A Meta-analysis of the Effects of Experimental Warming on Plant Physiology and Growth on the Tibetan Plateau

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Abstract Uncertainties about the response of plant photosynthesis and growth to elevated temperature make it difficult to predict how plant production will vary under future climatic warming in alpine regions. Here, we used a meta-analysis approach to synthesize 272 observations from 27 studies on the Tibetan Plateau. Warming significantly increased aboveground biomass by 19.1 % (95 % CI 6.0–40.7 %), belowground biomass by 26.7 % (95 % CI 3.0–87.5 %), and net photosynthetic rate (P_n) by 13.6 % (95 % CI 9.7–17.7 %). The increase of P_n was attributed to the increases in stomatal conductance, apparent quantum yield, chlorophyll content, non-photochemical quenching of chlorophyll fluorescence, soluble sugar, and peroxidase. A decoupling of plant photosynthesis and leaf N concentration occurred. Our findings imply that global warming may have a stronger effect on the alpine plants on the Tibetan Plateau than the global average. Our findings provided a better understanding of the physiological responses of alpine plants to future climatic warming.

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Introduction

By the end of this century, global surface temperature is predicted to increase by 1.8–4 °C (IPCC 2007). Such warming has affected global carbon sequestration in various terrestrial ecosystems, especially for alpine ecosystems at the high altitudes and latitudes (Lin and others 2010; Chen and others 2013). To better understand the responses of plant photosynthesis and growth to climatic warming, extensive field experiments have been conducted worldwide (Fu and others 2013; Ruiz-Vera and others 2013; Yang and others 2013). Moreover, several meta-analyses have also investigated the general tendency of warming effects on plant production (Rustad and others 2001; Lin and others 2010; Wu and others 2011). However, it remains unclear how plant physiology will vary under warming and how the change in plant physiology will affect plant photosynthesis. Concentrations of photosynthetic pigments, chlorophyll (Chl) fluorescence parameters, stomatal conductance (g_s), intercellular CO_2 concentration (C_i), maximum rate of carboxylation (V_{max}), apparent quantum yield (AQY), antioxidant enzymes, superoxide anion radicals (O_2^-), hydrogen peroxide (H_2O_2), and malondialdehyde (MDA) are important physiological parameters related to plant photosynthesis (Ruiz-Vera and others 2013; Yang and others 2013). All these physiological parameters are temperature-dependent and probably affected under climatic warming (Yin and others 2008; Han and others 2009; Shi and others 2010; Xu and others 2012; Yang and others 2012). For example, warming

significantly increased antioxidant enzymes of *Kobresia pygmaea* (Yang and others 2012). Increases in O_2^-, H_2O_2, and MDA within plants are harmful to plant photosynthesis because they likely result in physiological damage (Girotti 1985; Han and others 2009; Shi and others 2010). In contrast, plant photosynthesis benefits from increases in antioxidant enzymes, AQY, V_{max}, g_s, photosynthetic pigment concentrations, and Chl fluorescence parameters (Awada and others 2003; Shi and others 2010). Photoinhibition may generally occur as a result of high light intensity in high-elevation regions and warming may affect photoinhibition (Shi and others 2009). Warming enhanced the photoinhibition of *Elymus nutans*, but reduced the photoinhibition of *Potentilla anserina* (Shi and others 2010). In addition, plant photosynthetic capacity is positively related to leaf N concentration (Kattge and others 2009; Xu and others 2012) and warming significantly increased leaf N by 2.8 % across all terrestrial biomes (Bai and others 2013). Therefore, the change in net photosynthesis rate (P_n) under climatic warming is dependent on the relative change between beneficial and adverse photosynthetic parameters caused by warming.

Temperature and soil N availability are generally considered to be the most vital limiting factors for plant growth and biomass accumulation in alpine regions (Gugerli and Bauert 2001; Lin and others 2010). Warming likely accelerates net N mineralization and nitrification rates, resulting in an increase in nutrient availability (Rustad and others 2001; Bai and others 2013). The results indicated that the positive effect of warming on plant growth and biomass accumulation may result from the direct effect of enhanced temperature and indirect effect of warming-induced increases in nutrient availability. However, some studies showed that warming did not increase gross primary production or aboveground plant biomass in alpine ecosystems (Klein and others 2007; Fu and others 2013). A decoupling of plant biomass and soil N availability occurred on the Tibetan Plateau (Wang and others 2012; Jiang and others 2013). Wang and others (2012) indicated that warming significantly increased aboveground net primary production, but had little effect on soil N availability. In addition, N fertilization did not significantly alter aboveground net primary production (Wang and others 2012) and aboveground and belowground plant biomass in July and August (Jiang and others 2013). Some alpine plants on the Tibetan Plateau can directly use organic N (Xu and others 2006), and this ability is related to plant physiology (Chapin and others 1993).

In this study, we compiled data from 27 experimental warming studies across the Tibetan Plateau. The goal was to quantitatively identify the general tendency of the warming effects on 32 variables related to plant physiological and growth of "Earth's Third Pole". Climatic warming will increase P_n and plant productivity across all the biomes (Wu and others 2011; Lu and others 2013). Warming amplitude on the Tibetan Plateau (about 0.7 °C during 1971–2000) is much greater than the global average (about 0.5 °C during 1971–2000), and alpine ecosystems are more sensitive to climatic warming compared with other terrestrial ecosystems (Wu and others 2005; IPCC 2007). Therefore, we hypothesized that warming was beneficial to alpine plants, and the positive response magnitude to warming on the Tibetan Plateau was higher than the global average.

Materials and Methods

Data Compilation

We searched articles published before September, 2013 using the Web of Science and the China National Knowledge Infrastructure (Supporting information, Table S1). Our criteria were as follows: only studies conducted on the Tibetan Plateau were included; at least one of the variables considered here were measured; studies with laboratory incubation, temperature gradients, and growth chambers were excluded, and only field warming experimental studies were included; only data from control and warming treatments were used for multifactor experiments; only the latest results were used for multiple observations at different times from the same study site because the observations should be independent in a meta-analysis (Hedges and others 1999; Rosenberg and others 2000); means, standard deviations (or standard errors), and sample sizes were directly provided or could be calculated from the studies; multiple soil depths, warming magnitudes, or ecosystem types were treated as independent (Bai and others 2013; Lu and others 2013).

We collected latitude, longitude, elevation, mean annual temperature, mean annual precipitation, ecosystem types, warming method, warming duration, and the response variables. Soil temperature and moisture were also collected if reported. Warming duration was calculated in months. Data were extracted by GetData software if the studies provided the data in figures. We grouped all the studies into those analyzing forests and grasslands at the ecosystem level and into those analyzing trees and grasses at the species level. Warming methods included open top chambers and infrared heaters.

The compiled database included plant growth parameters [plant height, basal diameter, leaf length, shoot length, leaf area index (LAI), and specific leaf area (SLA)], biomass parameters [aboveground biomass (AGB), belowground biomass (BGB)], C pools (leaf starch and soluble sugar concentration), leaf N, P_n, plant antioxidant enzymes [superoxide dismutase (SOD), peroxidase (POD), catalase

(CAT), and ascorbate peroxidase (APX)], Chl fluorescence parameters [non-photochemical quenching (NPQ), photochemical quenching (Q_p), maximal PSII efficiency (F_v/F_m), and actual photochemical efficiency of PSII in the light (Yield)], photosynthetic pigment concentration [chlorophyll a (Chl$a$), chlorophyll b (Chl$b$), and carotenoids], and other parameters related to plant photosynthesis [O_2^-, H_2O_2, MDA, g_s, C_i, V_{max}, AQY, light compensation point (LCP), and saturation point (LSP)].

Statistical Analyses

In this study, we used METAWIN 2.1 software (Sinauer Associates Inc., Sunderland, MA, USA) (Rosenberg and others 2000) to perform the meta-analysis. The natural logarithm of the response ratio (R) without and with standardization by warming magnitude was used as the effect size (Hedges and others 1999),

$$\text{Log}_e R = \text{Log}_e\left(\frac{\overline{X_t}}{\overline{X_c}}\right) = \text{Log}_e\left(\overline{X_t}\right) - \text{Log}_e\left(\overline{X_c}\right) \quad (1)$$

$$\text{Log}_e R = \frac{\text{Log}_e\left(\frac{\overline{X_t}}{\overline{X_c}}\right)}{T_t - T_c} = \frac{\text{Log}_e\left(\overline{X_t}\right)}{T_t - T_c} - \frac{\text{Log}_e\left(\overline{X_c}\right)}{T_t - T_c} \quad (2)$$

where $\overline{X_c}$ and $\overline{X_t}$ are the mean values in the control and warming treatments, respectively. T_c and T_t are the air temperature in the control and warming treatments, respectively.

For each study, the inverse of the pooled variance ($1/v$) or sample size (N_{weight}) was used as the weighting factor (w),

$$v = \frac{S_t^2}{n_t \overline{X_t}^2} + \frac{S_c^2}{n_c \overline{X_c}^2} \quad (3)$$

$$N_{weight} = \frac{n_t \times n_c}{n_t + n_c} \quad (4)$$

where S_c^2 and S_t^2 are the standard deviations in the control and warming treatments, respectively; n_c and n_t are the sample sizes in the control and warming treatments, respectively.

Therefore, we obtain the mean effect size ($\overline{\text{Log}_e R}$) for all observations,

$$\overline{\text{Log}_e R} = \frac{\sum_{i=1}^{m} w_i \text{Log}_e R_i}{\sum_{i=1}^{m} w_i}, \quad (5)$$

where w_i and $\text{Log}_e R_i$ are w and $\text{Log}_e R$ of the ith observation, respectively.

A fixed effects model was used to test whether a variable had a significant response to warming (Rosenberg and others 2000). Mean effect size and 95 % bootstrap confidence intervals (CI) were generated. For a specific variable, if the 95 % bootstrap CI did not cover zero, the warming effect on this variable was statistically significant (Wan and others 2001). We transformed the mean effect size of a variable to the percentage change$(e^{\overline{\text{Log}_e R}} - 1) \times 100\%$. All statistical significance was examined at $P < 0.05$.

Results

Experimental warming had significant positive effects on plant height (+25.1 %; 95 % CI 13.0–40.4 %), basal diameter (+10.6 %; 95 % CI 4.9–17.5 %), leaf length (+40.1 %; 95 % CI 26.4–54.2 %), shoot length (+14.6 %; 95 % CI 12.7–17.8 %), LAI (+9.5 %; 95 % CI 4.9–15.2 %), SLA (+7.2 %; 95 % CI 3.7–9.9 %), aboveground biomass (+19.1 %; 95 % CI 6.0–40.7 %), and belowground biomass (+26.7 %; 95 % CI 3.0–87.5 %), when weighed by the inverse of the pooled variance (Fig. 1a). Experimental warming also significantly increased plant height by 23.1 % (95 % CI 11.3–37.3 %), basal diameter by 7.8 % (95 % CI 2.4–14.1 %), leaf length by 37.8 % (95 % CI 21.2–55.6 %), shoot length by 15.8 % (95 % CI 12.6–19.3 %), LAI by 12.5 % (95 % CI 4.8–23.1 %), SLA by 7.4 % (95 % CI 3.5–10.4 %), aboveground biomass by 26.6 % (95 % CI 10.8–48.1 %), and belowground biomass by 29.9 % (95 % CI 16.5–48.1 %), when weighed by sample size (Fig. 1b). A 1 °C increase of temperature significantly increased plant height by 19.9 % (95 % CI 7.7–35.0 %), basal diameter by 8.8 % (95 % CI 3.0–13.0 %), leaf length by 9.5 % (95 % CI 6.3–12.6 %), shoot length by 9.8 % (95 % CI 7.1–11.7 %), LAI by 3.2 % (95 % CI 1.4–5.3 %), SLA by 4.6 % (95 % CI 2.1–7.3 %), and aboveground biomass by 32.1 % (95 % CI 6.5–103.6 %), but insignificantly increased belowground biomass by 2.2 % (95 % CI −9.3–16.8 %), when weighed by the inverse of the pooled variance (Fig. 1c). Similarly, when weighed by sample size, a 1 °C increase of temperature significantly increased plant height by 13.5 % (95 % CI 4.6–24.2 %), basal diameter by 5.8 % (95 % CI 1.7–10.1 %), leaf length by 9.1 % (95 % CI 5.1–12.7 %), shoot length by 8.8 % (95 % CI 6.1–11.2 %), LAI by 5.3 % (95 % CI 1.3–11.7 %), SLA by 5.9 % (95 % CI 2.5–9.2 %), and aboveground biomass by 37.2 % (95 % CI 10.2–93.8 %), but insignificantly increased belowground biomass by 1.4 % (95 % CI −19.5–18.9 %) (Fig. 1d).

When weighed by the inverse of pooled variance, soluble sugar in leaves increased by 27.9 % (95 % CI 16.8–42.0 %) under warming conditions, whereas leaf

Fig. 1 Effect sizes of experimental warming on basal diameter (BD), leaf length (LL), shoot length (SL), plant height (PH), leaf area index (LAI), specific leaf area (SLA), aboveground biomass (AGB) and belowground biomass (BGB) weighting by the inverse of the pooled variance without standardization by warming magnitude (**a**), weighting by sample sizes without standardization by warming magnitude (**b**), weighting by the inverse of the pooled variance with standardization by warming magnitude (**c**), and weighting by sample sizes with standardization by warming magnitude (**d**). *Error bars* indicate effect sizes and 95 % bootstrap confidence intervals. The *dashed lines* are drawn at effect size = 0. The sample size for each variable is shown next to the *bar*
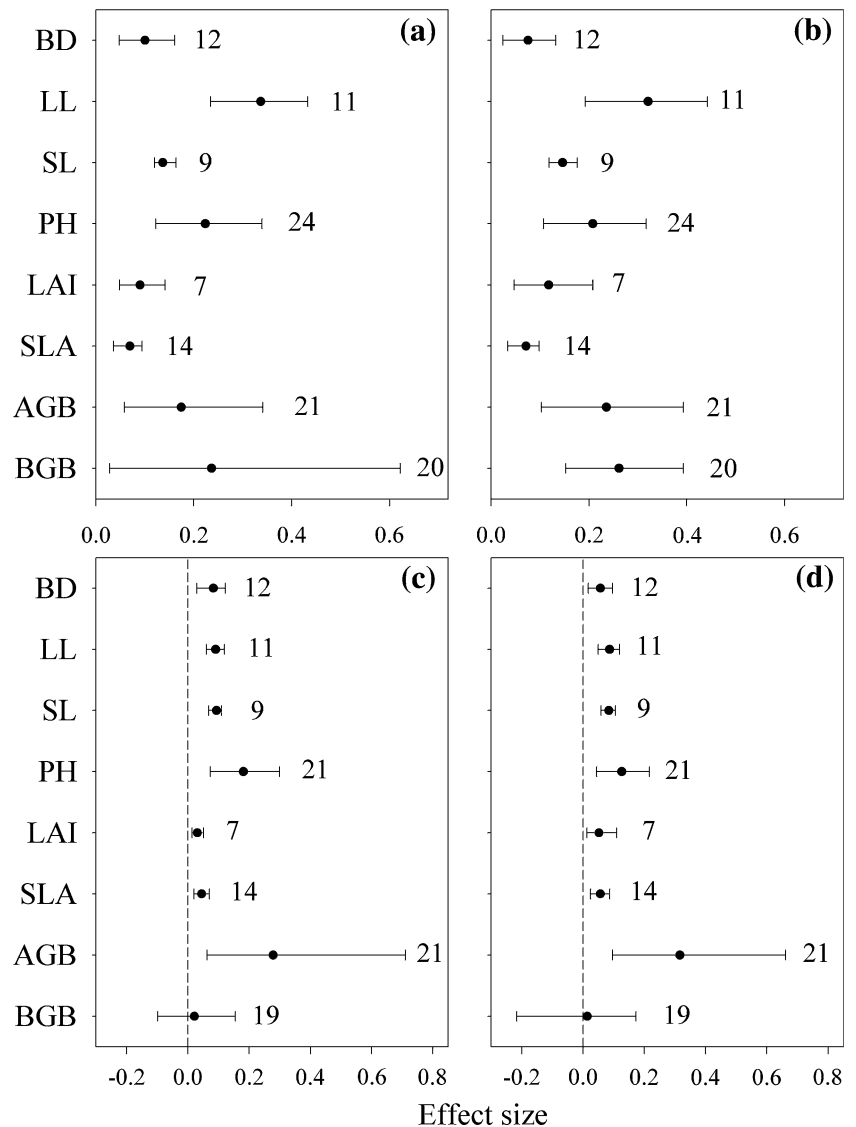
starch (95 % CI −24.7–17.2 %) and N (95 % CI −11.6–5.2 %) were not significantly affected (Figs. 2a, 3a). Experimental warming had a significant positive effect on POD (+22.2 %; 95 % CI 10.1–107.6 %), but did not significantly alter SOD (95 % CI −0.5–40.1 %), APX (95 % CI −3.4–101.0 %), CAT (95 % CI −12.1–30.1 %), MDA (95 % CI −16.2–19.8 %), O_2^- (95 % CI −16.1–2.9 %), and H_2O_2 (95 % CI −60.1–1.5 %) (Figs. 2a, 3a). In contrast, when weighed by sample size, soluble sugar in leaves increased by 29.7 % (95 % CI 16.8–44.0 %) under warming conditions, whereas leaf starch (95 % CI −25.1–16.4 %) and N (95 % CI −10.1–3.9 %) were not significantly affected (Figs. 2b, 4a). Experimental warming had a significant positive effect on POD (+36.8 %; 95 % CI 13.2–79.2 %), SOD (+27.9 %; 95 % CI 8.9–47.8 %), and APX (+41.8 %; 95 % CI 11.3–89.6 %), but a significant negative effect on H_2O_2 (−33.0 %; 95 % CI −71.4 to

−2.6 %) (Figs. 2b, 4a). In contrast, experimental warming did not significantly alter CAT (95 % CI −12.1–30.1 %), MDA (95 % CI −16.6–23.9 %), and O_2^- (95 % CI −14.4–5.9 %) (Figs. 2b, 4a). A 1 °C increase of temperature significantly increased soluble sugar by 11.2 % (95 % CI 5.1–18.6 %) and 12.2 % (95 % CI 5.3–19.6 %) and POD by 9.1 % (95 % CI 5.6–29.7 %) and 14.9 % (95 % CI 6.1–27.4 %), when weighed by the inverse of pooled variance and sample size, respectively (Fig. 2c, d). In contrast, a 1 °C increase of temperature significantly decreased O_2^- by 3.9 % (95 % CI −8.5 % to −0.5 %), when weighed by the inverse of pooled variance (Fig. 5a). A 1 °C increase of temperature significantly increased SOD by 14.5 % (95 % CI 3.7–25.3 %) and APX by 17.8 % (95 % CI 4.6–35.9 %), but significantly reduced H_2O_2 by 15.8 % (95 % CI −41.9 % to −0.7 %), when weighed by sample size (Figs. 2d, 6a).

Fig. 2 Effect sizes of experimental warming on starch, soluble sugar (SSugar), chlorophyll a (Chla), chlorophyll b (Chlb), carotenoid (Caro), maximal PSII efficiency (F_v/F_m), photochemical quenching (Q_p), non-photochemical quenching (NPQ), yield, maximum rate of carboxylation (V_{max}), light saturation point (LSP), catalase (CAT), superoxide dismutase (SOD), peroxide (POD), and ascorbate peroxidase (APX) weighting by the inverse of the pooled variance without standardization by warming magnitude (**a**), weighting by sample sizes without standardization by warming magnitude (**b**), weighting by the inverse of the pooled variance with standardization by warming magnitude (**c**), and weighting by sample sizes with standardization by warming magnitude (**d**). *Error bars* indicate effect sizes and 95 % bootstrap confidence intervals. The *dashed lines* are drawn at effect size = 0. The sample size for each variable is shown next to the *bar*
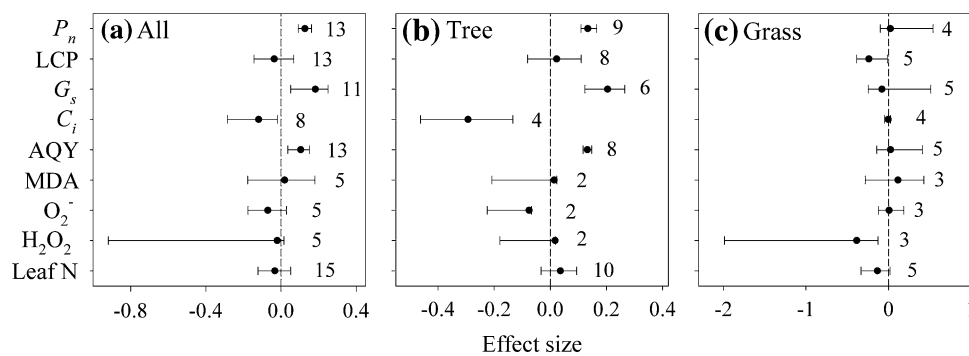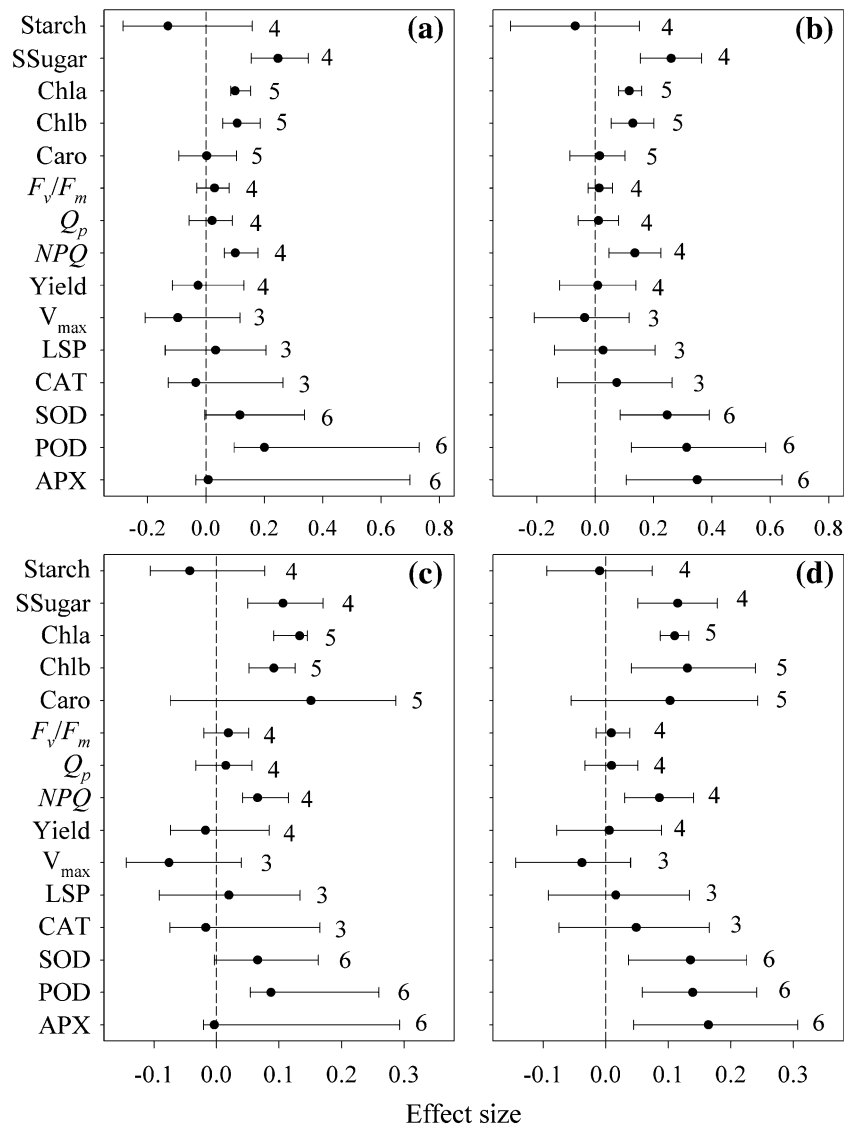

Fig. 3 Effect sizes of experimental warming on net photosynthesis rate (P_n), light compensation point (LCP), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), apparent quantum yield (AQY), malondialdehyde (MDA), superoxide anion radical (O_2^-), hydrogen peroxide (H_2O_2), and leaf N for Tree + Grass (**a**), Tree (**b**), and Grass (**c**) weighting by the inverse of the pooled variance without standardization by warming magnitude. *Error bars* indicate effect sizes and 95 % bootstrap confidence intervals. The *dashed lines* are drawn at effect size = 0. The sample size for each variable is shown next to the *bar*
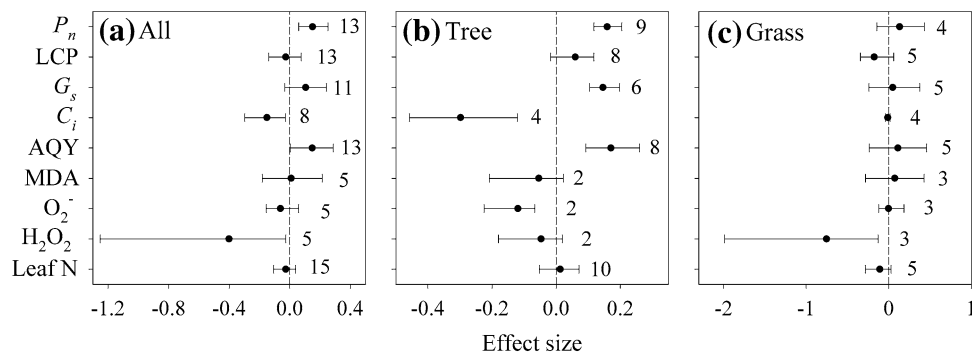
Fig. 4 Effect sizes of experimental warming on net photosynthesis rate (P_n), light compensation point (LCP), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), apparent quantum yield (AQY), malondialdehyde (MDA), superoxide anion radical (O_2^-), hydrogen peroxide (H_2O_2), and leaf N for Tree + Grass (**a**), Tree (**b**), and Grass (**c**) weighting by sample size without standardization by warming magnitude. *Error bars* indicate effect sizes and 95 % bootstrap confidence intervals. The *dashed lines* are drawn at effect size = 0. The sample size for each variable is shown next to the *bar*
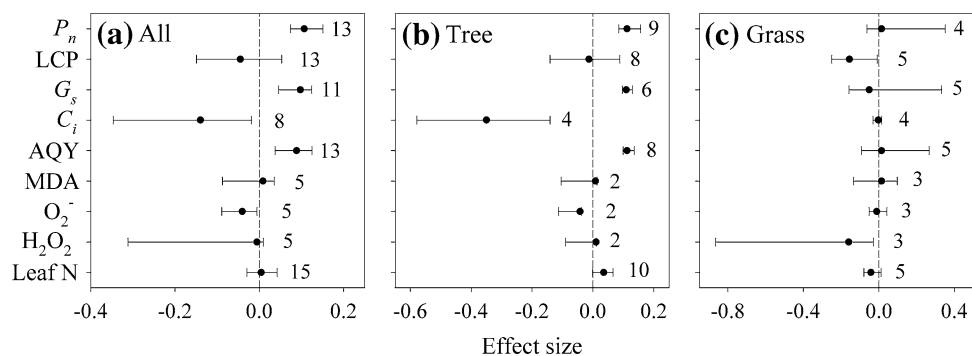

Fig. 5 Effect sizes of experimental warming on net photosynthesis rate (P_n), light compensation point (LCP), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), apparent quantum yield (AQY), malondialdehyde (MDA), superoxide anion radical (O_2^-), hydrogen peroxide (H_2O_2), and leaf N for Tree + Grass (**a**), Tree (**b**), and Grass (**c**) weighting by the inverse of the pooled variance with standardization by warming magnitude. *Error bars* indicate effect sizes and 95 % bootstrap confidence intervals. The *dashed lines* are drawn at effect size = 0. The sample size for each variable is shown next to the *bar*
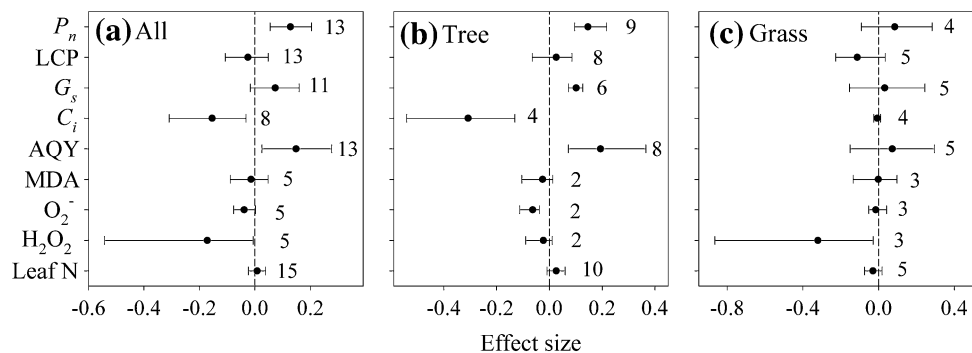
Fig. 6 Effect sizes of experimental warming on net photosynthesis rate (P_n), light compensation point (LCP), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), apparent quantum yield (AQY), malondialdehyde (MDA), superoxide anion radical (O_2^-), hydrogen peroxide (H_2O_2), and leaf N for Tree + Grass (**a**), Tree (**b**), and Grass (**c**) weighting by sample size with standardization by warming magnitude. *Error bars* indicate effect sizes and 95 % bootstrap confidence intervals. The *dashed lines* are drawn at effect size = 0. The sample size for each variable is shown next to the *bar*

When weighed by the inverse of pooled variance, experimental warming significantly increased P_n by 13.6 % (95 % CI 9.7–17.7 %), G_s by 20.0 % (95 % CI 5.4–28.7 %), and AQY by 11.1 % (95 % CI 3.9–16.4 %) (Fig. 3a). C_i was significantly reduced by 11.2 % (95 % CI −24.6 % to −1.8 %) (Fig. 3a). Warming had significantly positive effects on Chl*a* (+10.5 %; 95 % CI 8.8–16.5 %), Chl*b* (+11.3 %; 95 % CI 5.9–20.4 %), and *NPQ* (+10.6 %; 95 % CI

6.5–19.4 %) (Fig. 2a). In addition, warming had negligible effects on V_{max} (95 % CI −18.9–12.3 %), LCP (95 % CI −13.5–7.1 %), LSP (95 % CI −13.0–22.7 %), carotenoid (95 % CI −8.9–11.1 %), F_v/F_m (95 % CI −3.0–8.2 %), Q_p (95 % CI −5.7–9.4 %), and yield (95 % CI −10.8–13.8 %) (Figs. 2a, 3a). In contrast, when weighed by sample size, experimental warming significantly increased P_n by 16.3 % (95 % CI 6.1–28.7 %) and AQY by 16.0 % (95 % CI 0.3–33.4 %) (Fig. 4a). C_i was significantly reduced by 14.1 % (95 % CI −25.7 % to −2.8 %) (Fig. 4a). Warming had significantly positive effects on Chl$a$ (+12.4 %; 95 % CI 8.3–17.2 %), Chl$b$ (+13.8 %, 95 % CI 5.6–22.3 %), and NPQ (+14.5 %; 95 % CI 4.9–25.2 %) (Fig. 2b). In addition, warming had negligible effects on G_s (95 % CI −3.3–27.4 %), V_{max} (95 % CI −18.9–12.3 %), LCP (95 % CI −13.0–7.8 %), LSP (95 % CI −13.0–22.7 %), carotenoid (95 % CI −8.3–10.7 %), F_v/F_m (95 % CI −2.3–6.1 %), Q_p (95 % CI −5.6–8.3 %), and yield (95 % CI −11.5–15.0 %) (Figs. 2b, 4a). A 1 °C increase of temperature significantly increased Chl$a$ by 14.2 % (95 % CI 9.6–15.7 %) and 11.6 % (95 % CI 9.1–14.2 %), Chl$b$ by 9.6 % (95 % CI 5.3–13.4 %) and 14.0 % (95 % CI 4.2–27.1 %), NPQ by 6.8 % (95 % CI 4.3–12.2 %) and 8.9 % (95 % CI 3.1–15.1 %), P_n by 11.3 % (95 % CI 7.7–16.3 %) and 13.7 % (95 % CI 5.6–22.7 %), and AQY by 9.2 % (95 % CI 3.8–13.3 %) and 16.0 % (95 % CI 2.6–31.9 %), but significantly decreased C_i by 13.0 % (95 % CI −29.3 % to −1.9 %) and 14.3 % (95 % CI −26.6 % to −3.2 %) when weighed by the inverse of pooled variance and sample size, respectively (Figs. 2c, d, 5a, and 6a). In addition, a 1 °C increase of temperature significantly increased G_s by 10.2 % (95 % CI 4.7–13.2 %), when weighed by the inverse of pooled variance (Fig. 5a).

Experimental warming significantly increased P_n, G_s, and AQY, or decreased C_i and O_2^- of trees, but did not significantly affect those of grass (Figs. 3, 4, 5, and 6). In contrast, experimental warming significantly decreased H_2O_2 of grass, but did not significantly affect that of tree (Figs. 3, 4, 5, and 6). Experimental warming did not significantly alter LCP of tree (Figs. 3, 4, 5, and 6). Experimental warming significantly reduced LCP of grass, when weighed by the inverse of pooled variance (Figs. 3, 5), but did not significantly decreased it, when weighed by sample size (Figs. 4, 6). In addition, experimental warming had little effects on MDA and leaf N for both tree and grass (Figs. 3, 4, 5, and 6).

Discussion

Plant Growth and Biomass Accumulation

Warming stimulated plant growth and biomass accumulation, as indicated by increases in height, basal diameter, leaf area, leaf and shoot length, and component biomass.

To adapt to cold climates, alpine plants generally decrease their height (Friend and Woodward 1990) and allocate more carbon into roots compared to leaves and shoots (Weih and Karlsson 2001). The low height of alpine plants can increase the relative temperature of leaf, shoot, and soil (Friend and Woodward 1990; Li and others 2008). Warming-induced temperature increases in leaf, shoot and soil (Wang and others 2012; Lu and others 2013) may alleviate low temperature stress and decrease the relative carbon allocation into roots, which in turn cause an increase in plant height (Friend and Woodward 1990; Weih and Karlsson 2001).

In line with our hypothesis, the magnitude of the increase in plant biomass under warming in our analysis [aboveground biomass (+19.1 %, 95 % CI 6.0–40.7 %; +26.6 %, 95 % CI 10.8–48.1 %); belowground biomass (+26.7 %, 95 % CI 3.0–87.5 %; +29.9 %, 95 % CI 16.5–48.1 %)] was greater than that of Lin and others (2010) (12.3 %, 95 % CI 8.4–16.3 %), but comparable to that of Rustad and others (2001) (19 %, 95 % CI 15–23 %). The MAT values ranged from −6 to 12 °C and from −9 to 14 °C in this study and in Rustad and others (2001), respectively. However, a wider range of temperatures (from ≤−2 to >18 °C) was included in Lin and others (2010). The fact that warming does not affect plant biomass when MAT was greater than 18 °C may partially explain the different warming effects among the three studies.

Net Photosynthetic Rate and Photosynthetic Physiological Parameters

The magnitude of the increase in P_n caused by warming in our analysis (13.6 %, 95 % CI 9.7–17.7 %; +16.3 %, 95 % CI 6.1–28.7 %) was also greater than that of Lu and others (2013) (4.5 %, 95 % CI 2.6–6.4 %). This shows that in alpine ecosystems on the Tibetan Plateau, climatic warming will trigger a stronger positive response of plant photosynthesis than that of the global average effect of warming on photosynthesis. This was in line with our hypothesis. The increase in plant photosynthetic capacity may be attributed to increases in photosynthetic Chl content and AQY (Awada and others 2003) and favorable physiological conditions under warming conditions.

Our meta-analysis showed that warming did not increase plant stress in terms of negligible changes of MDA, H_2O_2, and O_2^- or significant decreases in H_2O_2 and O_2^-. In contrast, plants can produce some antioxidant enzymes, including SOD, POD, CAT, and APX, and can use some non-enzymes functions to protect themselves from oxidative stress and lipid peroxidation (Han and others 2009; Shi and others 2010). For example, carotenoids can protect Chl against photo-oxidative damage

(Agrawal and Rathore 2007), whereas *NPQ* can protect PSII from photo-oxidative damage by consuming the excessive light energy (Shi and others 2010). Soluble sugar and starch accumulation can protect enzymes, when excessive inorganic ion concentrations are present in plant cells (Sofo and others 2004). Therefore, increases in APX, SOD, POD, *NPQ,* and soluble sugar under warming conditions suggested that warming provided stronger antioxidant defense capacity against plant stress and also created more favorable physiological conditions for plant photosynthesis and growth.

In vivo Chl fluorescence can reflect the function of the photosynthetic apparatus and the capacity of plants to produce photosynthates (Yin and others 2008; Shi and others 2010). In high-elevation areas, photoinhibition generally occurred as a result of high light intensity (Yin and others 2008), thus warming did not aggravate photoinhibition in terms of negligible changes in F_v/F_m (Fig. 2). The changes of C_i and G_s can reflect whether or not the change in P_n was more closely associated with stomatal limitation than nonstomatal limitation (Farquhar and Sharkey 1982). Based on this conclusion, our meta-analysis showed that an increase of P_n under warming conditions was more closely associated with non-stomatal than with stomatal limitations in terms of an increase in G_s and a decrease of C_i, especially for trees (Figs. 3, 4, 5, and 6).

Many studies showed that plant photosynthetic capacity is positively related to leaf N concentration, because leaf N content is correlated closely with Rubisco content (Kattge and others 2009; Xu and others 2012). Warming did not affect leaf N, but significantly increased P_n in our meta-analysis across all studies or in forests (Figs. 3, 4, 5, and 6). The results imply that a decoupling of plant photosynthesis and leaf N concentration occurred, which may be attributed to the fact that Rubisco activity had still increased even when the Rubisco concentration decreased (Long and others 2004); also, Rubisco activity was not affected by warming because V_{max} was closely associated with Rubisco activity (Xu and others 2010) and not affected by warming (Fig. 2).

Conclusions

Our meta-analysis indicated that the magnitude of the response of alpine plants on the Tibetan Plateau was much greater than the global average in terms of P_n and plant biomass. The increase in P_n was probably associated with the increase in Chl content and AQY and favorable physiological conditions rather than on leaf N content. Our findings should be useful for understanding the underlying mechanisms of the response of alpine plants to global warming.

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