}$ was observed in short term but disappeared in medium- or long-term drought under $eCO_2$ ($p = 0.02$; Figure 6b; Table S8). The mean effect size for above-ground biomass and below-ground biomass decreased the most in the long-term treatment regardless of $CO_2$ treatments ($p < 0.05$; Figure 6a,b; Table S8). The negative effect of drought at $eCO_2$ on total plant biomass was weakest in the short-term treatment ($p = 0.04$; Figure 6b; Table S8). The drought × $eCO_2$ interaction increased leaf area only in the short-term treatment ($p = 0.03$; Figure 6c; Table S8). Above-ground biomass, below-ground biomass and total plant biomass in experiments using GC and OTC responded more strongly to $eCO_2$ than those using FACE under well-watered conditions ($p < 0.05$; Figure 7a; Table S9). The decreases in $\Psi_{predawn}$, $A$, above-ground biomass, below-ground biomass and total plant biomass in response to drought were stronger in pot than in field experiments regardless of $CO_2$ treatments ($p < 0.05$; Figure 8a,b; Table S10). The drought-induced reduction in $g_s$ was stronger in pot than in field experiments at $eCO_2$ ($p = 0.04$; Figure 8b; Table S10) rather than at $aCO_2$ ($p > 0.05$; Figure 8a; Table S10). Drought decreased $\Psi_{midday}$ to a greater extent in the experiments using big pots than in those using small pots at $aCO_2$ ($p = 0.03$; Figure S10a; Table S11), and there was positive interaction between drought and $eCO_2$ on $\Psi_{midday}$ in the experiments using big pots but not small pots ($p < 0.001$; Figure S10c; Table S11). The negative effects of drought on $g_s$, $A$, above-ground biomass, below-ground biomass and total plant biomass were strongest in Type III drought manipulation at both $aCO_2$ and $eCO_2$ compared with Type I and Type II manipulations ($p < 0.05$; Figure S11a; Table S12).

## 4 | DISCUSSION

### 4.1 | $eCO_2$ improves plant water relations without increasing SWC

We found that drought stress caused marked reductions in SWC regardless of $CO_2$ concentrations, resulting in a decrease in soil water availability. This is inconsistent with our expectation (H1) and some previous studies (Parvin, Uddin, Fitzgerald, et al., 2019; Robredo et al., 2007). It has been shown that the 44% decrease of $g_s$ in response to $eCO_2$ outweighed the 24% increase of leaf area, resulting in a slower soil water depletion under drought (Parvin, Uddin, Fitzgerald, et al., 2019); similar patterns of $g_s$ and leaf area responses to $eCO_2$ were observed in this study, which, however, did not translate into a higher SWC regardless of watering regimes, as recently reported by Jiang et al. (2021). A possible explanation is that $eCO_2$ enhances leaf temperature, which may partially counteract the reduction in plant transpiration due to the reduced $g_s$ caused by $eCO_2$ (Gray et al., 2016). Additionally, it has been shown that the conservation of soil moisture induced by $eCO_2$ mainly occurred at shallow soil layers (Manderscheid et al., 2014). However, soil evaporation is mainly from the upper soil layer, which likely speeds up the consumption of the soil water saved by the reduced transpiration under $eCO_2$ (Manderscheid et al., 2018). A process-based modelling also showed that $eCO_2$ did not increase soil moisture in spite of decreasing transpiration, but increased evaporation (Kellner et al., 2019). These findings suggest that changes in leaf area, leaf temperature and soil evaporation may collectively counteract the benefits of $eCO_2$ on soil water savings (Wilson et al., 1999).

Although no 'water saving effect' was detected, we found that $eCO_2$ improved leaf water status indicated by a higher LRWC under the combination of $eCO_2$ and drought stress. The improved leaf water status of droughted plants under $eCO_2$ has been shown to be accompanied by increases in $\Psi_{midday}$ and $\Psi_{predawn}$ (Robredo et al., 2007). However, a less negative $\Psi_{midday}$ rather than $\Psi_{predawn}$ was observed in the present study. This is consistent with the finding of Atwell et al. (2007) that the improved water status only occurred during daylight hours, suggesting that the effect of $eCO_2$ was a result of decreased transpiration rather than increased SWC (Field et al., 1995). Given that a higher $eCO_2$-induced increase in LRWC was observed only when drought occurred, the decreased sensitivity of $g_s$ to $eCO_2$ caused by drought suggests that there may be other mechanisms that contributed to the improved leaf water status. For example, root biomass production was preferentially stimulated by $eCO_2$ when plants were subjected to water stress, leading to a higher R/S. This proportionally larger investment of C in root growth may allow plants to have more extensive root systems and improve

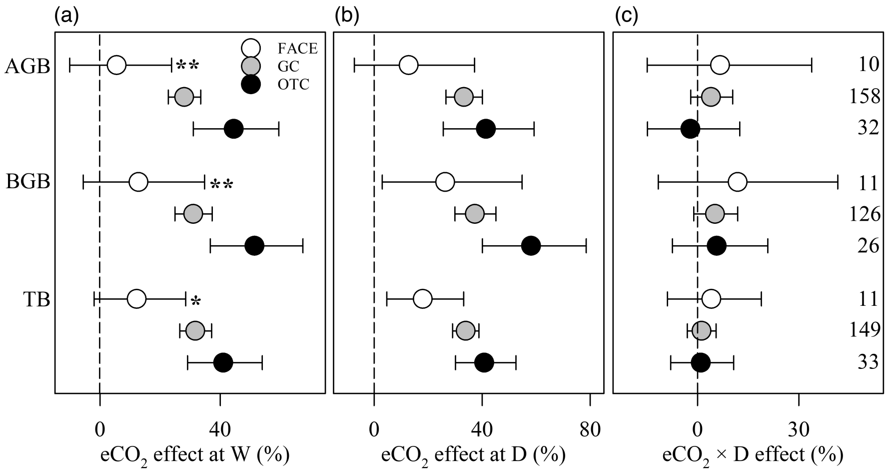

FIGURE 7 Effects of experimental protocols on plant responses to elevated $CO_2$ ($eCO_2$) and its interaction with drought (D). (a) The effect of $eCO_2$ at well-watered treatment (W). (b) The effect of $eCO_2$ at D. (c) The interactive effect of $eCO_2$ and D. The effect size is calculated as a percentage response (%). FACE, free-air $CO_2$ enrichment; GC, growth chamber; OTC, open top chamber. The error bars represent 95% confidence intervals. The asterisks indicate significant differences in the responses among the experimental protocols (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The numbers on the right represent the numbers of observations included. Refer to Figures 1–3 for the abbreviations

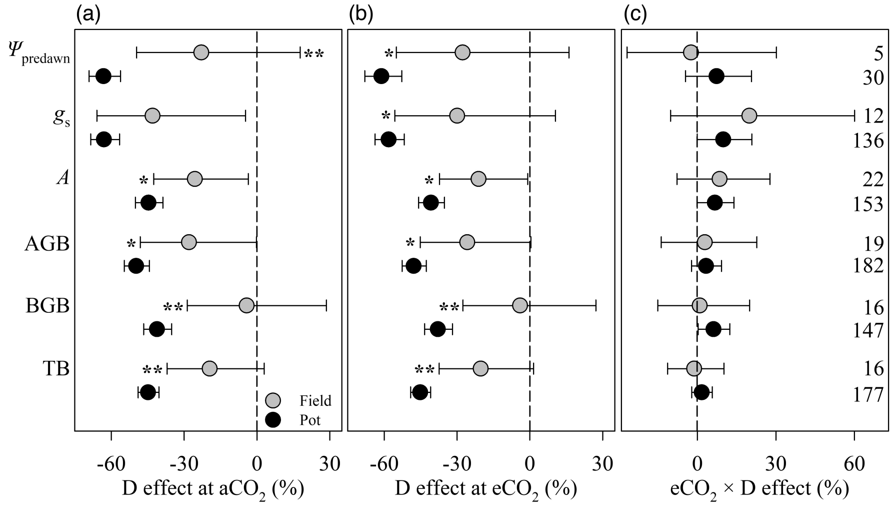

FIGURE 8 Effects of growth conditions on plant responses to drought (D) and its interaction with elevated $CO_2$ ($eCO_2$). (a) The effect of D at ambient $CO_2$ ($aCO_2$). (b) The effect of D at $eCO_2$. (c) The interactive effect of $eCO_2$ and D. The effect size is calculated as a percentage response (%). The error bars represent 95% confidence intervals. The asterisks indicate significant differences in the responses between the growth conditions (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The numbers on the right represent the numbers of observations included. Refer to Figures 1–3 for the abbreviations

their water acquisition (Idso & Idso, 1994; Wullschleger et al., 2002). These findings suggest that stomatal control and morphological adjustments jointly improve leaf water status under $eCO_2$ and drought (Jiang et al., 2021), and $eCO_2$ consequently mitigates the impacts of drought stress on plants even without changing SWC (De Kauwe et al., 2021).

## 4.2 | $eCO_2$ alleviates adverse effects of drought on photosynthesis

We found that the drought-induced reduction in $g_s$ was concurrent with the increase in leaf ABA concentration, suggesting that ABA may be involved in regulating stomatal closure under drought stress (Comstock, 2002). However, the drought-induced enhancement in leaf ABA concentration was less pronounced when plants were exposed to $eCO_2$. This negative interaction between drought and $eCO_2$ has been suggested to delay stomatal response to drought (Li et al., 2020), which was supported by our finding that the response of $g_s$ to drought was reduced by $eCO_2$. Similar responses have been observed in *Lycopersicon esculentum* (Liu et al., 2019), *Fagus sylvatica* and *Castanea sativa* (Heath, 1998). The smaller reduction in $g_s$ caused by drought at $eCO_2$ was also in accordance with the aforementioned finding that LRWC and $\Psi_{midday}$ were increased by $eCO_2$ at drought conditions. This result indicates that $eCO_2$ indirectly impacted leaf water status through its effect on $g_s$, which, in turn, affected the response of $g_s$ to drought. However, $eCO_2$ changed the magnitude of $g_s$ response to drought but not the direction, suggesting that SWC may play an important role in stomatal control, and that stomata respond to the factors that influence plant water status (Buckley, 2019).

Following the decreased $g_s$ under drought, there was a decrease in $C_i$, suggesting that drought imposed stomatal limitation on *A* (Flexas & Medrano, 2002). In contrast, $eCO_2$ alleviated stomatal limitation by stimulating $C_i$, resulting in a more pronounced enhancement in *A* under drought treatment than under well-watered treatment; this provides evidence for the 'low $C_i$ effects' hypothesis (Ellsworth et al., 2012; Kelly et al., 2016). In addition, the less sensitive of $g_s$ to drought for plants growing under $eCO_2$ may be another reason for the positive interaction between drought and $eCO_2$ on *A*. However, the $eCO_2$-induced stimulation of biomass was independent of water availability. This is likely because the growth response to $eCO_2$ increases with decreasing soil moisture only when $eCO_2$ produces relatively wet soil (Fatichi et al., 2016; Morgan et al., 2004; Ottman et al., 2001). Given that no 'water saving effect' was detected in this study, it is logical that there was no positive interaction between drought and $eCO_2$ on biomass.

## 4.3 | $eCO_2$ increases WUE, but the magnitude is scale dependent

At the leaf level, iWUE increased under $eCO_2$ as a consequence of the reduced $g_s$ and enhanced *A*, in line with previous meta-analyses (Ainsworth & Long, 2005; Wang & Wang, 2021). It has been suggested that the impact of $eCO_2$ on WUE was lower in plants under drought (De Kauwe et al., 2013; Robredo et al., 2007). However, drought did not affect the response of iWUE to $eCO_2$, which, combined with the finding of the proportional increase in iWUE with $eCO_2$ regardless of water availability, supports the optimal stomatal behaviour theory that $g_s$ and *A* are well coupled to maximize C uptake and minimize water loss (Medlyn et al., 2011; Walker et al., 2021; Wang & Wang, 2021). Similarly, it has been observed that when the $eCO_2$-induced stimulation of *A* was greatest, the reduction in $g_s$ was smallest, suggesting a tight coupling between *A* and $g_s$ (Pastore et al., 2019). Such an iWUE response to $eCO_2$ has been suggested to be regulated by three mechanisms, that is, maintaining a constant $C_i$, $C_i - C_a$ and $C_i$:$C_a$ (Saurer et al., 2004). The present meta-analysis extends previous empirical findings and model simulations by showing that *A* and $g_s$ are regulated in a way to keep the $C_i$:$C_a$ constant in response to $eCO_2$, which is independent of soil water availability; this suggests a consistent and moderate contribution of $eCO_2$ to the increase in iWUE (Ainsworth & Long, 2005; De Kauwe et al., 2013; Peñuelas et al., 2011).

At the individual level, there was also an $eCO_2$-stimulated $WUE_{plant}$, suggesting that the higher biomass production was not accompanied by a proportional increase in water use; this is in line with the large-scale evidence that increased terrestrial C uptake by $eCO_2$ does not cause an enhancement in water use because of the increased WUE (Cheng et al., 2017). It has been shown that $eCO_2$ improved $WUE_{plant}$ to a greater extent in drought treatment than in well-watered treatment (Qiao et al., 2010). However, no interaction between $eCO_2$ and drought was detected in this study, likely because of the lack of positive interaction between $eCO_2$ and drought on plant biomass.

There is evidence that the sensitivity of WUE to $eCO_2$ decreased from leaf to plant levels (Centritto et al., 1999; Kelly et al., 2016; Knauer et al., 2017), which was confirmed by the present study. This is likely because additional feedbacks may play a role in scaling up iWUE to the whole-plant level (Centritto et al., 1999; De Kauwe et al., 2013; Field et al., 1995; Knauer et al., 2017). First, the aforementioned larger leaf area under $eCO_2$ would reduce the physiological effects of $eCO_2$ on plant water use (Field et al., 1995). Second, the response magnitude of plant/stand-scale WUE to $eCO_2$ also depends on the coupling between the leaf and the atmosphere (De Kauwe et al., 2013). For example, Kelly et al. (2016) attributed the discrepancy between the responses of iWUE and $WUE_{plant}$ of *Eucalyptus* seedlings to $eCO_2$ to the weak coupling between plants and the surrounding air. Third, the difference in leaf-to-air vapour pressure deficit and responses of *A* and $g_s$ to $eCO_2$ can change vertically within canopies owing to changes in light availability (Barton et al., 2012).

## 4.4 | Factors affecting plant responses to drought and $eCO_2$

The interactive effect of drought and $eCO_2$ on *A* may depend on photosynthetic pathway (Leakey et al., 2006). Our study showed that the photosynthetic advantage of $C_3$ plants over $C_4$ plants under $eCO_2$ diminished with the onset of drought stress, which is consistent with the finding that the response of *A* to $eCO_2$ was more positive under reduced rainfall compared with ambient rainfall for $C_4$ grass but not for $C_3$ grass (Pastore et al., 2020). The distinct responses of $C_3$ and $C_4$ plants to the combination of $eCO_2$ and drought may be associated with the unique $CO_2$-concentrating mechanism of $C_4$ plants. Compared with $C_3$ plants, the initial slope of the $A/C_i$ curve of $C_4$ plants is much steeper, and *A* is $CO_2$ saturated at a lower $C_i$ and thus is less responsive to $eCO_2$ (Leakey, 2009). However, when $C_4$ plants are exposed to drought, the reduction in $g_s$ may decrease the operating $C_i$ to a value below the inflexion point of the $A/C_i$ curve, and *A* becomes more sensitive to $eCO_2$ (Leakey et al., 2009). Similarly, drought provoked a more pronounced $WUE_{plant}$ response of $C_4$ plants to $eCO_2$. This finding supports a model simulation that a stronger enhancement in $WUE_{plant}$ of *Zea mays* caused by $eCO_2$ occurred in drought treatment than in the wet treatment (Kellner et al., 2019). The benefits of $eCO_2$ on *A* and $WUE_{plant}$ of $C_4$ plants under water-limited environments may explain why the biomass of $C_4$ plants was enhanced only when $eCO_2$ and drought were combined (Leakey et al., 2006; Manderscheid et al., 2014; Ottman et al., 2001).

There were also significant differences in plant response to $eCO_2$ and drought among $C_3$ functional groups. The negative effects of drought on plant biomass of herbs were less than those of woody plants, which is generally consistent with the viewpoint that compared with woody plants, herbs have more strategies (e.g. dehydration escape; Kooyers, 2015) to cope with drought and thus are more drought tolerant (Volaire, 2018). Contrarily, woody plants exhibited significantly greater increases in *A* in response to $eCO_2$ than herbs, which is in line with previous findings that woody plants responded more strongly to $eCO_2$ (Ainsworth & Long, 2005).

Unexpectedly, the interaction between drought and $eCO_2$ on plants hardly changed with experimental factors such as drought manipulation type, experimental protocol, growth condition, drought duration, etc., which, however, mediated the individual effects of drought and $eCO_2$ on plants. For example, we found that the physiology and biomass production were more strongly constrained by drought for plants growing in pots than those growing in field. This is consistent with a previous meta-analysis that the effects of precipitation changes on root biomass in pot experiments did not mirror those in field experiments (Wang et al., 2020). Our finding implies that plants growing in pots were less drought tolerant than those growing in field, likely because pot size impacted root growth and development (Poorter et al., 2012); rooting volume, fine-root area and activity determine the capacity of the root system to take up water (Wullschleger et al., 2002). In addition, the negative effect of drought on plant biomass worsened as drought prolonged, possibly because the plant growth became C limited over long-term drought (Duan et al., 2013). Additionally, experimental protocol affected plant responses to $eCO_2$. Specifically, plant biomass in FACE experiments was less responsive to $eCO_2$, similar to the result by de Graaff et al. (2006). We also found that drought caused the greatest reductions in $g_s$, *A* and biomass for Type III manipulation; this suggested that plant physiology and growth were severely impaired when the water supply was totally withheld (Type III), whereas recurrent mild droughts (Type II) may increase plant drought resistance (Backhaus et al., 2014; Bréda et al., 2006).

## 5 | CONCLUSIONS

To detect whether $eCO_2$ can alleviate the negative effects of drought stress, we performed a worldwide synthesis on the interactive effects of $eCO_2$ and drought on plant water status, photosynthesis, WUE, biomass production and allocation. Our analysis showed that $eCO_2$ little affected SWC, but improved leaf water status under drought conditions (e.g. a higher LRWC and a less negative $\Psi_{midday}$) by reducing $g_s$ and increasing R/S. Elevated $CO_2$ enhanced WUE regardless of soil water availability, which was jointly driven by a lower $g_s$ response (associated with leaf ABA levels) and a higher *A* response to $eCO_2$ under drought, consistent with the optimal stomatal behaviour, but the magnitude of the $eCO_2$-induced enhancement in WUE decreased from the leaf to individual scales. $eCO_2$ reduced the magnitude of the effect of drought on $g_s$, but did not change the direction. The lower $g_s$ under drought caused stomatal limitations on *A*, while $eCO_2$ alleviated stomatal limitations by increasing $C_i$, which resulted in a greater *A* response to $eCO_2$ and drought, supporting the 'low $C_i$ effect' hypothesis. However, the magnitude of the increase in plant biomass caused by $eCO_2$ did not vary with water availability. The advantages of $eCO_2$ on $C_3$ plants over $C_4$ plants under well-watered conditions diminished under drought conditions. Compared with $C_3$ herbs, drought caused a greater reduction in biomass of woody plants. The negative effect of drought on plant biomass increased as drought prolonged. Plants growing in pots were less drought tolerant than those growing in field. The $eCO_2$-induced increase in biomass was observed in growth chamber and OTC experiments rather than in FACE experiments. These findings suggest that $eCO_2$ can alleviate the adverse impacts of drought by improving plant water status and *A*; they enhance our understanding of plant responses to and feedbacks on global changes.

Nevertheless, we realized several limitations in this study. First, although we found that $eCO_2$ improved plant water status, of which the exact mechanisms remain uncertain. One potential candidate is that $eCO_2$ may affect the rooting depth and vertical distribution of roots, which determine the water acquisition capacity of roots (Nadal-Sala et al., 2021; Wullschleger et al., 2002). Second, $eCO_2$ often increases non-structural carbohydrates, which may allow plants to increase osmotic adjustment and maintain a higher water potential (Miranda-Apodaca et al., 2018). Third, although normalizing plant responses to $eCO_2$ with the magnitude of $CO_2$ treatments did not change the directions of the responses, it increased the magnitudes by 38.8%–42.0% on average; nevertheless, the current dataset denied the normalization to drought and its interaction with $eCO_2$. Fourth, $eCO_2$ can also impact plant water supply through its effect on plant hydraulic conductance, with the specific effects depending on species and plant growth form (Domec et al., 2017). However, few data are available for synthesizing interactive effects of $eCO_2$ and drought on those aspects; the number of observations for SWC was also smaller than those of plant physiological variables, which may limit the power of this meta-analysis. Clearly, these limitations call for more studies, particularly on exploring responses of plant root characteristics (e.g. root length, root distribution), hydraulics (e.g. osmotic adjustment, plant hydraulic architecture) and SWC to the combination of $eCO_2$ and drought.

## AUTHOR CONTRIBUTIONS

Zhaoguo Wang and Chuankuan Wang designed the study. Zhaoguo Wang collected and analysed the data. Zhaoguo Wang and Chuankuan Wang drafted the manuscript. Zhaoguo Wang, Chuankuan Wang and Shirong Liu were involved in the revision.

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## CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13988.

## DATA AVAILABILITY STATEMENT

The database used in this meta-analysis is available from the Dryad Digital Repository https://doi.org/10.5061/dryad.zs7h44jcz (Wang et al. 2022).

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## SUPPORTING INFORMATION

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