

A meta-analysis of plant physiological and growth responses to temperature and elevated CO₂

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Received: 21 June 2010 / Accepted: 10 October 2011
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Abstract Atmospheric carbon dioxide (CO₂) and global mean temperature are expected to be significantly higher by the end of the 21st century. Elevated CO₂ (eCO₂) and higher temperature each affect plant physiology and growth, but their interactive effects have not been reviewed statistically with respect to higher chronic mean temperatures and abrupt heat stress. In this meta-analysis, we examined the effect of CO₂ on the physiology and growth of plants subjected to different temperature treatments. The CO₂ treatments were categorized into ambient (<400 ppm) or elevated (>560 ppm) levels, while temperature treatments were categorized into ambient temperature (AT), elevated temperature (ET; AT + 1.4–6°C), or heat stress (HS; AT + >8°C). Plant species were grouped according to photosynthetic pathways (C₃, C₄), functional types (legumes, non-legumes), growth forms (herbaceous, woody), and economic purposes (crop, non-crop). eCO₂

enhanced net photosynthesis at AT, ET, and HS in C₃ species (especially at the HS level), but in C₄ species, it had no effect at AT, a positive effect at ET, and a negative effect at HS. The positive effect of eCO₂ on net photosynthesis was greater for legumes than for non-legumes at HS, for non-crops than crops at ET, and for woody than herbaceous species at ET and HS. Total (W_T) and above- (W_{AG}) and below-ground (W_{BG}) biomass were increased by eCO₂ for most species groups at all temperatures, except for C₄ species and W_{BG} of legumes at HS. Hence, eCO₂ × heat effects on growth were often not explained by effects on net photosynthesis. Overall, the results show that eCO₂ effects on plant physiology and growth vary under different temperature regimes, among functional groups and photosynthetic pathways, and among response variables. These findings have important implications for biomass accumulation and ecosystem functioning in the future when the CO₂ level is higher and climate extremes, such as heat waves, become more frequent.

Communicated by Ram Oren.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2172-0) contains supplementary material, which is available to authorized users.

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Keywords Global change · Elevated CO₂ · Heat stress · Meta-analysis · Biomass · Photosynthesis

Abbreviations

A	Net CO ₂ assimilation rate (μmol m ⁻² s ⁻¹)
AT	Ambient temperature
ET	Elevated temperature
aCO ₂	Ambient CO ₂
eCO ₂	Elevated CO ₂
F _v /F _m	Photosystem II (PSII) efficiency
g _s	Stomatal conductance
HS	Heat stress
N _L	Leaf nitrogen concentration
N _R	Root nitrogen concentration
RA	Rubisco activity (μmol m ⁻² s ⁻¹)

SLA	Specific leaf area
W_T	Total plant weight (dry mass)
W_{AG}	Above-ground weight (dry mass)
W_{BG}	Below-ground weight (dry mass)

Introduction

As a consequence of human activities, global atmospheric carbon dioxide (aCO_2) and temperature, both key variables affecting plant growth, development, and function, have changed in the recent past and are predicted to increase in the future. Increases in aCO_2 and other greenhouse gases are largely responsible for recent increases in global mean surface temperatures, which rose by 0.6°C from 1990 to 2000 and are projected to increase by another 1.4–5.8°C by the year 2100 (Houghton et al. 2001; IPCC 2001, 2007). In addition to rising mean annual temperatures, there will also be increases in the frequency, duration, and severity of periods with exceptionally high temperatures (Wagner 1996; Haldimann and Feller 2004). Thus, plants in the future will not only be exposed to elevated levels of CO_2 (eCO_2), but will also likely experience more acute heat stress (HS), which can greatly impact ecosystem productivity (Ciais et al. 2005) and biodiversity (Davis 1986; Thomas et al. 2004).

The interactive effects of eCO_2 and temperature on the physiology and growth of a large number of plant species have been investigated, although mostly for increases in mean temperatures (i.e., chronic warming) (Morison and Lawlor 1999), rather than for abrupt temperature increases (Wang et al. 2008, and references therein). Since net CO_2 assimilation rate per unit area (A) is affected by the ratio of CO_2 and atmospheric oxygen (O_2) as they compete for carbon fixation and photorespiration at the active site of the enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), increased CO_2 reduces carbon loss through photorespiration. However, elevated temperature increases photorespiration due to the reduced solubility of CO_2 compared with O_2 and reduced specificity of Rubisco for CO_2 at higher temperatures (Sage and Monson 1999). It has therefore been predicted that photosynthetic response to eCO_2 in plants with C_3 metabolism will be larger at higher temperatures (Long 1991; Gifford 1995; Bowes et al. 1996). In contrast, it has been generally considered that C_4 species will show little CO_2 stimulation irrespective of temperature because of the CO_2 concentration mechanism in C_4 species. Recent studies, however, have shown substantial stimulation of both net photosynthesis and biomass in C_4 species under non-HS conditions (Ghanoum et al. 2000). Therefore, the response of C_4 species to

the interactive effect of temperature and CO_2 requires further examination.

Although a large number of empirical studies have examined effects of eCO_2 and elevated growth temperature (typically 3–5°C) on photosynthesis (reviewed by Morison and Lawlor 1999), the interactions between eCO_2 and HS (typically >8°C above the normal growth temperature) have been investigated in only a limited number of studies (Wang et al. 2008). The results have been variable and have not been reviewed statistically. One of the negative effects of HS on plants is the damage to photosynthesis, often by impairing photosystem II (PSII) in the light reactions (electron transport) (Berry and Bjorkman 1980; Heckathorn et al. 1998, 2002) and Rubisco activase in the Calvin-cycle (dark) reactions (Eckardt and Portis 1997; Crafts-Brandner and Law 2000; Crafts-Brandner and Salvucci 2000). While with mild temperature increases, eCO_2 has consistently positive effects on plants, at HS, eCO_2 can have positive (Faria et al. 1996, 1999; Huxman et al. 1998; Ferris et al. 1998; Hamerlynck et al. 2000; Taub et al. 2000), negative (Bassow et al. 1994; Roden and Ball 1996b; Huxman et al. 1998; Taub et al. 2000), or no effects (Coleman et al. 1991), or positive effects for C_3 species and negative effects for C_4 species (Wang et al. 2008) on plant photosynthesis and growth. Due to the contrasting effect of CO_2 at elevated temperatures (ET) and HS, it is critical to examine the role of CO_2 under different temperature treatments and for different functional groups to better understand plant responses to multiple environmental changes in the future.

In addition to temperature treatments and species groups, treatment duration and growth facility (pot or in-ground, growth chamber or greenhouse, etc.) might also affect CO_2 responses. In the short term, CO_2 fixation may be stimulated by eCO_2 ; however, in the long term, this effect may be partly lost as a result of a down-regulation of photosynthesis (Gunderson and Wullschlegel 1994). This down-regulation of photosynthesis might be associated with an over-production of assimilates relative to sink demand and may, therefore, be associated with an accumulation of non-structural carbohydrates in the leaves (van Oosten and Besford 1996) or decreased Rubisco activity and production caused by decreased nitrogen (N) concentration (Luo et al. 2004). Therefore, in this meta-analysis, we categorized reports into groups based on treatment duration and growth facility. Key physiological variables, such as Rubisco activity and N concentration, were analyzed based on different temperature treatments and species groups.

In order to assess the effects of eCO_2 and temperature on plant biomass and physiological performance, we conducted a comprehensive meta-analysis of CO_2 studies published before the end of 2010 in which plant

photosynthesis or growth was reported at different temperature and CO₂ treatments. In this meta-analysis, we summarized and interpreted 466 observations of CO₂ effects on plant physiology and growth under different temperature treatments extracted from 84 separate publications [Electronic supplementary material (ESM)].

The major objectives of this meta-analysis were two-fold: (1) to provide estimates of the magnitude and significance of eCO₂ effects on plant biomass accumulation and partitioning, net photosynthesis, PSII function, stomatal conductance, Rubisco activity, specific leaf area (SLA), and leaf and root N concentration under different global-warming scenarios; (2) to test for differences among plant functional groups and growth forms in affecting these responses. We hypothesized: (1) the enhancement of biomass and net photosynthesis by eCO₂ would be less pronounced at HS than at AT or ET, which might be associated with heat-damage effects on PSII function, g_s , or Rubisco activity; (2) C₄ species would have a smaller enhancement than C₃ species in biomass and net photosynthesis in response to eCO₂ at all temperature treatments due to the CO₂-concentrating mechanism in C₄ plants; (3) legume species would show a greater enhancement than non-legumes, especially at HS, as a consequence of higher tissue N concentrations, which can limit N-dilution effects on plant function under conditions of eCO₂.

Methods

Data collection

The peer-reviewed journal articles used to construct the database for this meta-analysis were obtained by searching the Science Citation Index (SCI) of the Institute of Scientific Information. The list of articles obtained were subsequently cross-checked with references cited in a large number of CO₂ review articles and books to ensure the inclusion of all articles containing data relevant for this meta-analysis. Any article published in English before the end of 2010 that met all of the following criteria was included: (1) aCO₂ treatment >250 and <400 $\mu\text{mol mol}^{-1}$ and eCO₂ treatment between 500 and 1,000 $\mu\text{mol mol}^{-1}$; (2) plants were treated at ambient temperature (AT) and with either ET or heat stress (HS) under conditions of both aCO₂ and eCO₂; (3) photosynthetic measurements were conducted at the growth CO₂ and temperatures. In those studies from which we collected data, the CO₂ treatment typically included ambient (320–400 $\mu\text{mol mol}^{-1}$) and elevated (560–1,000 $\mu\text{mol mol}^{-1}$) CO₂ concentrations. Only one study has aCO₂ at 250 $\mu\text{mol mol}^{-1}$ and one study has eCO₂ at 1,300 $\mu\text{mol mol}^{-1}$ (ESM). On average, for the aCO₂ and eCO₂ treatments included in the meta-analysis,

the CO₂ levels were 366 and 702 $\mu\text{mol mol}^{-1}$ at AT, 362 and 691 $\mu\text{mol mol}^{-1}$ at ET, and 364 and 711 $\mu\text{mol mol}^{-1}$ at HS, respectively. Response variables extracted from these articles include net photosynthesis (net CO₂ assimilation) (A), PSII efficiency (F_v/F_m measured in the dark), stomatal conductance to water vapor (g_s), Rubisco activity (RA), SLA, above-ground (W_{AG}), below-ground (W_{BG}), and total (W_T) weight of plant dry mass, and leaf (N_L) and root (N_R) N concentration. For multi-year studies on annual species, results from different seasons were considered independent, and all observations were included in this analysis. For multi-year studies on perennial species, only those studies with the longest CO₂ exposure were included. If a study included more than one species, all of the observations were considered to be independent and included in the database. If a study examined the interactive effects of CO₂ and non-temperature stress factors, only those measurements from the non-stressed experiments, e.g., low ozone or well-watered plants, were included.

Categorization of studies

For this analysis, temperature treatments were categorized into three levels: AT, ET (1.4–6°C above ambient), and HS (>8°C above ambient). Originally, the temperature categories used in this meta-analysis were intended to be categorized into AT and ET (AT + 1.4–5.8°C), as predicted by IPCC (2001, 2007), but this was modified to ET (AT + 1.4–6°C) and HS (AT + >8°C), since <6 and >8°C + AT were used most frequently in the reference papers. Thus, the temperature categories were essentially arbitrary and should not be considered as defining fixed boundaries for the specific temperature treatment. Plant species were categorized based on photosynthetic pathway (C₃ or C₄), N-fixing ability (legumes or non-legumes), growth form (herbaceous or woody), and economic purpose (crop or non-crop). Research facilities used to raise CO₂ concentration were divided into two broad classes: (1) semi-open systems, which include open-top chambers (OTC) and screen-aided CO₂ control (Leadley et al. 1997) and (2) closed systems, which include greenhouses and growth chambers. Pot size was grouped into <10 L, >10 L, or in-ground. These size classes have been previously used in similar meta-analytic review looking at tree responses to CO₂ (Curtis 1996; Wand et al. 1999).

Meta-analytical methods

This meta-analysis followed the techniques described in the work of Wang (2007). We used the natural logarithm-transformed ratio ($\ln r$) of plant responses at elevated to ambient levels of CO₂ to estimate the effect size of the CO₂ treatment (Hedges et al. 1999). In order to include the large

percentage of studies that did not adequately report sample sizes and variances, we performed unweighted analysis using the statistical software program MetaWin 2.0 (Rosenberg et al. 2000). A mixed-effects model was used in this analysis with the assumption that there were random variations in effect sizes among the diverse studies included in this synthesis. Consequently, the confidence intervals generated are larger than those of a fixed-effect model and can represent more conservative interpretations. Confidence intervals (CI) for effect-size estimates were generated by bootstrapping the unweighted data using MetaWin 2.0 with a resampling of 9,999 iterations. $e\text{CO}_2$ was considered to have a significant effect on a variable if the bootstrap CIs of its percentage change did not overlap zero. The response to $e\text{CO}_2$ was considered to be significantly different between temperature treatments if their CIs did not overlap. Significance was established at $p < 0.05$ unless otherwise noted.

For the significant effect of $\ln r$, we looked for the potential of publication bias in the meta-analysis. First, we calculated Spearman's rank-order correlation, r_s , a statistic that describes the relationship between the effect size ($\ln r$) and the sample size of the analysis (Begg and Mazumdar 1994). A significant correlation of r_s (i.e., $p < 0.05$) demonstrated significant bias, whereby, for example, larger effect sizes are more likely to be published than smaller effect sizes. We also calculated Rosenthal's fail-safe number with Meta-Win 2.0. This value yields the number of additional studies with a mean effect size of zero needed to eliminate the significance of a significant effect (Rosenthal 1979). If the fail-safe number is larger than a critical value of $5n + 10$, where n is the number of studies, then publication bias may be safely ignored (Rosenberg 2005). Publication bias will be reported if it existed for certain effect size and could not be ignored.

Results

Across all plants and environmental conditions synthesized in this analysis, $e\text{CO}_2$ impacted F_v/F_m and SLA by different magnitudes at different temperature treatments, but the $e\text{CO}_2$ effect was not significantly different among temperature treatments for A , g_s , RA , and N_L (Fig. 1). Elevated CO_2 increased A at AT (13.9%), ET (19.5%), and HS (14.3%) (Fig. 1a). In contrast, F_v/F_m was unaffected by $e\text{CO}_2$ at AT and ET, but was decreased by $e\text{CO}_2$ at HS (0.46 at $a\text{CO}_2$ and 0.43 at $e\text{CO}_2$) (Fig. 1b). There was a publication bias for the effect of $e\text{CO}_2$ on F_v/F_m at ET ($r_s = 0.58$, $p = 0.024$). Since the calculated Rosenthal's fail-safe number (84.4) was not above the critical value (85), the publication bias could not be ignored. Elevated CO_2 decreased g_s and RA at all temperature treatments, but

there were no significant differences among different temperature treatments (Fig. 1c, d). SLA was decreased by $e\text{CO}_2$ at AT (−10.7%), unchanged at ET, and increased at HS (17.2%) (Fig. 1e). N_L was decreased by $e\text{CO}_2$ at all temperature treatments (Fig. 1f).

Responses of A , F_v/F_m , and g_s to temperature \times $e\text{CO}_2$ varied in C_3 , C_4 , legume, and non-legume species (Fig. 2). For C_3 species, $e\text{CO}_2$ increased A by 15.3, 19.9, and 28.7% at AT, ET, and HS, respectively (Fig. 2a), and the difference in response at AT versus HS was significant. However, for C_4 species, $e\text{CO}_2$ had no effect at AT, increased A at ET by 17.7%, but had a negative effect on A at HS (−21.0%). $e\text{CO}_2$ increased A by 12.3 (not significant), 20.9, and 36.6% at AT, ET, and HS for legumes, and by 15.4, 19.1, and 6.4% (not significant for HS) for non-legumes; the response of legumes differed from that of non-legumes only at HS, wherein the effect of $e\text{CO}_2$ was greater in legumes than in non-legumes. For the F_v/F_m of C_3 species, $e\text{CO}_2$ had a slight positive effect at AT, no significant effect at ET, and a negative effect at HS. For C_4 and non-legume species, $e\text{CO}_2$ had a negative effect on F_v/F_m at AT and HS, but no effect at ET. For legume species, $e\text{CO}_2$ had a positive effect on F_v/F_m at AT, but no effect at ET and HS (Fig. 2b). The decrease of F_v/F_m by $e\text{CO}_2$ at HS was greater in C_4 than in C_3 species. For C_3 , C_4 , legume, and non-legume species, g_s was decreased by $e\text{CO}_2$ at all temperature treatments, with the difference between C_3 and C_4 species at AT and HS being significant; there was less of a decrease in g_s by $e\text{CO}_2$ in C_3 plants than in C_4 plants at AT, but more of an increase in C_3 than C_4 plants at HS (Fig. 2c).

$e\text{CO}_2$ increased A at AT, ET, and HS for all herbaceous, woody, crop, and non-crop species, and there were significantly different responses between ET and HS for non-crop species (Fig. 3a). Elevated CO_2 had no significant effect on F_v/F_m at AT, but it did have a negative effect at HS for all herbaceous, woody, crop, and non-crop species (Fig. 3b). The decrease of F_v/F_m by $e\text{CO}_2$ at HS was more in herbaceous than in woody species and more in non-crop than in crop species. At ET, $e\text{CO}_2$ had a positive effect on F_v/F_m in herbaceous and crop species, but no effect on woody and non-crop species. For all species groups, g_s was decreased by $e\text{CO}_2$ at all temperature treatments (except for woody at HS), with the difference being significant between AT or ET and HS for herbaceous species, between AT or ET and HS for crops, and between ET and AT or HS for non-crop species (Fig. 3c). At AT and ET, the decrease in g_s by $e\text{CO}_2$ was greater in herbaceous than in woody species, and greater in crop than in non-crop species.

$e\text{CO}_2$ decreased the N_L of C_3 species by 5.2, 5.7, and 16.5% at the AT, ET, and HS levels, respectively, and the difference was not significant among different temperature treatments. The N_L of C_4 species was not significantly

Fig. 1 Responses to elevated CO_2 (eCO_2) in net photosynthetic rate (A ; **a**), photosystem II (PSII) efficiency (F_v/F_m ; **b**), stomatal conductance (g_s ; **c**), rubisco activity (RA ; **d**), specific leaf area (SLA ; **e**), and nitrogen (N) content in leaf (N_L ; **f**) for plants grown under different temperatures (AT ambient temperature, ET elevated temperature, HS heat stress). Each data point represents the mean \pm 95% confidence interval (CI; *whiskers*). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * $p < 0.05$ and ** $p < 0.01$ for comparison between temperature treatment categories whose CIs do not overlap

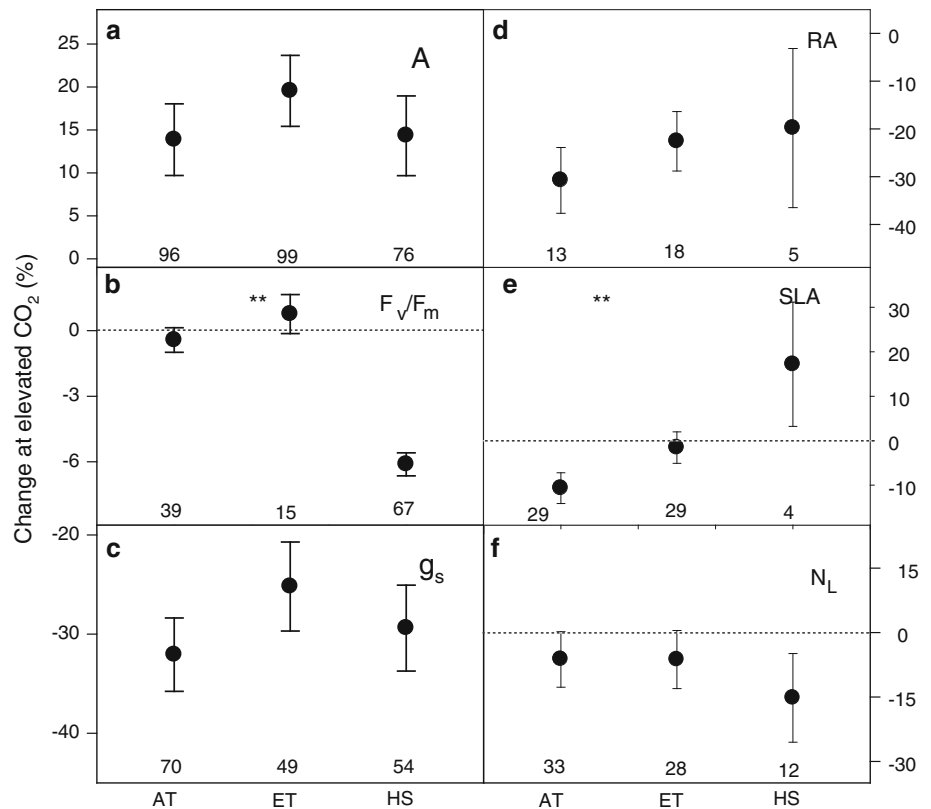


Fig. 2 Photosynthetic responses to eCO_2 in C_3 , C_4 , legume, and non-legume species at different temperature treatments for net photosynthetic rate (A ; **a**), PSII efficiency (F_v/F_m ; **b**), and stomatal conductance (g_s ; **c**). Each data point represents the mean \pm 95% CI (*whiskers*). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * $p < 0.05$ and ** $p < 0.01$ for comparison between temperature treatment categories whose CIs do not overlap

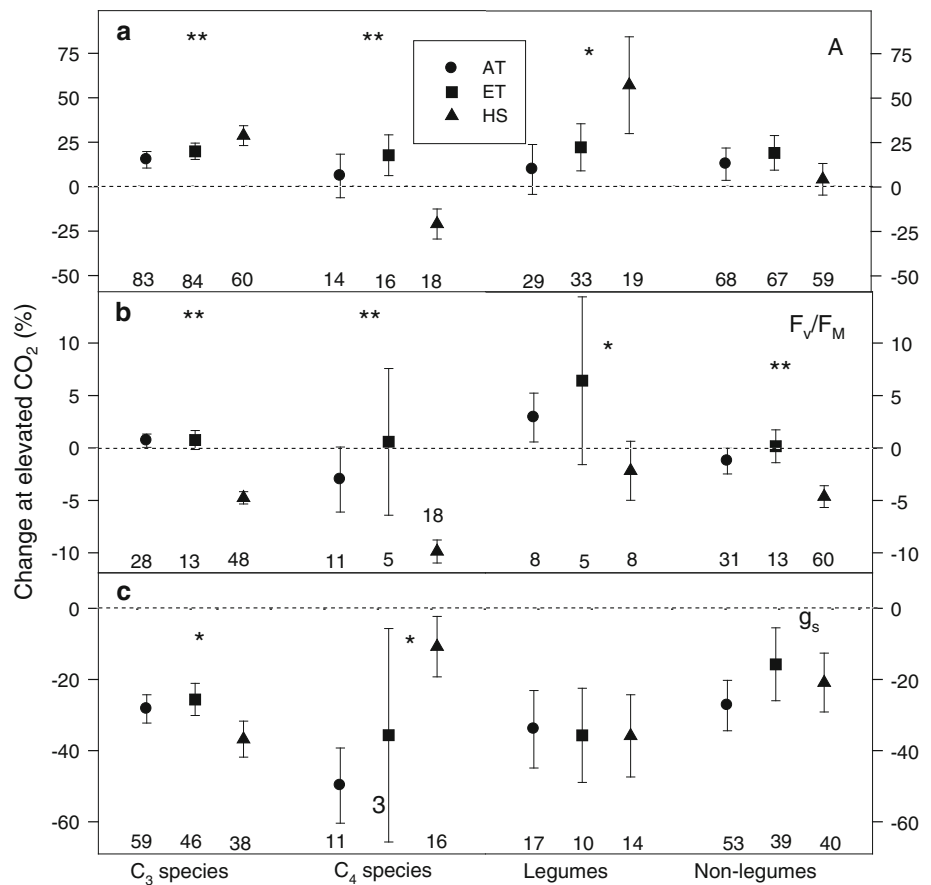
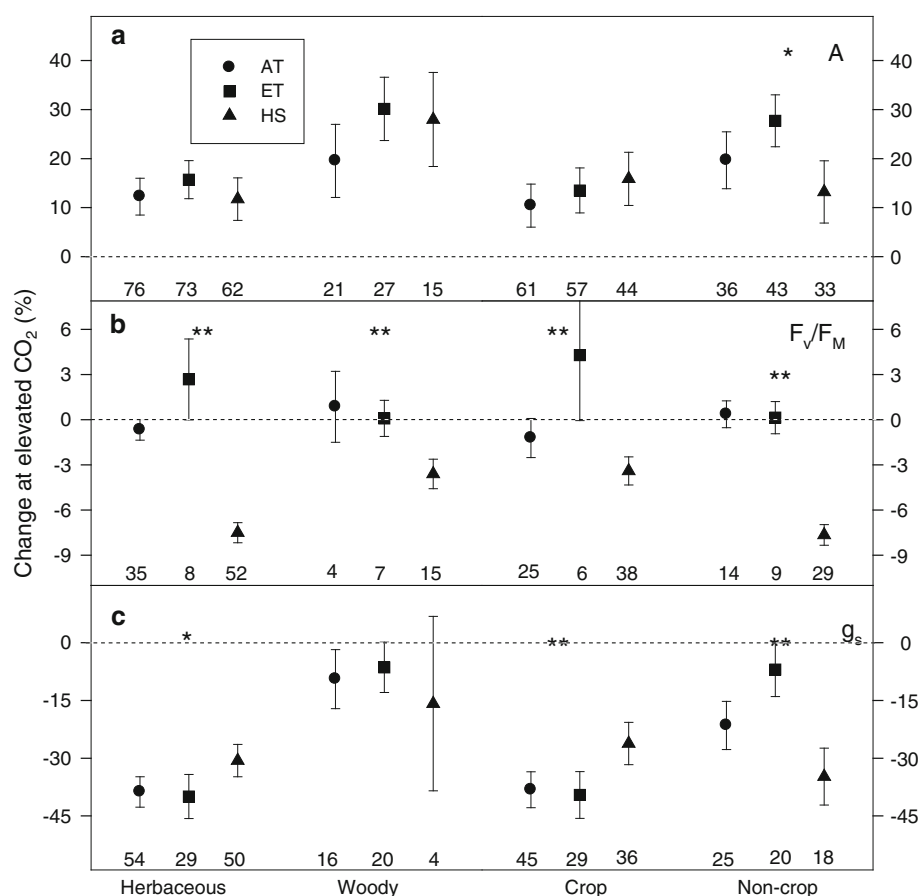


Fig. 3 Photosynthetic responses to eCO₂ in herbaceous, woody, crop, and non-crop species at different temperature treatments for net photosynthetic rate (*A*; **a**), PSII efficiency (F_v/F_m ; **b**), and stomatal conductance (g_s ; **c**). Each data point represents the mean \pm 95% CI (whiskers). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * $p < 0.05$ and ** $p < 0.01$ for comparison between temperature treatment categories whose CIs do not overlap



affected by eCO₂ at all temperature treatments (Fig. 4a), and the N_R of C₃ and C₄ species was not affected by eCO₂ at all temperatures (Fig. 4b). For N_R , there was publication bias for C₃ ($r_s = 0.83$, $p = 0.042$) and C₄ ($r_s = 0.83$, $p = 0.042$) species at HS, and in both cases, the publication bias could not be ignored based on Rosenthal's value.

The W_T , W_{AG} , and W_{BG} were all increased by eCO₂ in C₃, legume, and non-legume species at all temperature treatments (except for legumes at HS) (Fig. 5). For C₄ species, CO₂ had no effect on W_T , W_{AG} , and W_{BG} at AT, but it tended to have a positive effect at ET and HS, although the publication bias could not be ignored. Elevated CO₂ increased W_T , W_{AG} , and W_{BG} in herbaceous, woody, crop, and non-crop species at all temperature treatments (Fig. 6). At ET, the enhancement of W_T and W_{AG} by eCO₂ was greater in crops than in non-crops; the increase in W_{AG} and W_{BG} by eCO₂ in crops was greater than that in non-crops at AT (Fig. 6b).

At AT, the effect of eCO₂ on A was greater in plants grown in <10-L pots than in those in >10-L pots; at ET and HS, this effect did not differ between plants grown in smaller pots and those grown in larger ones. However, the effect of eCO₂ on A was smaller for plants grown in the ground at AT and ET than in those grown in pots (Fig. 7a). At ET and HS, the effect of eCO₂ on W_T was greater in

plants grown in >10-L-pots than on those grown in <10-L pots or in the ground (Fig. 7b).

Photosynthetic enhancement by eCO₂ was lowest in plants exposed to eCO₂ at AT for >1 year and greatest in plants exposed to eCO₂ for 1–30 days. The effect of eCO₂ on A was not different among exposure durations at ET. At HS, the effect of eCO₂ on A was higher in plants exposed to eCO₂ for 30–365 days than in those with a <1-day treatment (Fig. 8a). In addition, stimulation of A by eCO₂ tended to decrease in HS versus AT in plants exposed to eCO₂ for <1 or 1–30 days, but increase in heated versus AT plants in plants exposed to eCO₂ for 30–365 days. W_T always increased with eCO₂, regardless of the treatment duration. At ET, the enhancement of W_T was greater in plants exposed to eCO₂ for >1 year than in those exposed to eCO₂ for 30–365 days (Fig. 8b).

Discussion

In this meta-analysis, consistent with the prediction that high temperature stress is expected to be alleviated by eCO₂ due to improved photosynthesis in most species under hot conditions (Long 1991; Morison and Lawlor 1999), when averaged across all species, net photosynthesis was

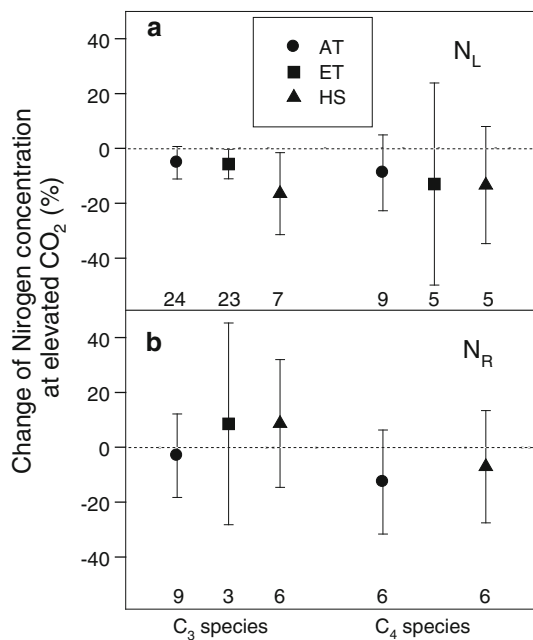


Fig. 4 Response of plant tissue nitrogen concentration to eCO₂ in C₃ and C₄ species at different temperature treatments for leaf N concentration (N_L; **a**) and root N concentration (N_R; **b**). Each data point represents the mean \pm 95% CI (whiskers). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * $p < 0.05$ and ** $p < 0.01$ for comparison between temperature treatment categories whose CIs do not overlap

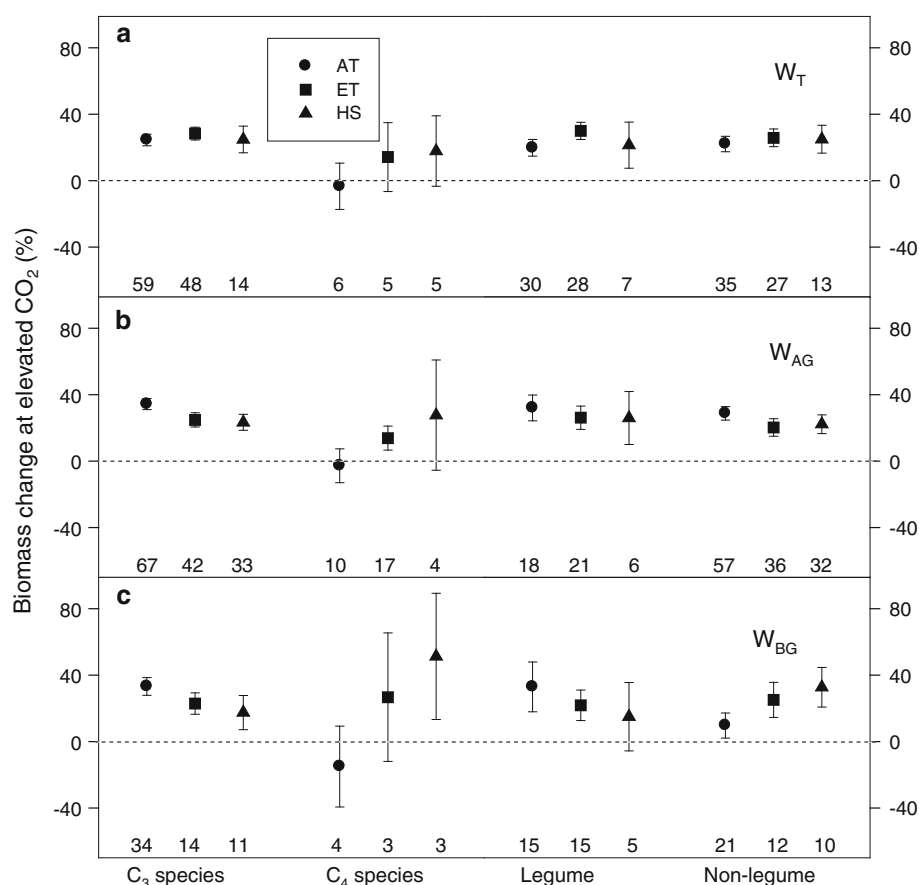
enhanced by eCO₂ at ET and HS (Fig. 1a). However, plants with different photosynthetic pathways responded differently to eCO₂ and temperature. In C₃ species, which comprise approximately 90% of all plant species, net photosynthesis was enhanced by eCO₂ at all temperatures, with the benefit being the greatest at HS and the least at AT. For C₄ species, eCO₂ had no effect at AT, a positive effect at ET (as in Wand et al. 1999), and a negative effect at HS (as in Wang et al. 2008) (Fig. 2a). In C₃ species, the benefits of eCO₂ at high temperatures are likely due to decreases in photorespiration that offset decreases in F_v/F_m , RA, g_s , or N_L . In C₄ species, however, which have low levels of photorespiration and are CO₂ saturated at the current CO₂ level, the negative effect of eCO₂ on net photosynthesis at HS may be related to decreased N_L or higher leaf temperatures caused by lower stomatal conductance (Wang et al. 2008). Growth temperature is known to strongly influence the response and tolerance of organisms and photosynthesis to HS (Barua and Heckathorn 2004). It has been reported that growing cool-season C₃ species at a lower temperature (25°C) increases the benefits of eCO₂ on the photosynthetic tolerance to HS of these plants compared with growing them at a higher temperature (30°C) (Wang et al. 2008). However, the average growth temperature for C₃ ($29.5 \pm 1.8^\circ\text{C}$, $n = 32$) and C₄ ($30.1 \pm 2.5^\circ\text{C}$, $n = 15$)

species was not significantly different in the HS treatment of this study. The enhancement of photosynthesis by eCO₂ was found to be greater for woody species than for herbaceous species at ET and HS, which might be due to the inclusion of the more-responsive juvenile and exponentially growing trees in many CO₂ studies (Wang 2007), and the benefit of eCO₂ was found to be greater in non-crop than crop species at ET (Fig. 2a). It is important to note that low sample sizes for some functional groups used in this analysis (e.g., C₄, legumes, and trees) require that some results in this analysis be interpreted with caution; nevertheless, results from these under-represented groups demonstrate that further study of these groups is critical, and these results provide hypotheses for future studies to test.

The response of g_s to eCO₂ is critical for modeling ecosystem and landscape-scale water flux. We found decreased stomatal conductance (g_s) at eCO₂ for all species groups (excluding woody species at HS), regardless of different temperature treatments, which is consistent with the findings from other reviews (Long et al. 2004; Ainsworth and Long 2005; Ainsworth and Rogers 2007). g_s was decreased less by eCO₂ for C₄ than for C₃ at HS, which suggested that the negative effect of eCO₂ on A for C₄ species was not directly caused by the decrease in g_s . The decrease of g_s by eCO₂ was less for woody than for herbaceous and for non-crop than for crop species at AT and ET. Hence, these results from this current study are similar to the trend reported for trees, shrubs, and forbs, showing a lower percentage decrease in g_s compared to C₃ and C₄ grasses and herbaceous crops (Saxe et al. 1998; Ainsworth and Rogers 2007). As suggested in Warren et al. (2011), the decrease in g_s may increase leaf temperature resulting from a decline in latent heat loss through evaporation, which may further affect net carbon balance.

It has been hypothesized that at supra-optimal temperatures, both electron transport capacity and Rubisco activase capacity can limit net photosynthesis at eCO₂ (Sage and Kubien 2007). In this analysis, PSII efficiency (F_v/F_m) was negatively affected by eCO₂ at HS (except for legumes), regardless of the photosynthetic pathway, indicating that eCO₂ enhanced photoinhibition at higher temperatures (as in Roden and Ball 1996a). More research is needed on the effect of CO₂ on PSII efficiency at ET, since the publication bias on this effect could not be ignored in this meta-analysis. At AT, elevated CO₂ increases F_v/F_m in legumes but decreases it in non-legumes, which indirectly supports the hypothesis that eCO₂ decreases photoinhibition under conditions of high N but increases photoinhibition under conditions of low N (Hymus et al. 2001). RA was negatively affected by eCO₂ at AT, ET, and HS (Fig. 1d). High-CO₂ effects on RA often closely match reductions in N content and increases in soluble carbohydrate levels (Körner 2006; Reich et al. 2006; Rustad 2006).

Fig. 5 Biomass response to $e\text{CO}_2$ in C_3 , C_4 , legume, and non-legume species at different temperature treatments for whole-plant dry weight (W_T ; **a**), above-ground dry weight (W_{AG} ; **b**), and below-ground dry weight (W_{BG} ; **c**). Each data point represents the mean \pm 95% CI (whiskers). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * $p < 0.05$ and ** $p < 0.01$ for comparison between temperature treatment categories whose CIs do not overlap



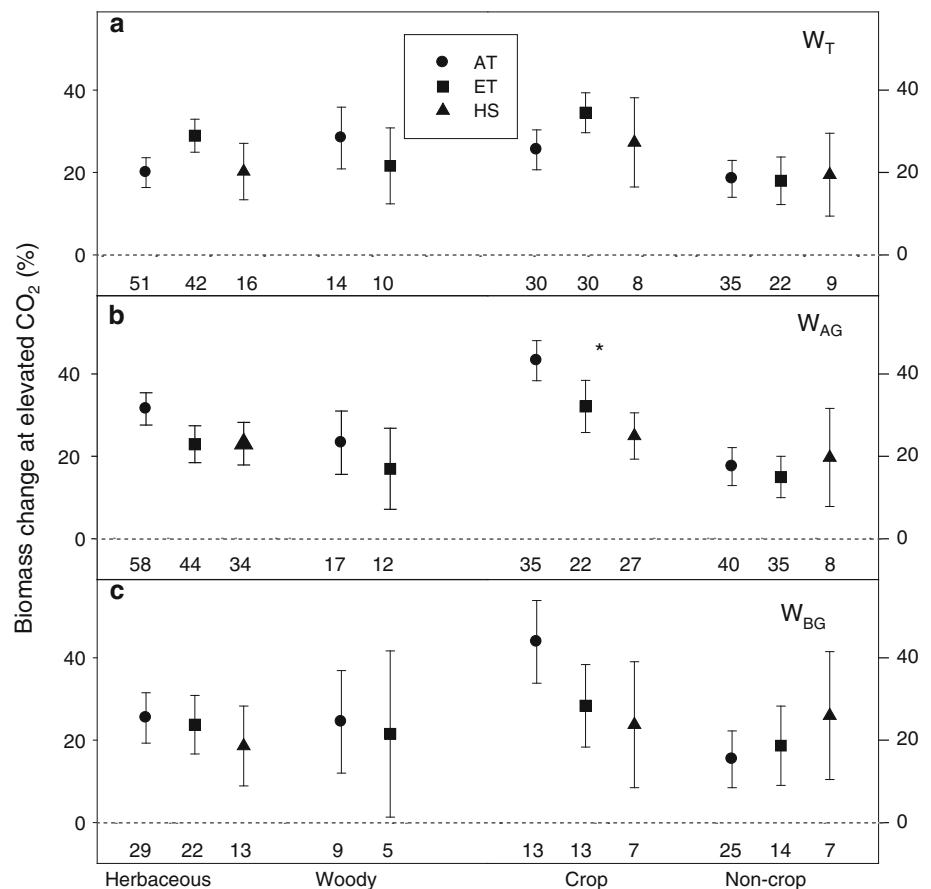
Decreased RA could be caused by reduced Rubisco content or by decreased specificity of Rubisco (Aranjuelo et al. 2005; Korner 2006; Gutschick 2007).

It has been well documented that the availability of mineral nutrients, particularly N, can greatly modify plant growth responses to $e\text{CO}_2$ (Diaz et al. 1993; Hebeisen et al. 1997; Luo et al. 2004; Reich et al. 2006). The negative effect of $e\text{CO}_2$ on net photosynthesis in C_4 species at HS, including F_v/F_m , might also be related to a decreased N concentration, which could result in the impaired synthesis of photosynthetic enzymes and protecting systems; such damage would not be compensated for by decreased photorespiration at $e\text{CO}_2$, as in C_3 species (Bunce 2000; Aranjuelo et al. 2005). Perhaps due to the smaller dataset, we were unable to detect a significant decrease of N_L for C_4 species at $e\text{CO}_2$. However, we did find that across all species, N_L tended to decrease at all temperatures with $e\text{CO}_2$ and that the magnitude of the decrease was greatest at HS, although it was not significantly different from that at AT and ET (Fig. 1f). We further tested this hypothesis by separating plants into legumes and non-legumes, on which $e\text{CO}_2$ imposed similar effects on A at AT and ET. However, at HS, $e\text{CO}_2$ had a significantly greater positive effect on legumes than on non-legumes (Fig. 2a), which indirectly suggests that

N_L might play a role in plant tolerance to HS at $e\text{CO}_2$. In this meta-analysis, due to the smaller sample sizes at HS, specific mechanisms of $e\text{CO}_2$ on N_L and N_R at ET and HS should be generalized with caution, and more studies are needed to further understand these $\text{CO}_2 \times$ temperature effects and their underlying causes, such as changes in leaf temperature and increases in heat-shock proteins (Wang et al., unpublished data), protective compatible solutes (Williams et al. 1992), and isoprene production (Velikova and Loreto 2005).

It is important to note that A per unit leaf area is not the most important factor for predicting overall plant growth (Korner 1991). The combination of carbohydrate production, which is determined by photosynthetic rate and leaf area, and the consumption of carbohydrates for growth, respiration, storage, and root exudation, account for most of the overall growth enhancement under conditions of $e\text{CO}_2$ (Morison and Lawlor 1999). The negative effect of $e\text{CO}_2$ on A in C_4 species at HS might be offset by the positive effects of $e\text{CO}_2$ on leaf area, respiration, and water use efficiency (Owensby et al. 1993, 1999; Hamerlynck et al. 1997), or the imbalance between source (photosynthesis) and sink (growth). Consistent with the finding that LMA (leaf mass per unit area, the inverse of SLA) increases at higher CO_2 levels (Poorter et al. 2009), in our

Fig. 6 Biomass response to eCO₂ in herbaceous, woody, crop, and non-crop species at different temperature treatments for whole-plant dry weight (W_T ; **a**), above-ground dry weight (W_{AG} ; **b**), and below-ground dry weight (W_{BG} ; **c**). Each data point represents the mean \pm 95% CI (whiskers). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * $p < 0.05$ and ** $p < 0.01$ for comparison between temperature treatment categories whose CIs do not overlap



study, at AT, SLA decreased at eCO₂ (Fig. 1e). SLA declines when the increase in leaf size is less than the increase in leaf mass at eCO₂ (Yin 2002). We found that the decrease in SLA with eCO₂ was less pronounced at ET than at AT (Fig. 1e). It has also been reported that C₃ and C₄ species differ in their response, with C₄ species showing a decrease in LMA (=an increase in SLA) at the higher CO₂ concentrations (Ackerly et al. 1992; Wolfe et al. 1998; Ghannoum et al. 2000; Poorter et al. 2009). Higher SLA is beneficial for obtaining a more extensive foliar display that captures more light for constant biomass investment (Niinemets 1999), which could contribute to the positive effect of CO₂ on biomass gain at HS for C₄ species, despite the negative effect on A. It has also been found that eCO₂ can reduce transpiration (Bruhn et al. 2002; Gonzelez-Meller et al. 2004; Bunce 2005). Reduced stomatal conductance at eCO₂ will slow the rate of transpiration and therefore decrease the onset, severity, and impact of water stress, which is often accompanied by high temperature stress (Morison 1993). More experiments are needed to assess the balance of these processes and the extent and direction of acclimation of these processes to temperature and CO₂ interaction.

It is essential that potential confounding factors be considered in a meta-analysis which synthesizes results

from a large number of studies that were conducted under a variety of growing conditions on different plant species. In our analysis, studies in which plants were grown under environmental stresses (e.g., drought, low nutrients, light deficiency, or elevated ozone) were excluded. A large variation in CO₂ effects on unstressed plants, however, was still found, due to differences in experimental protocols and temperature regimes in the empirical studies. Growth temperature might interact with CO₂ to influence the response of photosynthesis to temperature treatments. Trees from tropical and subtropical regions have been reported to be more susceptible to growth declines in a warmer climate than trees from higher latitudes (Way and Oren 2010). We found that the duration of the treatment was another important factor affecting plant responses to high-temperature treatments. Photosynthetic enhancement in plants exposed to eCO₂ for more than 1 year was not significant at AT (Fig. 8a). This temporal pattern suggests a down-regulation of photosynthesis relative to its initial capacity at eCO₂ and is consistent with results from earlier studies with spruce (van Oosten et al. 1992) and orange trees (Adam et al. 2004). Down-regulation of photosynthesis by eCO₂ has been suggested to be correlated with reduced protein content and enzyme activation, based on results relating to alterations in the expression of genes

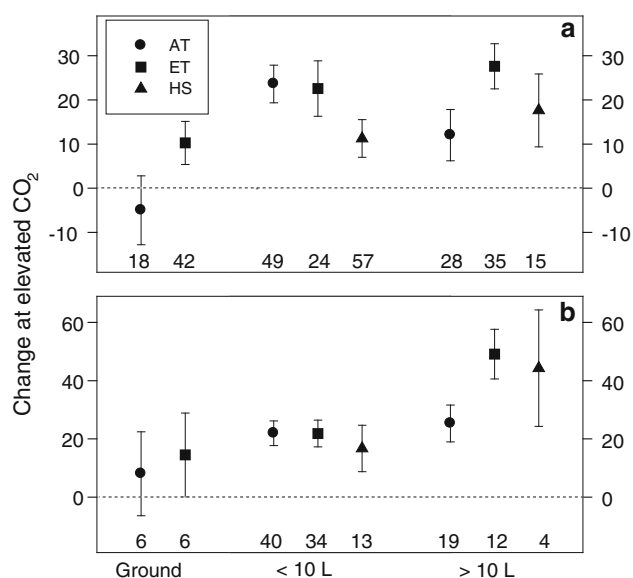


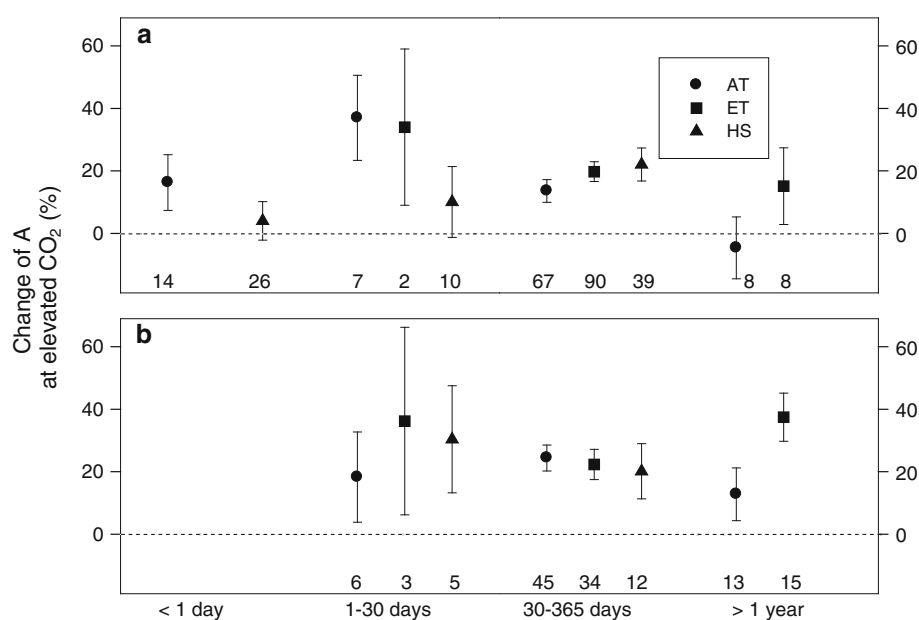
Fig. 7 Responses to eCO₂ in net photosynthetic rate (A; **a**) and whole-plant dry weight (W_T; **b**) by plants grown in the ground, in <10-L pots, or in >10-L pots and under different temperature treatments. Each data point represents the mean \pm 95% CI (whiskers). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * p < 0.05 and ** p < 0.01 for comparison between temperature treatment categories whose CIs do not overlap

encoding Rubisco at the transcriptional and/or post-transcriptional level (Van Oosten and Besford 1994; Moore et al. 1999). Species differences in the photosynthetic responses to eCO₂ could be ecologically important if they influence species productivity and distribution and, subsequently, species dynamics. Another issue of concern about the effects of eCO₂ has been centered on how much the

effects are influenced by the particular cultural or exposure systems used. The exposure systems used in the studies included in this meta-analysis were mostly closed systems, including greenhouses and growth chambers. This meta-analysis revealed no significant effect of exposure systems on photosynthetic responses to CO₂ or temperature. Pot size is also thought to be another important factor affecting the magnitude of photosynthetic responses to eCO₂, by implicating root sink strength (Arp 1991). Contrary to the expectation that the effect of eCO₂ on A would be smaller for plants grown in small pots, we found that the effect of eCO₂ on A was smallest for plants grown in the ground, which perhaps was mainly caused by the fact that many experiments in which plants were grown in the ground lasted for more than 1 year. These results on pot size should be interpreted with caution, since we do not have information on root temperature and the pot size-to-plant size ratios in studies used in this analysis, or the extent to which nutrients were flushed through the pots during growth (Korner 2003).

A third potential confounding factor we considered is the biased choice of species in the empirical studies, and hence unbalanced composition of species in different categories in this meta-analysis. For example, C₄ species, which are all non-legumes, might account for the lower photosynthetic and growth responses to eCO₂ in non-legumes, since the C₃ species used in this meta-analysis included a number of legumes. We excluded all C₄ species from the non-legumes and performed another analysis on plant species that were all C₃ species. The results showed that at AT and ET, photosynthetic responses to eCO₂ were similar for legumes and non-legumes; but at HS, eCO₂ had a more pronounced effect (36%, n = 19) for legumes than

Fig. 8 Responses to elevated CO₂ in net photosynthetic rate (A; **a**) and whole-plant dry weight (W_T; **b**) under different temperature treatments for different treatment (CO₂ \times temperature) durations. Each data point represents the mean \pm 95% CI (whiskers). The number of observations for each category used in the analysis is given at the bottom of each graph, under the corresponding CI. * p < 0.05 and ** p < 0.01 for comparison between temperature treatment categories whose CIs do not overlap



for non-legumes (18%, $n = 41$). These results demonstrate that the inclusion of C_4 species did not obscure the comparison between non-legumes and legumes.

In summary, we found significant interactive effects of eCO_2 and temperature on a number of plant physiological and growth variables. The most surprising result was that at HS, eCO_2 had a negative effect on photosynthesis in C_4 species, compared with a positive effect in C_3 species. Compared with legumes, non-legumes showed less enhancement of photosynthesis in response to eCO_2 at HS, suggesting that the interactive effects of heat and eCO_2 are partly dependent on N status. W_T responded positively to eCO_2 in all species group at all temperatures, except in C_4 species. The negative effects of eCO_2 in C_4 species on photosynthesis under HS may be alleviated by higher water-use efficiency and leaf area of C_4 species, especially in times of water stress, and the benefits of eCO_2 to C_3 species may be offset by likely changes in other environmental factors which influence thermotolerance differentially (e.g., changes in precipitation which might increase or decrease tolerance, and increasing ozone which might decrease tolerance). This meta-analysis highlights the importance of improving our mechanistic understanding of plant responses to the interactive effects of eCO_2 and other abiotic factors, particularly higher temperature, increased N deposition, and altered patterns of precipitation, all of which are expected in the future.

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