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 (Pn) and dark respiration rate (Rd) 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 Pn and Rd of terrestrial plants.

Important findings
Across all the plants included in the analysis, warming enhanced Pn and Rd significantly by 6.13 and 33.14%, respectively. However, the responses were plant functional type (PFT) specific. Specifically, photosynthesis of C4 herbs responded to experimental warming positively but that of C3 herbs did not, whereas their respiratory responses were similar, suggesting C4 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 Rd instead of Pn was observed. Although greater proportion of fixed C was consumed (greater Rd/Pn 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 contrasting 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

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 temperature 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 $R_q$ 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 Ov 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 (Armone 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 (Armone 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 ($P_n$), leaf dark respiration rate ($R_d$), 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 was calculated as: $SD = SE\sqrt{n}$, where $n$ was the sample size. If data were given with a mean and a confidence interval (CI), the SD was computed as: $SD = (CI_u - CI_l)\sqrt{n} / 2t_{a, n}$, where $CI_u$ and $CI_l$ were the upper and lower limits of CI, and $t_{a, n}$ was the significant level and equaled 1.96 when $a = 0.05$ and 1.645 when $a = 0.10$.

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 ($\bar{M}$) and the averaged standard deviation ($\bar{SD}$) were calculated using the following equations (Liao et al. 2008):

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

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

where $j$ was the sampling times ($\geq 2$), $M_i$, $SD_i$ and $n_i$ were mean, SD and sample size on the $ith$ 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 $P_n$ and $R_d$ 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 $P_n$ and $R_d$ were both from 0.3 to 20.0°C. According to the data conducted in soil, the ambient soil temperatures for $P_n$ and $R_d$ changed from 3.9 to 18.9°C and from 18.9 to 20.0°C, respectively. Soil warming magnitudes for $P_n$ and $R_d$ 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 $P_n$ 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), the $R_d/P_n$ ratios in the control and warming treatments and net C balance of leaves were calculated. The means of the $R_d/P_n$ 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 $(P_n - R_d)$. To examine the
weighted response of \((P_n - R_d)\) to elevated temperature, SD was estimated by \((SD_x^2 + SD_y^2)^{1/2}\), where \(SD_x\) and \(SD_y\) 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, \(\log_{RR} = \log_e(X_w / X_i)\), where \(X_w\) and \(X_i\) are the mean value in the warming and control treatment, respectively. The weighted log, \(RR\) and 95% confidence intervals were computed.

In meta-analysis, the total heterogeneity \((Q_t)\) can be partitioned into within-group heterogeneity \((Q_w)\) and between-group heterogeneity \((Q_b)\). The \(Q\) statistic approximately has a chi-square distribution (Curts 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% \((P < 0.05; \text{Fig. 1a})\). Responses of \(P_n\) for both herbaceous and woody plants were significantly positive (both \(P < 0.05; \text{Fig. 1a})\). 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 \((P < 0.01; \text{Table 1, Fig. 1a})\). 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 \((P < 0.05; \text{Table 1, Fig. 1b})\). In addition, the respiration enhancement of deciduous trees \((53.37\%)\) was greater than that of evergreen trees \((13.27\%; \text{Table 1, Fig. 1b})\). 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 \((R^2 = 0.69, P < 0.05; \text{Fig. 2a})\). 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 \((R^2 = 0.70, P < 0.01; \text{Fig. 3b})\).

**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 \((R^2 = 0.30, P = 0.05; \text{Fig. 4b})\).

**Changes in \(R_d/P_n\) ratio and \((P_n - R_d)\) value**

The \(R_d/P_n\) ratio under warming treatment \((0.14 \pm 0.02)\) was statistically greater than that at control \((0.12 \pm 0.01)\) \((P < 0.01; \text{Fig. 5})\). In addition, warming significantly enhanced the \((P_n - R_d)\) value by 8.72% \((R^2 = 0.69, P < 0.05; \text{Fig. 5})\). 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% \((\text{Fig. 6})\). The \((P_n - R_d)\) value of broadleaved and deciduous trees was 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 \((P < 0.05)\).

**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
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 C4 species; and warming significantly enhanced photosynthesis of C4 herbs but did not affect that of C3 herbs. Specifically, the positive response of C4 grass was greater than that of C3 grass, while the responses of C3 grass and C3 forbs were similar (not shown in the RESULTS section). The physiological structure of C4 species enables them benefit more at warm temperatures due to less O2 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).
compared with C₃ plants. Our results suggest that warming in the future may benefit C₄ plants more than C₃ plants. This is in line with the field experiments, which have shown an increased dominance of C₄ 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 Pn 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 2: dependence of the responses of Pn (a) and Rd (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 Pn (a) and Rd (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.
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
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 CO2 (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 climatic 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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