Water Deficit Modulates the CO₂ Fertilization Effect on Plant Gas Exchange and Leaf-Level Water Use Efficiency: A Meta-Analysis

Fei Li1,2, Dagang Guo1,2, Xiaodong Gao3,4,5* and Xining Zhao2,3,4*

1 College of Water Resources and Architectural Engineering, Northwest A&F University, Xianyang, China, 2 Key Laboratory of Agricultural Soil and Water Engineering in Arid and Semiarid Areas, Ministry of Education, Northwest A&F University, Xianyang, China, 3 Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, China, 4 National Engineering Research Center of Water Saving and Irrigation Technology, Yangling, China, 5 Institute of Soil and Water Conservation, Northwest A&F University, Xianyang, China

Elevated atmospheric CO₂ concentrations ([eCO₂]) and soil water deficits significantly influence gas exchange in plant leaves, affecting the carbon-water cycle in terrestrial ecosystems. However, it remains unclear how the soil water deficit modulates the plant CO₂ fertilization effect, especially for gas exchange and leaf-level water use efficiency (WUE). Here, we synthesized a comprehensive dataset including 554 observations from 54 individual studies and quantified the responses for leaf gas exchange induced by [eCO₂] under water deficit. Moreover, we investigated the contribution of plant net photosynthesis rate (Pn) and transpiration rates (Tr) toward WUE in water deficit conditions and [eCO₂] using graphical vector analysis (GVA). In summary, [eCO₂] significantly increased Pn and WUE by 11.9 and 29.3% under well-watered conditions, whereas the interaction of water deficit and [eCO₂] slightly decreased Pn by 8.3%. Plants grown under light in an open environment were stimulated to a greater degree compared with plants grown under a lamp in a closed environment. Meanwhile, water deficit reduced Pn by 40.5 and 37.8%, while increasing WUE by 24.5 and 21.5% under ambient CO₂ concentration ([CO₂]) and [eCO₂], respectively. The [eCO₂]-induced stimulation of WUE was attributed to the common effect of Pn and Tr, whereas a water deficit induced increase in WUE was linked to the decrease in Tr. These results suggested that water deficit lowered the stimulation of [eCO₂] induced in plants. Therefore, fumigation conditions that closely mimic field conditions and multi-factorial experiments such as water availability are needed to predict the response of plants to future climate change.

Keywords: CO₂ fertilization effect, water deficit, leaf gas exchange, meta-analysis, graphical vector analysis

INTRODUCTION

Global atmospheric carbon dioxide concentration ([CO₂]) has accelerated at an unprecedented pace of about 2.4 μmol mol⁻¹ per year during the last decade, and presently, it is 413 ppm (IPCC, 2019; NASA, 2020). [CO₂] is projected to be between 421–946 ppm by 2,100 depending on continued emission scenarios. This increase in [CO₂] might be accompanied by shifting
precipitation patterns and increasing extreme precipitation events (Bencze et al., 2014; Zhang et al., 2021). It is predicted that plants may be negatively affected by drought stress and yet may benefit from elevated CO₂ (e[CO₂]), known as the “CO₂ fertilization effect.” An increase in Pn and WUE are necessary for improve carbon-water cycle and plant productivity in terrestrial ecosystems. Therefore, understanding how soil water deficit affects “CO₂ fertilization effect” on plant is of great significance to projecting the potential risk of climate change on global bio-environment equilibrium.

Generally, e[CO₂] and drought stimulate or inhibit plant growth by changing leaf gas exchange including net photosynthesis rate (Pn), transpiration rate (T₁), stomatal conductance (Gᵢ), and leaf-level water use efficiency (WUE), which result in a significant impact on the global cycling of carbon-water in terrestrial ecosystems (McLaughlin et al., 2007; Lawson and Blatt, 2014). Water is a key reactant required by plants for various photochemical processes including as an electron donor in photosynthesis. Stomatal closure is one of the first visible drought tolerance mechanisms employed by plants to reduce excessive water loss (Hessini et al., 2009; Li et al., 2017). Drought reduces Gᵢ by triggering abscissic acid (ABA) production in plants (Paoletti and Grulke, 2005; Yamaguchi et al., 2019; Li S. et al., 2020). Meanwhile, Gᵢ is regulated by guard-cell water potential (Assmann, 1999; Raschke et al., 2003). Drought stress negatively affects plant physiology, which usually results in reduced Pn, as Pn is closely associated with Gᵢ and mesophyll conductance leading to CO₂ diffusion, especially in C₃ plants (Luomala et al., 2005; Haworth et al., 2013; Xu et al., 2016). Short-term water stress results in stomatal defense and increased WUE, which is associated with delayed drought (Ameye et al., 2012). Drought stress results in stomatal and non-stomatal limitations; for instance, a reduction in Pn may occur as a result of conditions favoring ribulose 1,5-bisphosphate (RuBP) oxygenation rather than carboxylation, resulting in a reduction of chlorophyll content (Farquhar and Sharkey, 1982; Ameye et al., 2012; Drake et al., 2017; Birami et al., 2020).

Atmospheric [CO₂] is another pivotal factor affecting various biochemical processes of photosynthesis (Xu, 2015). Plants consume more CO₂ to stimulate the carboxylation efficiency of ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) to increase plant growth for most C₃ plants while competitively reducing photorespiration and dark respiration when increasing atmosphere [CO₂] (Leakey et al., 2006, 2007; Reddy et al., 2010; Robredo et al., 2010; Birami et al., 2020). However, the boost extent of photosynthesis induced by e[CO₂] may be related to the plant growth environment. There are serious potential limitations in using enclosure systems when conducting experiments to explore the effect of elevated [CO₂] on plants (Ainsworth, 2008). However, a study showed that the more closely fumigation conditions mimicked field conditions, the smaller was the stimulation of yield by elevated [CO₂] (Ainsworth and Long, 2005). Additionally, some plants may begin to develop an adverse response to enriched CO₂ environments, when beyond certain CO₂ concentration limits (Cotrufo et al., 1998; Long et al., 2006; Taub et al., 2008; Xu, 2015). Meanwhile, the response of plant gas exchange to e[CO₂] may be limited by other abiotic factors, such as high-temperature stress, low N/P, and low water availability (Bajji et al., 2001; Hessini et al., 2009; Zhao et al., 2016; Gorthi et al., 2019; Jiang et al., 2020). For example, high temperature can affect photosynthesis by reducing the activities of key metabolic enzymes in plants (Luomala et al., 2005); N deficiency can lead to inadequate sink strength and thus limit plant growth (Hyvönen et al., 2007); Severe drought conditions counteract e[CO₂] improvements in physiological performance and yield in soybeans (Casteel et al., 2008). Additionally, in contrast to C₃ plants, Pn of C₄ plants may not be influenced by e[CO₂] because [CO₂] is not rate-limiting to photosynthesis (Zhang et al., 2021). However, under e[CO₂], C₄ species may have certain advantages over C₃ plants regarding high WUE, especially under drought conditions (Barton et al., 2012). Studies have shown that WUE of maize and sorghum improved owing to direct or indirect stimulation of photosynthesis at e[CO₂] (Allen et al., 2011; Yan et al., 2016), and other groups have reported that enhanced WUE results due to reduction in Gᵢ and transpiration (Morison, 1985; Wu and Wang, 2000). Stomatal control is regulated by water stress, resulting in the maintenance of high plant water status at e[CO₂] (Ferris and Taylor, 1994; Polley et al., 1999; Torralbo et al., 2019). However, contradictory results were found in Brassica napus regarding minimizing water loss by following the e[CO₂]- induced stomatal closure (Faralli et al., 2017). Unfortunately, despite several studies on the response of plants to e[CO₂], previous analyses have focused on how e[CO₂] alleviates the adverse effects of drought on plant growth and physiology. Consequently, the impact of water deficit conditions in regulating the effect of e[CO₂] on plants is poorly understood, particularly on photosynthesis and WUE.

Rising [CO₂] levels in this century are predicted to stimulate the growth of C₃ species, counteracting the negative impacts of greater drought on plant growth and crop yield (Parry et al., 2004; Bencze et al., 2014). However, a few studies have shown that the stimulation of crop yield by e[CO₂] diminished to zero as drought intensified (Gray et al., 2016; Zheng et al., 2020). Conflicting results stemming from differences in experimental design have hampered the potential to draw general conclusions. In addition, as with several control experiments, many experimental tests for CO₂ response have been conducted in a limited environment such as enclosed spaces and weak light intensity, which limits the inferences that can be drawn from previously published literature. These limitations highlight the need for quantitative analysis of the available experimental data to better predict and implement adaptation policies related to future climate change scenarios and limited water availability for agricultural irrigation. Here, we used meta-analysis to address three key questions: (1) What extent does water deficit modulate the response of plant gas exchange to e[CO₂]? (2) How does e[CO₂] and water deficit affect leaf-level WUE, and what is the nature of the interaction between e[CO₂] and water deficit? (3) Do these responses differ by plant type, photosynthetic pathway, and growing conditions? Meta-analysis was used to test the effects of water availability on plant responses to e[CO₂] by hypothesizing that: the CO₂ fertilization effect on photosynthesis is reduced by water deficit (H1); water deficit × e[CO₂] has no effect on WUE because water...
availability has a greater effect on plants than that of e[CO₂] (H2); the more closely the fumigation conditions mimic field conditions, the stronger the stimulation of Pₚ by e[CO₂] (H3). Hypothesis H1 was generally consistent with previous studies on the mitigation of stress by e[CO₂], while H2 and H3 have no consensus. In this study, the synthetic power of meta-analysis was combined with graphical vector analysis (GVA) to investigate the contribution of plant Pₚ and Tₚ to WUE under water deficit and e[CO₂].

**MATERIALS AND METHODS**

**Literature Search and Study Selection**

We used the Web of Science¹ and China National Knowledge databases (CNKI²) to search for peer-reviewed papers related to water deficit × CO₂ interactions in plants. Various keyword combinations were used for the search, including (drought OR water deficit OR water supply) AND (CO₂ enrichment OR doubled ambient CO₂ OR rising CO₂ OR CO₂ rise) AND (gas exchange OR plant physiology). A total of 554 observations from 54 published papers were included in this meta-analysis (Appendix and Supplementary Material).

Only experiments on e[CO₂] and water deficit were included, and the few available studies simultaneously testing a third variable, such as temperature or nutrient levels, were omitted. Factorial experiments included at least two water treatments in addition to two CO₂ concentration treatments. The “well-watered,” “water deficit,” “ambient [CO₂]”(a[CO₂]), and “elevated [CO₂]” (e[CO₂]) treatments followed the definition of the authors of the original experiment (Wang et al., 2015). Meanwhile, the two most common methods of water control were chosen: dry days and field water capacity (FWC). All studies included plants growing in pots. We extracted response variables for leaf gas exchange, including Pₚ, Gₚ, Tₚ, and instantaneous WUE, which was calculated from Pₚ/Tₚ by authors. For those studies that included only Pₚ and Tₚ data but not WUE, we supplemented the WUE values with the equation:

\[
\text{WUE} = \frac{P}{T},
\]

WUE = Pₚ/Tₚ. Data were taken from tables or digitized from figures using the software GetData Graph Digitizer, 2008 (ver. 2.22, Russian Federation).

The factorial experiments included four treatments: (i) ambient CO₂ (a[CO₂]) + well-watered (CₐWₚ); (ii) e[CO₂] + well-watered (CₑWₚ); (iii) a[CO₂] + water deficit (CₐWₚ); and (iv) e[CO₂] + water deficit (CₑWₚ). In our dataset, a[CO₂] treatments ranged from 350 to 450 ppm, while e[CO₂] ranged from 500 to 1,200 ppm. The e[CO₂] treatments were grouped into seven categories: 500–550, 551–600, 601–650, 651–700, 701–750, 751–800, and >800 ppm. In addition, CO₂ exposure was either in a closed environment (growth chamber, greenhouse, and glasshouse), or an open or semi-open environment; free-air CO₂ enrichment (FACE) and open top chamber (OTC). Water treatments were categorized into well-watered and water deficit, with the water-deficit treatment grouped into three categories for FWC: 65–55, 54–40, and <40%.

Dry days were not grouped because of the small amount of data. Additionally, several explanatory variables in our meta-analysis may affect leaf gas exchange under water deficit and e[CO₂], including plant type (grass, tree, legume, shrub, or crop), source of light (lamp or solar), and photosynthetic pathways (C₃ or C₄) as described in the Supplementary Tables 1, 2.

**Meta-Analytical Methods**

We considered a[CO₂] and well-watered treatments as the baseline, whereas e[CO₂] and water deficit were the experimental treatments. The individual effect sizes for water and CO₂ manipulation (rₑ and rₚ, respectively) were calculated as follows:

\[
rₚ^\text{aCO₂} = \frac{X_{CₐWₚ}}{X_{CₑWₚ}} \text{ under a[CO₂] treatment,}
\]

\[
rₚ^\text{eCO₂} = \frac{X_{CₑWₚ}}{X_{CₑWₚ}} \text{ under e[CO₂] treatment,}
\]

\[
rₚ^\text{Wₑ} = \frac{X_{CₑWₚ}}{X_{CₑWₚ}} \text{ under well - watered treatment,}
\]

\[
rₚ^\text{Wₑ} = \frac{X_{CₑWₚ}}{X_{CₑWₚ}} \text{ under water - deficit treatment,}
\]

where \( X, Cₐ, Cₑ, Wₑ, \) and \( Wₑ \) represented the mean, e[CO₂], a[CO₂], well-watered, and water-deficit treatments, respectively (Jiang et al., 2020). The water deficit × CO₂ interaction term was calculated from factorial experiments as described by Lajunesse (2011). The water deficit and e[CO₂] interaction effect size, or the effect of water deficit on the e[CO₂] responses was calculated as follows:

\[
r = \frac{X_{CₑWₚ}}{X_{CₑWₚ}} / \frac{X_{CₑWₚ}}{X_{CₑWₚ}}
\]

\[
\text{r was log-transformed to linearize this metric as follows:}
\]

\[
\text{Ln}(r) = \text{Ln} \left( \frac{X_{CₑWₚ}}{X_{CₑWₚ}} \right) - \text{Ln} \left( \frac{X_{CₑWₚ}}{X_{CₑWₚ}} \right)
\]

Based on the additive property of variance (Curtis and Wang, 1998; Baig et al., 2015; Jiang et al., 2020), the variance of the water deficit by the CO₂ interaction (v) response ratio was calculated as follows:

\[
v = \frac{\text{SD}^2_{CₑWₚ}}{\text{n}_{CₑWₚ}} + \frac{\text{SD}^2_{CₑWₚ}}{\text{n}_{CₑWₚ}} + \frac{\text{SD}^2_{CₑWₚ}}{\text{n}_{CₑWₚ}} + \frac{\text{SD}^2_{CₑWₚ}}{\text{n}_{CₑWₚ}}
\]

An overall interaction term was estimated using weighted means, with greater weighting given to experiments with greater precision. A random-effects model was selected because the between-study variance was statistically significant. A multivariate linear mixed-effects model was then used to estimate the mean and the 95% confidence interval (CI) of the log-transformed response ratios for each individual variable, weighted by the variance of individual studies described in

¹http://apps.webofknowledge.com
²http://www.cnki.net
Supplementary Tables 1, 2. Effect sizes were reported as the antilog $r$ converted to the mean percentage change from the baseline treatment ($[r - 1] \times 100$). Meta-analysis and $\ln(r)$ calculations were conducted using OpenMEE software for ecological and evolutionary meta-analysis (Wallace et al., 2017).

Graphic Vector Analysis Methodology
Graphical vector analysis was first developed to simultaneously compare the effect of experimental treatments on plant biomass, nutrient concentration, and nutrient content using an integrated graph (Haase and Rose, 1995). It is widely used because the comparison may be interpreted independently of predetermined critical levels or ratios.

In this analysis, GVA was used according to Wang et al. (2015); Couture et al. (2017), and Li Z. et al. (2020) to complement the meta-analysis of WUE. The magnitude of change in leaf-level WUE is determined by $P_n$ and $T_r$. Responses of leaf-level WUE to the experimental treatment relative to the control fell into one of the following seven categories:

1. “Steady-state” increase, where WUE is unchanged owing to the parallel increases in leaf $P_n$ and $T_r$,
2. “Steady-state” decrease, where WUE is unchanged owing to the parallel decreases in leaf $P_n$ and $T_r$,
3. “$T_r$” positive effect, where WUE increases because $T_r$ decreases faster than $P_n$,
4. “$T_r$” negative effect, where WUE decreases because $T_r$ increases faster than $P_n$,
5. “$P_n$” positive effect, where WUE increases because $P_n$ increases faster than $T_r$,
6. “$P_n$” negative effect, where WUE decreases because $P_n$ decreases faster than $T_r$,
7. $P_n$ and $T_r$ work together, where WUE decreases/increases, despite $P_n$ and $T_r$ remaining unchanged, or $P_n$ increases and $T_r$ decreases.

All variables were plotted to illustrate the percent change in water deficit, $e[CO_2]$, and their interactions (value at $C_w W_d$ divided by those at $C_w W_w$ and multiplied by 100, value at $C_w W_w$ divided by those at $C_w W_w$ and multiplied by 100, value at $C_w W_d$ divided by those at $C_w W_w$ and multiplied by 100). $T_r$ (y-axis) was plotted against $P_n$ (x-axis) with WUE as the diagonal axis (y-axis) in a square-shaped diagram. Plotting the $P_n$ and WUE data automatically positioned the points along the diagonal lines representing the z-axis value for $T_r$, allowing simultaneous examination of the three related variables on a two-dimensional diagram.

RESULTS

Overview of Data Availability
The dataset was derived from 54 studies of 554 valid data points of gas exchange ($P_n$, $G$, $T_r$, and WUE) under $e[CO_2]$ and water deficit. Under $e[CO_2]$, $P_n$ was increased by an average of 11.9 and 16.4% for well-watered and water-deficit treatments, respectively, for all plants, whereas the interaction of water deficit and $e[CO_2]$ slightly decreased $P_n$ by 8.3%. That is, the $e[CO_2]$-induced stimulation of $P_n$ was reduced by the water deficit (Figures 1B,C). In contrast, water deficit reduced $P_n$ by 40.5 and 37.8% because of a[CO2] and e[CO2] treatments, respectively, and WUE was increased by 24.5 and 21.5% (Figure 1B). The negative effects of water deficit on plant $P_n$ were relieved at e[CO2] (Figures 1A–C).

In contrast to $P_n$, e[CO2] reduced $G$ and $T_r$ by 23.3 and 14.4% under water-deficit treatments, respectively. However, a greater e[CO2] reduction was observed in well-watered plants (28.5 and 19.1%, respectively). Similarly, water-deficit treatment reduced $G$ and $T_r$ by 56.7 and 45.2%, respectively, under e[CO2] treatment (Figures 1A,B). In comparison, WUE was increased due to the e[CO2] and water deficit. e[CO2] increased WUE by 29.3 and 28.8% under well-watered and water-deficit treatments, respectively, and water deficit increased WUE by 24.5 and 21.5%, respectively, under a[CO2] and e[CO2] treatment (Figures 1A,B). In addition, the interaction between water deficit and e[CO2] and the impact on $G$, $T_r$, and WUE were not statistically significant.

Net Photosynthetic Rate Responses
$P_n$ responded to changes in water and CO2 treatments, types of light sources, and fumigation methods. The stimulation of $P_n$ by e[CO2] was 50.7% lower under water-deficit treatments than the well-watered treatments using solar radiation (Figure 1), whereas the stimulation of CO2 on $P_n$ under water deficit was almost the same as that under well-watered treatment using lamp radiation. Additionally, under e[CO2] conditions, water deficit decreased plant $P_n$ by 41.8 and 35.6% when using the field capacity and drought days methods to control the water conditions, respectively. A greater increase in $P_n$ was observed when plants were exposed to e[CO2] in a free-air CO2 enrichment system (FACE, 64.2%) than in closed glasshouses (35.3%), greenhouses (14.1%), or growth chambers (4.3%) (Figure 1B). However, the e[CO2]-induced increase in $P_n$ was significantly reduced by water deficit compared with well-watered plants in any growing environment (Figure 1C).

The stimulatory effect of increasing [CO2] on $P_n$ reached a maximum at 551 to 600 ppm in well-watered plants. However, the e[CO2]-induced increase in $P_n$ was significantly reduced by water deficit (43.4%) at 551–600 ppm (Figure 2A). Very strong CO2 fertilization effects on $P_n$ were observed when the [CO2] increased from 601 to 800 ppm, and became >800 ppm during water deficit compared with the well-watered treatment (Figure 2A). The water deficit effect size magnitudes for $P_n$ were $-0.343$, $-0.408$, and $-0.75$ at 55–65%, 40–54%, and <40% soil water at [CO2], respectively, indicating that the highest water deficit resulted in the greatest inhibition (Figure 3A).

Plant $P_n$ significantly increased by 11.2 and 21.5% when the soil water was between 65–55% and 54–40%, respectively, in conditions of e[CO2] compared to a[CO2] treatment. However, e[CO2] increased the inhibition after water-deficit treatment by 3.9% when the soil water was <40% (Figure 3A). The effect size of $P_n$ decreased linearly with increasing drought days, with $R^2$ values of 0.19 (Figure 4A; $p = 0.0321$) and 0.26 (Figure 4A; $p = 0.0164$) at [CO2] and e[CO2], respectively, in a closed growing environment. However, there was no significant correlation between plant $P_n$ response and drought days in open...
Additionally, the water-deficit effect sizes of grass and legume treatment by 11.1% (G crop2 except in shrubs, regardless of the CO2 concentration. Water deficit reduced the plant Gs response to e[CO2]: red, blue, and black boxes represent positive, negative, and statistically neutral effects, respectively. Response variables are as follows: net photosynthesis (Pn), stomatal conductance (Gs), transpiration rate (Tr), and leaf-level water use efficiency (WUE = Pn/Tr). Water-deficit and e[CO2] treatment effect on plant Pn was classified according to light source, control methods of water, and CO2 fumigation methods; Gs was classified according to plant type and control methods of water; Tr was classified according to photosynthetic pathways, plant type, and CO2 fumigation methods; and WUE was classified according to light source and photosynthetic pathways (all separated by dotted lines). Dots and error bars represent means and 95% CI, respectively, of the log-transformed response ratio estimated based on a random effect model. LnRR(++) represent weighted mean response ratios. Number of data entries for each variable is denoted as n, labeled on the right y-axis. The treatment response was significant (p < 0.05) if the CI did not intersect with the red vertical dotted line on each plot (k = 6).

and semi-open environments, possibly owing to the relatively small sample size (n = 8) (Figure 4B).

Stomatal Conductance Responses
Water-deficit treatment reduced the plant Gs for most plants except in shrubs, regardless of the CO2 treatment. Tree and crop Gs were significantly reduced by e[CO2] after water-deficit treatment by 11.1% (n = 53) and 14.5% (n = 20), respectively. Additionally, the water-deficit effect sizes of grass and legume Gs were −1.067 and −1.344 under a[CO2], which increased by 16.3 and 0.6% compared with that in e[CO2] conditions, respectively, (Figure 1). Similarly, e[CO2] reduced all plant Gs, regardless of the drought treatment, except for shrubs. The e[CO2] effect sizes of crop, legume, tree, and grass Gs were −1.229, −1.718, −1.057, and −1.519 under well-watered conditions; and −0.406, −0.376, −0.251, and −0.204 under water-deficit treatments, respectively (Figure 1). Therefore, water deficit reduced the e[CO2] response. In contrast, the effect size of shrubs was positive (0.135); however, the 95% CI included zero. The effects of the two water control methods on Gs were also not significant. The interactions of water deficit and e[CO2] on Gs were not statistically significant for plant type and control methods of water because the 95% CI included zero.

When the CO2 concentration was higher than 650 ppm (651–700, 701–750, 751–800, and >800 ppm), Gs decreases significantly in conditions of well-watered treatment (Figure 2B). Similarly, water-deficit treatment reduced Gs. The water-deficit effect size of Gs was −0.577, −0.74, and −1.594 when the FWC was 65–55, 54–40, and <40% after a[CO2] treatment, respectively. However, the water-deficit effect size of Gs was −0.552, −0.487, and −1.226 when the FWC was 65–55, 54–40, and <40% after e[CO2] treatment (Figure 3B).

Transpiration Rate Responses
Water deficit reduced the Tr of C3 plants to a greater degree than C4 plants, whereas e[CO2] reduced the Tr of C4 plants more than that of C3 plants. Meanwhile, water deficit reduced the Tr of grasses, trees, and legumes more than crops regardless CO2 concentration. Additionally, water deficit reduced the Tr by 29.7, 26, 0.52, and 56.5% in OTC, greenhouse, FACE, and growth
chambers, respectively, under a[CO₂] (Figure 1B). However, water deficit increased the $T_r$ by 9.6% in FACE under e[CO₂] treatment (Figure 1A). Moreover, e[CO₂] reduced $T_r$ regardless of the water condition and CO₂ fumigation method except for OTC. However, the interactions of drought and e[CO₂] on $T_r$ were statistically insignificant for legumes and crop species.
The decrease in $T_r$ for plants resulted in a much larger decrease in $T_a$ at >750 ppm CO$_2$ compared with 551–750 ppm CO$_2$ (Figure 2C). However, there was no significant influence on $T_r$ at 500–600 ppm CO$_2$ (Figure 2C). The water deficit effect size of $T_r$ was $-0.436$, $-0.68$, and $-1.306$ when FWC was 65–55, 54–40, and <40%, respectively (Figure 3C).

**Leaf-Level Water Use Efficiency Responses**

Graphical vector analysis showed that increased leaf-level WUE under C$_e$W$_w$ treatment compared to the control (C$_a$W$_w$) may be due to the common effect of $P_n$ and $T_r$ (Figure 5). However, increased WUE caused by water deficit (C$_a$W$_d$) is attributable to the $"T_r"$ positive effect (Figure 5). Water deficit induced a larger increase in WUE under solar grown plants compared to plants grown under a lamp, regardless of [CO$_2$]. e[CO$_2$]-induced stimulation of WUE was attributable to a $"P_n"$ positive effect when grown in sunlight (Figures 6A,B). There were no significant interaction effects for C$_3$ plants in WUE (Figures 1A–C). Water deficit increased the WUE of C$_3$ plants by 32.8 and 21.4% in the a[CO$_2$] and e[CO$_2$] treatments, respectively, but it had no effect on the WUE of C$_4$ plants. Instead, water deficit resulted in a parallel decrease in $P_n$ and $T_r$ of C$_4$ plants ("steady-state" decrease) under a[CO$_2$] (Figures 6C,D). Meanwhile, e[CO$_2$] increased the WUE of C$_3$ and C$_4$ plants by 31.7 and 53.3%, respectively, in the well-watered treatments, and by 20 and 95.8%, respectively, in the water-deficit treatments.

Water use efficiency reached a maximum of 0.593 (81.0%) and 0.483 (62.1%) when the CO$_2$ concentration was 601–650 ppm in water deficit and well-watered treatments, respectively. The e[CO$_2$]-induced increases in WUE were less prominent in the water deficit treatment than in the well-watered treatment at 500–550, 551–600, 601–650, and 651–700 ppm [CO$_2$] (0.246 vs. $-0.05$; 0.334 vs. 0.18; 0.593 vs. 0.483; 0.31 vs. 0.228; and 0.512 vs. 0.278, respectively) (Figure 2D). However, the e[CO$_2$]-induced increase in WUE during water deficit treatment was 1.8 and 2.53 times greater than that of the well-watered treatments at 751–800 ppm CO$_2$ and >800 ppm CO$_2$, respectively (Figure 2D).

**DISCUSSION**

**Soil Water Deficit Constrains the Positive e[CO$_2$] Effect on Gas Exchange**

It has been suggested that the positive effects of e[CO$_2$] cannot be maintained when other environmental factors (nutrients,
temperature, and availability of water) are limited (Carter et al., 2007; Elliott et al., 2014; Fernando et al., 2019). Our meta-analysis results supported our H1 hypothesis that the e[CO₂]-induced stimulation of $P_n$ was reduced by water deficit treatment (Figures 1B,C). e[CO₂] leads to a delay in the onset of drought stress due to increased stomatal closure preventing water loss (Paoletti and Grulke, 2005; Yamaguchi et al., 2019; Jiménez et al., 2020). However, this delay only existed under mild drought stress because further stomatal closure leads to decreases in intercellular CO₂ and reduces carbon assimilation (Figure 7). e[CO₂] did not weaken the inhibition by water deficit treatment when soil water was <40% FWC (Figure 3A). This result indicates that the effect of soil water deficit is stronger than that of e[CO₂] when under severe water-deficit stress. In general, water deficit negatively affected the $P_n$ of most C₃ plants due to favoring RuBP oxygenation over carboxylation. Meanwhile, water deficit induced the stomatal closure reduced $T_r$, thereby inhibiting the uptake of N, which was associated with reductions in the amount and/or activity of Rubisco (Figure 7). Additionally, Zheng et al. (2020) found that the regularity of stomatal distribution pattern was dramatically reduced by e[CO₂] when winter wheat plants were constrained to moderate and severe stresses, implying that soil moisture conditions partly determined the response of stomatal distribution pattern to e[CO₂] (Figure 7). The effect size of $P_n$ decreased linearly with increasing drought days, regardless of [CO₂], also suggesting that water stress had a greater impact on plant growth than e[CO₂] when plants are under severe stress.

### Soil Water Deficit Modulated the [CO₂] Effect on Leaf-Level Water Use Efficiency

Stomatal optimization theory states that stomatal opening to allow CO₂ uptake inevitably comes at the expense of H₂O loss (Ferris et al., 2002; Robredo et al., 2010). Therefore, climate change will affect not only the rate of carbon fixation in plants, but also water loss. Evidence was found to support our H2 hypothesis that both water deficit and e[CO₂] treatment...
improved leaf-level WUE, but the underlying mechanisms for maintaining high water availability may be different. In general, an increased WUE is a rapid response to drought by closing stomata through root-generated xylem-born ABA (Ferris et al., 2002; Zhang et al., 2018, 2021). Conversely, e[CO₂] changes stomatal aperture (SA) by increasing intercellular [CO₂] for a short-term response (Xu et al., 2016; Li S. et al., 2020). Additionally, stomatal density (SD) also decreased when plants were exposed to high [CO₂] for a long time (Lin et al., 2001; Zhang et al., 2019). This study showed that water deficit and e[CO₂] significantly increased WUE by 24.5 and 29.3%, respectively (Figure 1A). Increases in WUE under the C₅W₅ treatment are attributable to the “Tᵣ” positive effect (Figure 5), whereas increases in WUE under the C₅W₆ treatment may be due to the common effect of Pₚ and Tᵣ (Figure 7). Meanwhile, water deficit increased the WUE of C₃ plants by 32.8 and 21.4% in the a[CO₂] and e[CO₂] treatments, respectively, implying that the water deficit induced increase of WUE may also be modulated by [CO₂]. In contrast, e[CO₂] had a greater effect on WUE of C₄ plants than C₃ plants in water deficit treatment, which is consistent with previous studies (Pearcy and Ehleringer, 1984). C₄ plants have higher light energy use efficiency because photosynthesis is completed by the combination of vascular bundle sheath cells and mesophyll cells (Pearcy and Ehleringer, 1984; Ainsworth and Long, 2005). Therefore, C₄ plants have higher CO₂ assimilation rates, less transpiration and water loss, and higher WUE compared with C₃ plants (Pearcy and Ehleringer, 1984; Conley et al., 2001). In addition, e[CO₂]-induced stimulation of WUE is attributable to a “Pₚ” positive effect when growing under sunlight regardless of water concentration. Hence, higher light appears to stimulate the effect of e[CO₂] on plants more efficiently than lamps.

**Effects of Growing Environment and Plant Type on Plant Gas Exchange Response to e[CO₂]**

It is widely reported that e[CO₂] stimulates Pₚ through the “CO₂ fertilization effect” because the current CO₂ concentration limits the photosynthetic ability of plants (Xu, 2015;
Fitzgerald et al., 2016). Our meta-analysis demonstrated that the % increase in $P_n$ by e[CO$_2$] treatments depended on the fumigation method; $P_n$ was stimulated to a greater magnitude when plants were exposed to e[CO$_2$] in an open environment than in a closed environment, especially when compared to the growth chamber. In contrast, another meta-analysis studying the effects of e[CO$_2$] indicated that the more closely the fumigation conditions mimicked field conditions, the smaller the stimulation of rice yield (Ainsworth, 2008). It is important to note that earlier studies were conducted at lower control [CO$_2$] than recent studies owing to changes in atmospheric CO$_2$. For example, earlier FACE and chamber studies were conducted at 339 and 330–360 ppm control CO$_2$, respectively (Baker et al., 1990; Teramura et al., 1990), whereas recent control experiments used approximately 400 ppm (Zinta et al., 2014; van der Kooi et al., 2016; Zheng et al., 2020). In addition, there were differences in the light conditions used. For example, FACE and OTC rely on natural light, and some greenhouse/glasshouse studies also used natural light but were covered by transparent material at the top, whereas almost all plants growing in growth chambers used lamps as a light source. Enclosed growing environments may be limited through the downregulation of photosynthesis (Ainsworth and Long, 2005; Zhang et al., 2021). Under high light conditions, plants are generally better able to take advantage of increased [CO$_2$] due to altered N partitioning within the photosynthetic apparatus to favor light-harvesting complexes (Yu et al., 2012; Kizildeniz et al., 2021). However, at low light levels, light-dependent reactions limit the rate of photosynthesis (Assmann, 1999; Yu et al., 2012). Our meta-analysis supported these conclusions since the $P_n$ of plants grown under natural light was higher than that under lamps. Therefore, light levels and CO$_2$ concentration may contribute to a smaller stimulation of $P_n$ by e[CO$_2$] in a closed–CO$_2$ fumigation system.

Our results showed that e[CO$_2$] reduced $G_s$, but the extent of the decrease varied according to plant type. The $G_s$ of legumes are more sensitive to [CO$_2$] which may be due to the decrease in total K content of legumes in high CO$_2$ environments, and the decrease in K$^+$ concentration increases stomatal resistance resulting in stomatal closure (Pearcy and Ehleringer, 1984). Moreover, $G_s$ reached a minimum when the [CO$_2$] was >800 ppm, while the $P_n$ did not decrease, implying that $G_s$ was not the cause of $P_n$ variation (Figure 1B). However, this result contradicts previous conclusions stating that changing photosynthesis and $G_s$ is evidence of stomatal control over photosynthesis (Lawson and Blatt, 2014; Xu et al., 2016). It is possible that the decreased $G_s$ may be the result rather than the cause of decreased photosynthesis. This may be related to e[CO$_2$], resulting in an increase in the concentration of ions and organic molecules; thus, guard cells swell to balance the water potential inside and outside the cell, reducing stomatal openness. Nevertheless, it should be noted that this study did not compare the long-term and short-term fumigation time of plants with high CO$_2$ concentration mainly due to the limited data and small sample size in previous literatures. Therefore, further studies with long-term multi-factor experiments are needed to fully understand the mechanisms and processes governing the interactions between e[CO$_2$] and water deficit on many plant types for comparing the “long-term” and “short-term” effects of e[CO$_2$] on plants under future climate change.

CONCLUSION

Our meta-analysis demonstrated that e[CO$_2$] generally augmented $P_n$, but the magnitude of the increase varied depending on the CO$_2$ fumigation method and light conditions. The greatest increases occurred when plants were exposed to e[CO$_2$] in an open environment under natural light. Previous projections based on the results of earlier e[CO$_2$] experiments may underestimate the “CO$_2$ fertilization effect” in future global terrestrial ecosystems, because the CO$_2$ fertilization effect on plant $P_n$ may be limited by the enclosed experimental methods and low light. Our results also indicated that both water deficit and e[CO$_2$] improved leaf-level WUE. However, e[CO$_2$]-induced stimulation of WUE is attributable to the $P_n$ and $T_r$ common effect, whereas water deficit induced increases of WUE are attributable to the “$T_r$” positive effect. Additionally, water deficit may result in a greater impact on the $P_n$ and WUE than e[CO$_2$], that is, the “CO$_2$ fertilization effect” may be modulated by soil water conditions under future climate change. Therefore, fumigation conditions that more closely mimic field conditions and multi-factorial experiments such as water availability, high temperature, low N/P, and elevated O$_3$ are needed to predict the response of plants to future climate change.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

AUTHOR CONTRIBUTIONS

FL, XG, and XZ designed the study. FL and DG performed the literature collection and data extraction. FL performed data analysis and wrote the initial manuscript with additional input from XG and XZ. All authors edited and approved this version of the manuscript.

FUNDING

This work was jointly supported by the National Natural Science Foundation of China (42125705), the Cyrus Tang Foundation, Shaanxi Key Research and Development Program (2020ZDLNY07-04), and the “111” project (Grant No. B12007).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2021.775477/full#supplementary-material
REFERENCES

Ainsworth, E. A. (2008). Rice production in a changing climate: a meta-analysis of responses to elevated carbon dioxide and elevated ozone concentration. Glob. Chang. Biol. 14, 1642–1650. doi: 10.1111/j.1365-2486.2008.01944.x

Ainsworth, E. A., and Long, S. P. (2005). What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. New Phytol. 165, 351–371. doi: 10.1111/j.1469-8137.2004.01224.x

Allen, L. H., Kakani, V. G., Vu, J. C. V., and Boote, K. J. (2011). Elevated CO₂ increases water use efficiency by sustaining photosynthesis of water-limited maize and sorghum. J. Plant Physiol. 168, 1909–1918. doi: 10.1016/j.jplph.2011.05.005

Amey, M., Wertz, T. M., Bauweraerts, L., McGuire, M. A., Teskey, R. O., and Steppe, K. (2012). The effect of induced heat waves on Pinus taeda and Quercus rubra seedlings in ambient and elevated CO₂ atmospheres. New Phytol. 196, 448–461. doi: 10.1111/j.1469-8137.2012.04267.x

Assmann, S. M. (1999). The cellular basis of guard cell sensing of rising CO₂. Plant Cell Environ. 22, 629–637. doi: 10.1046/j.1365-3040.1999.00408.x

Baig, S., Medly, B. E., Mercado, L. M., and Zaehle, S. (2015). Does the growth response of woody plants to elevated CO₂ increase with temperature? A model-oriented meta-analysis. Glob. Chang. Biol. 21, 4303–4319. doi: 10.1111/gcb.12962

Bajji, M., Lutts, S., and Kinet, J. M. (2001). Water deficit effects on solute Bencze, S., Bamberger, Z., Janda, T., Balla, K., Varga, B., Bedo, Z., et al. (2014). Constraints and potentials of future irrigation water availability on agricultural production under climate change. Proc. Natl. Acad. Sci. U.S.A. 111, 3239–3244. doi: 10.1073/pnas.1222474110

Farquhar, G. D., and Sharkey, T. D. (1982). Stomatal conductance and photosynthesis. Annu. Rev. Plant Biol. 33, 317–345. doi: 10.1146/annurev.pp.33.060182.001533

Faralli, M., Grove, I. G., Hare, M. C., Kettlewell, P. S., and Fiorani, F. (2017). Rising CO₂ from historical concentrations enhances the physiological performance of Brassica napus seedlings under optimal water supply but not under reduced water availability. Plant Cell Environ. 40, 317–325. doi: 10.1111/pce.12868

Fernando, N., Florentine, S. K., Naiker, M., Panozzo, J., and Chauhan, B. S. (2019). Annual ryegrass (Lolium rigidum Gaud) competition altered wheat grain quality: a study under elevated atmospheric CO₂ levels and drought conditions. Food Chem. 276, 285–290. doi: 10.1016/j.foodchem.2018.09.145

Ferris, R., Long, L., Bunn, S. M., Robinson, K. M., Bradshaw, H. D., Rae, A. M., et al. (2002). Leaf stomatal and epidermal cell development: identification of putative quantitative trait loci in relation to elevated carbon dioxide concentration in poplar. Tree Physiol. 22, 633–640. doi: 10.1093/treephys/22.9.633

Ferris, R., and Taylor, G. (1994). Stomatal characteristics of four native herbs following exposure to elevated CO₂. Ann. Bot. 73, 447–453. doi: 10.1006/anbo.1994.1055

Fitzgerald, G. J., Tausz, M., O’Leary, G., Mollah, M. R., Tausz-Posch, S., Seneewera, S., et al. (2016). Elevated atmospheric CO₂ can dramatically increase wheat yields in semi-arid environments and buffer against heat waves. Glob. Change Biol. 22, 2269–2284. doi: 10.1111/gcb.13362

Gorith, A., Volenc, J. J., and Welp, L. R. (2019). Stomatal response in soybean during drought improves leaf-scale and field-scale water use efficiencies. Agric. For. Meteorol. 271:107629. doi: 10.1016/j.agrformet.2019.107629

Gray, S. B., Demody, O., Klein, S. P., Locke, A. M., McGrath, J. M., Paul, R. E., et al. (2016). Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. Nat. Plants 2:16132. doi: 10.1038/nplants.2016.132

Haase, D. L., and Rose, R. (1995). Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. For. Sci. 41, 54–66. doi: 10.1093/forestscience/41.1.54

Haworth, M., Elliott-Keating, C., and McElwain, J. C. (2013). Coordination of physiological and morphological responses of stomata to elevated CO₂ in vascular plants. Oecologia 171, 71–82. doi: 10.1007/s00442-012-2406-9

Hessini, K., Pablo Martínez, J., Gandon, M., Albouchi, A., Soltani, A., and Abdell, C. (2009). Effect of water stress on growth, osmotic adjustment, cell wall elasticity and water-use efficiency in Spartina alterniflora. Environ. Exp. Bot. 67, 312–319. doi: 10.1016/j.envexpbot.2009.06.010

Hyvönen, R., Agren, G. I., Linder, S., Persson, T., Cotrufo, M. F., Ekblad, A., et al. (2007). The likely impact of elevated CO₂ nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. New Phytol. 173, 463–480. doi: 10.1111/j.1469-8137.2007.01967.x

IPCC (2019). “Summary for Policymakers,” in Climate Change and Land: An IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fossil Fuels in Terrestrial Ecosystems, eds P. R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H. O. Pörtner, D. C. Roberts, et al. (Geneva: IPCC).

Jiang, M., Caldararu, S., Zhang, H., Fleischer, K., Crous, K. Y., Yang, J., et al. (2020). Low phosphorus supply constrains plant responses to elevated CO₂: a meta-analysis. Glob. Chang. Biol. 26, 5856–5873. doi: 10.1111/gcb.15277

Jiménez, S., Fattahi, M., Bedis, K., Nasrolahpour-moghadam, S., Irigoyen, J. J., and Gogorcena, Y. (2020). Interaction effects of climate change factors on the water status, photosynthetic rate, and metabolic regulation in peach. Front. Plant Sci. 11:43. doi: 10.3389/fpls.2020.00043

Kizilduzen, T., Pascual, I., Irigoyen, J. J., and Morales, F. (2021). Future CO₂ warming and water deficit impact white and red Tempranillo grapevine.
photosynthetic acclimation to elevated CO₂ and biomass allocation. *Physiol. Plant* 172, 1779–1794. doi: 10.1111/ppl.13388

Lajeunesse, M. J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology* 92, 2049–2055. doi: 10.1890/11-0423.1

Lawson, T., and Blatt, M. R. (2014). Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiol.* 164, 1556–1570. doi: 10.1104/pp.114.237107

Leakey, A., Xu, F., Gillespie, K., Ainsworth, E., Long, S., and Ort, D. (2007). Physiological, biochemical and molecular analysis of the coordinated up-regulation of photosynthetic, respiratory and biosynthetic metabolism in soybean leaves under free-air CO₂ enrichment. *Photosynthesis Res.* 91, 246–247.

Leakey, A. D. B., Uribelarrea, M., Ainsworth, E. A., Naidu, S. L., Rogers, A., Ort, D. R., et al. (2006). Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant Physiol.* 140, 779–790. doi: 10.1104/pp.105.073957

Li, S., Li, X., Wei, Z., and Liu, F. (2020). ABA-mediated modulation of elevated CO₂ on stomatal response to drought. *Curr. Opin. Plant Biol.* 56, 174–180. doi: 10.1016/j.pbi.2019.12.002

Li, Y., Li, H., Li, Y., and Zhang, S. (2017). Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat. *Crop J.* 5, 231–239. doi: 10.1016/j.cj.2017.01.001

Li, Z., Yang, J., Shang, B., Xu, Y., Couture, J. J., Yuan, X., et al. (2020). Water stress rather than N addition mitigates impacts of elevated O₃ on foliar chemical profiles in poplar saplings. *Sci. Total Environ.* 707:135935. doi: 10.1016/j.scitotenv.2019.135935

Lin, J. X., Jach, M. E., and Ceulemans, R. (2001). Stomatal density and needle anatomy of Scots pine (*Pinus sylvestris*) are affected by elevated CO₂. *New Phytol.* 150, 665–674. doi: 10.1046/j.1469-8137.2001.00124.x

Long, S. P., Ainsworth, E. A., Leakey, A. D. B., Noesberger, J., and Ort, D. R. (2006). Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science* 312, 1918–1921. doi: 10.1126/science.1114722

Luomala, E. M., Laitinen, K., Sutinen, S., Kellomäki, S., and Vapaavuori, E. (2005). Stomatal density, anatomy and nutrient concentrations of Scots pine needle cells are affected by elevated CO₂ and temperature. *Plant Cell Environ.* 28, 733–749. doi: 10.1111/j.1365-3040.2005.01319.x

McLaughlin, S. B., Nosal, M., Wallischegler, S. D., and Sun, G. (2007). Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. *New Phytol.* 174, 109–124. doi: 10.1111/j.1469-8137.2007.02018.x

Morison, J. I. L. (1985). Sensitivity of stomata and water use efficiency to high CO₂. *Plant Cell Environ.* 8, 467–474. doi: 10.1111/1365-3040.12685.10.1111/2016.10.00124.x

NASA (2020). Global Climate Change: Vital Signs of the Planet. Available online at: https://climate.nasa.gov/413pp QUOTES (accessed May 4, 2020).

Paoletti, E., and Grulke, N. E. (2005). Does living in elevated CO₂ atmosphere affect photosynthesis and plant productivity? *Curr. Sci.* 99, 46–57. doi: 10.1371/journal.pone.0011405

Robredo, A., Perez-Lopez, U., Lacuesta, M., Mené-Petite, A., and Munoz-Rueda, A. (2010). Influence of water stress on photosynthetic characteristics in barley plants under ambient and elevated CO₂ concentrations. *Biol. Plant.* 54, 285–292. doi: 10.1007/s10035-010-0050-y

Sustainability - MIT. (2019). Differential regulation of stomatal conductance as a strategy to cope with ammonium fertilizer under ambient versus elevated CO₂. *Front. Plant Sci.* 10:597. doi: 10.3389/fpls.2019.00597

van der Kooi, C., Reich, M., Loew, M., De Kok, L. J., and Tausz, M. (2016). Growth and yield stimulation under elevated CO₂ and drought: a meta-analysis on crops. *Environ. Exp. Bot.* 122, 150–157. doi: 10.1016/j.envexpbot.2015.10.004

Wallace, B. C., Lajeunesse, M. J., Dietz, G., Dahabreh, I. J., Trizkalis, T. A., Schmid, C. H., et al. (2017). OpenNEMI: intuitive, open-source software for meta-analysis in ecology and evolutionary biology. *Methods Ecol. Evol.* 8, 941–947. doi: 10.1111/2041-210X.12708

Wang, X., Taub, D. R., and Jablonski, L. M. (2015). Reproductive allocation in plants as affected by elevated carbon dioxide and other environmental changes: a synthesis using meta-analysis and graphical vector analysis. *Oecologia* 177, 1075–1087. doi: 10.1007/s00442-014-3191-4

Wu, D. X., and Wang, G. X. (2000). Interaction of CO₂ enrichment and drought on growth, water use, and yield of broad bean (*Vicia faba*). *Environ. Exp. Bot.* 43, 131–139. doi: 10.1016/S0098-8472(99)00053-2

Xu, M. (2015). The optimal atmospheric CO₂ concentration for the growth of winter wheat (*Triticum aestivum*). *J. Plant Physiol.* 184, 89–97. doi: 10.1016/j.jplph.2015.07.003

Yan, W., Zhong, Y., and Shangguan, Z. (2016). A meta-analysis of leaf gas exchange and water status responses to drought. *Sci. Rep.* 6:20917. doi: 10.1038/srep20917

Yu, J., Chen, L., Xu, M., and Huang, B. (2012). Effects of elevated CO₂ on physiological responses of tall fescue to elevated temperature, drought stress, and the combined stresses. *Crop Sci.* 52, 1848–1858. doi: 10.2135/cropsci2012.01.0030

Zhao, M. L., Wang, L. H., Sun, X. M., Li, Y., and Li, L. (2016). Accumulation and distribution dynamics of soluble carbohydrate in Helianthus tuberosus under drought stress. *Plant Dis. Pers.* 7, 36–40.

Zhang, D. S., Li, A., Lam, S. K., Li, P., Zong, Y. Z., Gao, Z. Q., et al. (2021). Increased carbon uptake under elevated CO₂ concentration enhances water-use efficiency of G. hirsutum millet under drought. *Agr. Water Manag.* 245:106631. doi: 10.1016/j.agwat.2020.106631

Zhang, H., Jiang, H., Song, X., Jin, J., and Zhang, X. (2018). The responses of plant leaf CO₂/H₂O exchange and water use efficiency to drought: a meta-analysis. *Sustainability* 10:551. doi: 10.3390/su10050551

Zhang, H., Pan, C., Gu, S., Ma, Q., Zhang, Y., Li, X., et al. (2019). Stomatal movements are involved in elevated CO₂-mitigated high temperature stress in tomato. *Plant Physiol.* 165, 569–583. doi: 10.1104/pp.118.02752Z

Zheng, Y., He, C., Guo, L., Hao, L., Cheng, D., Li, F., et al. (2020). Soil water status triggers CO₂ fertilization effect on the growth of winter wheat (*Triticum aestivum*). *Agric. For. Meteorol.* 291:108097. doi: 10.1016/j.agrformet.2020.108097

Zinta, G., AbdElgawad, H., Domagalska, M. A., Vergauwen, L., Knapen, D., Nijs, L., et al. (2014). Physiological, biochemical, and genome-wide transcriptional analysis reveals that elevated CO₂ mitigates the impact of combined heat wave
and drought stress in Arabidopsis Thaliana at multiple organizational levels. *Glob. Chang. Biol.* 20, 3670–3685. doi: 10.1111/gcb.12626

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Publisher’s Note:** All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

*Copyright © 2021 Li, Guo, Gao and Zhao. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.*