

# A meta-analysis of experimental warming effects on woody plant growth and photosynthesis in forests

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**Abstract** Increasing field experiments have been conducted in forests to better understand the response of plant growth and photosynthesis to climatic warming. However, it is still unknown whether there is a general pattern in relation to how and to what extent warming impacts woody plants in forests. In this study, a meta-analysis was conducted to investigate the warming effects. When temperatures increased between 0.3 and 10 °C, specific leaf area (SLA) was significantly increased by 5.9%, plant height by 7.8%, biomass by 21.9%, foliar calcium (Ca) and manganese (Mn) concentrations by 20.7% and 39.6% and net photosynthetic rate ( $P_n$ ) by 9.9%. Enhanced growth and  $P_n$

may have a relationship with changing SLA, efficiency of PSII (photosystem II), photosynthetic pigment concentrations and foliar nutrients. The results will be useful to understand the underlying mechanisms of forests responding to global warming.

**Keywords** Forest · Global warming · Meta-analysis · Photosynthesis · Plant growth

## Introduction

Forest ecosystems cover approximately 35% of the world's land surface, contribute to ~ 70% of terrestrial net primary productivity, and are responsible for 66% of worldwide photosynthesis (Meyer and Turner 1992; Melillo et al. 1993; Nagy et al. 2000; Valentini et al. 2000). Studies suggest that climate change, especially increasing temperatures, may fundamentally alter ecosystem functioning through its effect on plant growth and photosynthesis (Eamus and Jarvis 1989). Previous experiments have been carried out in an effort to better understand the effects of climate warming on growth and photosynthesis (Luomala et al. 2005; Fu et al. 2014). However, a general pattern of these effects is lacking.

Warming could affect production and physiology via impacting temperature-dependent parameters (Fu et al. 2014). These include concentrations of photosynthetic pigments, chlorophyll (Chl) fluorescence parameters, stomatal conductance ( $g_s$ ), rates of carboxylation ( $V_{cmax}$ ), apparent quantum yield of the photochemical efficiency of PSII, and the fluorescence parameter ratio (Fv/Fm) (Yin et al. 2008; Yang et al. 2013). The effect of warming on these parameters could be positive, negative or neutral depending upon the species and experimental conditions.

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For example, warming decreased  $g_s$  and Fv/Fm of *Betula albosinensis* Burkill (Chinese red birch), but had no effect on *Abies faxoniana* Rehd & Wilson (Farges fir) (Duan et al. 2014). Studies show that photosynthesis generally benefits from increases in  $g_s$ , Chl pigments concentration,  $V_{cmax}$  and AQY, but is inhibited by  $H_2O_2$  and MDA (malondialdehyde) (Shi et al. 2010). Thus, changes in growth and photosynthesis under climate warming are the results of overall changes of parameters (Fu et al. 2014).

Temperature is also a driving force for nutrient cycling which might affect foliar nutrients, including mineral and mobile nutrients (Coley 1998; Sager and Hutchinson 2005). For example, N (nitrogen), P (phosphorous), K (potassium), S (sulphur), and Cu (copper) concentrations in needles of *Pinus sylvestris* L. were decreased by warming treatment, while Ca (calcium), Mg (magnesium), B (boron), Zn (zinc), and Mn (magnesium) concentrations in needles were increased (Luomala et al. 2005). However, these trends were condition-dependent. Kellomaki and Wang (1997) found elevated temperatures increased foliar N concentration in Scots pine. Moreover, because foliar nutrients are closely related to biochemical capacity for photosynthesis and growth (Luomala et al. 2005), warming could affect them indirectly through changes in nutrients.

Increasing, decreasing or neutral impacts of experimental warming have been observed for biomass and/or photosynthesis in forest ecosystems (Bruhn et al. 2007; Yin et al. 2008; Bronson and Gower 2010; Yang et al. 2011; Lavola et al. 2013; Li et al. 2013). Yin et al. (2008) found that warming stimulated a significant increase in biomass accumulation and photosynthetic performance of *Picea asperata* Mast. seedlings. Yang et al. (2011) reported that height and biomass of *Abies fabri* (Mast.) Craib. were decreased by artificially simulated warming at the nearby Gongga Alpine Forest Ecosystem Observation Station which might be caused by a shortage in nitrogen supply. Bronson and Gower (2010) reported that neither photosynthesis or nor respiration of *Picea mariana* (Mill.) BSP was affected after 3 years of warming. This result is consistent with a growing number of experiments which have shown species acclimation to increased temperatures for photosynthesis and/or respiration (Gunderson et al. 2000). However, we do not know to what extent warming impacts woody plant biomass and photosynthesis in forest ecosystems.

A meta-analytic method was used in this study to summarize the effects of climatic warming on woody plant physiology and growth and to evaluate the direction and magnitude of the effects of experimental warming. Studies at a global scale have demonstrated that experimental warming could stimulate plant growth (Wu et al. 2011). Forest ecosystems have the most terrestrial net primary productivity (Meyer and Turner 1992; Melillo et al. 1993;

Nagy et al. 2000; Valentini et al. 2000) and are large  $CO_2$  sinks (Valentini et al. 2000). We hypothesize that warming is beneficial to woody plants, and the positive response magnitude would be higher than the global average.

## Materials and methods

### Data collection

Journal articles published before December 2015 were searched using the Web of Science database, and the keywords 'forest' and 'warming', 'plant' or 'forest', and 'temperature' and 'plant'. The literature survey was intended to be comprehensive with studies on woody species, including trees, shrubs and lianas. Publication years were restricted between 1996 and 2015. Papers published in Chinese were searched in the CNKI database (<http://www.cnki.net/>). A total of 522 observations from 52 papers (Table S1 and S2) were selected and the database included 24 variables related to woody plant growth and physiology. The final database included data from 25 forest sites. Most data were located between latitudes ( $30^\circ$ – $60^\circ$  N and S) (See Table S1).

The collected variables included: (1) plant growth parameters of height, basal diameter, shoot length, specific leaf area (SLA), total biomass and ratio of root/shoot (R/S); (2) foliar nutrient content, including nitrogen, carbon/nitrogen (C/N), phosphorus, potassium, calcium, magnesium, aluminum, and manganese; (3) photosynthetic parameters of net photosynthetic rate ( $P_n$ ), leaf transpiration ( $E$ ), stomatal conductance ( $g_s$ ),  $V_{cmax}$ , maximum photosynthetic rate ( $A_{max}$ ), Fv/Fm, yield, concentration of chlorophyll a (Chla), chlorophyll b (Chlb), and carotenoids (Carot).

For each study, we collected latitude, longitude, elevation, species, warming magnitude and duration, and the response variables. In addition, the variables warming magnitude and experimental duration were divided into three classes to reveal general patterns of plant response to warming (for warming magnitude ( $^\circ C$ ),  $\leq 2$ , 2–5,  $> 5$ ; for warming duration (month),  $\leq 12$ , 12–36,  $> 36$ ). Data in tables were directly extracted, and data with graphs, were digitized with GetData software (<http://getdata-graph-digitizer.com/>). For experiments along warming gradients, data were only collected at both ends. We identified the means, standard deviations (SD), standard errors (SE), and sample sizes (N). SE was transformed to SD when studies only provided the SE value. When SD or SE was missing, SD was estimated from van Groenigen et al. (2011). We first calculated coefficient of variation (CV) for each dataset and then averaged all CVs. The missing SD was estimated by multiplying the reported mean value by the average CV.

Selection criteria were: (1) only studies conducted in forest ecosystems were included, including natural and planted forests; (2) laboratory incubation studies were not included; only field warming manipulation studies were selected; (3) studies included pair-wise control and experimental treatments. Warming and control plots had the same ecosystem and soil types; (4) the warming method, magnitude and experimental duration were clearly recorded, and the measurements of variables in the control and experimental groups were performed at the same temporal and spatial scales; (5) only data from woody plants were used; (6) at least one of the selected variables was measured; and, (7) for multifactorial studies, only control and warming treatment data were used.

### Meta-analysis

In this study, Metawin v.2.0 (Rosenberg et al. 2000) was used to perform the meta-analysis. As a metric for the response of variables to experimental warming, we used the natural log of the response ratio (R), defined as the 'effect size' (Hedges et al. 1999). For a given variable, R was calculated as the ratio of its value in the warming treatment group  $\bar{X}_t$  to that in the control group  $\bar{X}_c$ , without and with standardization by warming magnitude (Eqs. 1, 2).

$$\log_e R = \log_e \left( \frac{\bar{X}_t}{\bar{X}_c} \right) = \log_e(\bar{X}_t) - \log_e(\bar{X}_c) \quad (1)$$

$$\log_e R = \frac{\log_e \left( \frac{\bar{X}_t}{\bar{X}_c} \right)}{T_t - T_c} = \frac{\log_e(\bar{X}_t)}{T_t - T_c} - \frac{\log_e(\bar{X}_c)}{T_t - T_c} \quad (2)$$

where  $T_t$  and  $T_c$  are the airtemperature in the control and warming treatments, respectively.

The variance of  $\log_e R$  ( $v$ ) was approximated using the following formula:

$$v = \frac{s_t^2}{n_t \bar{X}_t^2} + \frac{s_c^2}{n_c \bar{X}_c^2} \quad (3)$$

where  $s_c^2$  and  $s_t^2$  are the standard deviations in the control and warming treatments,  $n_c$  and  $n_t$  are the sample sizes in the control and warming treatments.

To determine if warming had a significant effect on a variable, we employed a fixed-effects model (Rosenberg et al. 2000). Confidence intervals (CIs) on the weighted effect size were generated using bootstrapping (9999 iterations). If the 95% CI values of the effect size for a variable did not overlap with 0, the effect of warming on the variable was considered significant. The warming effects of different groups were considered to be significantly different from each other if their 95% CIs did not overlap (Wan et al. 2001). We transformed the mean effect size of a variable to percentage change  $\left( e^{\overline{\log_e R}} - 1 \right) \times 100\%$ .

Generally, positive or negative data in ecological studies are more likely to be published than neutral data. Therefore, we examined whether our datasets were publication-biased or not (Peters et al. 2006; Yang et al. 2014). First, Spearman correlation analysis was performed between the standardized effect size of raw data and sample size. Spearman correlation analysis assesses how well the relationship between two variables can be described using a monotonic function. If no correlation was found, the dataset had no publication bias; or else, we needed to estimate fail-safe number to confirm whether publication bias would influence the final conclusions. A fail-safe number is the number of studies that would have to be added to change the results of the meta-analysis from significant to non-significant (Rosenberg et al. 2000). In this study we used Rosenthal's fail-safe calculation of  $5N + 10$  where  $N$  is the original number of studies.

## Results

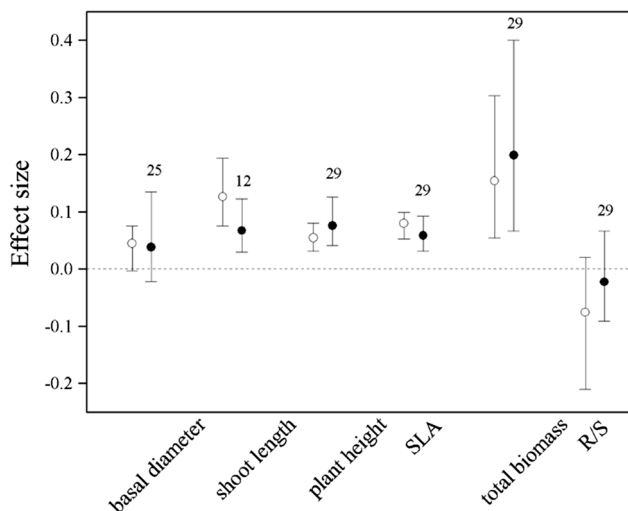
### Publication bias test

Publication bias was examined for each dataset of parameters. Spearman correlation analysis showed significant correlation between standardized effect size and sample size for height, yield and foliar Ca content datasets (Spearman  $r = 0.435$ ,  $P = 0.016$  for height,  $r = 0.711$ ,  $P = 0.021$  for yield and  $r = 0.424$ ,  $P = 0.049$  for foliar Ca content). Statistics suggested that there was slight publication bias for these three datasets. No publication bias was detected in other datasets as no correlation was found.

The fail-safe numbers were 304.1, 149.8 and 268.6 for height, yield and foliar Ca content while the respective  $5N + 10$  values were 155, 60 and 120. This indicated that although there was slight publication bias for these datasets, it would not change the overall meaning of the results.

### Growth response to warming

Without standardization by warming magnitude, the effect size and 95% CI of experimental warming on shoot length, height, SLA, and total biomass were 0.1264 (0.0757–0.1938), 0.0547 (0.0313–0.0804), 0.0798 (0.0529–0.0992), and 0.1542 (0.0542–0.3029), respectively, and their 95% CI did not cover zero (Fig. 1), suggesting a significantly positive effect of warming on plant growth. Warming increased shoot length by 13.5%, height by 5.6%, SLA by 8.3%, and total biomass by 16.7%. Basal diameter (0.0449, –0.0033 to 0.0752) and R/S (–0.0757, –0.2104 to 0.0203) did not respond to warming treatment.

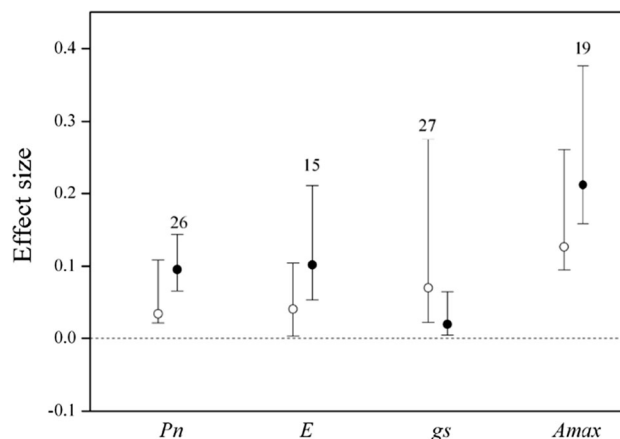


**Fig. 1** Effect sizes of experimental warming on basal diameter, shoot length, plant height, specific leaf area (SLA), and total biomass, without (hollow points) and with (solid points) standardization by warming magnitude. Error bars indicate effect sizes and 95% bootstrap confidence intervals. The dashed lines are drawn at effect size = 0. The sample size for each variable is shown next to the bar

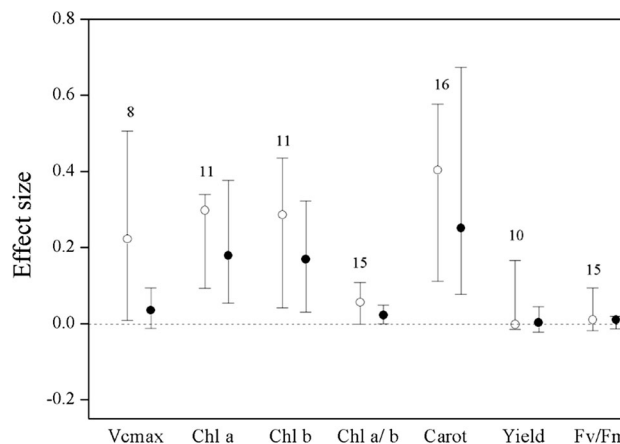
With standardization by warming magnitude, the effect size and 95% CI of experimental warming on shoot length, SLA, plant height and total biomass were 0.0661 (0.0281–0.1245), 0.0577 (0.0299–0.0916), 0.0746 (0.0397–0.1241) and 0.1979 (0.0649–0.3990), respectively, and their 95% CI did not cover zero, also suggesting a significantly positive effect of warming on growth. Warming increased shoot length by 6.8%, SLA by 5.9%, height by 7.8% and total biomass by 21.9%. Basal diameter (0.0372, –0.0232 to 0.0595) and R/S (–0.0240, –0.0927 to 0.0648) did not respond to warming treatment (Fig. 1).

### Photosynthesis and related parameters response to warming

Without standardization by warming magnitude, the effect size and 95% CI was 0.0349 (0.0164–0.1180) for net photosynthetic rate ( $P_n$ ), 0.0411 (0.0012–0.1045) for transpiration ( $E$ ), 0.0702 (0.0218–0.2748) for  $g_s$ , 0.2226 (0.0081–0.5064) for  $V_{cmax}$ , 0.1265 (0.0950–0.2602) for  $A_{max}$ , 0.2976 (0.0927–0.3393) for Chla, 0.2860 (0.0414–0.4349) for Chlb, 0.4034 (0.1107–0.5767) for carotenoid (Carot). Warming significantly increased  $P_n$  by 3.6%, transpiration by 4.2%,  $g_s$  by 7.3%,  $V_{cmax}$  by 24.9%,  $A_{max}$  by 13.5%, Chla by 14.2%, Chlb by 34.7%, and carotenoid by 49.7%. The effect of experimental warming on Chla/b (0.0556, –0.0016 to 0.1088), yield (–0.0023, –0.0147 to 0.1663), Fv/Fm (0.0097, –0.0187 to 0.0935) were not significant (Figs. 2, 3).

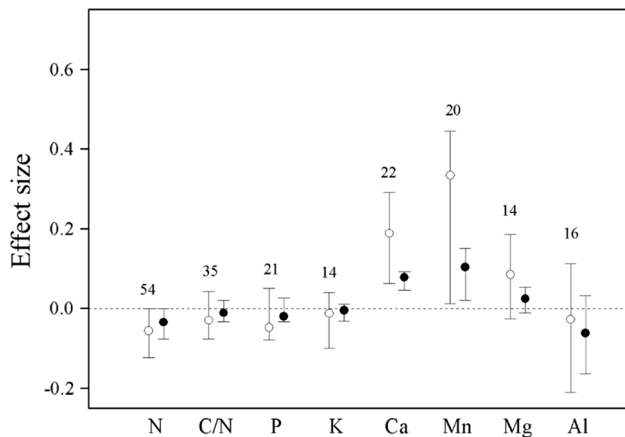


**Fig. 2** Effect sizes of experimental warming on net photosynthetic rate ( $P_n$ ), transpiration ( $E$ ),  $g_s$ , and  $A_{max}$ , without (hollow point) and with (solid point) standardization by warming magnitude. Error bars indicate effect sizes and 95% bootstrap confidence intervals. The dashed lines are drawn at effect size = 0. The sample size for each variable is shown next to the bar



**Fig. 3** Effect sizes of experimental warming on  $V_{cmax}$ , Chla, Chlb, Chla/b, carotenoid (carot), yield, and Fv/Fm, without (hollow point) and with (solid point) 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

With standardization by warming magnitude, the effect size and 95% CI was 0.0946 (0.0653–0.1429) for  $P_n$ , 0.1008 (0.0351–0.2132) for transpiration, 0.0179 (0.0034–0.0639) for  $g_s$ , 0.2108 (0.1574–0.3752) for  $A_{max}$ , 0.1768 (0.0485–0.3746) for Chla, 0.1668 (0.0278–0.3211) for Chlb, 0.2494 (0.0753–0.6435) for carotenoid, respectively, and their 95% CI did not cover zero (Figs. 3, 4). Warming significantly increased the  $P_n$  by 9.9%, transpiration by 10.6%,  $g_s$  by 1.6%,  $V_{cmax}$  by 21.9%,  $A_{max}$  by 23.5%, Chla by 19.3%, Chlb by 18.2%, carotenoid by 28.3%. The effect of experimental warming on  $V_{cmax}$ , Chla/b, yield, Fv/Fm, was not significant (Figs. 2, 3).



**Fig. 4** Effect sizes of experimental warming on foliage concentration of N, C/N, P, K, Ca, Mn, Mg, and Al, without (hollow point) and with (solid point) 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

### Foliage nutrients response to warming

Without standardization by warming magnitude, the effect size and 95% CI of experimental warming on leaf N was  $-0.0555$  ( $-0.1224$  to  $-0.0005$ ), Ca  $0.1879$  ( $0.0620$ – $0.2906$ ), Mn  $0.3337$  ( $0.0116$ – $0.4446$ ) and their 95% CI did not cover zero. Warming significantly increased the foliage content of Ca by 20.7%, Mn by 39.6%, and decreased N content by 5.5%. The effect of experimental warming on C/N, P, K, Mg, Al were not significant (Fig. 4).

With standardization by warming magnitude, the effect size and 95% CI of experimental warming on leaf N was  $-0.0369$  ( $-0.0789$  to  $-0.0034$ ), Ca  $0.0754$  ( $0.0428$ – $0.0908$ ), Mn  $0.1013$  ( $0.0164$ – $0.1464$ ) and their 95% CI did not cover zero. Warming significantly increased the foliage content of Ca by 7.8%, Mn by 10.7%, Mg by 2.3%, and decreased N content by 3.6%. The effect of experimental warming on C/N, P, K, Mg, Al were not significant (Fig. 4).

### Response to warming magnitude and experimental duration

Warming significantly stimulated woody plant biomass when the magnitude was  $< 5$  °C. However,  $P_n$  was not significantly affected when the warming magnitude was  $> 2$  °C. When the magnitude was  $< 2$  °C, the biomass and  $P_n$  enhancement was significantly higher than that at the warming magnitudes of 2–5 °C (Fig. S1).

Temperature manipulations caused significant increments in plant biomass at durations of  $< 12$  months and  $> 36$  months, but not between 12 and 36 months.  $P_n$  of woody plants did not show significant enhancement at durations  $> 12$  months (Fig. S1).

## Discussion

Our meta-analysis provided evidence that when the temperature was between 0.3 and 10 °C, growth and photosynthetic rate was significantly increased by 21.9 and 9.9% respectively. These increases were greater than the growth stimulation (12.3%, with a 95% CI of 8.4–16.3%) reported by Lin et al. (2010), and  $P_n$  stimulation reported by Lu (2013) (4.5%, with a 95% CI of 2.6–6.4%). Lin et al. (2010) and Lu et al. (2013) studied terrestrial plants at a global scale while we focused on forest ecosystems. In forest ecosystems, climatic warming may trigger a stronger positive response of plant growth and photosynthesis than that of global averages. These results verified our hypothesis.

Based on our results, increased growth and net photosynthesis by woody plants may have a relationship with changes of temperature-dependent parameters. From our analysis, warming increased the content of photosynthetic pigments (Fig. 4). These increases may promote photosynthetic capacity (Carter et al. 2000; Yin et al. 2008). Warming also increased Fv/Fm and quantum yield, indicating higher excitation energy transfer and higher efficiency of using light which reflected higher photosynthetic efficiency (Fu et al. 2014). As stomatal conductance ( $g_s$ ) could affect photosynthesis, increased  $g_s$  in our analysis may indicate higher passage rates of CO<sub>2</sub> which might have a positive relationship with photosynthetic rates. In addition, other studies have shown that increased temperatures can improve the activity of RuBisCo (Ribulose biphosphate carboxylase oxygenase) to enhance photosynthesis (Farquhar et al. 1980). Increased carboxylation rates ( $V_{cmax}$ ) due to warming in our study indicated either enhanced RuBisCo activity or higher concentrations. As leaf nitrogen, which has a close relationship with RuBisCo concentration, did not increase under warming treatments (Farquhar et al. 1980),  $V_{cmax}$  increase might be caused by improved RuBisCo enzyme activity rather than higher concentrations.

Root/shoot (R/S) ratios reflect the carbon allocation between above-ground and below-ground. Research suggests that R/S ratios may be more reasonable to assess experimental effects on plants than root or shoot biomass alone (Agathokleous et al. 2016). From our results, warming did not affect biomass allocation between roots and shoots, and reflected the same stimulation of above- and below-ground growth. In addition, the effect of warming on R/S ratios was similar to leaf C/N in our study. This similarity might fit the biomass allocation model (Reynolds and Thornley 1982) which shows that R/S ratios should show similar shifts as tissue C/N ratios because when C/N ratios rise, N will become more limiting relative



to C and biomass allocation to roots will increase. Specific leaf area (SLA) is highly correlated with light exposure (St Clair and Lynch 2004), so increased SLA by warming might have a relationship with  $P_n$ .

Previous studies have found that climate warming could increase soil organic matter decomposition (Rustad et al. 2001; Henry and Moise 2015) which is usually associated with increased release of acidic matter (D'Orangeville et al. 2014). The production of acidic matter can result in soil acidification (Vancelev et al. 1990; Simandi et al. 2005). Acidic inputs can lead to the leaching of basic cations such as calcium (Ca) and increase the availability of potentially phytotoxic trace metals such as manganese (Mn) (D'Orangeville et al. 2014). Thus increased Mn and Ca concentrations in plant tissues due to warming might be the result of soil acidification in forest ecosystems (Sager and Hutchinson 2006; Tian et al. 2016). Because foliar concentrations of Ca and Mn are highly correlated with biochemical capacity for plant growth and photosynthesis (Farquhar and Sharkey 1982; Fischer et al. 2015; Hochmal et al. 2015), the observed changes of plant growth and  $P_n$  by warming maybe the indirect outcome in changes of foliar Ca and Mn concentrations.

Most data used in our analysis is located between latitudes 30°–60° N and S (See Table S1). The biomass and  $P_n$  of woody plants varied with warming magnitude and experimental duration. In order to identify the response of plants to climate warming at a global scale more clearly, and to distinguish the role of photosynthetic parameters in this process, multiple field experiments that span various environmental gradients and duration are urgently needed.

Results in this and previous meta-analyses provide evidence that warming generally increases terrestrial net primary productivity (Lin et al. 2010) at a forest ecosystem scale and a global scale. The increased growth and net photosynthesis rates by a forest ecosystem could be attributed to the integrated changes of various parameters. Our findings will be useful to predict the response of plant functioning to global climate warming.

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