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# Global patterns of the responses of leaf-level photosynthesis and respiration in terrestrial plants to experimental warming

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## Abstract

***Aims***
The balance between leaf photosynthesis and respiration of terrestrial plants determines the net carbon (C) gain by vegetation and consequently is important to climate–C cycle feedback. This study is to reveal the global patterns of the responses of leaf-level net photosynthesis and dark respiration to elevated temperature.

***Methods***
Data for leaf-level net photosynthesis rate ($P_n$) and dark respiration rate ($R_d$) in natural terrestrial plant species with standard deviation (or standard error or confidence interval) and sample size were collected from searched literatures on Web of Science. Then a meta-analysis was conducted to estimate the effects of experimental warming on leaf-level $P_n$ and $R_d$ of terrestrial plants.

***Important findings***
Across all the plants included in the analysis, warming enhanced $P_n$ and $R_d$ significantly by 6.13 and 33.14%, respectively. However, the responses were plant functional type (PFT) specific. Specifically, photosynthesis of $C_4$ herbs responded to experimental warming positively but that of $C_3$ herbs did not, whereas their respiratory responses were similar, suggesting $C_4$ plants would benefit more from warming. The photosynthetic response declined linearly with increasing ambient temperature. The respiratory responses linearly enhanced with the increase in warming magnitude. In addition, a thermal acclimation of $R_d$, instead of $P_n$, was observed. Although greater proportion of fixed C was consumed (greater $R_d/P_n$ ratio), warming significantly enhanced the daily net C balance at the leaf level. This provides an important mechanism for the positive responses of plant biomass and net primary productivity to warming. Overall, the findings, including the contrastive responses of different PFTs and the enhancement in daily leaf net C balance, are important for improving model projection of the climate–C cycle feedback.

***Keywords***: acclimation, meta-analysis, plant functional type, photosynthesis, respiration

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## INTRODUCTION

Photosynthesis and respiration of terrestrial plants are two opposite but interdependent metabolic pathways (Kromer 1995; Raghavendra and Padmasree 2003). At the organelle level, respiration in mitochondria depends on carbon (C) substrates provided by photosynthesis in chloroplasts, while photosynthesis relies on respiration for the supply of ATP and C skeletons, and protection against photoinhibition (Raghavendra and Padmasree 2003). At the ecosystem level, the net balance between photosynthesis and respiration determines net primary production (NPP) of an ecosystem (Chapin III *et al.* 2002a). At the global scale, photosynthesis and respiration are two critical processes in the global C cycle (Chapin III *et al.* 2002b). Since both processes are temperature dependent (Luo 2007; Tjoelker and Zhou 2007), the metabolic balance of the two processes under climate warming plays a critical role in regulating the climate–C cycle feedback (Schimel 1995; King *et al.* 2006).

Irrespective of the increasing reports on the photosynthetic and respiratory responses of terrestrial plants to elevated temperature, there are great discrepancies among studies: experimental warming has been shown to stimulate (Bunce and Ziska 1996; Griffin *et al.* 2002a, 2002b; Bunce 2004; Danby and Hik 2007; Wan *et al.* 2009), suppress (He and Dong 2003; Rachmilevitch *et al.* 2006; Jochum *et al.* 2007), or have neutral effects (Tjoelker *et al.* 1998; Loik *et al.* 2000; Llorens *et al.* 2004; He *et al.* 2005) on net photosynthesis and/or respiration rates. The contradictory findings pose great challenges for projecting the responses and feedbacks of terrestrial ecosystems to climate change.

One possible reason for the contradictory findings may be that photosynthetic and respiratory responses of terrestrial plants to elevated temperature vary with plant species and functional types (PFT; Larigauderie and Korner 1995; Niu *et al.* 2008). In the Great Basin of North America, warming enhances photosynthesis of a widely distributed evergreen shrub but reduces that of a coexisting deciduous shrub (Shaw *et al.* 2000). In a subalpine meadow, warming leads to permanent closure of photosystem II (PSII) in a forb but not in an evergreen shrub (Loik *et al.* 2000). Given >300 000 terrestrial plant species on the Earth (Millennium Ecosystem Assessment 2005), vegetation is represented as patches of plant functional types to simplify parameterization in many ecological models (Bonan *et al.* 2002; Tian *et al.* 2010). Therefore, knowledge of photosynthetic and respiratory responses to elevated temperature of PFTs instead of species across the world will facilitate the prediction of terrestrial C-cycle feedback to climate warming.

Temperature condition in which plants live may be another possible reason for the contradictory findings. King *et al.* (2006) have indicated that tropical vegetation has a smaller positive respiratory response to warming than boreal vegetation. Another synthesis research has also revealed that aboveground plant productivity shows a greater positive response to elevated temperature in colder ecosystems (Rustad *et al.* 2001). In addition, foliar respiration has been observed to be less sensitive to warming with increasing temperature (Atkin and Tjoelker 2003). Given that temperature change associated with climate warming is greater and low-temperature limitation is stronger in colder conditions (IPCC 2007; Way *et al.* 2010), terrestrial plant species growing under lower ambient temperatures are expected to be more sensitive to warming than those under higher ambient temperatures (Shaver *et al.* 2000; Root *et al.* 2003; Parmesan 2007). However, a global synthesis of the responses of photosynthesis and respiration to warming at the leaf level is still lacking.

As thermal sensitive processes, both plant photosynthesis and respiration are expected to increase initially with temperate elevation (Atkin and Tjoelker 2003). However, plants can physiologically adjust to sustained changes in growth temperature (Atkin *et al.* 2000; Atkin and Tjoelker 2003; Loveys *et al.* 2003). The physiological acclimation can lead to smaller enhancements of plant photosynthesis and respiration under warmer conditions than predicted with photosynthesis/respiration–temperature relationships (Tjoelker *et al.* 1999a, 1999b; Gunderson *et al.* 2000; Yamori *et al.* 2005; Dwyer *et al.* 2007; Niu *et al.* 2008). Previous studies on thermal acclimations of $P_n$ and $R_d$ have often come up with conflicting findings, including full acclimation (Tjoelker *et al.* 1999a, 1999b; Gunderson *et al.* 2000; Turnbull *et al.* 2002; Yamori *et al.* 2005; Atkin *et al.* 2006), partial acclimation (Battaglia *et al.* 1996) and no acclimation (He and Dong 2003; Gielen *et al.* 2007). In addition, Xiong *et al.* (2000) and Ow *et al.* (2008a, 2008b) have shown that respiration acclimates to experimental warming, but photosynthesis does not. The conflicting results have restrained the validity of climate change analyses and C-cycle models (King *et al.* 2006; Atkin *et al.* 2008). Thus, quantifying whether thermal acclimations of plant photosynthesis and respiration exist globally is critically needed.

Given the tight interdependence of plant photosynthesis and respiration, the balance between the two processes determines the growth of terrestrial plants under climate warming (Chapin III *et al.* 2002a). The ratio of respiration to photosynthesis ($R/P$) has been used to express the proportion of consumed to fixed C of plants (Arnone and Korner 1997; Loveys *et al.* 2002, 2003; Atkin *et al.* 2007; Campbell *et al.* 2007). The $R/P$ ratio has been observed to be enhanced (Atkin *et al.* 2007; Campbell *et al.* 2007) or maintained (Arnone and Korner 1997; Gunn and Farrar 1999; Loveys *et al.* 2003) under warming. The observations suggest that a greater or similar proportion of fixed C will be consumed, implying a decline or no response of the net amount of C fixed by leaves. However, several synthetic studies across multiple terrestrial plant species and ecosystems have illustrated enhancement of both plant biomass (Lin *et al.* 2010; Way *et al.* 2010) and NPP (Rustad *et al.* 2001; Wu *et al.* 2011) in response to warming. Hence, it is possible that the change in $R/P$ ratio may not accurately represent the net C balance of leaves. Instead, the balance between daily C assimilation and release may be more effective to interpret the responses of terrestrial plants at individual and ecosystem scales to warming.

In this study, a meta-analysis has been conducted to reveal general patterns of leaf-level photosynthesis and respiration of terrestrial plants in response to warming. The main objectives of this study are trying to answer the following four questions: (i) How do leaf photosynthesis and respiration of different PFTs respond to warming? (ii) How do photosynthetic and respiratory responses to warming vary with ambient temperature and warming magnitude? (iii) Do photosynthesis and respiration acclimate to warming? and (iv) How does climate warming affect the net C balance at the leaf level?

## MATERIALS AND METHODS

### Data collection

A comprehensive literature search with the terms of 'warming + photosynthesis' and 'warming + respiration' was conducted using ISI Web of Science database. Articles met the following criteria were included in our analysis: (i) both control and warming treatment were included; (ii) reported net photosynthesis rate and/or respiration rate at the leaf level (data obtained from more than one single leaf or shoot of some small plants (e.g. *Arabidopsis thaliana*) were also included); (iii) species reported in the studies were in natural terrestrial ecosystems; and (iv) means, standard errors (SE) or standard deviations (SD) or confidence interval, and sample sizes were provided in both control and warming treatments. According to the above criteria, studies investigating photosynthetic and respiratory responses to experimental warming at individual and community level, and agricultural and horticultural species, were excluded from the analysis. Warming method included infrared heater, greenhouse, open top chamber , soil heating cable and controlled growth chamber, etc. Data from daytime, night-time and diurnal warming were all included. Leaf net photosynthesis rate ($P_{\mathrm{n}}$), leaf dark respiration rate ($R_{\mathrm{d}}$), measured unit, species name, ambient temperature, warming magnitude and exposure time were collected. Information that showed where temperature was measured (air or soil) were also collected. In addition, studies including experimental warming together with other treatments were also included in our synthesis. In these studies, if the measurement of other treatments was given, we took this measurement as the control, and the combined treatment as the warming treatment. For instance, there were four treatments in Callaway *et al.* (1994), including (i) ambient $CO_2$ and ambient temperature (ACAT); (ii) ambient $CO_2$ and elevated temperature (ACET); (iii) elevated $CO_2$ and ambient temperature (ECAT); and (iv) elevated $CO_2$ and elevated temperature (ECET). We collected two groups of data. In the first group, we took ACAT as the control and ACET as the warming treatment. In the second group, we took ECAT as the control and ECET as the warming treatment. In some studies, measurements were taken at a set temperature (e.g. 20°C), while most measurements were conducted at the prevailing growth temperature in the control and warming treatments, respectively. There was no significant difference between the photosynthetic and respiratory responses of plants measured at the prevailing growth temperature and those of plants measured at a set temperature (both $P > 0.05$). Hence, data obtained from measurements at a set temperature were also used in the analyses, including in the ambient-gradient and warming magnitude analyses. When the data presented in graphs, they were extracted by digitizing the figures using SigmaScan (Systat Software Inc., San Jose, CA, USA). When means and SE were reported, the SD were calculated as: $\mathrm{SD} = \mathrm{SE}\sqrt{n}$ , where $n$ was the sample size. If data were given with a mean and a confidence interval (CI), the SD was computed as: $\mathrm{SD} = (\mathrm{CI}_u - \mathrm{CI}_l)\sqrt{n} / 2u_P$ , where $\mathrm{CI}_u$ and $\mathrm{CI}_l$ were the upper and lower limits of CI, and $u_P$ was the significant level and equaled 1.96 when $\alpha = 0.05$ and 1.645 when $\alpha = 0.10$.

In the present analysis, if more than one result from the same article or field site or laboratory were available, results of each species observed in the same year were synthesized. The averaged mean ( $\overline{M}$ ) and the averaged standard deviation ( $\overline{\mathrm{SD}}$ ) were calculated using the following equations (Liao *et al.* 2008):

$$\overline{M} = \sum_{i=1}^{j} \frac{M_i}{j}$$

$$\overline{\mathrm{SD}} = \sqrt{\frac{\sum_{i=1}^{j} \mathrm{SD}_i^2 (n_i - 1) n_i}{\left(\sum_{i=1}^{j} n_i - 1\right) \sum_{i=1}^{j} n_i}}$$

where $j$ was the sampling times (≥2), $M_i$, $\mathrm{SD}_i$ and $n_i$ were mean, SD and sample size on the $i$th sampling data, respectively.

To estimate the photosynthetic and respiratory responses of PFTs to warming, plants were divided into different PFTs—Group 1: herbaceous and woody plants; Group 2: forbs and grass; Group 3: annual and perennial herbs; Group 4: $C_3$ and $C_4$ herbs; Group 5: broadleaved and coniferous trees; and Group 6: deciduous and evergreen trees.

Because of the various warming methods, temperature measurements were conducted in either air or soil. According to the data conducted in air, the ambient air temperatures for $P_{\mathrm{n}}$ and $R_{\mathrm{d}}$ ranged from 3.6 to 31.0°C and from 7.0 to 25.0°C with median 15.2 and 15.0°C, respectively. Air warming magnitudes for $P_{\mathrm{n}}$ and $R_{\mathrm{d}}$ were both from 0.3 to 20.0°C. According to the data conducted in soil, the ambient soil temperatures for $P_{\mathrm{n}}$ and $R_{\mathrm{d}}$ changed from 3.9 to 18.9°C and from 18.9 to 20.0°C, respectively. Soil warming magnitudes for $P_{\mathrm{n}}$ and $R_{\mathrm{d}}$ varied from 0.5 to 29.6°C and from 0.8 to 7.0°C, respectively. In the analyses of the dependences of the responses on ambient temperature and warming magnitude, only temperatures measured in air were used. Ambient air temperature was divided to ranks at an interval of 5°C. Studies with a warming level <10°C were banded at an interval of 1°C, and the rest studies were banded together.

In our dataset, exposure time (i.e. how long plants were exposed to warming) ranged from <10 days to >10 years. To analyze the possible different responses under various warming durations, data with a exposure time <3 years were banded at an interval of 1/3 month (i.e. 10 days), and those >3 years were banded together.

When both $P_{\mathrm{n}}$ and $R_{\mathrm{d}}$ of one species with the same unit were provided in one study (including measurements conducted on the same leaves/individuals and those across individuals), the $R_{\mathrm{d}}/P_{\mathrm{n}}$ ratios in the control and warming treatments and net C balance of leaves were calculated. The means of the $R_{\mathrm{d}}/P_{\mathrm{n}}$ ratio were compared using paired $t$-test. In addition, we assumed that day- and night-time durations were both 12 hours to estimate the response of daily net C balance of leaves to warming. The daily net C balance was simply calculated by ($P_{\mathrm{n}}$–$R_{\mathrm{d}}$). To examine the weighted response of ($P_n$–$R_d$) to elevated temperature, SD was estimated by $(SD_P{}^2+SD_R{}^2)^{1/2}$, where $SD_P$ and $SD_R$ were the SD of $P_n$ and $R_d$, respectively.

### Meta-analysis

The method used in this meta-analysis followed that described by Hedges *et al.* (1999), Wan *et al.* (2001) and Luo *et al.* (2006). The effect of experimental warming was estimated for each observation as the natural logarithm transformed response ratio, $\log_e RR = \log_e(X_w / X_c)$, where $X_w$ and $X_c$ are the mean value in the warming and control treatment, respectively. The weighted $\log_e RR$ and 95% confidence intervals were computed.

In meta-analysis, the total heterogeneity ($Q_T$) can be portioned into within-group heterogeneity ($Q_W$) and between-group heterogeneity ($Q_B$). The $Q$ statistic approximately has a chi-square distribution (Curtis and Wang 1998), which allows a significance test of the null hypothesis that all response ratios are equal. Heterogeneity test in the present analysis was conducted following Wan *et al.* (2001). A $Q_B$ larger than a critical value indicated that there was significant difference between categories. Warming was considered to have a significant effect on a variable if 95% confidence intervals of response ratio did not overlap zero. Responses of categories were considered different if their 95% confidence intervals did not overlap (Gurevitch and Hedges 1993). In the present study, it was applied to compare the responses among different PFTs, ambient temperatures, warming magnitudes, and exposure times. Statistical significance was tested at the $P < 0.05$ level. In this study, the meta-analysis was accomplished using MetaWin 2.1 (Sinauer Associates Inc., Sunderland, MA, USA).

## RESULTS

### Photosynthetic and respiratory responses across different PFTs

Across all terrestrial plants included in the present analysis, experimental warming increased $P_n$ significantly by 6.13% ($P < 0.05$; Fig. 1a). Responses of $P_n$ for both herbaceous and woody plants were significantly positive (both $P < 0.05$; Fig. 1a). Within the herbaceous plants, warming enhanced the $P_n$ of grass significantly by 12.3% ($P < 0.05$) but had no influence on that of forbs, and the effect on grass was greater than that on forbs ($P < 0.01$; Table 1, Fig. 1a). Warming significantly stimulated the $P_n$ of perennial herbs ($P < 0.05$) but not annual herbs. In addition, $P_n$ of $C_4$ herbs responded to warming positively ($P < 0.05$), whereas that of $C_3$ herbs neutrally. Within the woody plants, there was no difference in the photosynthetic response to experimental warming between broadleaved and coniferous trees or between deciduous and evergreen trees.

Across all the PFTs included in the meta-analysis, $R_d$ was enhanced significantly by 33.14% ($P < 0.05$) under elevated temperature (Fig. 1b). In addition, the stimulations of $R_d$ were significantly larger than zero for all the PFTs, varying from 13.27% for evergreen trees to 57.74% for forbs. In contrast to their photosynthetic responses, the respiratory change of forbs (57.74%) was substantially greater than that of grass (20.33%) under experimental warming ($P < 0.05$; Table 1, Fig. 1b). In addition, the respiration enhancement of deciduous trees (53.37%) was greater than that of evergreen trees (13.27%; Table 1, Fig. 1b). However, no difference was observed between annual and perennial herbs, $C_3$ and $C_4$ herbs, or broadleaved and coniferous trees (Table 1, Fig. 1b).

### Dependence of photosynthetic and respiratory responses upon ambient temperature and warming magnitude

Across the data with temperature measurement conducted in air, photosynthetic response declined linearly with increasing ambient air temperature ($R^2 = 0.69$, $P < 0.05$; Fig. 2a). For dark respiration, no relationship with ambient air temperature was observed (Fig. 2b). In addition, there was no relationship between photosynthetic response and the magnitude of temperature elevation (Fig. 3a), whereas the respiratory response increased linearly with warming magnitude ($R^2 = 0.70$, $P < 0.01$; Fig. 3b).

### Dependence of photosynthetic and respiratory responses upon exposure time

Photosynthetic response of terrestrial plants to warming was independent of exposure time (Fig. 4a). In contrast, respiratory response declined logarithmically with the increase in exposure time ($R^2 = 0.30$, $P = 0.05$; Fig. 4b).

### Changes in $R_d/P_n$ ratio and ($P_n$–$R_d$) value

The $R_d/P_n$ ratio under warming treatment (0.14 ± 0.02) was statistically greater than that at control (0.12 ± 0.01) ($P < 0.01$; Fig. 5). In addition, warming significantly enhanced the ($P_n$–$R_d$) value by 8.72% (Fig. 6). However, the response was PFT-specific. Warming did not affect the ($P_n$–$R_d$) value of herbs, but significantly elevated that of woody plants by 20.97% (Fig. 6). The ($P_n$–$R_d$) value of broadleaved and deciduous trees were enhanced significantly by 23.59 and 31.58%, respectively (both $P < 0.05$), while that of coniferous and evergreen trees did not respond to warming (both $P > 0.05$). No difference was observed between grass and forbs, $C_3$ and $C_4$ herbs, broadleaved and coniferous trees, or deciduous and evergreen trees (all $P > 0.05$).

## DISCUSSION

### Photosynthetic and respiratory responses across different PFTs

In this study, both $P_n$ and $R_d$ were positively affected by experimental warming. However, the responses were PFT-specific. The positive response of photosynthesis to elevated temperature was greater for grass than forbs, whereas climate warming stimulated respiration of forbs

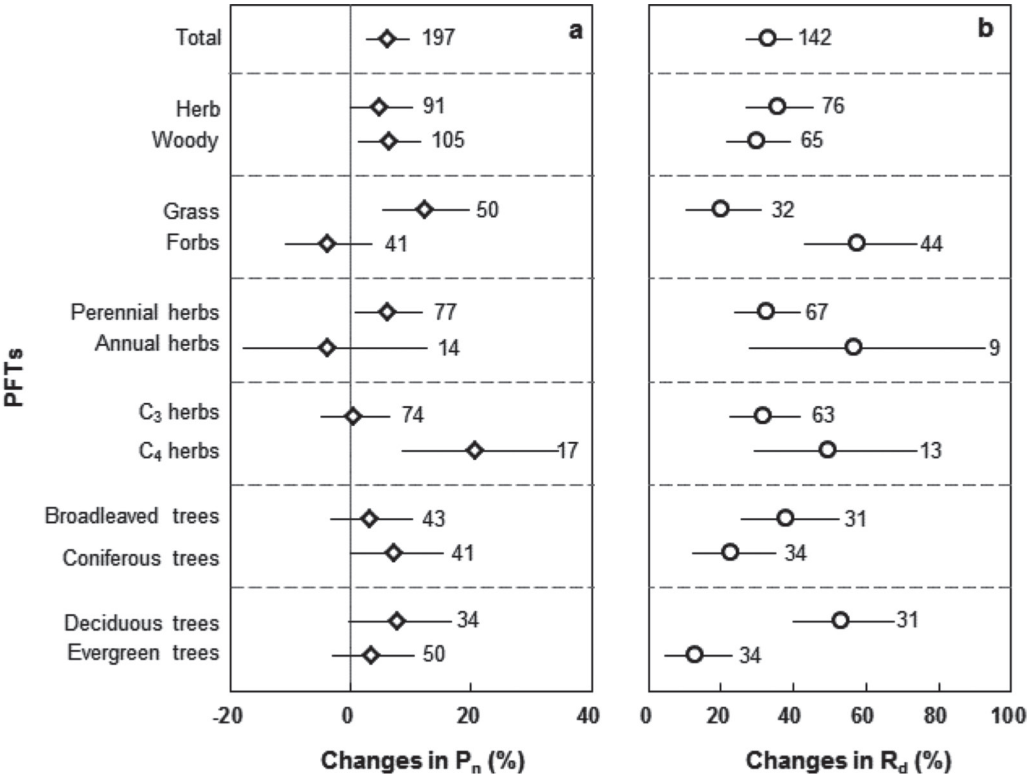

**Figure 1:** (a) photosynthetic ($P_n$) and (b) respiratory ($R_d$) responses of plant functional types (PFTs) to warming. Mean ± 95% confidence intervals. The number of observations for each PFT used in the analysis is shown near the bar.

**Table 1: between-group heterogeneity ($Q_B$) of warming effect size of net photosynthesis rates ($P_n$) and respiration rates ($R_d$) between group comparisons of plant functional types (PFTs).** *N* **is the number of observations for each PFT used in the analysis**

| PFTs | | $P_n$ | | | $R_d$ | | |
|---|---|---|---|---|---|---|---|
| | | *N* | $Q_B$ | *P* | *N* | $Q_B$ | *P* |
| Group 1 | Herbaceous plants | 91 | 0.14 | 0.71 | 76 | 0.83 | 0.36 |
| | Woody plants | 105 | | | 65 | | |
| Group 2 | Grass | 50 | 10.29 | < 0.01 | 32 | 17.90 | < 0.001 |
| | Forbs | 41 | | | 44 | | |
| Group 3 | Perennial herbs | 77 | 1.61 | 0.20 | 67 | 3.12 | 0.08 |
| | Annual herbs | 14 | | | 9 | | |
| Group 4 | $C_3$ herbs | 74 | 10.02 | < 0.01 | 63 | 2.72 | 0.10 |
| | $C_4$ herbs | 17 | | | 13 | | |
| Group 5 | Broadleaved trees | 43 | 0.64 | 0.42 | 31 | 3.16 | 0.08 |
| | Coniferous trees | 41 | | | 34 | | |
| Group 6 | Deciduous trees | 34 | 0.63 | 0.43 | 31 | 25.97 | < 0.001 |
| | Evergreen trees | 50 | | | 34 | | |

more strongly than that of grasses. These results suggest that forbs may accumulate lower biomass and become less competitive than grasses under warming conditions. Further analysis indicates that it is because the group of grass includes more $C_4$ species; and warming significantly enhanced photosynthesis of $C_4$ herbs but did not affect that of $C_3$ herbs. Specifically, the positive response of $C_4$ grass was greater than that of $C_3$ grass, while the responses of $C_3$ grass and $C_3$ forbs were similar (not shown in the RESULTS section). The physiological structure of $C_4$ species enables them benefit more at warm temperatures due to less $O_2$ inhibition and photorespiration (Björkman 1973), greater water use efficiency and nitrogen use efficiency (Pearcy *et al.* 1987; Jones *et al.* 1992; Tieszen *et al.* 1997; Long 1999)

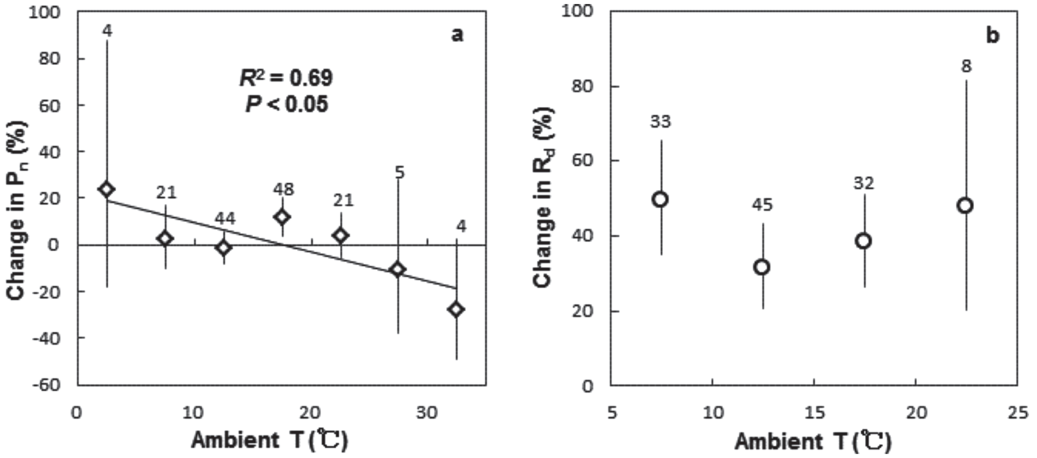

**Figure 2:** dependence of the responses of $P_n$ (a) and $R_d$ (b) of terrestrial plants on the ambient air temperature (T). Mean ± 95% confidence intervals. The ambient temperature has been divided to ranks at an interval of 5°C. Only temperatures measured in air have been used. The number of observations for each rank of ambient air temperature is shown near the bar. Linear regression was used to determine the significance of the trend.

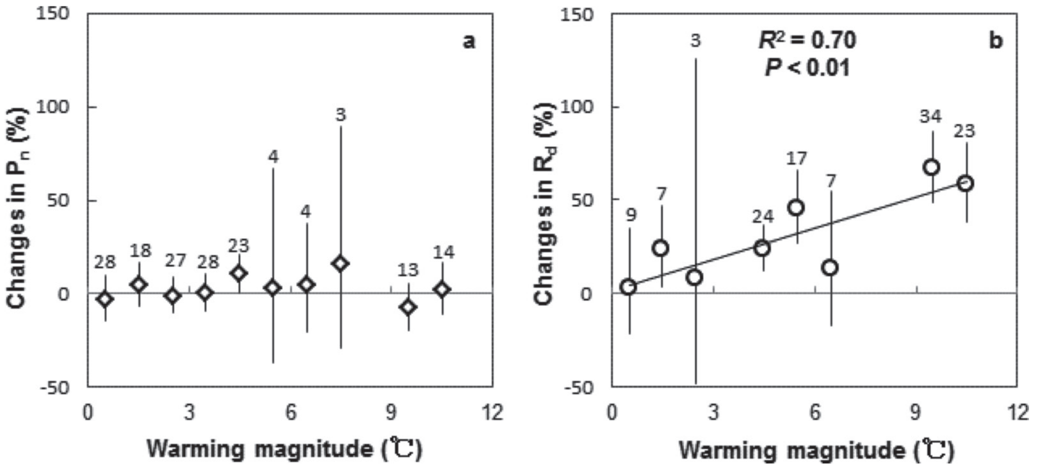

**Figure 3:** dependence of the responses of $P_n$ (a) and $R_d$ (b) of terrestrial plants on warming magnitude. Mean ± 95% confidence intervals. Studies with a warming level <10°C were banded at an interval of 1°C, and those >10°C were banded together. Only temperatures measured in air have been used. The number of observations for each rank of warming magnitude is shown near the bar. Linear regression was used to determine the significance of the trend.

compared with $C_3$ plants. Our results suggest that warming in the future may benefit $C_4$ plants more than $C_3$ plants. This is in line with the field experiments, which have shown an increased dominance of $C_4$ plants under warming (Field and Forde 1990; White *et al.* 2001; Niu *et al.* 2010). We also found that respiratory response of deciduous trees has been observed to be greater than that of evergreen trees, providing an explanation for the findings in Welp *et al.* (2007) that ecosystem respiration responds to spring warming greater in deciduous than evergreen forest.

Light and vapor pressure deficit (VPD) are also two critical factors affecting leaf photosynthesis in addition to temperature, and they may influence the responses of terrestrial plants to warming. Plant photosynthesis enhances with the increase in photosynthetically active radiation below the light saturation point (Taiz and Zeiger 2010). However, the majority studies included in our dataset have measured leaf photosynthesis at the light saturation. Hence, photosynthetic responses investigated in the present study were at ideal conditions without light limit, which may not reflect the real responses of leaf net photosynthesis under climate warming. The effect of VPD should not be ignored either because it can be enhanced by warming (Cohen *et al.* 2002; Lu *et al.* 2009; Xie *et al.* 2010). Increased VPD depresses stomatal conductance (Ludlow and Jarvis 1971; Sanford and Jarvis 1986; Mcdowell *et al.* 2004) and consequently results in a significant reduction in plant C assimilation (Day 2000; Sinclair *et al.* 2007; Allen and Vu 2009). Although warming induced changes in VPD and leaf temperature could both significantly affect $P_n$ rate, it is difficult to separate the contributions from the two factors in a synthetic study like ours. Overall, ignoring the effects of light and VPD may lead to inaccurate estimate and the results should be extrapolated with caution.

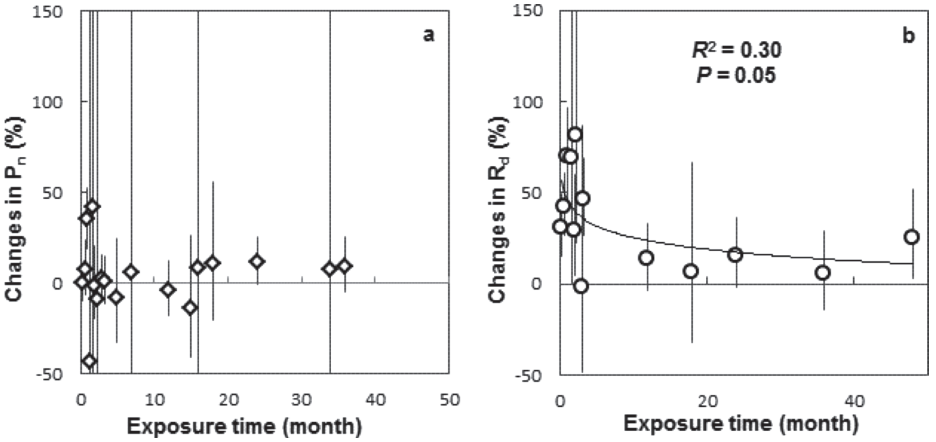

**Figure 4:** dependence of the response ratios of $P_n$ (a) and $R_d$ (b) of terrestrial plants on the exposure time. Mean ± 95% confidence intervals. Data with a exposure time <3 years were banded at an interval of 1/3 month (i.e. 10 days), and those >3 years were banded together. Logarithmic regression was used to determine the significance of the trend.

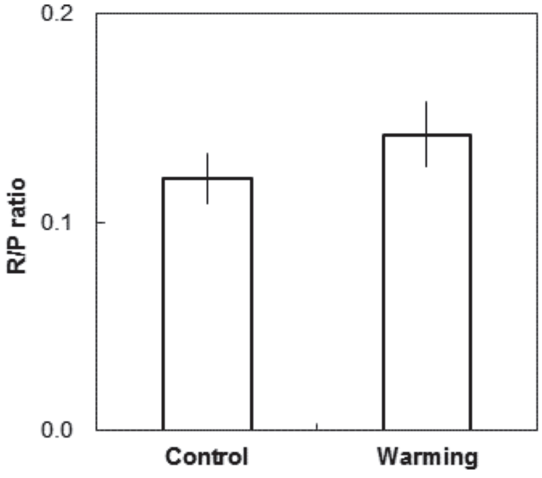

**Figure 5:** $R_d/P_n$ ratios at control and warming treatment. The $R_d/P_n$ ratio is calculated when both $P_n$ and $R_d$ of one species with the same unit were provided in one study (including measurements conducted on the same leaves/individuals and those across individuals). Hence the number of subset is 56. The $R_d/P_n$ ratios are compared using paired *t*-test. Mean ± SE.

## Dependence of photosynthetic and respiratory responses upon ambient temperature and warming magnitude

Both low-temperature limitation and the magnitude of warming are greater at cold than warmer conditions (IPCC 2007; Way *et al.* 2010). Therefore, it is reasonable to expect that plants live in the cold habitats would respond to climate warming greater than those in the warm habitats. The current study has shown that the photosynthetic response to warming declines linearly with the increase in ambient temperature. This indicates that the enhancement of C assimilation via leaf photosynthesis is greater for plants live in lower than those in higher ambient temperature. Actually, previous studies have demonstrated that the growth of plants in colder habitats can benefit more from warming than those in warmer habitats (Rustad *et al.* 2001; Root *et al.* 2003; King *et al.* 2006; Parmesan *et al.* 2007; Way *et al.* 2010). However, the dependence of

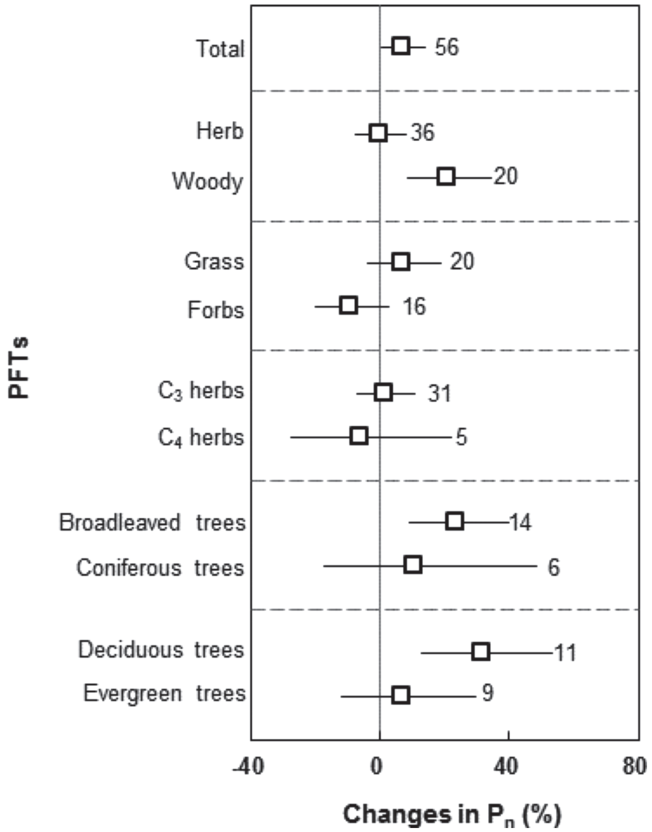

**Figure 6:** responses of the net foliage C balance of plant functional types (PFTs) to warming. The net foliage C balance is computed by ($P_n$–$R_d$) when both $P_n$ and $R_d$ of one species with the same unit were provided in one study (including measurements conducted on the same leaves/individuals and those across individuals). Mean ± 95% confidence intervals. The number of observations for each group used in the analysis is shown near the bar.

the photosynthetic responses on ambient temperature does not imply similar response trend with latitudinal gradient. One possible reason is that the temperature gradient does not necessarily reflect a latitudinal gradient because of the influence of elevation (Ackerman and Knox 2012). In addition, the general patterns may be obscured by precipitation. For example, along a north–south European gradient of temperature and precipitation, no warming effect on $P_n$ was found due to the decisive effect of rainfall (Llorens *et al.* 2004).

In addition to ambient temperature, the magnitude of temperature increase is another important factor that influences the responses of terrestrial plants to warming (Alexander *et al.* 1995). In the present analysis, respiratory response increases linearly with warming magnitude, which is mainly caused by the warming-induced stimulation of plants' biochemical reactions (Taiz and Zeiger 2010).

### Thermal acclimations of leaf photosynthesis and respiration

The findings in the present meta-analysis suggest that $P_n$ does not acclimate to warming. In contrast, the respiratory response shows significant decline with increasing exposure time, suggesting a thermal acclimation of $R_d$ to warming exists. The analysis extends the findings in Xiong *et al.* (2000) and Ow *et al.* (2008a, 2008b), i.e. respiration of terrestrial plants can acclimate to climate warming, but photosynthesis cannot.

The thermal acclimation of $R_d$ could minimize the effects of climate warming on C loss via plant respiration (Gifford 1995; Ziska and Bunce 1998; Dewar *et al.* 1999; Loveys *et al.* 2002) and mitigate the positive feedback between climate change and atmospheric $CO_2$ (King *et al.* 2006; Atkin *et al.* 2008). Recently, increasing ecological models take thermal acclimation of respiration into account (Hanson *et al.* 2005; Wythers *et al.* 2005; King *et al.* 2006; Atkin *et al.* 2008; Ziehn *et al.* 2011). When thermal acclimation of leaf respiration was taken into consideration, predicted C release via plant respiration would decrease (Atkin *et al.* 2008) and annual net ecosystem C exchange would increase (Hanson *et al.* 2005).

### Changes in $R_d/P_n$ ratio and the net C balance of leaves

The changes in $P_n$ and $R_d$ can profoundly affect the net C balance of terrestrial plants (Chapin III *et al.* 2002a). In the present analysis, the response of $R_d$ is greater than that of $P_n$ and consequently leads to significant enhancement in leaf $R_d/P_n$ ratio. This is consistent with a number of previous studies (Tjoelker *et al.* 1999a; Loveys *et al.* 2002; Atkin *et al.* 2007; Campbell *et al.* 2007). Although the enhanced $R_d/P_n$ ratio suggests a greater proportion of fixed C will be consumed, it does not necessarily imply that the net C balance would reduce. The calculated $R_d/P_n$ ratios are 0.12 and 0.14 at control and warming treatment in the current study. It means that the absolute value of $P_n$ is much greater than that of $R_d$. Hence, the absolute change in photosynthesis is not necessarily lower than that in respiration even though the fractional change in photosynthesis is much lower. Actually, the result in the current study shows that daily net C balance of leaves increases in response to warming. It provides an explanation, in addition to high leaf biomass (Lin *et al.* 2010) and prolonged growth season (Myneni *et al.* 1997), for the enhancement of terrestrial plant biomass (Lin *et al.* 2010; Way *et al.* 2010) and NPP (Rustad *et al.* 2001; Wu *et al.* 2011) in response to warming. Yet in our analysis we estimated daily net C balance of leaves with ($P_n$–$R_d$) value, assuming that 1) $P_n$ can represent the net C assimilation during day time and drop to 0 during night time; 2) $R_d$ can represent the C release during the night time, and 3) day-time duration is 12 hours. Hence, the calculated net C balance is a rough estimation based on the limited but best data available and it should be used with caution. Additional researches measuring 24-hour leaf-level C balance are needed.

## CONCLUSIONS

Changes in leaf photosynthesis and respiration induced by climate warming have important implications for the C balance of terrestrial biosphere under global climate change. Our meta-analysis demonstrated that warming could enhance both leaf photosynthesis and respiration in terrestrial plants, depending on plant functional types. The declining trend of photosynthetic response with increasing ambient temperature suggests that plants in cold than warmer habitats benefit more from warming. The thermal acclimation of respiration indicates that the magnitudes of C release from terrestrial plants to the atmosphere will be smaller than expected. The enhancement in daily net C balance of leaves provides a plausible mechanism for the positive responses of terrestrial plant biomass and NPP to warming.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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